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THE MIGRATIONS OF EAST COAST HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*)

PhD UP 1994

THE MIGRATIONS OF EAST COAST HUMPBACK WHALES
(*MEGAPTERA NOVAEANGLIAE*).

by

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Submitted in partial fulfilment of the
requirements for the degree of
Philosophiae Doctor
or
Doctor of Philosophy
or Ph.D.
in the
Faculty of Science
University of Pretoria
Pretoria

January 1994

The migrations of east coast humpback whales (*Megaptera novaeangliae).*

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South Africa

ABSTRACT

Southern hemisphere humpback whales undertake annual migrations from summer Antarctic feeding grounds, to breeding grounds in coastal sub-tropical and tropical waters in winter. *En route* the whales utilise extreme coastal waters as migratory corridors. After severe depletion by commercial whaling between 1904 and 1963, the species is showing a recovery off the east coast of southern Africa. The close proximity of the migration to the coast allowed for a recovery - monitoring programme to be carried out through shore-based visual surveys from Cape Vidal, northern Natal. Surveys of the northward migration were undertaken each winter from 1988 to 1991, and a survey of the southward migration was undertaken in 1990. Daily observations were carried out from an approximately 60 m high vantage point on a headland, during which attempts were made to measure migration characteristics for each group observed, including distance offshore, speed and bearing (measured by theodolite) and group size (estimated by observers and confirmed by interception of groups by ski-boat). Characteristics of the northward migration were unaffected by environmental parameters (sighting conditions, wind speed or

direction, and time of day) or interactive parameters (other migration characteristics). Each year's northward migration was comprised of waves, and apart from the distance offshore, there was no difference in the migration characteristic of each wave. Significant differences were found in group size, distance offshore and speed of the northward migration between years. No differences were found between the mean group sizes or speeds of the northward and southward migrations in 1990, although the southward migration was found to be significantly further offshore than its northward counterpart.

The measurement of migration characteristics has played an integral part in population estimation, and in the choice of optimum periods to monitor annual abundance.

Results of the 1988 and 1989 surveys suggested that not all groups within view were sighted by observers. Independent-observer surveys were therefore carried out in both 1990 (22 days) and 1991 (51 days), to determine the proportion of the population within the survey area that was being missed by observers using a single mark-release model. Results were stratified into three distance intervals from the shore and three sighting - condition intervals; there were constant sighting probabilities from the south tower under different sighting conditions, while those from the north tower increased slightly as sighting conditions improved. Sighting probabilities of both towers were highest in the intermediate distance interval, and decreased in both the inshore and offshore regions.

Daily densities (expressed as the number of groups crossing the midline in front of the towers), adjusted for groups missed with distance from the shore and under different sighting conditions, were multiplied by the mean group size of the survey year, and resulting daily densities of individuals were summed to provide totals of whales passing the towers during each survey. The abundance estimate of 1711, made during the northward migration of 1990, was considered the most reliable estimate of population size made, although no associated cv could be calculated. The estimate of 1777 made during the 1991 survey had an associated cv of 0.12 calculated by bootstrapping of daily data. The time series of four years is too short to provide an estimate of the recovery rate of the population, but the numbers sighted show the population to have undergone considerable recovery since protection in October 1963.

A line-transect survey undertaken in August and September 1991, to establish the distribution and abundance of humpback whales in coastal waters of southern and central Mozambique, showed whale densities to be highest in the southern region between 33° and 35° 30' E, a region characterised by shallow banks and where the strong

Mozambique Current flowed further offshore. The high proportion of cow - calf pairs (14.8%) in the northern Sofala Bank region implied that this region is a calving or nursery area. A hazard - rate model applied to the sighting data stratified into northern and southern areas indicated a population size of 1954 (cv 0.38), although the northern limit of the breeding ground was not determined, the proportion of the population present on the breeding ground was unknown, and it was assumed that all animals were seen on the trackline.

A limited collection of identification photographs was made from the east and west coasts of South Africa, Mozambique, Madagascar, and the Antarctic Areas II and III. No inter-region, or inter-year resightings were made (or would be expected given the limited sample size and the estimated size of the population). Estimation of the size of the population from mark-recapture analyses of photo-identified individuals was precluded.

Two humpback whale calves (of lengths of 6.45 and 6.15 m) were recorded from temperate waters of the west coat of South Africa in summer. The 6.45 m individual (estimated at an age of 6.5 months) stranded at St Helena Bay in February 1982, while the 6.15 m individual (estimated at 4.5 months old) was found ensnared in the buoy line of a lobster trap off Saldanha Bay. Although the 6.45 m individual was emaciated when stranded, the 6.15 m individual had been feeding on stomatopod prey, indicating that some individuals feed opportunistically during the migrations off the west coast of South Africa.

This thesis presents the first population estimates (albeit minimum estimates) of the African east coast breeding population of humpback whales, which presumably feed in Antarctic Area III. The Cape Vidal estimates must however be considered to be biased downwards by the proportion of the population passing offshore of observers and because the proportion of groups that were missed by observers within their field of view may have been underestimated. The Mozambique population was underestimated by the failure to survey the entire breeding ground, and the assumption made that all whales were sighted on the trackline.

ACKNOWLEDGMENTS

I am indebted to numerous people and organisations for the support, be it personal, logistic, financial or academic, they have shown this project.

I am first and foremost indebted to Dr Peter B Best for his supervision, valuable time in the field each year (and especially in the supervision of the 1989 survey), for his organisation of, and liaison with Earthwatch for, the Mozambique survey, and for providing an essential back-up while I was in the field.

I thank my colleague Keiko Sekiguchi for her voluntary assistance in the field (in 1989, 1990 and 1991), and with computer analyses, and Peter Bartlett who undertook five months of observations in 1990. I am enormously indebted to the numerous volunteers who undertook observations including, Michael Meyer (1988, 1989, 1990), Martin Haupt (1988, 1989), Gus van Dyk (1989, 1990), Dave Rundgren (1989), Jacki Portuesi (1989), Peter Chadwick (1990), Anton Rossouw (1990), Rob Faure (1990), Sean Patrick (1990), Dave Baker (1990), Vic Peddemors (1990), Paddy Cook (1990), Peter Leitner (1991), Stefan Swanson (1991), Keith Benkenstein (1991), Robyn Lovemore (1991), Nicole Godenir (1991), Pierre de Groot (1991), Brian Morris (1991), Michelle Yates (1991), Sabena Wintner (1991), Sean Blyth (1991), Debbie Grant (1991), Warren Backler (1991), Marliese Teuschner (1991), Ed Parsons (1991), Jenny Christal (1991), Cameron Dallas (1991), Leon Liebenberg (1991), Ingrid Rencken (1991), Leshack Karjzmarski (1991), and Price Kerfoot (1991).

I am indebted to the Director and staff of the Natal Parks Board for allowing access to Cape Vidal, and for the logistic support they have shown the project, in particular for providing boat time for interception of whale groups. The staff of Cape Vidal including Lionel and Wendy van Schoor, Frank and Wendy Cowley, Callum and Leanne Beattie and Robin and Ivana Allen must especially be thanked for the support shown to the project, and the friendship shown me at Cape Vidal.

I thank the University of Pretoria, the Director of the Mammal Research Institute, Professor J D Skinner, Dr P B Best, Computer Notions, and the Wildlife Society of Southern Africa for providing funding for equipment and field work of Cape Vidal. I am personally indebted to The Council for Scientific and Industrial Research, and The

University of Pretoria for post - graduate bursaries, and to the Boards of Trustees of the Charles Astley Maberly and Bob Blundell Memorial Scholarships for financial assistance, which allowed me to undertake this study.

I am indebted to Earthwatch USA without whose support and funding the Mozambique survey would have been impossible, and to the Earthwatch volunteers who partook in the survey, including Marion Bowers, "Cash" Register, Alessandro Piva, Bill Jenkins, Jim and Gerry Pratt, Frank Perkins, John Walker, Mary Beth Pratt, Andre von Korak, Tom Didier, Alison Middleton, "AB" Asmussen and Eric Wolfers. I am indebted to the Secretaria de Estado das Pescas, Mozambique for permission to undertake the survey in Mozambique territorial waters. Vic Peddemors and Domingo Gove must be thanked for their participation in the survey as must the staff of *Zanj Sea Safari's* their running of the ship, and Rod Hastier for his boat handling and crewing of the *Zanj*.

Michael Meyer and the staff of the Marine Mammal Laboratory of the Department of Environment Affairs, and Blake Abernethy of the Mammal Research Institute must be thanked for supplying identification photographs from the west coast. The staff of the Oceanographic Research Institute, Durban, are thanked for photographs from Madagascar. Mr Michail Shcheketov of the P.P. Shirshov Institute for Oceanology, Russia, and Dr Matthias Stehmann of the Bundesforschungsanstalt fur Fischerei, Germany, provided photographs from Walters Shoal for which I am grateful.

Further thanks must be extended to the Marine Mammal Laboratory of the Department of Environment Affairs, and to the Director, Natal Sharks Board, for loan of equipment for use in the field, David Borchers must be thanked for statistical advice, including giving up a week of his time for an on-site inspection of the field methods, and I thank Vic and Barbara Peddemors for hospitality shown to me whenever I needed a place to stay in Durban.

I am indebted to Dr R. B. Manning of the Smithsonian Institution for identification of the stomatopod prey items described in chapter 8, to Dr Patti Wickens for calculation of the cv presented in chapter 5, and to Carlos Villacastin-Herero for assistance with spectral analyses in chapter 3.

Last and not least I thank my parents for their support shown to me throughout the project, and my wife, Belinda for support and encouragement and advice.

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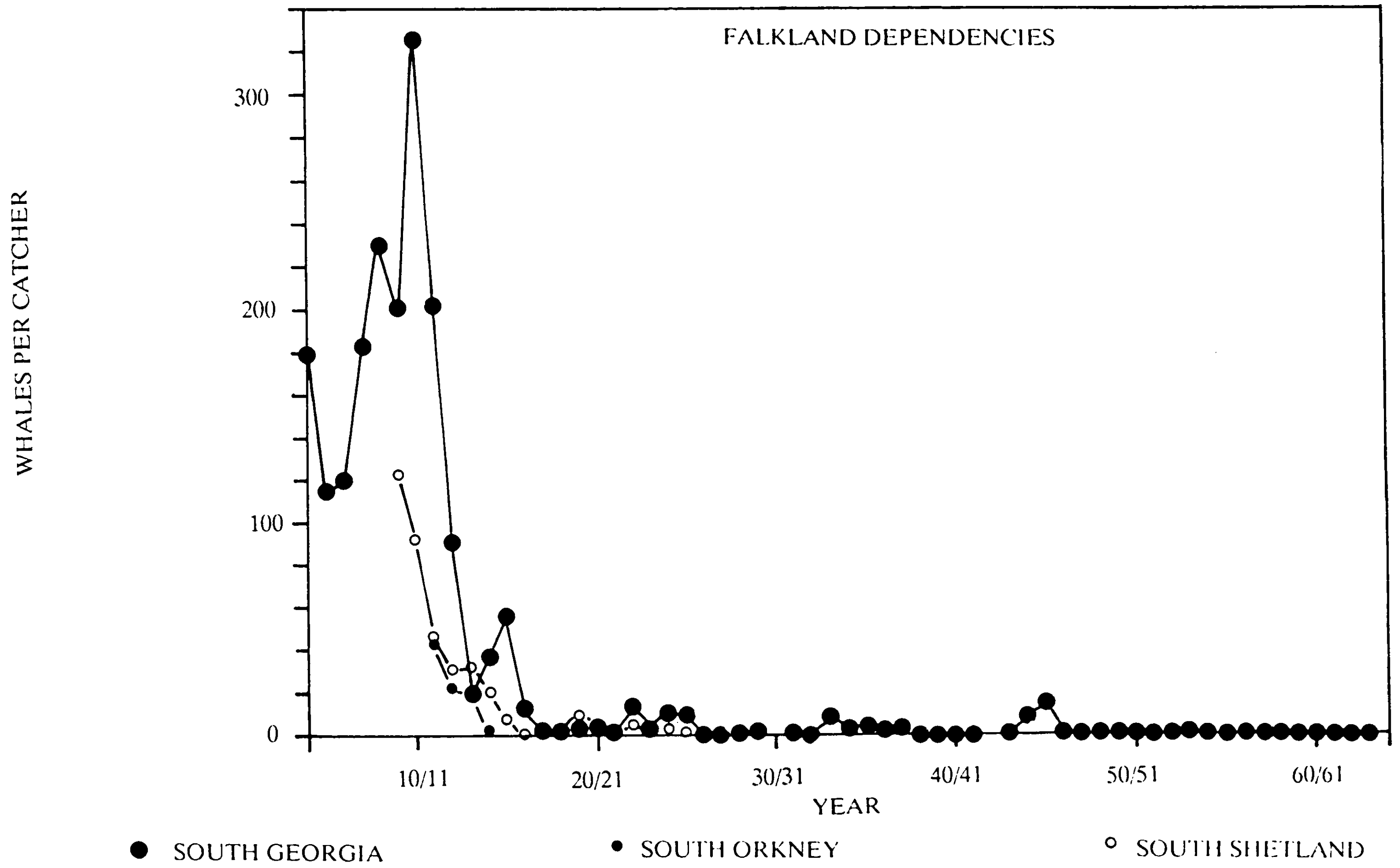
CHAPTER 1

INTRODUCTION

Southern hemisphere humpback whales (*Megaptera novaeangliae*) undertake annual migrations from summer Antarctic feeding grounds, where they feed almost exclusively on krill (*Euphausia superba*), to winter breeding grounds in tropical or sub-tropical coastal waters (Risting 1912, Olsen 1914, Kellogg 1929, Harmer 1928, 1931, Matthews 1938, Mackintosh 1942, Dawbin 1956, 1966, Chittleborough 1965). *En route* between the breeding and feeding grounds southern hemisphere humpback whales utilise extreme coastal waters of continents as migratory corridors (Risting 1912, Olsen 1914, Kellogg 1929, Matthews 1938, Chittleborough 1965, Dawbin 1956, 1966), while their northern hemisphere counterparts appear to utilise more open ocean migration routes (Clapham and Matilla 1990). The coastal migratory and breeding habits of southern humpback whales resulted in the species being particularly susceptible to catches from coastal whaling operations in temperate and tropical waters. Furthermore catches from the Falkland Island Dependencies were large during the southern summer, and between 1904 and 1963 over 90 000 humpback whales were estimated to have been taken from southern hemisphere waters (Committee for whaling statistics 1942-1964, Tonnesen and Johnsen 1982). As the majority of early evidence for the locations of feeding and breeding grounds and possible migratory links between them arose from the history and distribution of catches on both the feeding and breeding grounds, it is appropriate to review these briefly.

Modern humpback whaling in the southern hemisphere commenced in the summer of 1904/05 in South Georgia and terminated in October 1963. As noted for many new grounds by Risting (1912), the initial catch at South Georgia largely comprised humpback whales. Between the 1904/05 and 1913/14 seasons some 29 000 whales were taken at South Georgia and the Falkland Island Dependencies (Committee for whaling statistics, 1942-1964), of which 69 % were believed to be humpback whales. The marked decline in the annual availability of humpback whales (Figure 1.1) after 1904/05 is clearly evident in South Georgia, South Orkneys and South Shetlands. Despite some attempt at regulation of catches of humpback whales off South Georgia after the 1918/19 season (as only 131 humpbacks had been taken during the 1917/18 season), catches thereafter remained low (although this could, in part, be ascribed to catch selectivity for the more



<u>Figure 1.1</u> Annual catch per catcher of humpback whales from shore-based stations in the Falkland Island Dependencies between 1904/05 and 1963. Information from Committee for Whaling Statistics, 1942-1964.

valuable blue and fin whales). Shore-based humpback whaling ceased in the Falkland Dependencies in 1955, only 136 individuals being taken off South Georgia after 1949.

Initiation of pelagic whaling in Antarctic waters in 1923 opened the ice-edge feeding grounds to catchers (Figures 1.2a and 1.2b). Some 28 000 humpback whales were taken by pelagic whalers between 1930 and 1963, although catch trends in Antarctic pelagic whaling have been affected to some extent by regulation (Tonnesen and Johnsen 1982). Humpback whales south of 40° S were totally protected by the International Agreement for the Regulation of Whaling (ARW), 1937, between 1938 and 1949, apart from catches by the Japanese (who at the time were not members of the ARW) in the 1938/1939 season and the lifting of protection for the 1940/1941 season. From 1949 an annual global Antarctic quota of 1250 whales was granted, on condition that weekly catch returns were reported so that catches could be terminated four days after the quota had been filled. However, the high catches within the four-day period of grace in 1950 resulted in the season between restricted to four days between the 1953/54 and 1962/63 seasons, and Tonnessen and Johnsen (1982) noted that catches after 1953 were extremely variable. Humpback whaling throughout the southern hemisphere officially ceased after October 1963.

Modern whaling in southern African waters began in 1908 after reports of the abundance of whales off the southern African coast were received in Norway. The success of entrepreneurial whaling companies in South Africa in 1909 and 1910 resulted in a whaling boom in the region, and by 1913 11 floating factories and 17 land stations were operating between Gabon and Mozambique (Best and Ross 1989), processing an estimated 7263 humpback whales (Best in press). Humpback whaling probably began off the coast of Madagascar in 1910, when the *Mangoro* took only 79 unspecified whales from this coast (Budker 1954). Two years later the factory ship *Horatio* took only 25 humpback whales from this region. Good catches were recorded to the south of Madagascar in 1937 and 1938, and although the exact locations of these catches are not recorded by the Bureau of Whaling Statistics, Budker (1954) notes that they were "a good way" south of Madagascar.

Between 1908 and 1917 about 25 000 humpback whales were taken off the southern African coast (Best in press), although as shown in Figure 1.3 and 1.4, availability at most stations had declined markedly by 1914 (Committee for whaling statistics 1942-1964). Of particular interest in Figure 1.3 are the trends off Gabon,

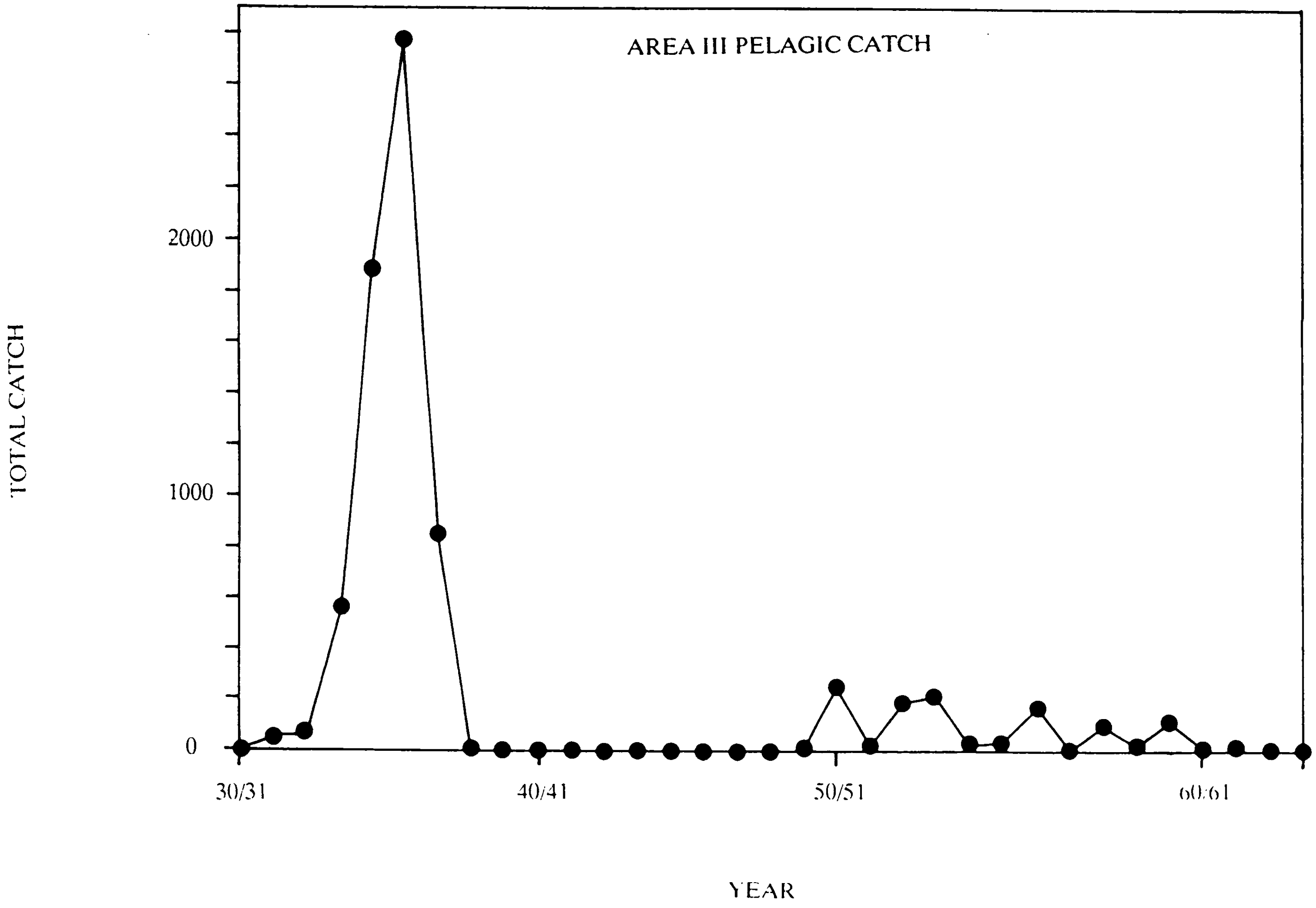
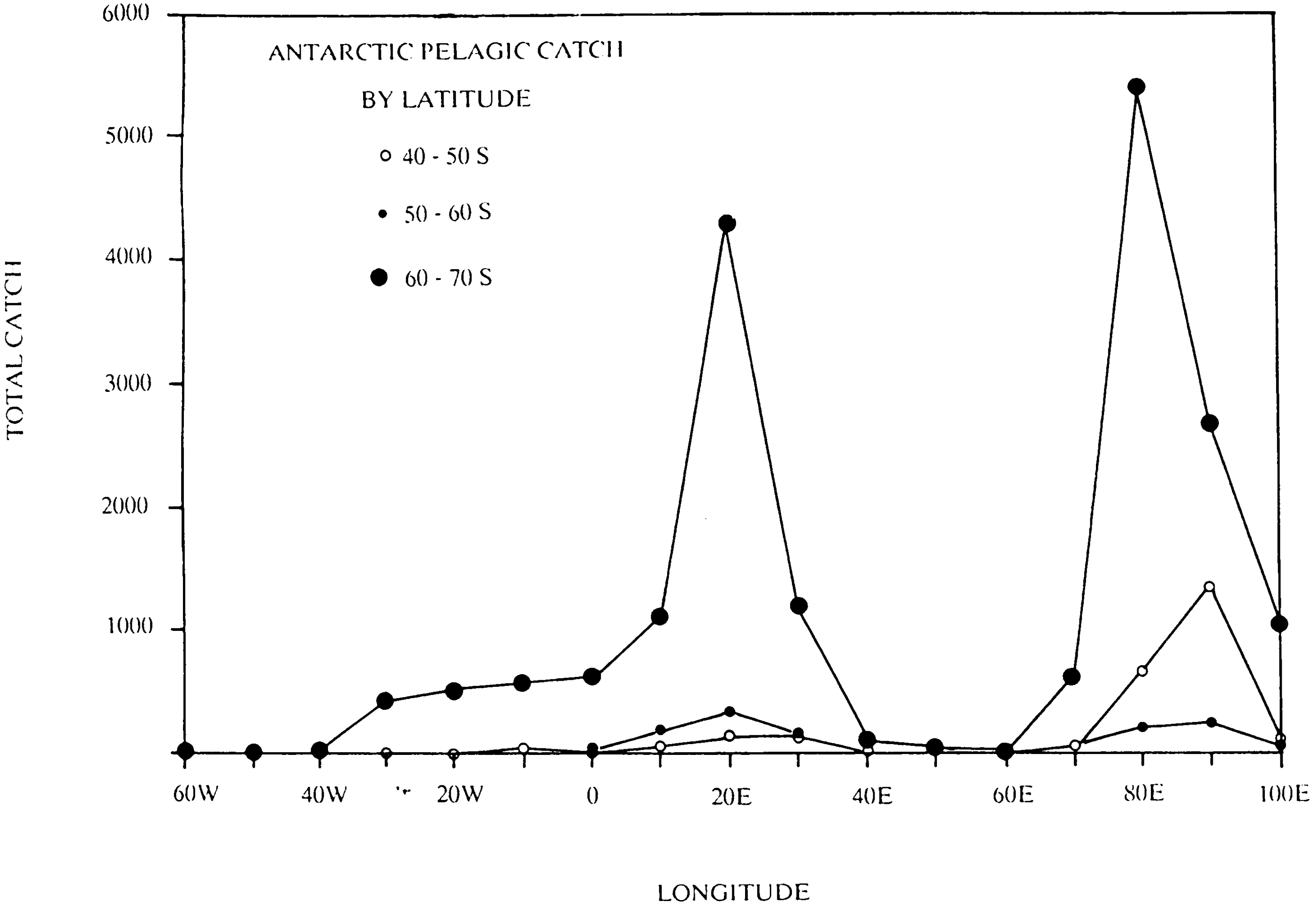


Figure 1.2 (a) Annual catch of humpback whales from Antarctic Area III between 1930/31 and 1963. Information from Omura (1973).



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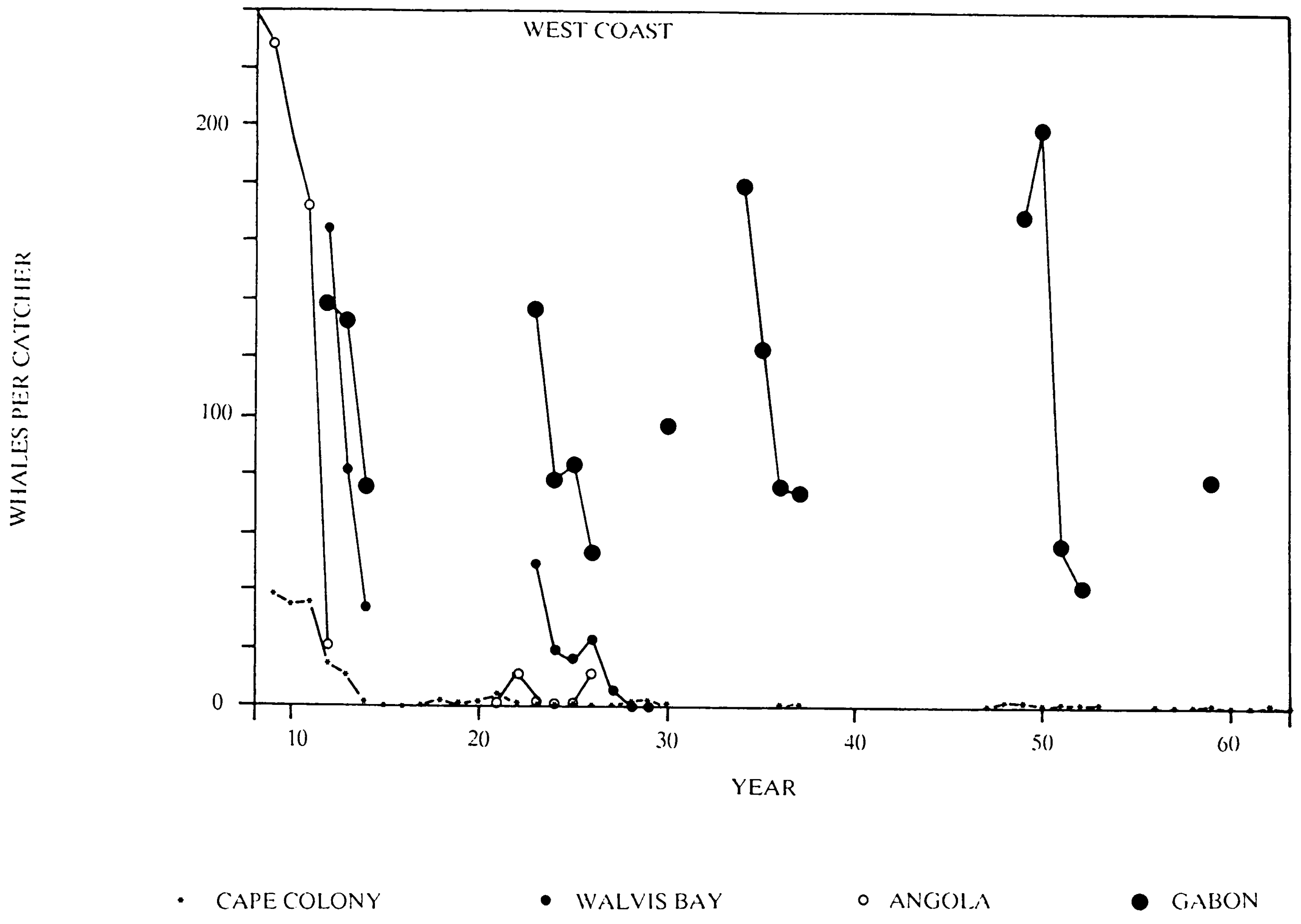


Figure 1.3 Annual catch per catcher of humpback whales from shore-based stations on the west coast of southern Africa between 1904/05 and 1963. Information from Committee for Whaling Statistics, 1942-1964.

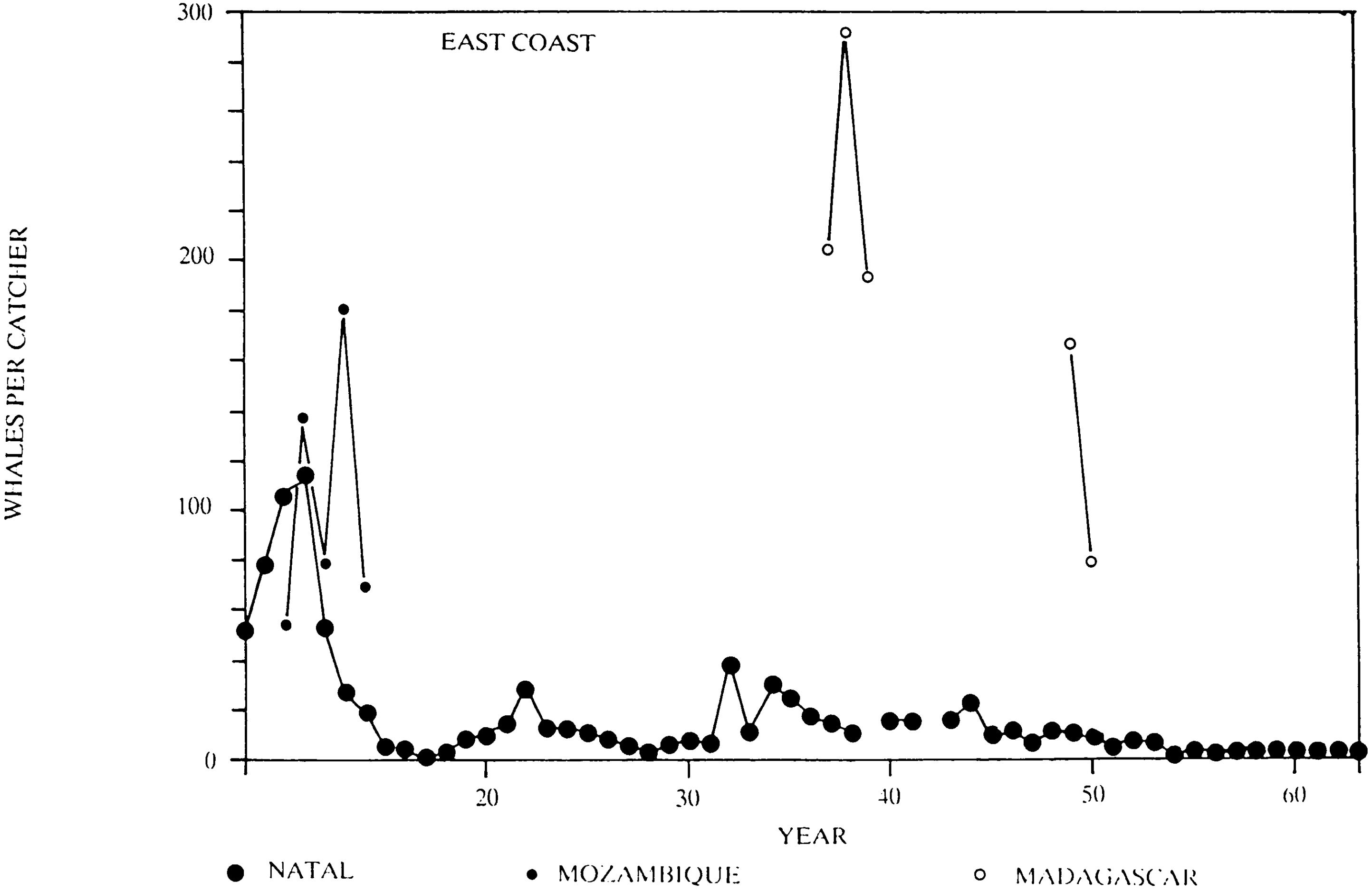


Figure 1.4 Annual catch per catcher of humpback whales from shore-based stations on the east coast of southern Africa between 1904/05 and 1963. Information from Committee for Whaling Statistics, 1942-1964.

which as a single species fishery, was forced to close when catches of humpback whales declined. Although Figure 1.3 suggests that four cycles of depletion (and closure of the fishery) were followed by three "recoveries" off Gabon, the short time period between periods of catches suggest "recoveries" resulted from strong localised fidelity to this breeding ground, as no such "recoveries" were recorded on other grounds on the west coast. A similar possible recovery was recorded at Madagascar (a single species fishery), if the 1937-1938 catches and the 1949-1950 catches were from the same region. Such recoveries may well have been facilitated at single-species grounds, as humpback whales in multi-species whaling grounds would not have been afforded the protection of a closed fishery (although it must be noted that catches may have been biased by selectivity of more valuable species in multi-species fisheries). Although the Mozambique ground was largely a single species fishery, the east coast humpback whale stock was never afforded protection as whaling to the south off Natal was continuous from 1908 to 1963. Furthermore, off neither Gabon nor Madagascar were populations reduced to such low levels of availability as in the multi-species fisheries.

Modern humpback whaling in Australasia began at Whangamumu, New Zealand, in 1910, although a net fishery for humpback whales had been operating from Whangamumu from 1890 onwards (Ommanney 1933). Three centres of shore-based whaling existed in New Zealand waters after 1911, one at Whangamumu (which closed in 1931), a second at Kaikoura between 1917 and 1922 (during which 68 whales were taken), and a third in the Tory Channel, Cook Strait (including the Perano family's station) which took humpback whales up until 1963 (Dawbin 1956; Grady 1982). Annual catches of humpback whales from the Tory Channel stations ranged from 6 taken in 1911 to a maximum of 226 taken in 1960 (Grady 1982).

In 1909 the Norwegian consul in Sydney, Australia, drew Norwegian whalers' attention to the presence of whales in Australian waters, and by 1911 ten companies had expressed interest in whaling in Australian waters. Of these, four never initiated operations, while a shore station operated at Jervis Bay, New South Whales, between 1912 and 1913 (Tonnesen and Johnsen 1982). Three co-operative companies continued whaling off the Australian west coast (at Albany and Point Cloates) after 1913, when high catches of humpback whales led authorities to introduce catch regulations. These stations closed after the 1916 season, and the Point Cloates station re-opened in 1922, although profitable catches were only recorded after 1925. The station closed again in 1929 after a dispute over government tariffs.

Shore-based humpback whaling resumed on both the east and west coasts of Australia in 1949, after a period of extensive whaling in western Australian waters by foreign fleets between 1935 and 1939. Over 22 700 humpback whales were taken from shore-based stations in Australian and New Zealand waters between 1949 and 1962 (Tonnesen and Johnsen 1982). Figure 1.5(a) shows the annual catch and catch per number of catchers of humpback whales off Australia (east and west coasts combined between 1912 and 1963, and total catch on each of the east and west coasts between 1949 and 1962). Figure 1.5(b) shows the annual catch, catch per catcher and sightings made in New Zealand waters between 1910 and 1963.

Although crude indices of catch per unit effort have been calculated for each of the two African, the Falkland Island Dependency and Antarctic pelagic catch histories, the calculation of pre-exploitation stock sizes through Leslie or De Lury analyses is precluded by the lack of information on stock identity, by uneven catch effort (change in catcher efficiency) with time, and by a possible change in selectivity in later years due to a preference for the more valuable blue whales (*Balaenoptera musculus*) and fin whales (*B. physalus*).

Hjort, Lie and Ruud (1932, 1933a, 1933b, 1934, 1935, 1937, 1938, all in Mackintosh 1942) and Bergersen, Lie and Ruud (1939, in Mackintosh 1942) divided the whaling grounds in Antarctic waters into five regions, namely

I. The area around the South Shetland Islands.

II. 60° W to 0°, including the coastal waters of the Falkland Island Dependencies.

III. 0° to 70° E off the coast of Queen Maud Land.

IV. 70° to 130° E to the south west of Western Australia.

V. 130° E to 170° W, south of New Zealand and including the Ross Sea.

Mackintosh (1942) found that humpback whales aggregated in feeding regions in the Bellinghausen Sea, the

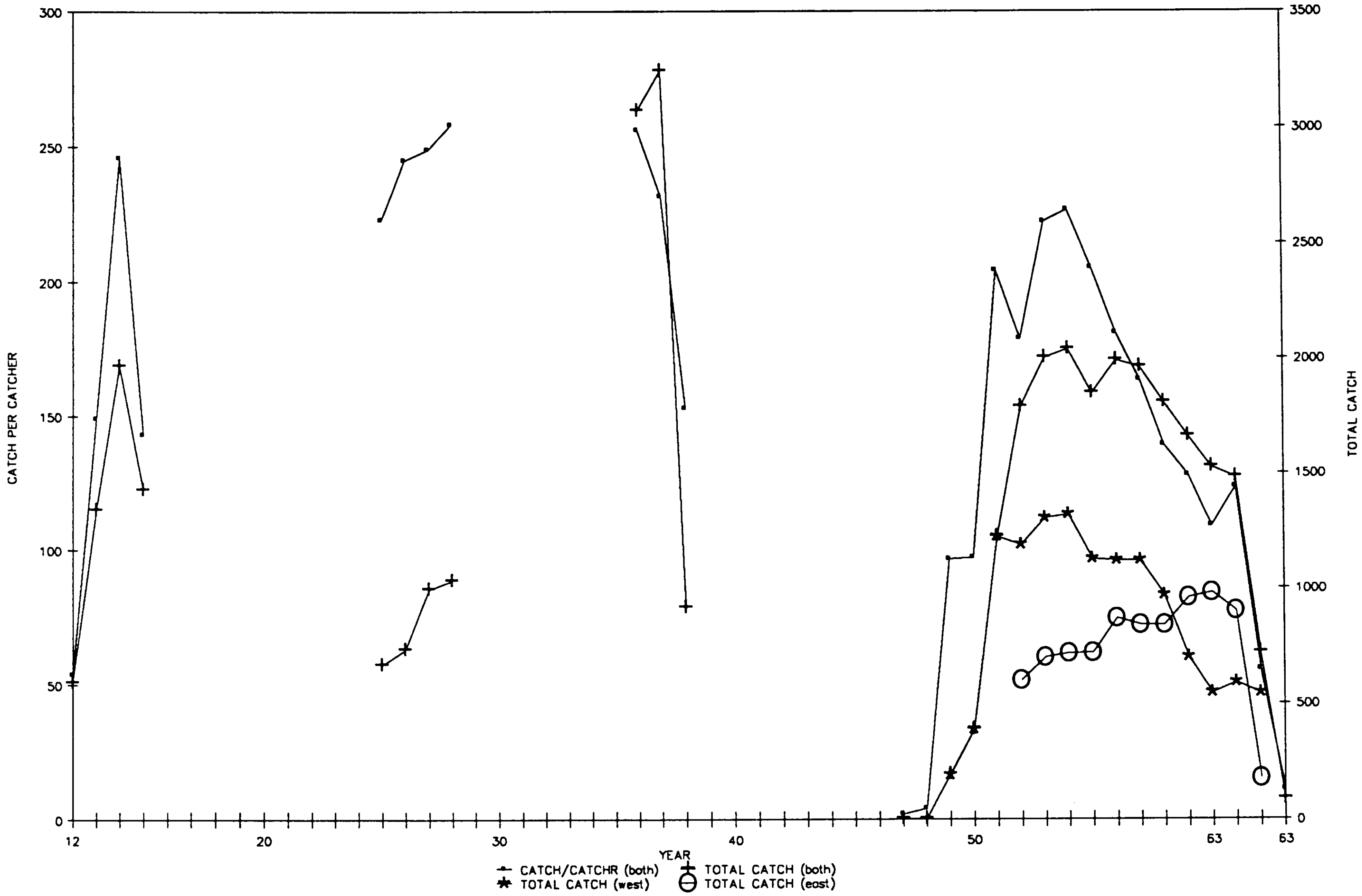


Figure 1.5 (a) Annual catch and catch per catcher of humpback whales from Australian waters (east and west coasts combined) between 1912 and 1963, and annual catches from each of the east and west coasts between 1949 and 1962. Information from Committee for Whaling Statistics, 1942-1964, and Chittleborough (1965).

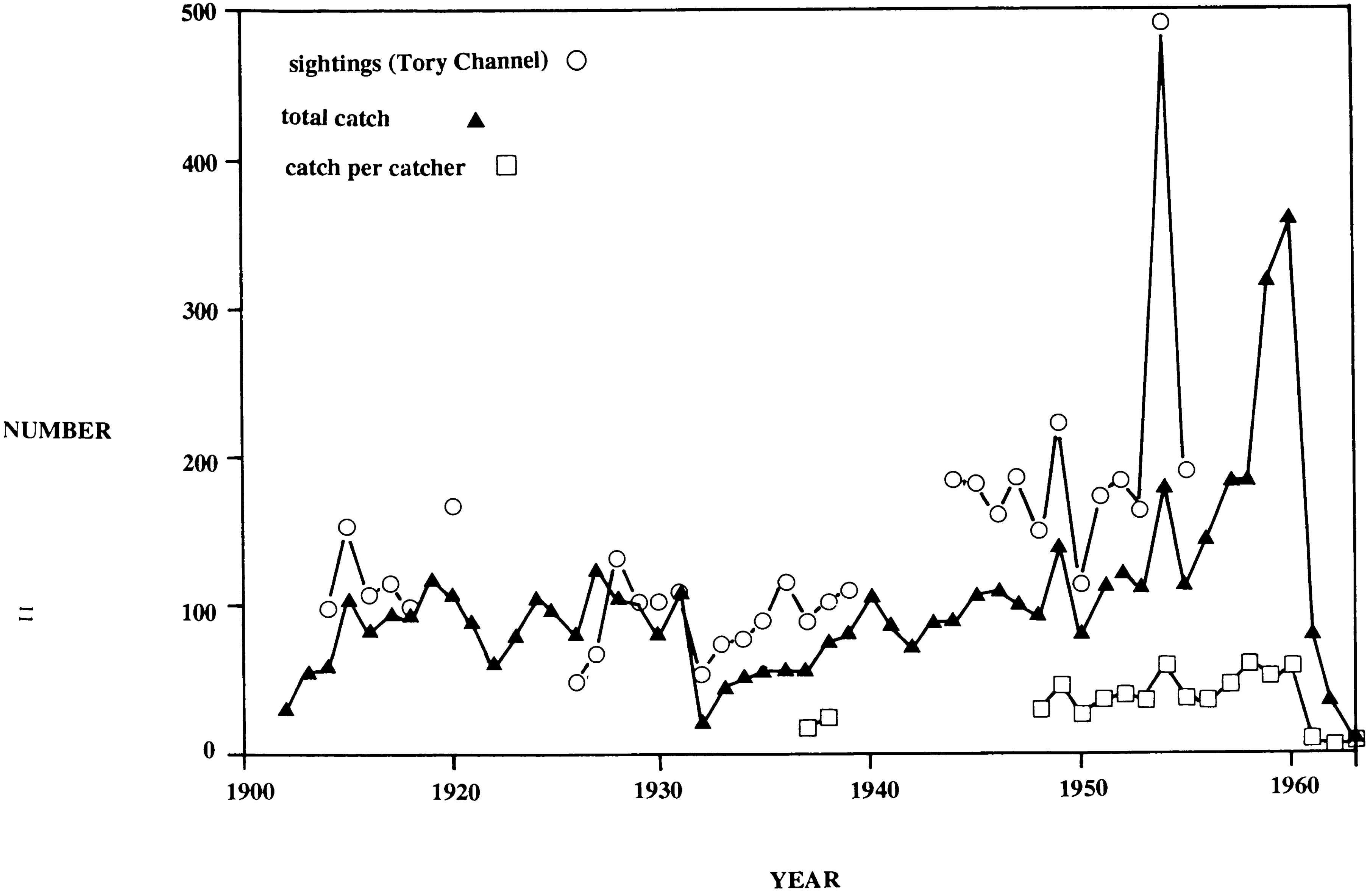


Figure 1.5 (b) Annual catch, catch per catcher and sightings from New Zealand waters between 1910 and 1963. Sightings are from the Tory Channel stations only. Information from Committee for Whaling Statistics, 1942-1964 and Dawbin (1956).

south-west Atlantic Ocean, in the region to the south of South Africa, in a region to the southwest of Western Australia, and in a region to the south of New Zealand, and noted the similarity to Hjort, Lie and Ruud's Areas II to V stock delineations. In 1957 the IWC suggested that the Antarctic feeding grounds should be divided into Areas I to VI, largely based on the Area delineations mooted by Mackintosh (Donovan 1991). Omura (1973) analysed the distribution of humpback whale catches in waters south of 40° S by pelagic whaling between the 1931/32 and 1938/39 and between the 1945/46 and 1962/63 seasons, and found three concentrations, one corresponding to each of the Area III, IV and V stocks.

Kellogg (1929) linked summer feeding grounds to winter breeding grounds occurring off the east and west coasts of South America, South Africa (including the southern and eastern coasts of Madagascar) and Australia, and in the Pacific Islands to the north of New Zealand (Figure 1.6); the links suggested by Mackintosh (1942) appear to be based on those mooted by Kellogg. With respect to African migrations, both Kellogg (1929) and Mackintosh (1942) suggested that the breeding grounds of the African east coast (namely off Madagascar and Mozambique) were linked to the feeding ground off Queen Maud Land, and that the breeding grounds off the west coast of Africa were linked to the feeding grounds off South Georgia and possibly to feeding grounds off Queen Maud Land. Although Mackintosh (1942) cited the two mark returns reported by Rayner (1940) (between the Queen Maud Land coast and the southern coast of Madagascar) as evidence for the east coast link, the west coast link is tentatively based on a similar catch history in the eastern Scotia Sea, and the fact that there was never a sizeable fishery for humpback whales off the eastern coast of South America. This suggested link between the Area II feeding ground and the African west coast possibly has its origin in a statement made by Morch (1911) :-

"During the months May to October especially, the Humpback Whales have been observed in great numbers and mostly off the coast of Portuguese West Africa. I think the question may reasonably be raised whether we have not here the great bulk of the Humpbacks from the South Georgia region on their annual migratory route ?"

At the time, the African west coast and the Falkland Island Dependencies were the two largest known humpback grounds and it is possible that this statement reflects lack of knowledge of the distribution elsewhere, rather than a link between the two grounds. Although this migration link has been suggested by

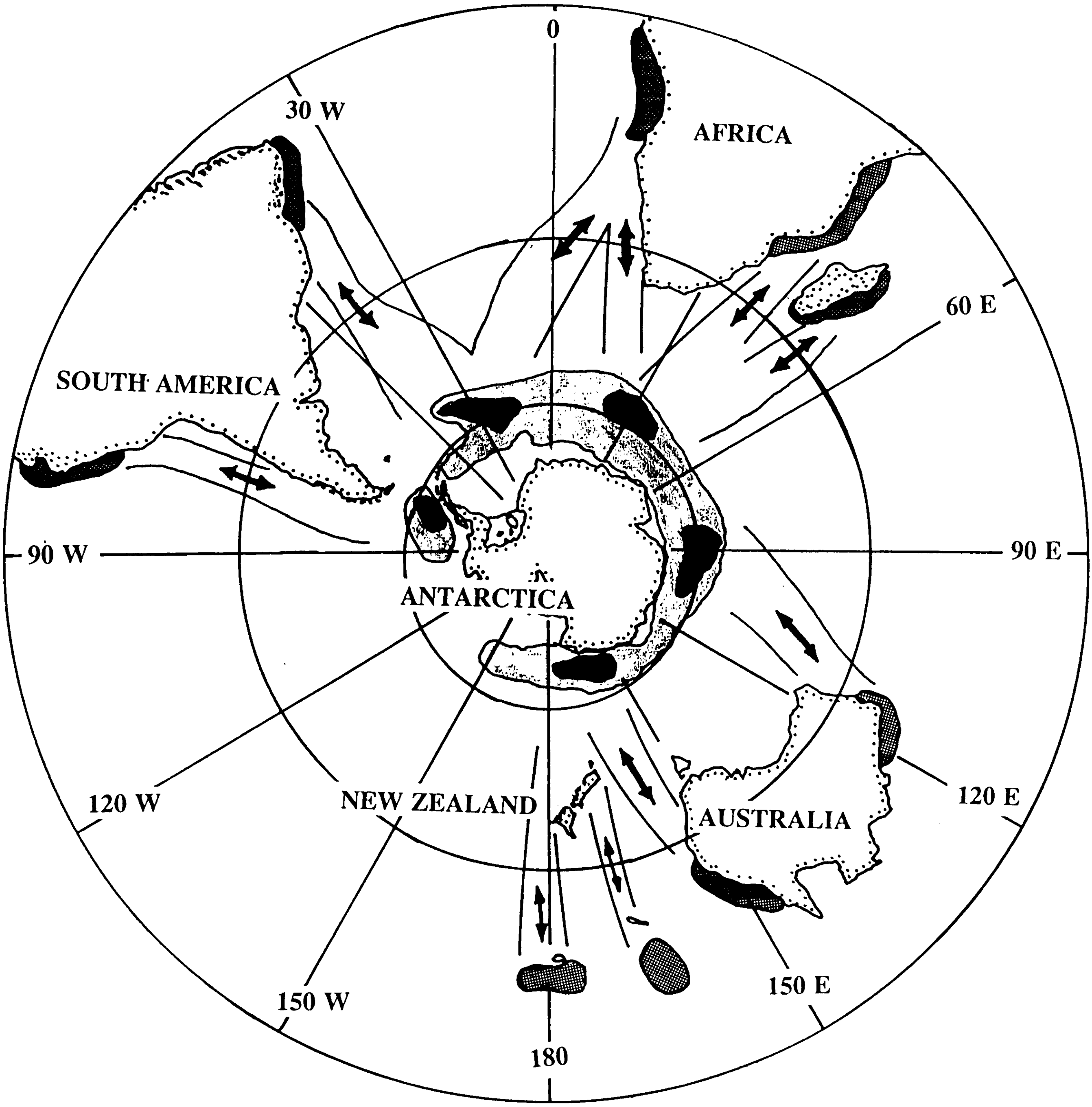


Figure 1.6 Positions of breeding and feeding grounds of southern hemisphere humpback whales and suggested migration links between grounds (after Mackintosh 1942).

Risting (1912), Kellogg (1929) and Mackintosh (1942), Chapman (1974) subsequently suggests that the African west coast humpbacks feed in Area III along with the African east coast humpbacks.

Despite the coasts of Mozambique and Madagascar being identified as the principal breeding grounds in the western Indian Ocean, Brown (1957) noted sightings of humpback whales in the northern Indian Ocean in the southern winter, and suggested that some individuals migrate north of the equator. Although Slijper, Van Utrecht and Naaktgeboren (1964) agreed that humpbacks found in the northern Indian Ocean during the austral winter belonged to the southern hemisphere Group III stock, they suggested that humpback whales found in the region during the boreal winter migrated from the northern Pacific Ocean. While Winn and Winn (1985) and Whitehead (1985) suggested that there was a resident humpback whale stock in the northern Indian Ocean, Reeves, Leatherwood and Papastavrou (1990) note that at present it is impossible to determine how far north the Area III humpbacks migrate during winter.

Morch (1911) reported a possible segregation of three colour forms (white-bellied, marble-bellied and dark-bellied) of humpback whales in the catches off South Georgia in 1910 and 1911, and Hinton (1925) suggested that these three different colour types formed separate races in the southern hemisphere. Matthews (1938) felt that this may be a consequence of Goodall's (1913) statement that all the whales seen at Durban were of a marble-bellied class. Matthews noted Hinton's small sample size, and that both his (Matthew's) data from Durban and Olsen's (1914) findings do not support this observation. Lillie (1915) classified the humpback whales of New Zealand into seven (four main and three intermediate) colour types. Comparison of the colouration of humpback whales inspected by Discovery staff at South Georgia and South Africa (combined) with those inspected off New Zealand by Lillie (1915) showed the South Georgian and South African forms to be darker (Matthews 1938) and led Matthews (op cit) to note that despite all colour forms occurring in each locality, they occurred in different proportions in different localities.

Evidence for migrations

Seasonal abundance patterns

Probably the best evidence for humpback whale migrations along the African coast arose from the seasonal abundance patterns recorded as catch per unit effort in whaling grounds at various latitudes. In such seasonal abundance patterns, a single mode suggested that the northern or southernmost destination of the migration had been reached, while a bimodal trend would suggest a northward and southward movement of whales through the ground. Seasonal abundance trends recorded in southern African grounds are shown in Table 1.1. Olsen (1914) noted that the main body of the humpback whale migration on the west coast struck the coast to the north of Saldanha Bay (resulting in the low catches in this region), and then migrated northwards. One factor of particular interest in Table 1.1 is the latitudinal difference in the position of the breeding grounds on the east and west coasts, the migration becoming unimodal at latitudes of 24° S on the east coast, but only at 6-18° S on the west coast. This presumably reflects the northward movement of cool water by the Benguela Current on the west coast, and the southward movement of warm water carried by the Agulhas Current on the east coast. Both breeding grounds are in comparable surface water temperatures of about 24° C (Climate Diagnostics Bulletin 1990), which is similar to breeding ground water temperatures of around 25° C reported by Dawbin (1966).

Table 1.1. The seasonality of humpback whale catches from shore- based stations at different latitudes on the east and west coasts of southern Africa.

Station	Latitude	Seasonality	Source
West coast			
Cape	33°-34° S	Bimodal	Olsen (1914)
Saldanha Bay and Hangklip	33°-34° S	Touch the coast to the north of the Cape	Harmer (1931)
Walvis Bay	23° S	Bimodal	PAN Files
Angola	6°-18° S	Bimodal	Harmer (1931)
Gabon	0°-4° S	Unimodal	Budker and Collignon 1952
East coast			
Durban	30° S	Bimodal	Olsen (1914)
	30° S	Bimodal	Harmer (1931)
	30° S	Bimodal	Matthews (1938)
	30° S	Bimodal	Bannister and Gambell (1965)
Linga-linga	24° S	Unimodal	Olsen (1914)
Madagascar	15°-25° S	Unimodal	Angot (1951)

Whale Marking

Further evidence of migration patterns arises from the three whale-marking programmes carried out in the southern hemisphere. The first of these, the Discovery marking programme, was carried out in Antarctic waters between the 1932/33 and 1938/39 season during which 566 humpback whales were marked. Of these, 37 or 6.5% were returned by the 1974/75 season (Brown 1977). Rayner (1940) presented results of the Discovery marking programme up to December 1939, and listed 36 marks returned from humpback whales. The second marking programme, the International programme, started in the 1945/46 season and by the 1974/75 season a total of 573 humpback whales had been marked in Antarctic waters, of which 14 or 2.6% had been recovered. A further 2251 humpback whales were marked outside Antarctic waters between 1949 and 1975, of which 1333 and 915 were marked in Australian and New Zealand waters respectively. Chittleborough (1965) reported the mark returns from whales marked in Australian waters, while Dawbin (1966) summarised the mark returns from whales marked in Australian and New Zealand waters. A third marking programme was carried out by the U.S.S.R. after the 1952/53 season. Brown (1977) reports 517 humpback whales marked during this programme of which 63 or 12.2 % were returned. Ivashin (1970) reports 517 humpback whales marked in Antarctic waters and 13 humpback whales marked outside Antarctic waters during this project.

Only two mark returns linking African breeding and Antarctic feeding grounds have been recorded in humpback whales (Rayner 1940). One of these whales was marked to the south of South Africa (62° 18' S 10° 41' E), and the other in the southern Indian Ocean (at 64° 00' S 54° 03' E) and both were recovered from whales caught in coastal waters of Madagascar (Table 1.2). The few recoveries recorded off the African coast presumably result from (a) the marking being carried out after the major decline in catches in the African whaling grounds, and (b) the fact that relatively few humpback whales were marked in Antarctic Areas II and III (the possible feeding grounds for African humpback whales) or off the African coast.

Table 1.2. Marks returned from humpback whales from southern African waters (after Rayner 1940).

Mark number	Date		Position	
	fired	recovered	fired	recovered
9326	14-3-37	17-8-38	62° 18' S 10° 41' E	25° 36' S 44° 52' E
2779	16-1-35	24-8-38	64° 00' S 54° 03' E	25° 03' S 47 °10' E

The numerous mark returns from the Area IV and V populations (reported by Chittleborough 1965, Dawbin 1966), show little interchange between breeding grounds off the east and west coasts of Australia. Chittleborough (1965) notes that the distribution of catches in Antarctic Areas IV and V suggests little interchange between feeding grounds, but notes that there was a movement of Area V animals into the eastern region of Area IV in the 1958/1959 summer. However mark returns from the Antarctic must be regarded with caution as the distribution of catches (and therefore of mark returns) were largely determined by where whaling fleets were operating during the four-day humpback whale season, and need not reflect the true distribution of the whales on their feeding ground.

Dawbin (1966) suggested that Area V humpback whales segregate after feeding in Antarctica, with components of the population returning separately to the Australian and New Zealand coasts, although Chittleborough (1965) noted that this segregation decreased after 1959.

Since the cessation of humpback whaling, research into migration patterns has continued through techniques, independent of the whaling industry.

Photo-identification

The extent of variation in the pigmentation patterns and scarification of humpback whales has long been noted (Matthews 1938, Lillie 1915), but it was not until after the cessation of humpback whaling and humpback whale marking, that research into migration patterns through photo-identification of individuals began. The majority of this research, however, has occurred in the North Atlantic and North Pacific Oceans. Humpback whales can be individually recognised from variation in scarification and pigmentation patterns on the ventral surface of the tail, in the serrated edge of the posterior edge of the tail, in the scarification and shape of the dorsal fin, and in the scarification and pigmentation patterns on the left and right flanks of the individual (Katona, Baxter, Brazier, Kraus, Perkin and Whitehead 1979; Katona and Whitehead 1981; Chu and Nieukirk 1987). Over 10 000 humpback whales have been identified worldwide, providing information on migrations in the northern Atlantic (Katona and Beard 1990), the northern Pacific (Baker, Herman, Perry, Lawton, Straley, Wolman, Kaufman, Winn, Hall, Reinke, and Ostman 1986, Darling and Jurasz 1983, Calambokidis, Cubbage, Steiger, Balcomb and Bloedel 1990, Darling and Cerchio 1993) and southern hemisphere (Kaufman, Osmond, Ward, Forestell 1990, Stone, Florez-Gonzalez and Katona 1990) and population characteristics in the North Pacific (Glockner-Ferrrari and Ferrari 1984, 1990, Baker, Perry and Herman 1987, Baker, Straley and Perry 1992), and the Atlantic

(Clapham and Mayo 1990), and population sizes through mark-recapture analyses (eg. Whitehead 1982, Whitehead, Chu, Perkins, Bryant and Nichols 1983, Balcomb and Breiwick 1984, Perkins, Balcomb, Nichols, Hall, Smultea and Thumser 1985, Whitehead and Glass 1985, Balcomb, Katona and Hammond 1986, Baker and Herman 1987, Alvarez, Aguayo, Rueda and Urban 1990, Katona and Beard 1990, 1991 and Baker *et al.* 1992).

Mitochondrial DNA (mtDNA) analyses.

The analysis of mitochondrial DNA haplotype distribution is a powerful technique for identifying geographical genetic variation in the maternal lineages of populations. Despite maternal limitation mtDNA has several advantages over nuclear genetic markers, including the rapid rate of mtDNA evolution compared to nuclear DNA and the fact that the effective size of the mtDNA genome is one quarter that of the nuclear genome. Baker, Palumbi, Lambertsen, Weinrich, Calambokidis and O'Brien (1990) analysed the distribution of mtDNA haplotypes in the northern Pacific Ocean using restriction-fragmentation-length-polymorphism (RFLP) analyses and concluded that their results substantiate the maternally directed fidelity to feeding grounds suggested by Baker *et al.* (1986). Baker, Slade, Bannister, Abernethy, Weinrich, Lien, Urban, Corkeron, Calambokidis, Vasquez and Palumbi (in prep) analysed mtDNA haplotype diversity in six stocks of humpback whales in the North Pacific, North Atlantic and Southern Oceans. Their results supported a division of the North Pacific population into central and western breeding stocks, and a division between the east and west Australian breeding stocks, but showed no significant division in western North Atlantic feeding stocks.

Research into song structure.

Payne and McVay (1971) first described the complex vocalisations made by humpback whales. Subsequent research on songs and song structures has been reviewed by Helweg, Herman, Yamamoto and Forestell (1990), and has shown singers to be male whales (Glockner 1983, Winn, Bischoff and Taruski 1973), singing to be largely limited to the breeding grounds, and whales on the same breeding grounds to sing the same song.

Geographically isolated stocks of humpbacks (ie in different oceanic basins) have been shown to have substantial song differences (Payne and Guinee 1983, Winn, Thompson, Cummings, Hains, Hudnall, Hays, and Steiner 1981). Songs recorded on isolated breeding grounds within one ocean, however, may be similar (Payne and

Guinee 1983, Winn *et al.* 1981, Helweg *et al.* 1990). Payne and Guinee (1983) suggest three possible vectors for such similarity :-

1) Singing whales visit more than one breeding ground each season.

2) Singing whales visit different wintering grounds in subsequent seasons.

3) Some song information is passed between breeding stocks when they mix on common feeding grounds.

Conclusions

The studies carried out to date suggest major differences between patterns of migrations in different oceans. Humpback whales in the western North Atlantic Ocean show strong fidelity to five distinct feeding grounds (Gulf of Maine, Gulf of St. Lawrence, Newfoundland and Labrador, Greenland and Iceland) and mix in the breeding grounds off the Dominican Republic, Puerto Rico and the Virgin Islands in the West Indies (Katona and Beard 1990, 1991). Under this model all humpback whales in the western North Atlantic Ocean would comprise one genetic stock, which is suggested by the distribution of mtDNA haplotypes analysed by Baker *et al.* (in prep). Migration patterns of eastern North Atlantic humpback whales are largely unknown at present.

The migration patterns of humpback whales in the North Pacific Ocean are more complex, with breeding grounds off Hawaii (linked to feeding grounds off Alaska), Mexico (linked to feeding grounds off California) and the Bonin, Ryukyuan, and Marianas Islands south of Japan (historically linked to feeding grounds in the Chukchi, Bering and Okhotsk Seas off Asia (Nishiwaki 1966, Helweg *et al.* 1990). Although song analyses suggest some intermixing of individuals between these breeding grounds (Helweg *et al.* 1990), the mtDNA analyses of Baker *et al.* (in prep) show a division between the Hawaiian and Mexican breeding grounds. Photo- identification analyses show that humpback whales in the central and eastern North Pacific neither form isolated sub-populations, nor mix randomly between years, but rather form geographically isolated feeding aggregations (Baker *et al.* 1986, Perry *et al.* 1990).

The mark return data (Chittleborough 1965, Dawbin 1966), song analyses (Dawbin and Eyre 1991), and results from mtDNA haplotype distribution analyses (Baker *et al.* in prep) suggest that whales migrating on the east and west coasts of Australia show a strong fidelity to breeding grounds and may occasionally mix on their Antarctic feeding grounds. Dawbin (1966) suggested that the Area V humpback whales segregate on the breeding ground, with some components of the population returning to the New Zealand (and southwest Pacific Island) coasts and others to the east Australian coast. Chittleborough (1965) noted that this segregation broke down after 1959 as the population declined.

Although the degree of interchange of individuals between other southern hemisphere breeding grounds is unknown, limited interchange of genetic material could have important ramifications for the gene pool size of isolated breeding populations recovering from severe depletion. Population recovery has been demonstrated in the east Australian component of the Area V humpback whale stock at rates of 0.097 (Paterson and Paterson 1989) and 0.144 per year (Bryden, Kirkwood and Slade. 1990) and in the Area IV stock at a rate of 0.088 per year (Bannister, Kirkwood and Wayte 1991). These recovery rates can be compared with those measured in the western North Atlantic stock at 0.138 (Sigurjonsson and Gunnlaugsson 1990) and at 0.094 (Katona and Beard 1990). Best (1993) noted that the values of 0.144 for the east Australian component of the Area V stock, and 0.138 for the western North Atlantic stock are somewhat high given the likely gross recruitment rates of 0.11 calculated for humpback whales (Clapham and Mayo 1990).

RATIONALE AND OBJECTIVES

During the 1980's it became apparent that the South African east coast humpback whale population was recovering. Not only were increasing numbers of incidental sightings being reported, but increasing numbers of humpback whales were seen on annual aerial surveys for right whales. No humpback whales were sighted in such surveys between 1971 and 1984, and increasing numbers were sighted each year thereafter to 1987.

The east coast population was chosen for monitoring rather than the west coast population for three reasons :-

a) as annual catches of humpback whales (in the ten years prior to protection) at Durban were approximately ten times those at Donkergat, Saldanha Bay, it is assumed that the east coast population is currently larger than its west coast counterpart.

b) the oblique orientation of the Natal coast to the general direction of the northward migration probably results in the whales converging on the northern Natal coast (see Dawbin 1966).

c) from the seasonality of catches, it appears that humpback whales migrate further north on the west coast, and much of this migration probably strikes the coast to the north of South Africa.

The ultimate objective of this programme is to use the unique opportunity provided by the proximity of a recovering whale stock in southern African waters to determine its size, rate of increase and measure relevant demographic parameters through shore-based monitoring. Such shore-based monitoring has been carried out for Californian gray whales (Rugh and Braham 1979, Reilly, Rice and Wolman 1980, 1983, Reilly 1984, Rugh 1984, Breiwick, Rugh, Withrow, Dahlheim and Buckland 1988, Rugh, Ferrero and Dahlheim 1990), bowhead whales at Pt. Barrow, Alaska (Zeh, Ko, Krogman and Sonntag 1986a, 1986b, Gentleman and Zeh 1987, Krogman, Rugh, Sonntag, Zeh and Ko 1989, Zeh, George, Raftery and Carroll 1991) and humpback whales off the east coast of Australia (Bryden 1985, Bryden *et al.* 1990, Paterson and Paterson 1984, 1989 and Paterson 1991). Furthermore, as humpback whales feed almost exclusively on krill, monitoring could provide baseline information from which the effects of potential krill harvesting in the Southern Ocean on humpback whale population recovery could be examined. Essential initial research however, is the determination of the optimal period in the migration and the most appropriate techniques for monitoring long term trends in the population.

Key questions posed in this project are :-

1) What are the characteristics (eg. timing, direction, intensity, speed, width of migration path, pod size and composition) of the migrations of humpback whales off the east coast of southern Africa?

Not only are the above characteristics of interest themselves, but they are also critical in the determination of annual population size, and in the comparison of population estimates between years.

2) What is the optimum period during the migration for monitoring annual changes in abundance?

Long term population monitoring will require a series of surveys to determine changes in abundance. Although such surveys need not be carried out each year (eg. a break of five years between three annual surveys would be suitable), they must be undertaken at a comparable and optimal period of the migration. Aspects to be considered include the density and behaviour of whales present and the suitability of weather conditions for monitoring.

3) With what feeding areas in the Antarctic is the east African migration stream associated?

4) With what breeding areas in the Indian Ocean is the east coast migration stream associated?

The latter two key questions will be addressed through photo-identification of individual animals, although constraints on the accessibility of the Antarctic feeding areas and certain sections of the east African breeding grounds may compromise this aspect of the project.

CHAPTER 2

STUDY AREA

This study was carried out on the east coast of southern Africa (Figure 2.1), shore-based visual surveys being undertaken at Cape Vidal (28° 07' S; 32° 33' E) on the northern Natal coast, South Africa, and a shipboard survey being undertaken in the coastal waters of Mozambique between Maputo (25° 58' S 32° 32' E) and 18° 00' S.

The oceanography of the east coast of southern Africa is dominated by the southerly-flowing Agulhas Current, which forms part of the western boundary current system of the southern Indian Ocean. The Agulhas Current water arises from both Tropical and Sub-tropical surface water (from the Mozambique and East Madagascar Currents), and has surface salinities of 35.2 to 35.4 ppt. Peace (1977) defined three regions in the surface layer of the Current :-

1) the western region inshore of the western 1 m.s^{-1} isotach.

2) the core region where the current speeds exceed 1 m.s^{-1}.

3) the eastern region offshore of the eastern 1m.s^{-1} isotach.

Heydorn, Bang, Pearce, Flemming, Carter, Schleyer, Berry, Hughes, Bass, Wallace, van der Elst, Crawford and Shelton (1978) stated that four regions were present in the Agulhas system, the fourth arising from Pearce's (1977) western region being divided into an inshore region and a boundary region.

Pearce (1977)found the mean peak current speed of the core to be 1.36 m.s^{-1}, although speeds of up to 2.45 m.s^{-1} were recorded. Grundlingh (1977) and Barlow (1931, in Harris 1978) recorded peak current speeds of 2.6 and 2.5 m.s^{-1} respectively. The current is constrained by the coastal shelf edge, so that the distance of the current core from the coastline varies with the shelf width. Pearce (1977) found that in the region of Richards Bay (approximately 100 km south of Cape Vidal) the maximum speed of the current is just offshore of the shelf

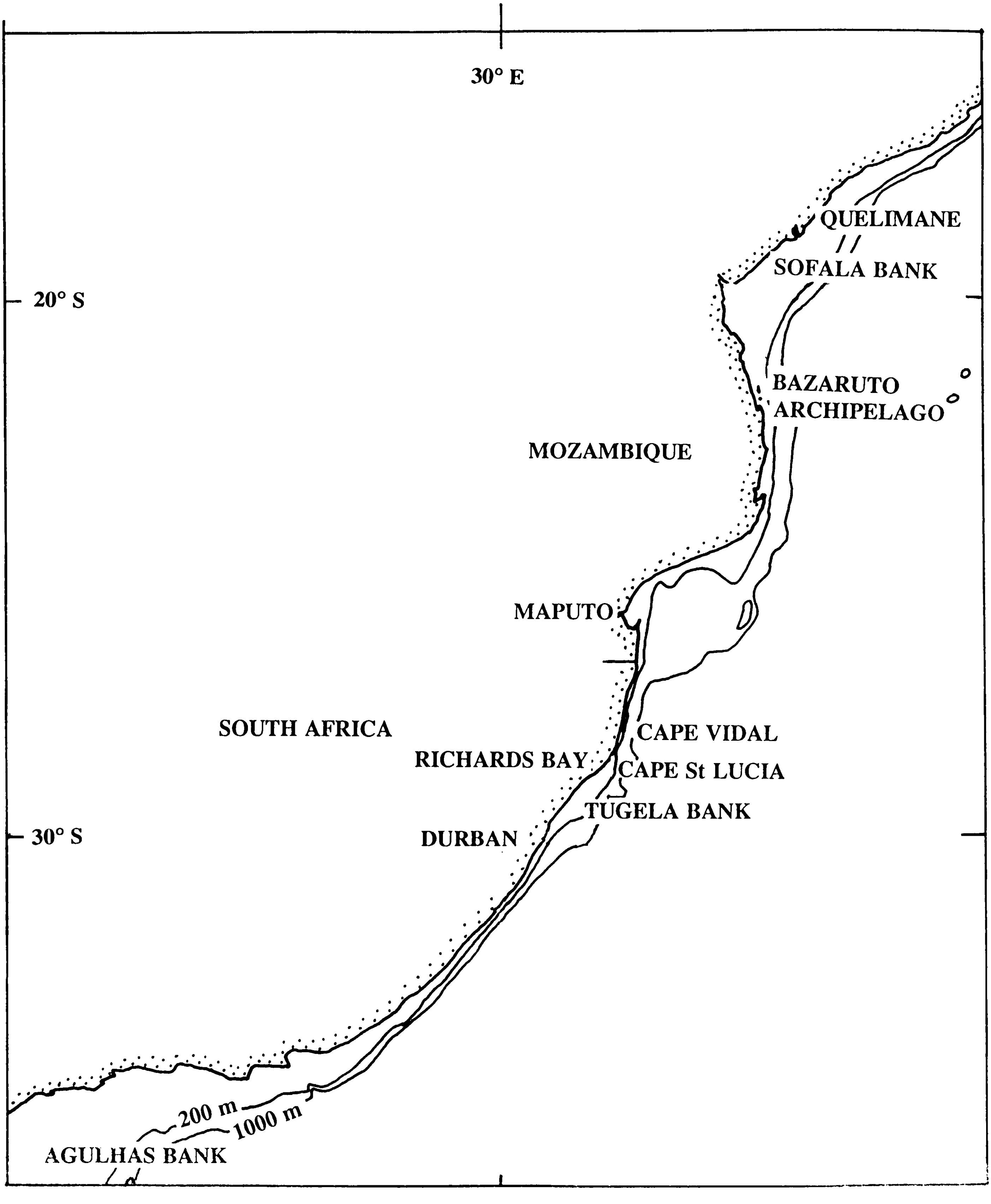


Figure 2.1 The east coast of southern Africa showing locations referred to in the text.

break which lies less than 10 km from the shore, while off Durban the maximum current speed was about 40 to 50 km offshore. Schumann (1987) notes that in the region of Cape St Lucia, the Current comes to within a few kilometres from the coast. Harris (1978) noted the limited current data from the northern Natal coastline, and that the only current observations are from a limited data set on the drift of ships parallel to, and about 2 km from, the coast. In the region of Sordwana Road to Cape Vidal, 17 % of observations showed northward drift, 79 % showed southward drift and 4 % showed slack water, while in the region from Cape Vidal to Cape St Lucia, northward drift comprised 12 %, southward drift 76 % and slack water 12 % of observations. The bathymetry of the east coast of southern Africa and localities referred to in the text are shown in Figure 2.1.

Harris (1978) stated that the Agulhas Current commonly meanders from its mean migration path as it flows southward along the Natal coastline. Pearce (1977) and Pearce, Schumann and Lundie (1978, in Schumann 1987) note however that this behaviour is less pronounced in the region of, and to the north of, Richards Bay than off Durban where the continental shelf is wider.

The site was chosen as it has a headland, and is sufficiently far north for the migratory corridor to have formed (as the orientation of the coast relative to the general south to north migration results in congregation of whales on the coast). Adequate infrastructure was also available, as the area formed part of a Natal Parks Board reserve. Observations were carried out from two vantage points (termed north and south tower) on a vegetated sand dune approximately 60 m high (above sea level). North and south towers had an horizontal uninterrupted view through 190 and 180 degrees respectively and shared a 160 degree view. The distance to the horizon was approximately 23 km. South tower was constructed in 1988, while north tower was constructed in 1990, after it had become apparent that not all groups within view were being sighted by observers. Both towers were timber constructions and each was topped by an approximately 3m x 3m work platform. The distance between towers was 22m and the heights of the south and north towers were 61.5 and 60.3m above mean sea level respectively. Protection from wind and sun on the south tower was provided by a canvas shelter in 1988 and 1989 and a corrugated iron shelter thereafter. The canvas shelter was used on north tower in 1990 and 1991.

Figure 2.2 shows the mean daily sighting conditions recorded at hourly intervals during each years survey

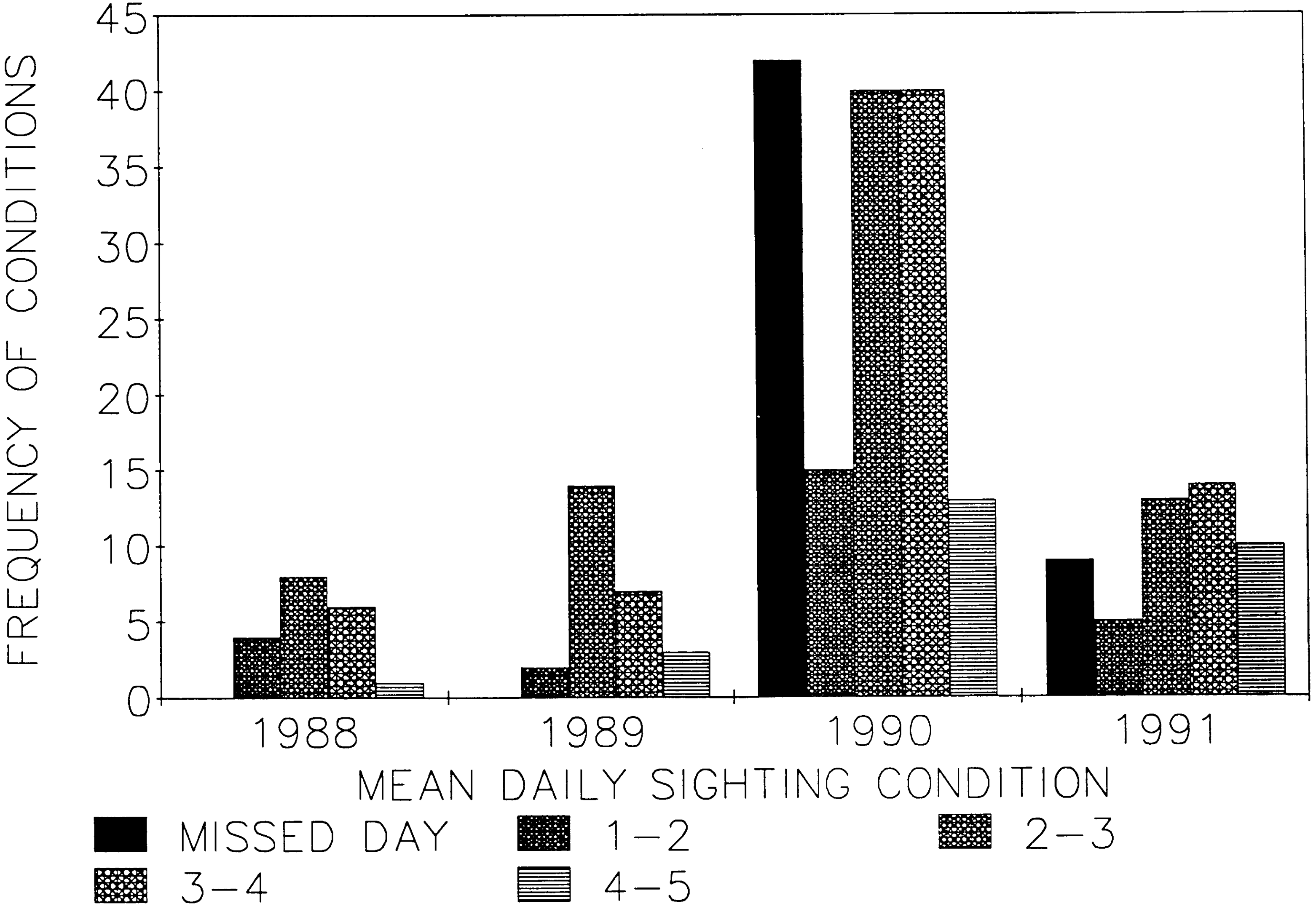


Figure 2.2 Frequencies of mean daily sighting conditions recorded at hourly intervals at Cape Vidal between 1988 and 1991.

undertaken from Cape Vidal. Observations were not carried out during periods of inclement weather (wind speeds of over 25 knots, rain or air visibility of less than 5 km from the shore). Poor air visibility occasionally resulted from haze from the burning of inland sugar plantations and light offshore winds. Included in the hourly weather records were wind speed and direction, sea surface state (Beaufort), cloud cover, swell and air visibility and a general index of sightability taking all weather conditions into consideration (1 = very poor, 2 = poor, 3 = acceptable, 4 = good, 5 = very good). No correlations were found between sighting condition and time of day (Figure 2.3, $r^2 = 0.07\%$, $p > 0.50$, $n = 1128$), wind speed and time of day (Figure 2.4, $r^2 = 0.11\%$, $p > 0.50$, $n = 1128$) or sea surface state by time of day (Figures 2.5, $r^2 = 0.13\%$, $p > 0.50$, $n = 1128$). Sea surface state was positively correlated to wind speed (Figure 2.6, $r^2 = 0.65$, $p < 0.05$, $n = 1128$), and sighting condition was negatively correlated to wind speed (Figure 2.7, $r^2 = 0.57$, $p < 0.05$, $n = 1128$).

The line-transect survey of the distribution and abundance of humpback whales was carried out in Mozambique waters between Maputo and Quelimane and between the 9 m and 183 m isobaths. Staff and volunteer changes were carried out at Magaruque Island in the Bazaruto Archipelago. The bathymetry of the region is shown in Figure 2.8. The oceanography of this region is dominated by the warm southerly flowing Mozambique Current which forms the Agulhas Current to the south. As with the Agulhas Current, the distance of the Mozambique Current from the coast varies with shelf width so that over the Sofala Bank and Zavora Bank the current lies some distance from the coast, off the shelf edge.

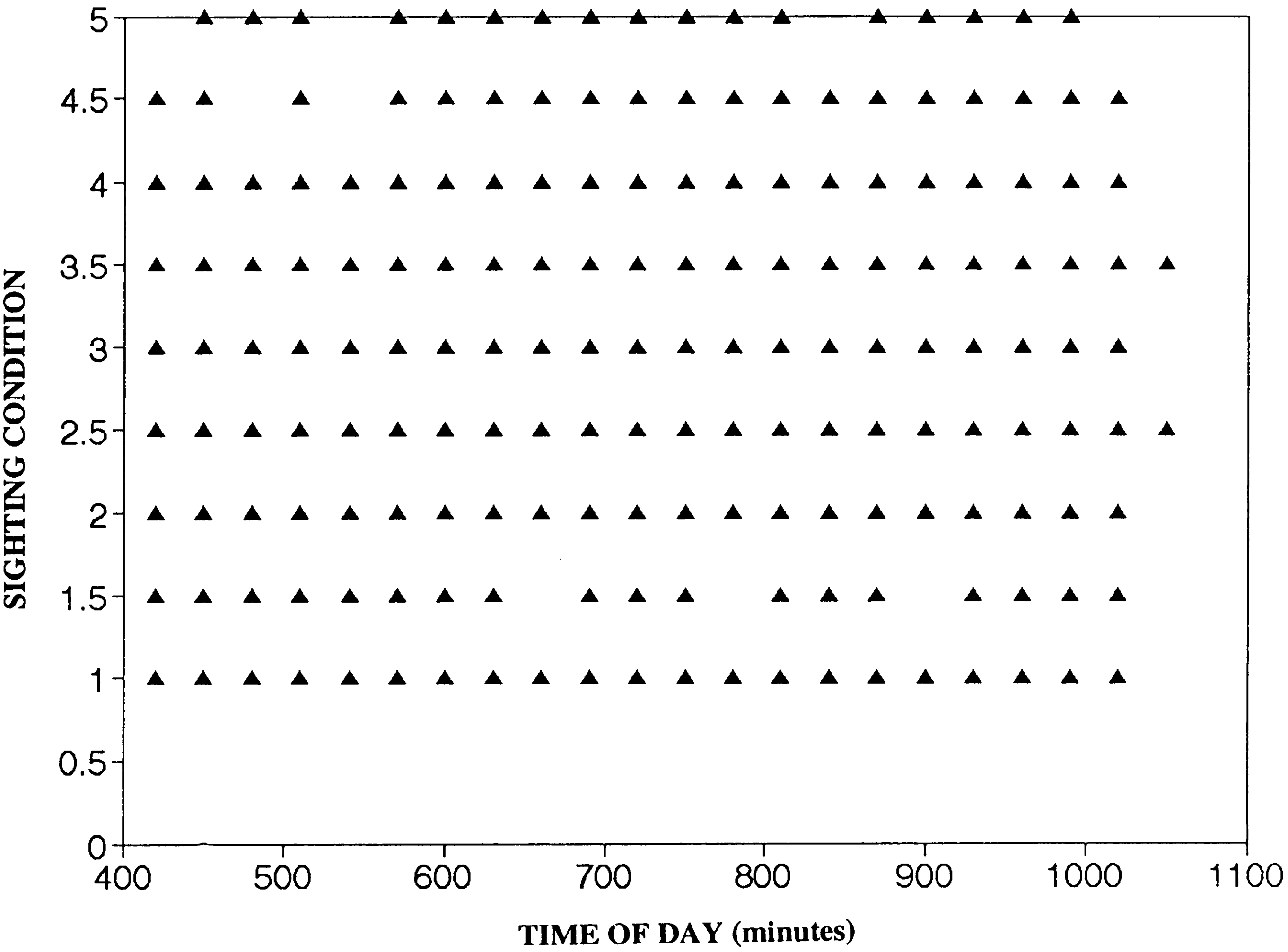


Figure 2.3 Sighting conditions recorded by time of day (minutes) during days of observations at Cape Vidal between 1988 and 1991.

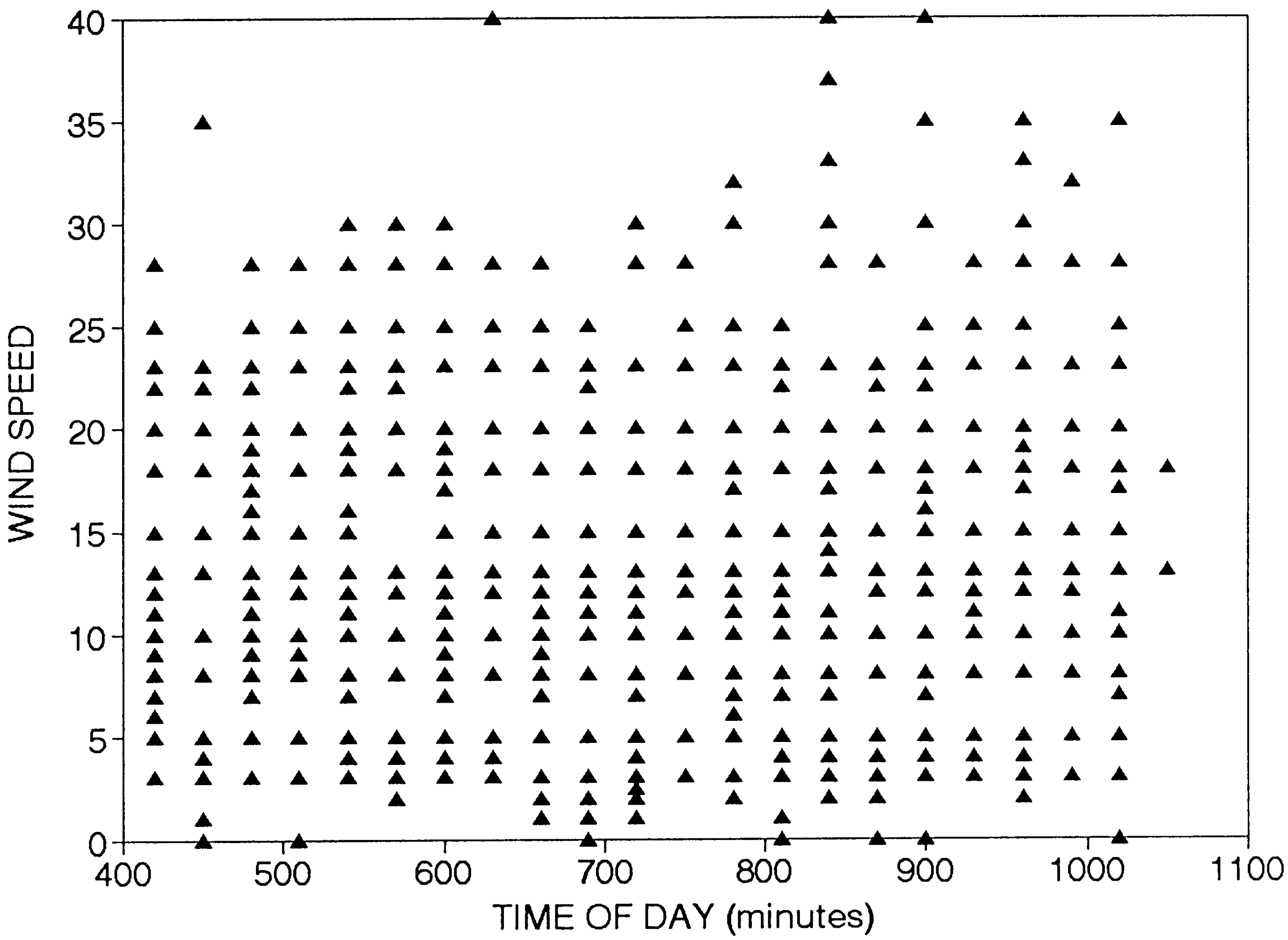


Figure 2.4 Wind speed (knots) recorded by time of day (minutes) during days of observations at Cape Vidal between 1988 and 1991.

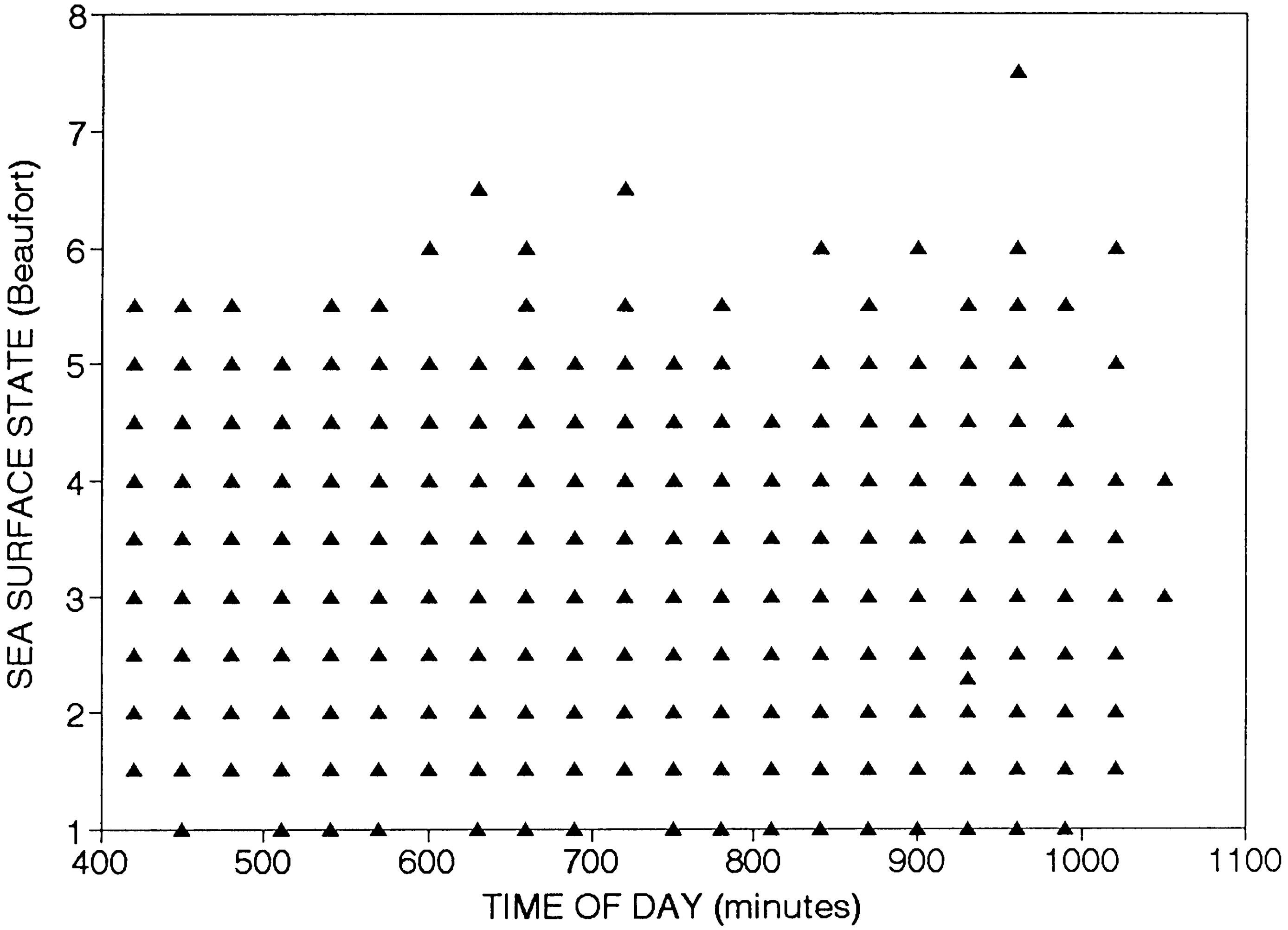


Figure 2.5 Sea surface state (Beaufort) recorded by time of day (minutes) during days of observations at Cape Vidal between 1988 and 1991.

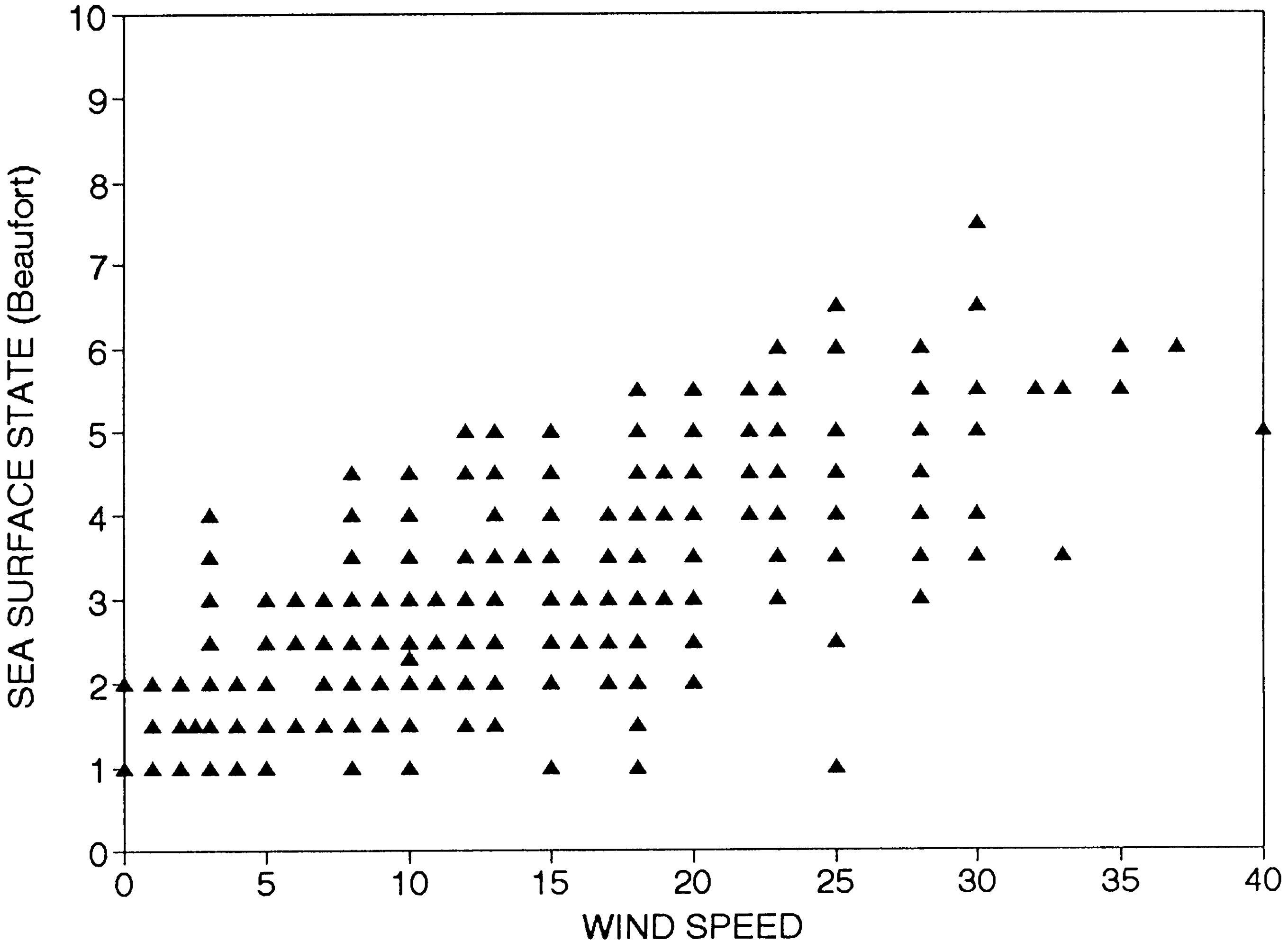


Figure 2.6 The relationship between wind speed (knots) and sea surface state (Beaufort) recorded at hourly intervals during days of observation at Cape Vidal between 1988 and 1991.

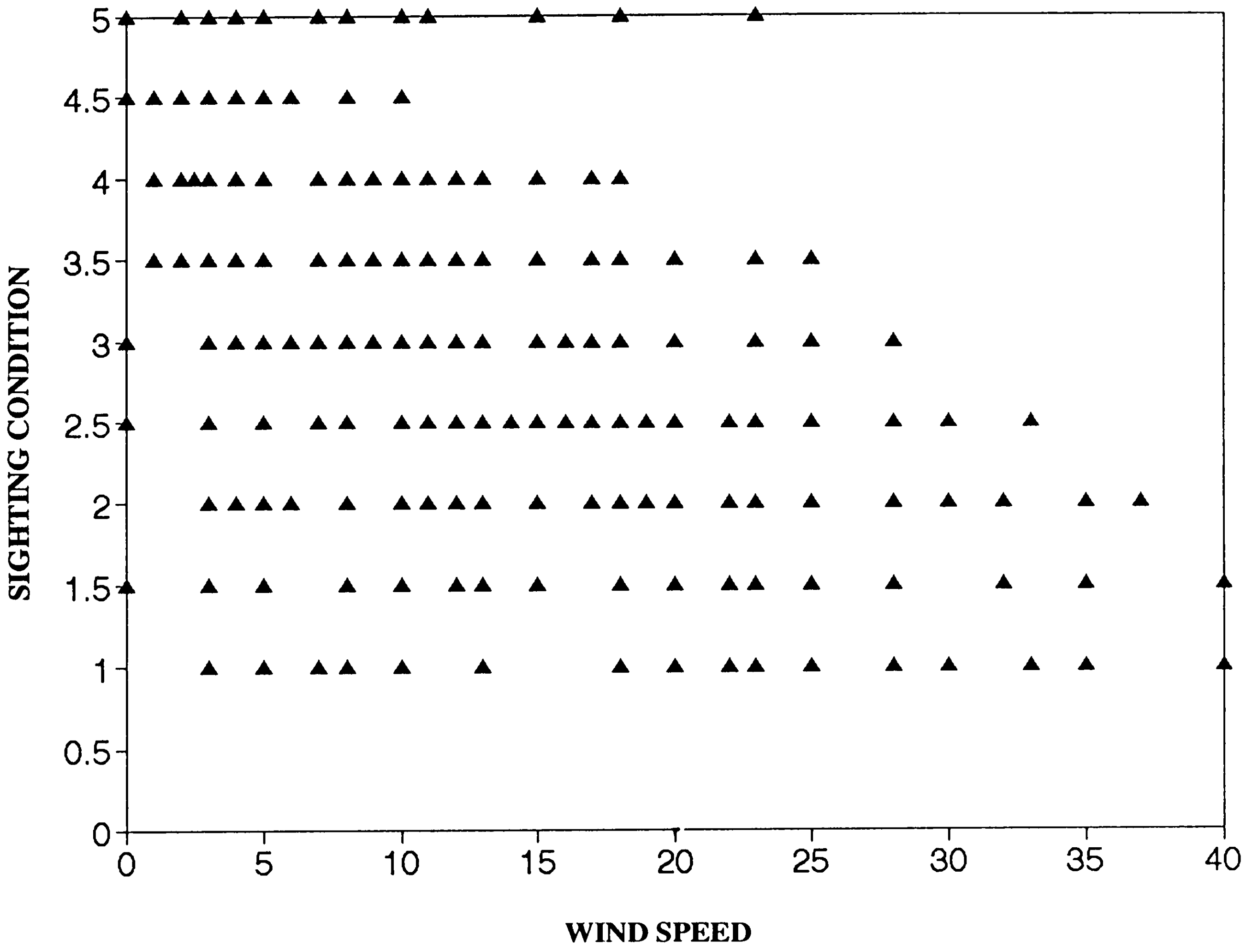


Figure 2.7 The relationship between wind speed (knots) and sighting conditions recorded at hourly intervals during days of observation at Cape Vidal between 1988 and 1991.

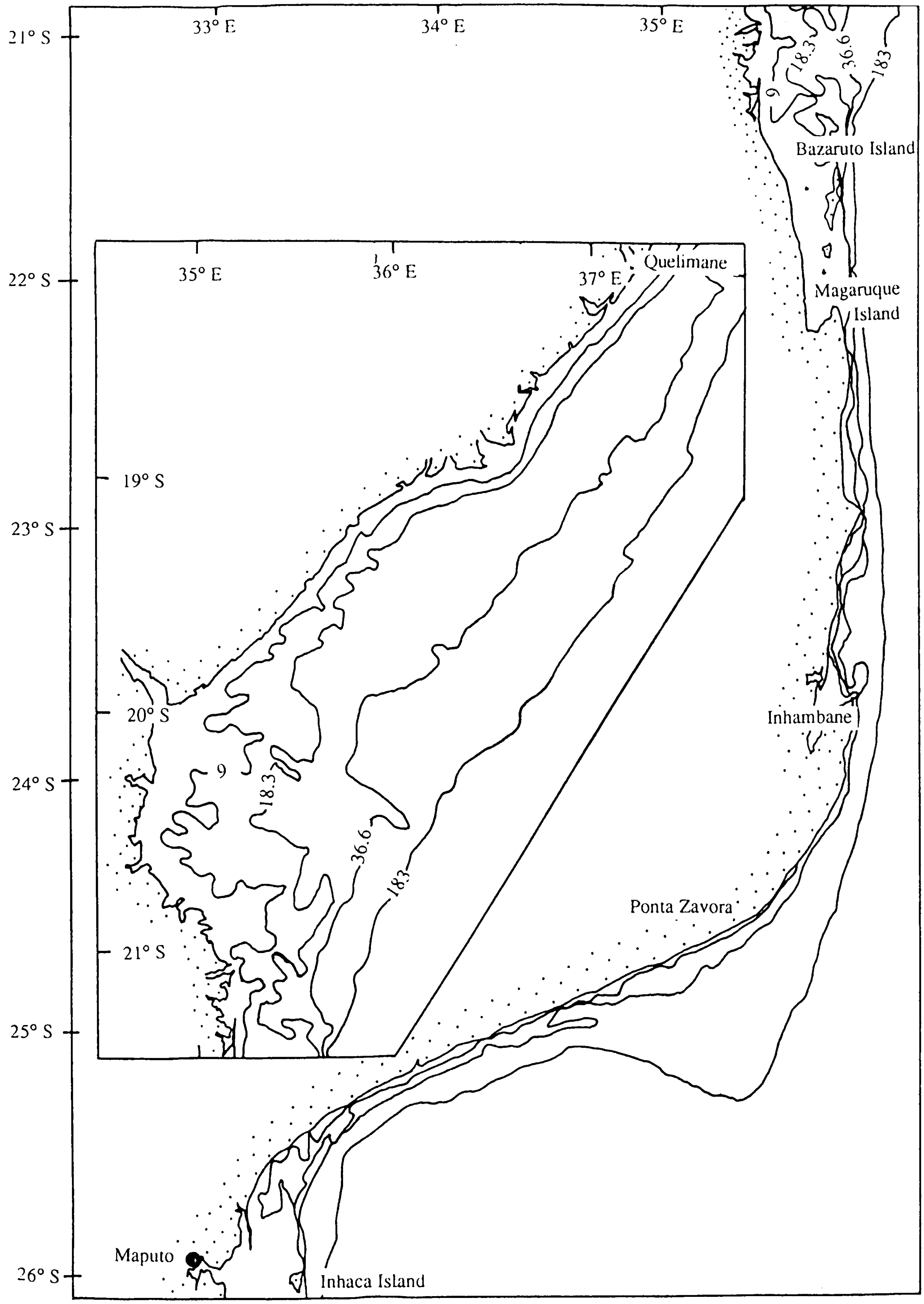


Figure 2.8 The bathymetry of the study area off Mozambique.

CHAPTER 3

CHARACTERISTICS OF HUMPBACK WHALE MIGRATIONS OFF CAPE VIDAL ON THE AFRICAN EAST COAST.

INTRODUCTION

The fact that humpback whales (*Megaptera novaeangliae*) undertake annual migrations from summer polar feeding grounds to winter breeding grounds in tropical and sub-tropical waters, has long been known from seasonal variations in abundance in whaling grounds at various latitudes (Risting 1912, Olsen 1914, Harmer 1928, 1931, Matthews 1938, Mackintosh 1942). Five feeding grounds have been identified off the Antarctic coast (Bergersen, Lie, and Ruud 1939 (in Mackintosh 1942), Hjort, Lie and Ruud 1932, 1933a, 1933b, 1934, 1935, 1937, 1938 (all in Mackintosh 1942), Mackintosh 1942, Omura 1973), each of which has been linked to a breeding ground in the coastal waters of South America, Africa (including Madagascar), Australia, New Zealand or the islands of the south-western Pacific Ocean (Kellogg 1929, Rayner 1940, Mackintosh 1942). *En route* between breeding and feeding grounds humpback whales utilise the coastal waters of southern hemisphere continents as migratory corridors. Historical catch records have indicated two such corridors in southern African waters: the east coast corridor conveys whales to breeding grounds off Mozambique (Olsen 1914) and possibly Madagascar (Angot 1951), while the west coast corridor takes whales as far north as breeding grounds off Gabon (Budker and Collignon 1952).

Modern humpback whaling from shore-based stations in southern Africa began in 1908, and catches of humpback whales amounted to approximately 23 000 animals between 1908 and 1915 (Committee for Whaling Statistics 1942 -1964). By 1914 the populations on both coasts had declined to the extent that stations relying entirely on humpback catches were forced to close. Despite such high catches, little actual biological data (apart from catch data) has been collected or published on African humpback whales, apart from information published by Risting (1912), Olsen (1914) and Matthews (1938). Humpback whaling continued until October 1963, by which time annual catches off the east coast amounted to about thirty-five. Winn and Reichley (1985) suggested a post-exploitation stock size of 340 whales for the western Indian Ocean, but the origins of this estimate were not given.

The coastal migratory habits of humpback whales, which made them particularly susceptible to shore-based modern whaling, now result in the species being ideally suited for shore-based monitoring. Such monitoring of large cetacean populations has been carried out for Californian gray whales (Reilly, Rice and Wolman 1980, 1983, Rugh and Braham 1979, Rugh 1984, Reilly 1984), bowhead whales (Zeh, Ko, Krogman and Sonntag 1986a, 1986b, Gentleman and Zeh 1987, Krogman, Rugh, Sonntag, Zeh and Ko 1989), and humpback whales in Australia (Bryden 1985, Bryden Kirkwood and Slade 1990, Paterson and Paterson 1984, 1989 and Paterson 1991).

Shore-based surveys of humpback whales have provided both annual abundance indices (Paterson and Paterson 1989) and rates of recovery (Bryden *et al.* 1990) for the Australian component of the Area V population. However, the importance of migration characteristics (speed, distance offshore, width of migration path, direction, or group size and composition) has largely been ignored in these studies. This paper presents attempts to provide estimates of most of these parameters for humpback whales migrating along the east coast of South Africa.

METHODS

Field methods

Shore-based surveys of migrating humpback whales have been undertaken at Cape Vidal, northern Natal, each year since 1988. Surveys were undertaken from an approximately 60m high vantage point from 4 July to 22 July 1988, from 27 June to 22 July 1989, from 2 June to 28 October 1990, and 17 June to 6 August 1991. During the July 1990 and the 1991 surveys, concurrent independent observations were made from a second tower (at a similar altitude and 22 m to the north of the primary tower) to determine observer efficiency under different weather conditions, and with distances from the coast (the results of which are reported in chapter 4). For the purposes of the present paper, only sightings made from the primary (southern) tower will be analysed.

Observations were undertaken for ten hours per day (07h00 to 17h00), weather permitting, except during the five-month survey in 1990, when five hours observation were undertaken each day outside of the expected peak migration periods (1 July to 23 July and 15 September to 15 October).

Observations were carried out by two observers per tower at all times, generally with one observer searching offshore with 7 x 35 wide-angle binoculars and the other searching the entire area by naked eye, with roles being reversed approximately every 15 minutes. Positions of groups were measured using a Wild T1 or T1A theodolite (orientated daily on a standard reference object on the shoreline) with fixes being taken on successive surface activity behaviour (as carried out by Wursig, Cipriano and Wursig 1991). The time of each fix was measured to the nearest second. Position fixes were measured as vertical and horizontal angles of the group from the centre of the earth and True North respectively, and were immediately plotted onto a chart. Angles were measured to at least the nearest 20 seconds in 1988 and the nearest 3 seconds in subsequent years. Immediate plotting not only provided an error check for recorded positions, but also eliminated confusion when two groups were migrating in close proximity, and assisted tracking in providing a rough indication of where the group would next surface. Estimates of group size and heading (north or south) were noted at each position fix, and animals had to be within five body lengths of each other to be classified as a group.

A record of search activity was kept wherein the times at which searching began, ended or was interrupted (eg for the tracking of a group of whales) and subsequently resumed were noted. Environmental observations (wind direction and speed, sea surface state (Beaufort), swell, cloud cover, visibility, and a general index of sightability) and the number of ski-boats and ships visible were recorded every hour, starting one hour after the commencement of observations. Watch was discontinued during rain, when visibility dropped to less than five kilometres, or when wind speeds exceeded 25 knots.

When possible, a ski-boat was launched to intercept passing groups of whales for confirmation of estimates of group size made from the tower and for collection of identification material. Exemption for this work was granted in terms of the Sea Fisheries Act (no 58 of 1973) and the Fishery Act (no 12 of 1988). During independent observer surveys, only groups determined to have been seen by both towers were intercepted, so that a tower was not cued to the presence of a whale by ski-boat activity. Such determination was made by a third party on the basis of radio reports of positions given independently by each tower. The ski-boat was directed onto the group by radio contact from the north tower.

Analyses

All observation effort has been regarded as being of equal intensity, and periods during which whales were tracked have been included as observation effort. Although this may result in a density-dependent underestimate of whales passing the platform, such a bias is thought to be balanced by increased observer awareness during tracking periods. From 1990, the amount of tracking of each group was limited to three consecutive fixes or twenty minutes, whichever came first.

Group size estimates were refined at each fix, and the sizes used in analyses were the final estimates of group size. Where the final estimate of group size was recorded as a range, the group size used in analysis was the mean of the range rounded to the nearest integer. Group size estimates from the tower were compared to group sizes confirmed during interception of the same groups by ski-boat. Groups of indeterminate size (where no estimate was made) were excluded from these analyses, but included in daily density analyses as single individuals.

The vertical and horizontal angles recorded by theodolite for each position were converted to distances from the platform (radial distance) and bearings from true north using a BASIC application programme (Appendix I). This algorithm took into consideration both the curvature of the earth and a tropical and temperate region refraction correction factor. Thereafter, having established co-ordinate positions for each fix, the migration speed and heading of each group and their distance from the shore (coastal distance) could be calculated. Migration speeds were calculated using the distance travelled between the first and last definite fixes of each migration track and the elapsed time between these fixes, while the mean heading of each track was calculated as the heading between the first and last definite fix. The coastal distance was calculated as the distance of the midpoint of the track to the shore directly to the east of it. Migration speeds and headings were calculated for all migrating groups for which more then two definite fixes were obtained, while coastal and closest radial distances were calculated for all groups for which at least one definite position fix was obtained.

To establish how many groups passed Cape Vidal during the period of watch, migration tracks of whales that were not seen to have crossed the midline were projected northwards or southwards to the midline along the mean heading of that particular track. The time of crossing the midline was calculated using the mean speed of the track over the projected distance, and the group was correspondingly scored to have crossed the midline inside or outside the observation period. Where only one position was noted, the direction of migration was taken as the direction noted in the field record (ie. north or south), while the heading and speed used were the mean heading and speed for that year (calculated from groups for which more than two fixes were obtained). Daily densities of northward and southward migrating groups were calculated from the sum of all northward or southward migrating groups observed to have crossed (or projected to cross) the midline during observation periods. Groups with an indeterminate migration direction were apportioned to the northward or southward migration densities of that day on a *pro rata* basis, taking into account the proportion of groups crossing the midline of total groups seen.

Examination of the pattern of daily densities suggested that the migration comprised a series of waves, as peak densities were recorded over similar time periods each year. Densities recorded on the same day each year were compared using Spearman's rank correlation test. Thereafter spectral analysis (BMDP Statistical software) was carried out on each year's data, and on all years' data combined to determine any periodicity in the migration waves.

The data collected for each group can be subdivided into migration-dependent parameters (speed and direction of migration, distance offshore, and group size and composition) and environmentally-dependent parameters (time of day, weather and other environmental conditions). The effects of migration-dependent and environmentally-dependent parameters were tested on group size, distance offshore, and migration speed and heading using both univariate and multivariate (multiple regression (BMDP 1R)) analyses. Due to the obvious correlation between wind speed and sea surface state, migration characteristics have not been analysed by sea surface state. While results of univariate analyses of environmentally-dependent parameters will be presented separately, results of univariate analyses pertaining to migration-dependent parameters will be presented together. Results of multiple regression analyses follow after the results of multiple regression analyses.

RESULTS

Observations

The observation effort and number of sightings recorded each year are shown in Table 3.1. The high proportion of humpback whales in the identified whales suggests that essentially all the unidentified whales were humpback whales, and they have been analysed as such. Other identified whales, including southern right whales (*Eubalaena australis*) and minke whales (*Balaenoptera acutorostrata*), have been excluded from analyses.

Table 3.1. Results of shore-based surveys undertaken at Cape Vidal in 1988, 1989, 1990 and 1991.

YEAR	OBSERVATION EFFORT	WHALES OBSERVED Groups (individuals)			
	Hours	Humpback	Other (R = southern right whale; M = minke whale)		Unidentified
			R	M	
1988	166	46 (115)	0 (0)	0(0)	17 (31)
1989	199.5	44 (91)	1 (2)	0 (0)	14 (20)
1990	618.25	291 (525)	3 (6)	2 (4)	89 (119)
1991	363	126 (254)	1 (1)	2 (3)	105 (154)

The observation effort recorded each day is shown in Figures 3.1. The proportion of effort lost to poor weather each month (Table 3.2) shows the inclement weather characteristic of the region from August to October, in the 1990 results. Weather conditions were clearly most optimum for monitoring during the earlier, northward migration.

Table 3.2. Percentage of monthly observation effort lost to poor weather conditions (wind speeds of over 25 knots, rain or visibility of less than approximately 5 km).

YEAR	MONTH	EFFORT (hours)	PERCENTAGE TIME LOST
1988	June	166	23 %
1989	June/July	199.5	17 %
1990	June	88.34	39 %
	July	185.92	30 %
	August	72.92	53 %
	September	149.27	38 %
	October	121.73	43 %
1991	June	108.9	22 %
	July	203.5	27 %
	August (6 days)	50.8	15 %

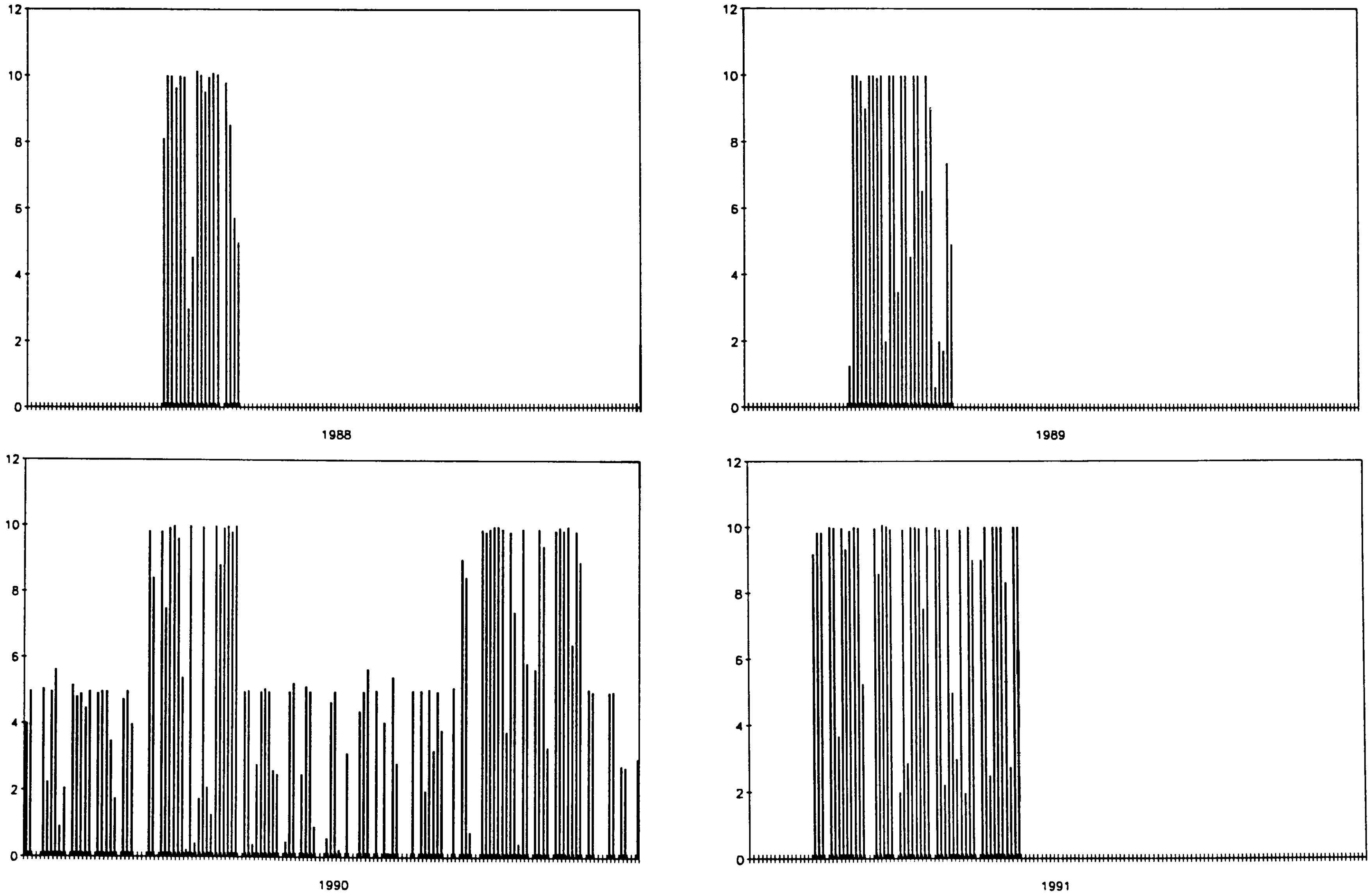


Figure 3.1. Daily observation effort (hours) carried out from the south tower at Cape Vidal between 2 June and 28 October in 1988, 1989, 1990 and 1991.

Daily densities

Daily densities of northward migrating whales observed each year on days for which observations were made, are shown in Figure 3.2, while the daily densities of southward migrating whales in 1990 are shown in Figure 3.3. The first group seen migrating southward in 1990 was on 7 July, while the last group migrating northwards was recorded on 13 October. Figure 3.4 shows the switch in the north to south migration occurring between 5 and 25 August, although the exact timing is impossible to establish, and suggests milling seems to occur in the area during August. Matthews (1938) found the mid-season catch in the Durban whaling grounds to comprise a high proportion of juvenile animals, and suggested that juvenile humpback whales did not migrate as far north as mature individuals.

The northward migration each year was composed of waves, occurring over the periods 1-10 July, 11-20 July and 21-31 July (Figure 3.5). Spearman rank correlation of daily densities recorded each year showed significant correlation between the 1989 and 1991 daily densities ($r_S = 0.5098$, $p = 0.011$, $n = 26$), but no correlation between daily densities recorded in other years (Table 3.3). Unfortunately, the 1988 and 1989 surveys ended prior to the peak migration period of 21-31 July, and the lack of correlation may arise from this or the fact that the 1-10 July wave did not appear in 1990, possibly owing to the presence of an oil slick some 100 km to the south of Cape Vidal. Spectral analysis with missing values replaced by means (BMDP Statistical software) showed a periodicity at 10.2 days in 1988, 1989 and 1991 and at 8.5 days in 1990, although these were not significant at the 5% level (Table 3.4). Spectral analysis carried out on mean daily densities of all four years showed asignificant periodicity at 10.2 days (Table 3.4). For ease of reference these waves have been numbered 1-5 as in Figure 3.5. In both 1990 and 1991, the impression was gained that wave number 4 comprised large whales (KPF pers. obs.), but no measurement of size was attempted.

Although the southward migration appears to comprise similar waves, the data are too few for inter-year comparison.

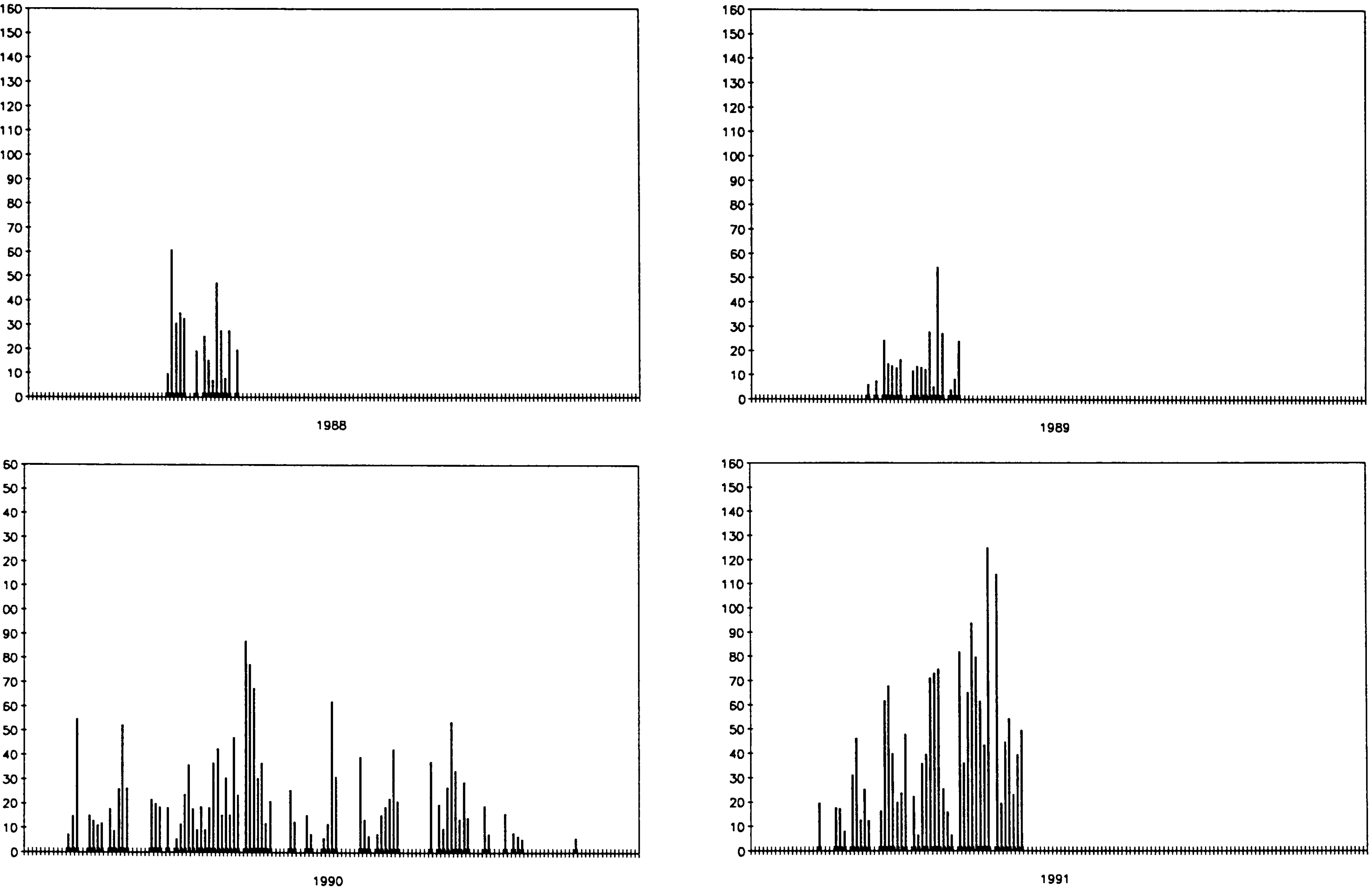


Figure 3.2. Estimates of daily densities of northward migrating humpback whales passing Cape Vidal between 2 June and 28 October made from the south tower in 1988, 1989, 1990 and 1991.

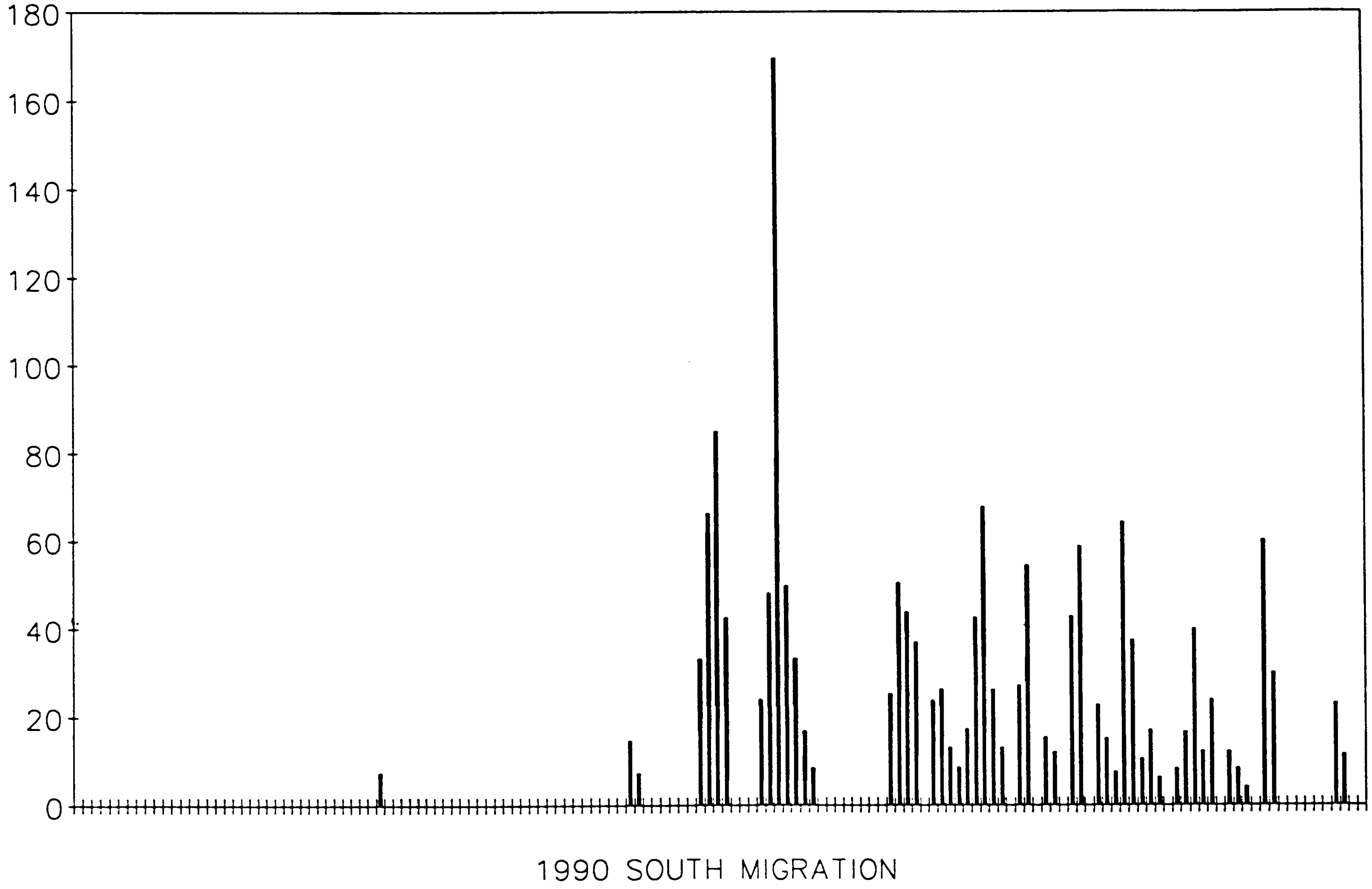


Figure 3.3 Daily densities of southward migrating humpback whales passing Cape Vidal as estimated from the south tower between 2 June and 28 October in 1990.

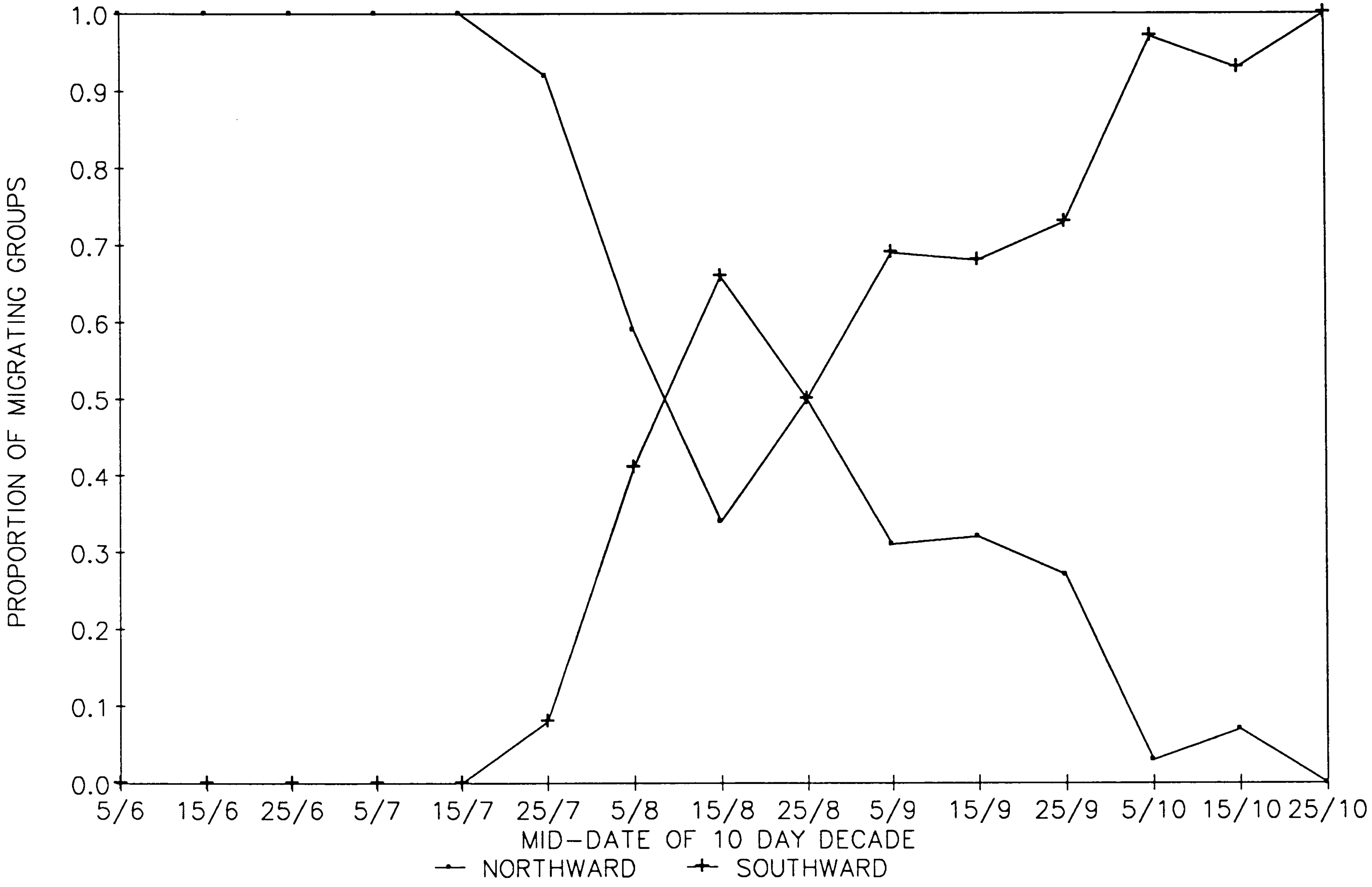


Figure 3.4 The proportions of northward- and southward-migrating groups sighted off Cape Vidal by decade in 1990.

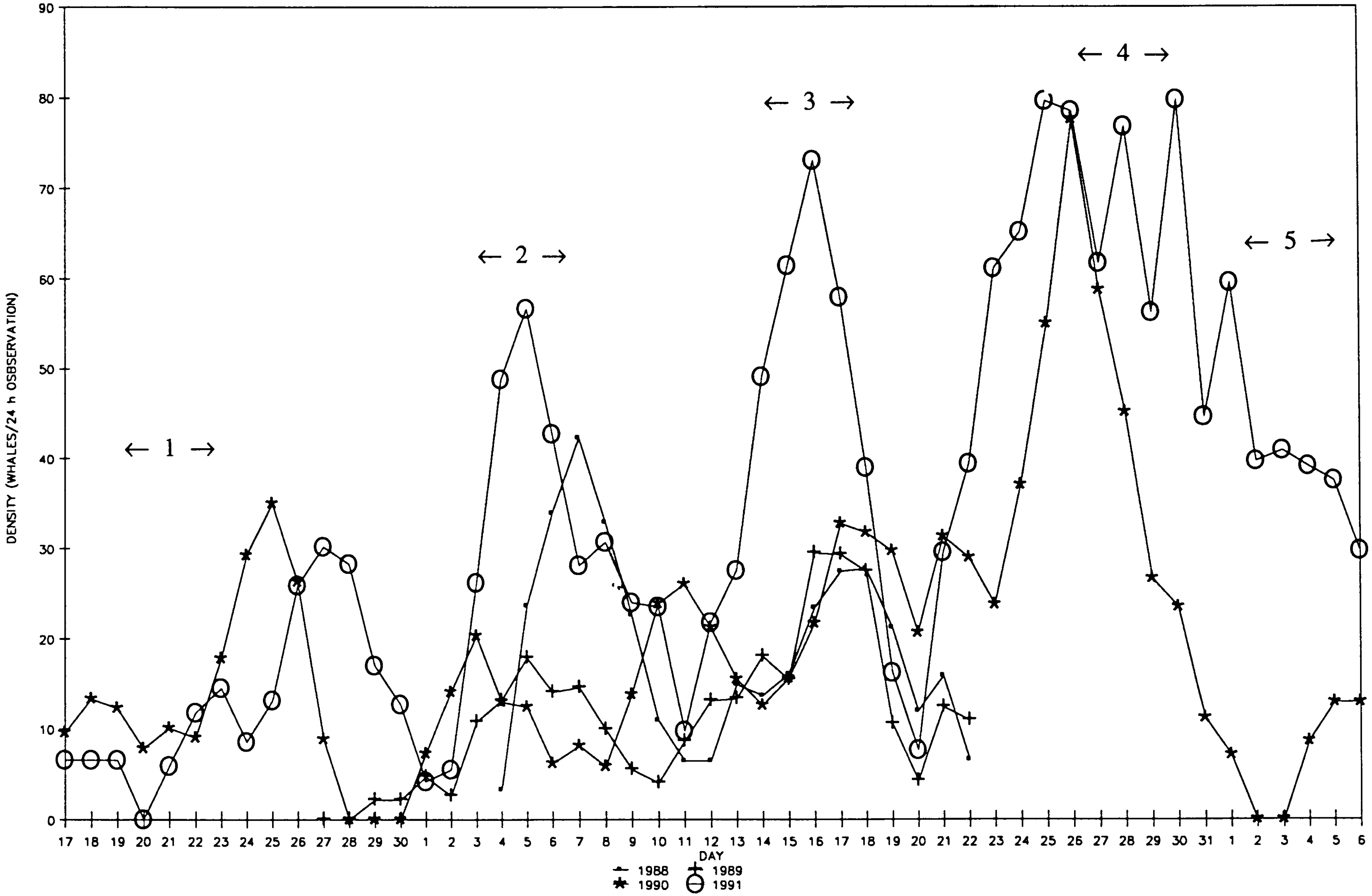


Figure 3.5 Three-day running means of daily densities of northward migrating humpback whales passing Cape Vidal (south tower) between 17 June and 6 August each year.

Table 3.3. Results of pair -wise Spearman rank correlation analyses of daily densities of humpback whales migrating past Cape Vidal each year between 1988 and 1991.

YEAR		1989	1990	1991
1988	coefficient	0.2766	0.0151	0.2355
	sample size	19	19	19
	sig. level	0.241	0.949	0.318
1989	coefficient	-	0.325	0.5098
	sample size		26	26
	sig. level		0.104	0.011
1990	coefficient	-	-	0.2181
	sample size			51
	sig. level			0.1230

Table 3.4. Results of the spectral analysis (BMDP) carried out on daily densities of humpback whales recorded migrating northwards past Cape Vidal each year.

UNIVARIATE SUMMARY STATISTICS (based on cases occurring in the interval day =1 through day = 51)								
VAR	COUNT	MEAN	SLOPE	ST. DEV.	MIN. VALUE	FIRST OCCUR.	MAX. VALUE	FIRST OCCUR
DAY	51	26	1	15	1	1	51	51
1988	19	19.4	-0.35	17.0	0.0	18	61	20
1989	26	11.2	0.68	13.0	0.0	11	54.8	31
1990	51	19.6	0.31	20.0	0.0	5	87.3	39
1991	51	34.8	1.08	31.0	0.0	1	125.1	43
ALL	51	24.8	0.68	21	0.0	5	90.7	39

PERIODOGRAM		VARIABLE				
CYCLE/DA	PERIOD	1988	1989	1990	1991	ALL
0.0000		8.246E-11	2.968E-01	2.852E-11	4.822E-11	2.318E-10
0.0196	51.00	3.135E+02	8.926E+02	1.861E+03	5.514E+03	3.075E+03
0.0392	25.50	2.167E+02	2.282E+01	9.331E+02	2.067E+03	1.114E+03
0.0588	17.00	1.485E+02	3.135E+01	1.052E+03	4.412E+02	6.168E+02
0.0784	12.75	2.955E+02	1.707E+02	2.573E+02	3.526E+02	2.026E+02
0.0980	10.20	5.200E+02	2.535E+02	7.834E+02	3.461E+03	1.761E+02
0.1176	8.500	3.347E+02	1.200E+02	1.095E+03	1.068E+03	5.524E+01
0.1373	7.286	8.193E+01	2.624E+01	6.006E+02	9.017E+01	1.171E+02
0.1569	6.375	7.603E+01	6.857E+01	5.797E+01	1.221E+03	5.179E+01
0.1765	5.667	1.472E+02	1.015E+02	8.986E+00	3.249E+02	5.688E+00
0.1961	5.100	7.999E+01	7.817E+01	5.106E+02	4.667E+01	1.376E+02
0.2157	4.636	4.314E+00	1.230E+02	3.017E+02	7.789E+00	5.065E+01
0.2353	4.250	1.485E+01	9.547E+01	9.762E+01	5.401E+02	2.099E+02
0.2549	3.923	4.400E+01	1.326E+01	4.653E+02	3.593E+02	7.437E+01
0.2745	3.643	5.407E+01	1.999E+01	3.136E+02	3.501E+02	1.943E+02
0.2941	3.400	2.451E+01	5.748E+01	1.727E+02	1.086E+02	6.967E+01
0.3137	3.188	1.325E+01	5.634E+01	2.752E-01	4.643E+02	4.913E+01
0.3333	3.000	1.769E+02	3.014E+01	1.224E+02	4.209E+02	1.451E+02
0.3529	2.833	3.931E+02	2.599E+01	1.821E+02	1.126E+03	5.399E+02
0.3725	2.684	3.325E+02	6.889E+01	2.533E+02	3.919E+02	2.691E+02
0.3922	2.550	9.482E+01	1.074E+02	5.742E+01	6.562E+02	7.684E+01
0.4118	2.429	8.263E+00	6.266E+01	3.340E+00	1.047E+03	2.187E+02
0.4314	2.318	4.799E+01	4.247E+01	4.621E+02	1.456E+03	6.266E+02
0.4510	2.217	2.304E+01	9.933E+01	1.559E+02	1.370E+03	2.938E+02
0.4706	2.125	9.107E+00	7.506E+01	1.219E+02	5.680E+02	2.245E+02
0.4902	2.040	7.588E+01	1.352E+01	9.510E+01	1.121E+03	4.857E+02
ΣI_J[a]		14556.6	8527.75	48475	20147.5	10782.5
Peak value[b] (period)		5.200E+02 (10.2)	2.535E+02 (10.2)	1.095E+03 (8.5)	3.461E+03 (10.2)	1.761E+03 (10.2)
Test statistic[c]		0.0357	0.029	0.0403	0.0713	0.1633
Significance[d]		not sig.	not sig.	not sig.	not sig.	significant

a : $\Sigma I_J = 1/2[(n-1)(sd^2)$ - final value]; b : Peak variable value in periodgram, c :Test statistic = peak variable value/ΣI_J; d : Critical value (95% level), m = [1/2(n-1)]) = 0.0739.

Univariate analyses

Environmentally dependent parameters

Group size

The frequencies of group sizes recorded each year are shown in Figure 3.6. Estimates of group sizes were refined at each theodolite fix, and a significant difference was found between mean sizes of groups estimated from two or less and from more than two fixes (Kruskal - Wallis test statistic, $H = 42.07$, d.f. = 1, $p = 0.0001$, $n = 576$). Although the position-fixing of small groups may be more difficult, so that the larger groups may be tracked for longer periods (due to their increased visibility), Figure 3.6 possibly suggests the size of groups of which few fixes were taken were underestimated.

No difference was found between confirmed and estimated group sizes of each intercepted group after log transformation (two tailed Student's t test, $t = 1.3598$, $p = 0.1808$, $n = 50$). However, there was a significant difference between the mean size estimates of intercepted and non-intercepted groups ($H = 9.036$, d.f. = 1, $p = 0.001$, $n = 576$). This difference could arise as a result of selection of larger groups for confirmation, from more attention being paid to such groups when directing the ski-boat onto them, or the underestimation of groups which were only briefly observed. No significant difference was found between the mean group size of intercepted and non-intercepted groups for which more than two fixes were available ($H = 0.608$, d.f. = 1, $p > 0.13$, $n = 251$). Furthermore, sequential group size estimates made at each fix on groups for which more than five fixes were taken (both northward- and southward-migrating groups) showed that the first two estimates underestimated group size (Figure 3.7, $H = 3.383$, d.f. = 1, $p = 0.0007$, $n = 314$). Consequently, only groups for which more than two fixes were taken were used in group size analyses.

The mean group sizes by year and migration wave are shown in Tables 3.5 and 3.6 respectively. A significant difference in mean group sizes of the northward migration was found between years ($H = 12.15$, d.f. = 1, $p = 0.006$, $n = 251$), but no difference was found between the mean group size of migration waves ($H = 3.53$, d.f. = 4, $p = 0.473$, $n = 251$) in the northward migration or between the northward and southward migrations in 1990 ($H = 0.636$, d.f. = 1, $p = 0.142$, $n = 259$). The difference in mean group sizes recorded between years results from the larger group size recorded in 1988 as no difference was found between mean

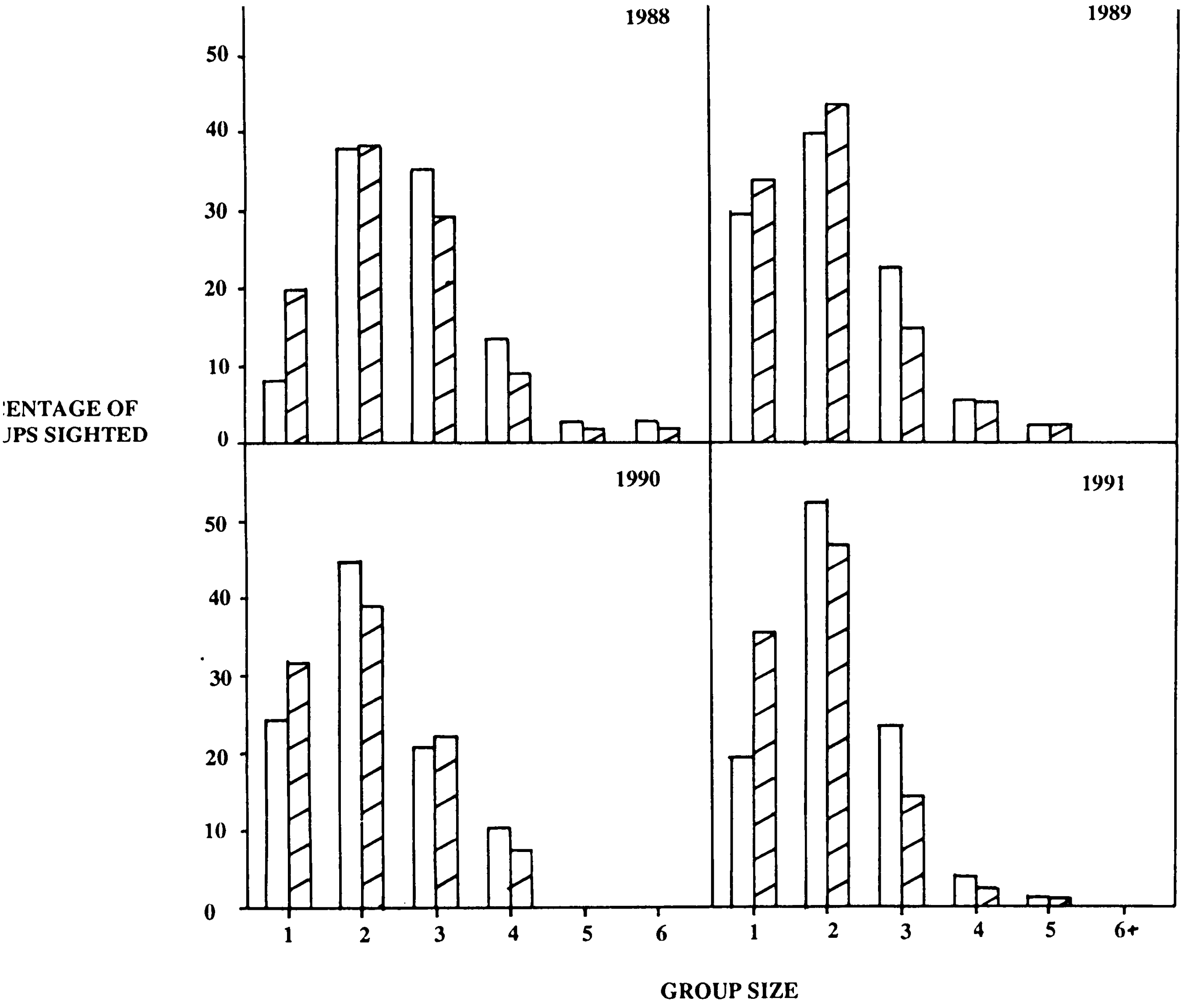


Figure 3.6. Frequencies of group sizes for which two or less (hatched), or more than two fixes (hatched) were taken from south tower, 1988 -1991.

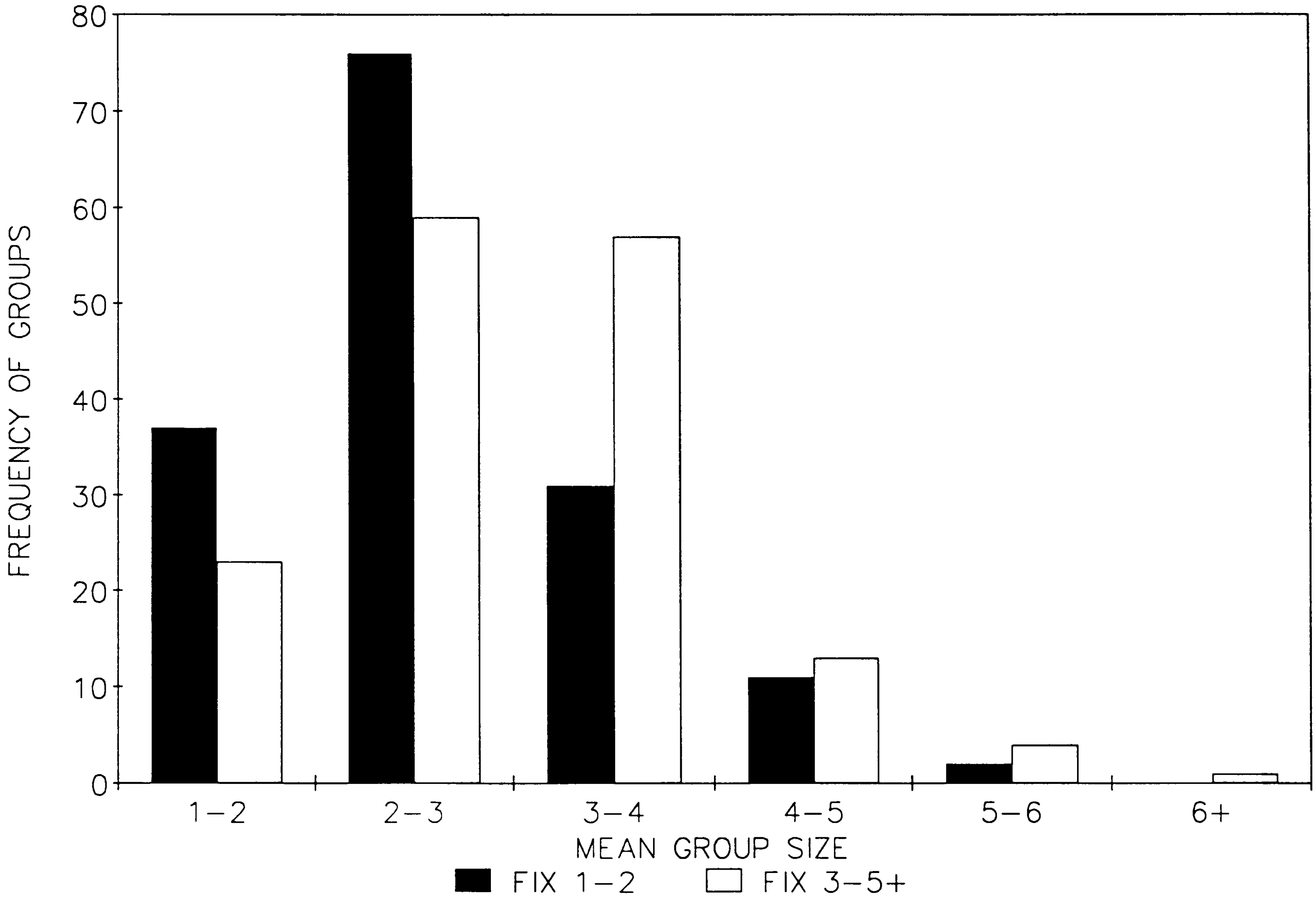


Figure 3.7 Frequencies of mean group size estimates made during (unhatched) the first two, and solid the next three fixes of all groups for which five or more fixes were taken.

group sizes recorded in 1989, 1990 and 1991 (H = 1.63, p = 0.175, n = 211).

Table 3.5. Mean group size, migration speed, distance offshore and migration heading (and associated standard errors) recorded during the northward and southward migrations past Cape Vidal each year between 1988 and 1991.

YEAR	GRP SIZE	SPEED (km/h)	DISTANCE km	HEADING degrees
Northward migration				
1988	2.73	4.49	5.20	16.59
	(0.18)	(0.48)	(0.53)	(3.80)
1989	2.10	5.41	4.01	9.56
	(0.16)	(0.59)	(0.62)	(5.43)
1990	2.11	4.62	4.70	15.44
	(0.11)	(0.30)	(0.33)	(3.60)
1991	2.22	3.63	3.50	15.09
	(0.09)	(0.21)	(0.16)	(3.13)
ALL	2.25	4.38	4.26	14.74
	(0.61)	(0.17)	(0.16)	(1.95)
Southward migration				
1990	2.18	5.26	6.21	195
	(0.17)	(0.37)	(0.48)	(3.01)

Table 3.6. Mean group size, migration speed, distance offshore and migration heading (and associated standard errors) recorded during each wave of the northward migration past Cape Vidal in all of the four years of monitoring.

WAVE	GRP SIZE	SPEED (km/h)	DISTANCE km	HEADING degrees
1	2.04	3.48	4.20	14.39
	(0.15)	(0.44)	(0.36)	(4.84)
2	2.43	4.21	4.51	9.56
	(0.15)	(0.37)	(0.41)	(4.64)
3	2.33	4.54	3.60	15.93
	(0.10)	(0.30)	(0.26)	(2.52)
4	2.07	4.59	3.13	17.92
	(0.16)	(0.37)	(0.18)	(4.51)
5	2.08	4.68	6.43	17.10
	(0.15)	(0.54)	(0.54)	(6.56)
ALL	2.25	4.38	4.26	14.74
	(0.62)	(0.17)	(0.16)	(1.94)

No significant difference was found between group sizes recorded by hourly interval (Figure 3.8, $H = 7.97$, d.f. = 9, $p = 0.436$, $n = 251$). No difference was found in mean group sizes by sighting condition (Figure 3.9, $H = 7.07$, d.f. = 4, $p = 0.529$, $n = 251$) or wind direction (Figure 3.10, $H = 1.40$, d.f. = 1, $p = 0.510$, $n = 251$) and no correlation was found between group size and wind speed (Figure 3.11, $r^2 = 0.38\%$, $p > 0.50$, $n = 251$), although no groups larger than three individuals were recorded in wind speeds of over 20 knots.

No correlation was found between group sizes and perpendicular distance from the coast (Figure 3.12, $r^2 = 0.02\%$, $p > 0.50$, $n = 251$) in the northward migration, although groups larger than three individuals were not recorded more than 10 km from the coast. Larger groups would be expected to provide more sighting cues than smaller groups and should consequently have a greater probability of being sighted with distance than smaller groups (Reilly, Rice and Wolman 1980) or under poorer weather conditions. This lack of large groups recorded over 10 km distant (Figure 3.12) or under higher wind speeds (Figure 3.11), may result from an underestimation of group size with increasing distance or deteriorating sea conditions. However, no

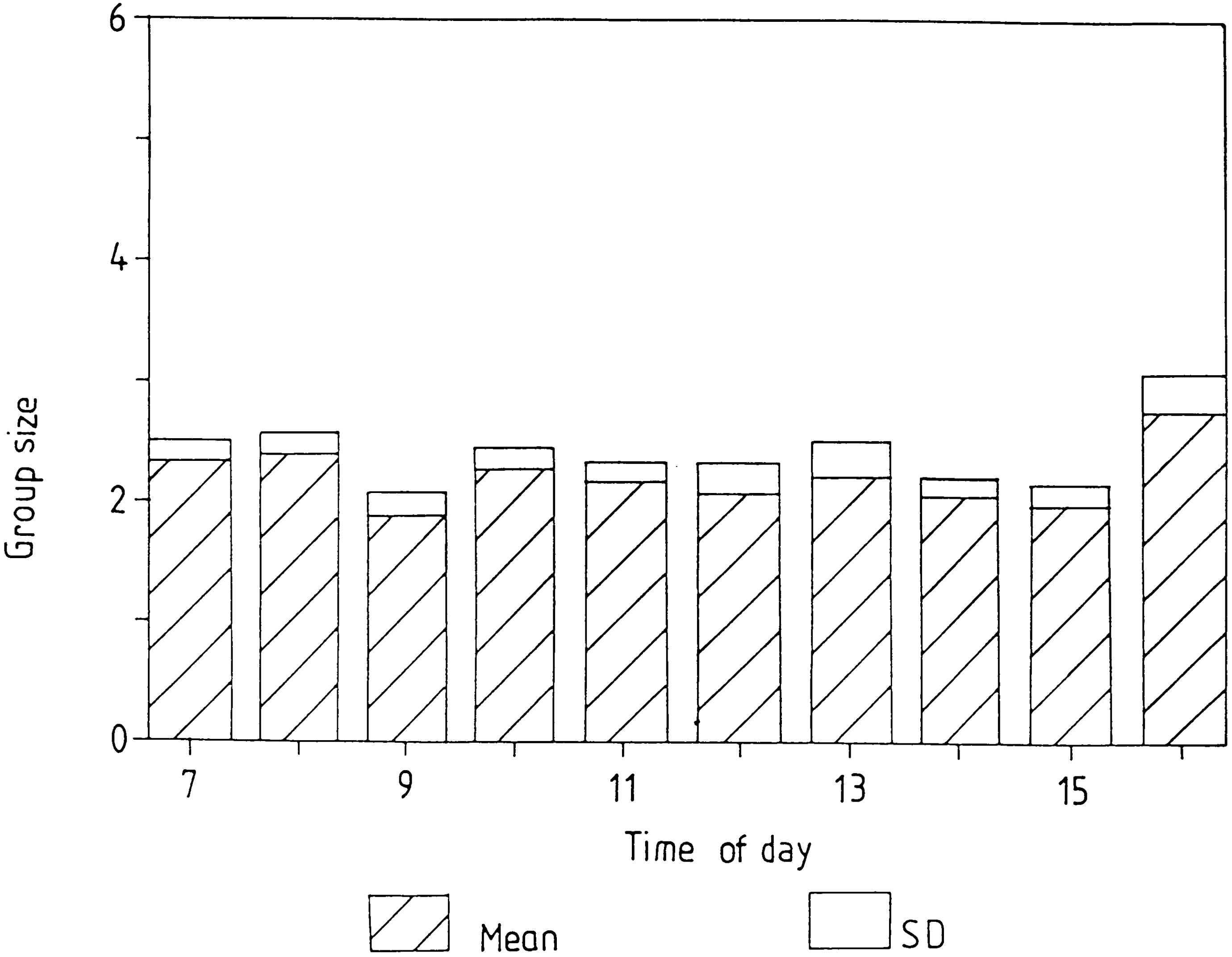


Figure 3.8 Mean sizes of groups recorded migrating northwards past Cape Vidal by hourly interval.

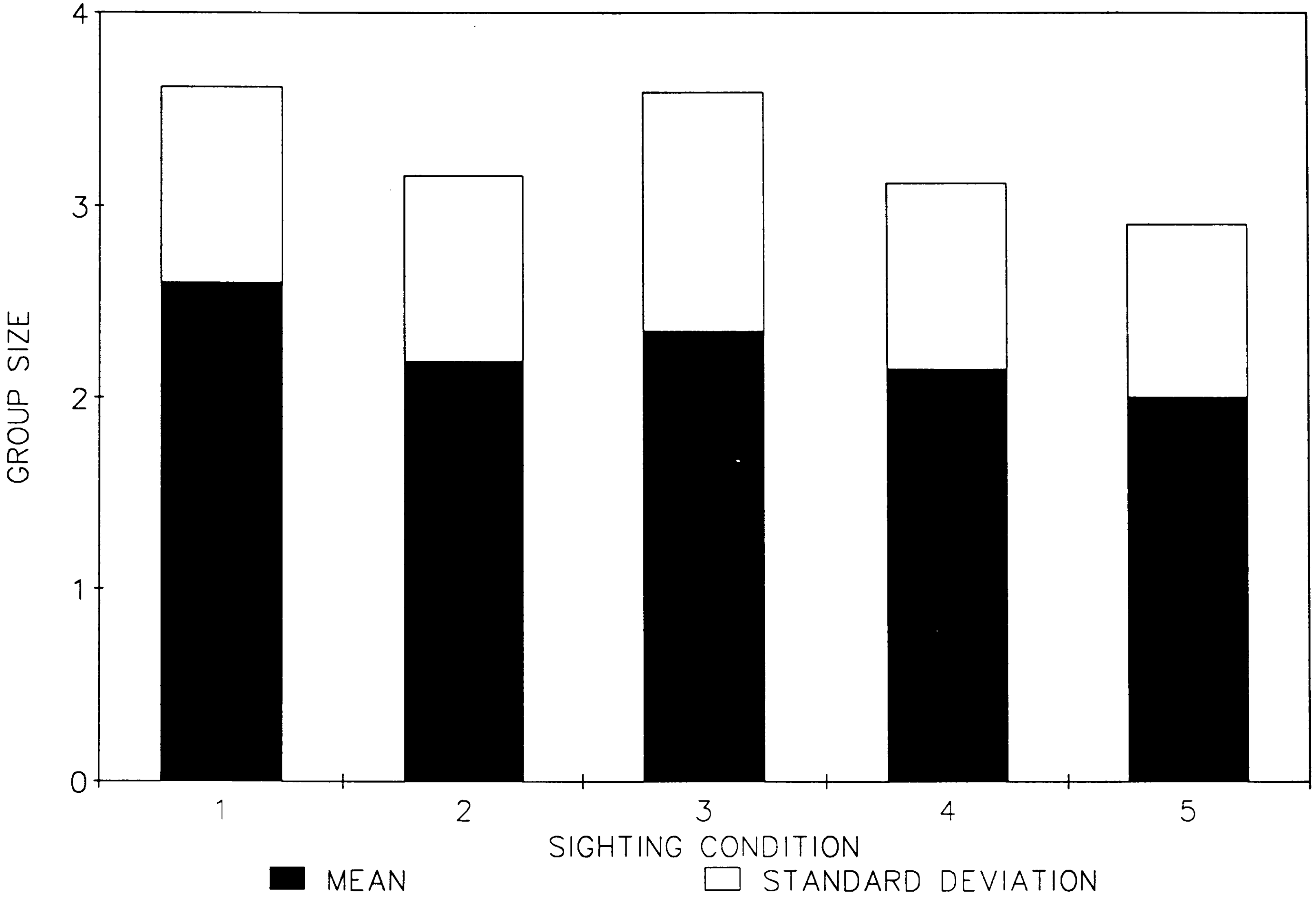


Figure 3.9 Mean sizes of groups recorded migrating northwards past Cape Vidal in each sighting condition.

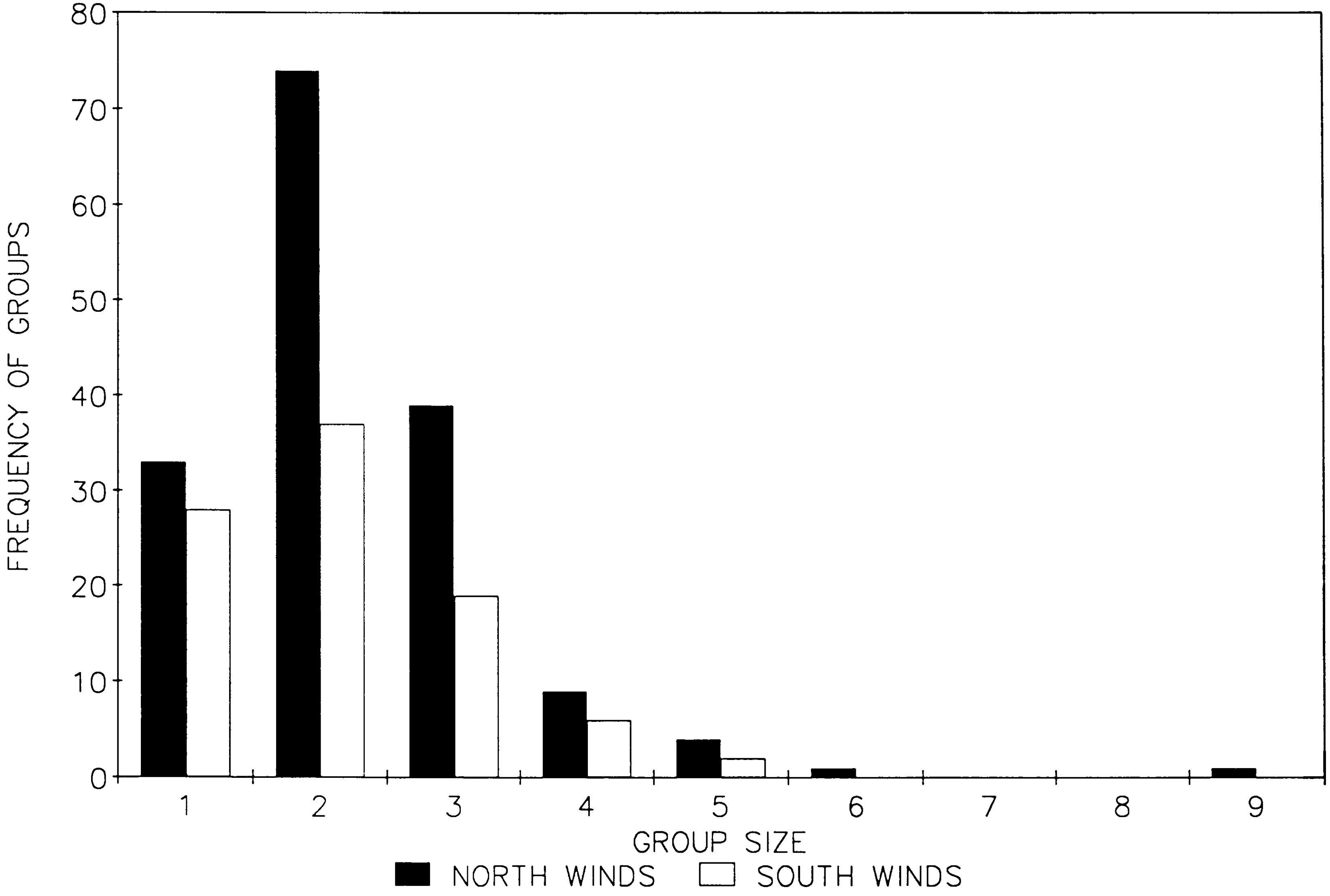


Figure 3.10 Frequencies of group sizes recorded migrating northwards past Cape Vidal in northerly and southerly winds.

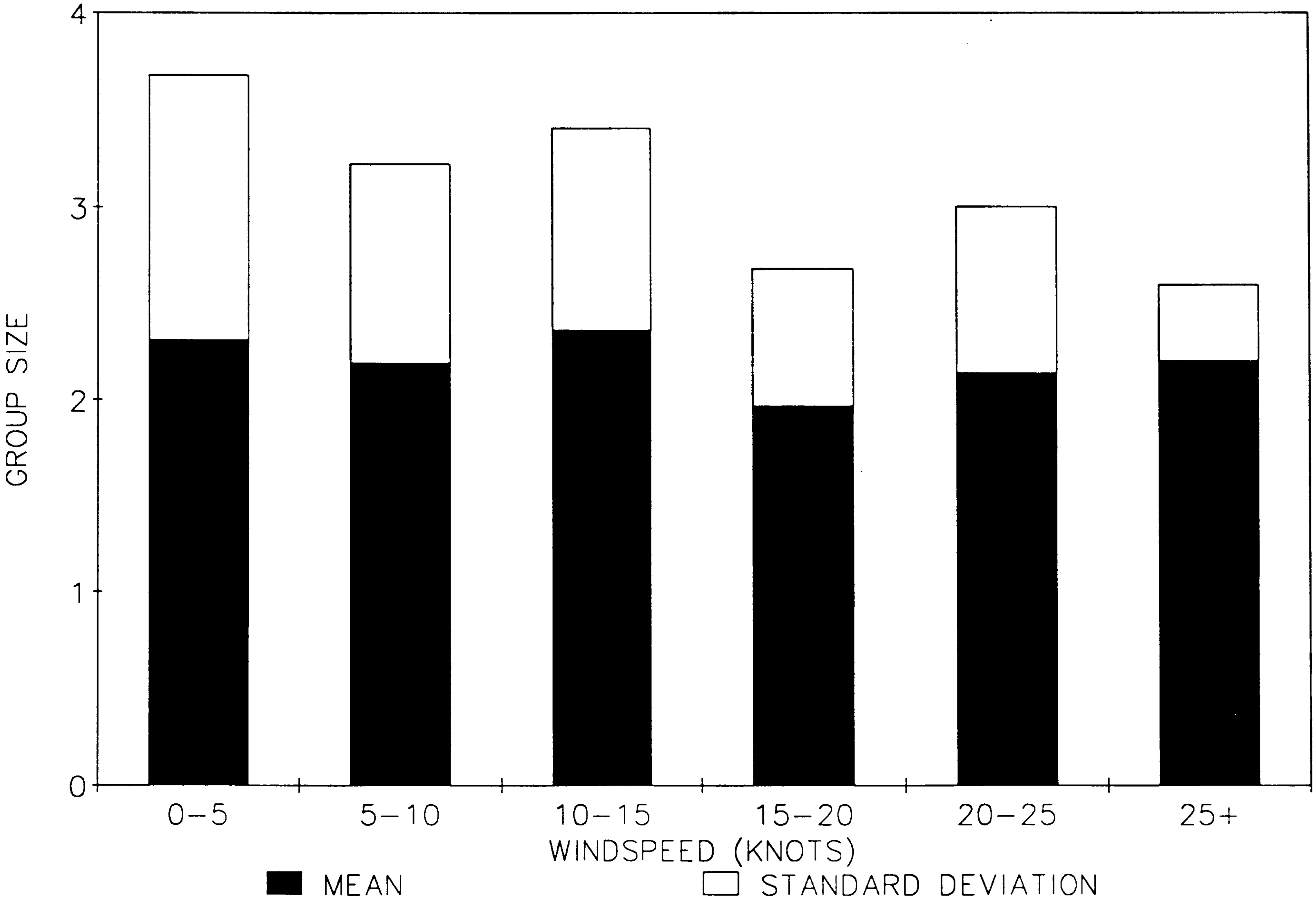


Figure 3.11 Sizes of groups recorded migrating northwards past Cape Vidal in different wind speeds.

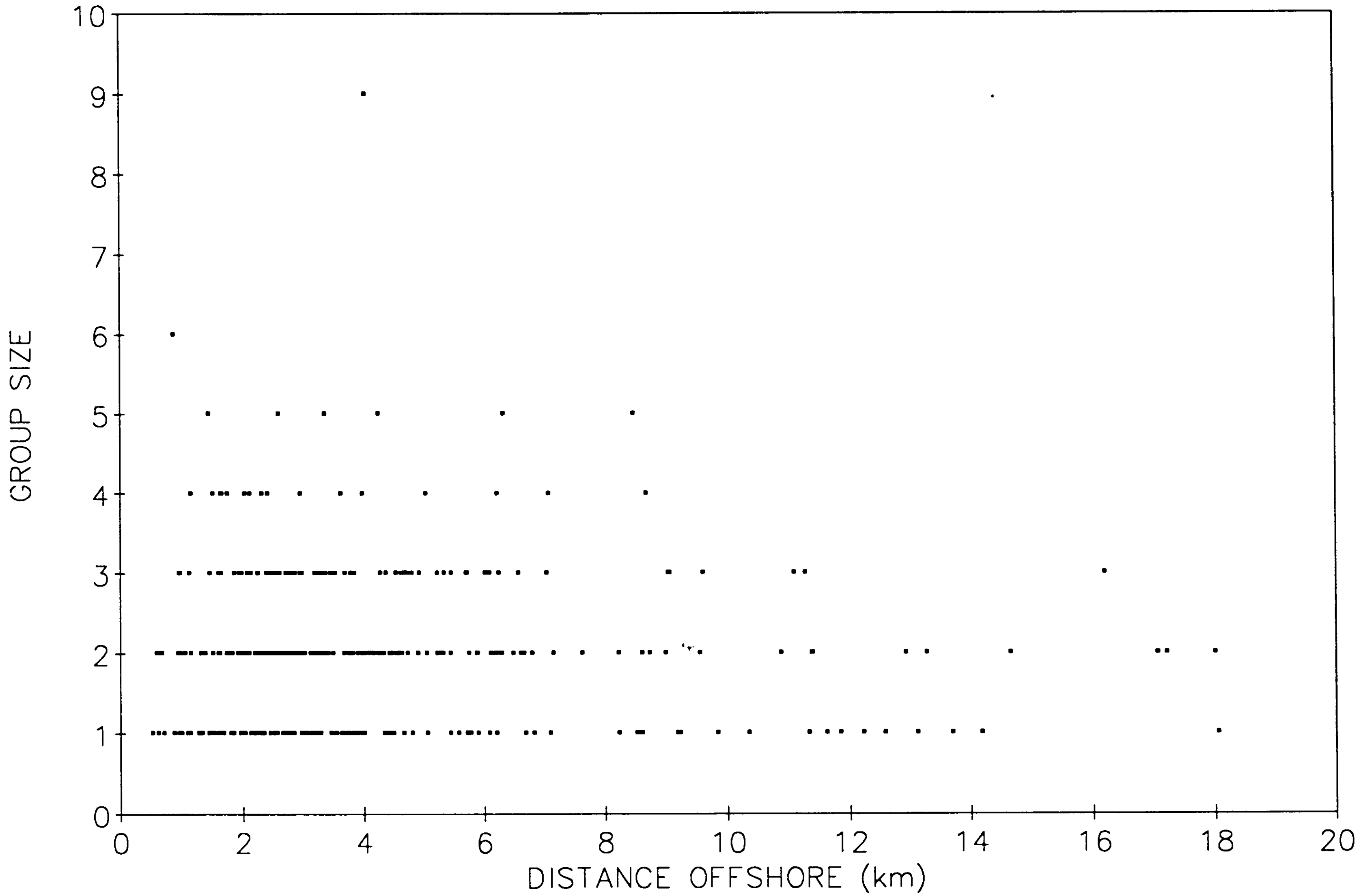


Figure 3.12 Sizes of groups recorded migrating northwards past Cape Vidal at different perpendicular distances offshore.

correlation was found between the ratio of estimated to confirmed group sizes and the radial distance from the observer (Figure 3.13, $r^2 = 0.009\%$, $p > 0.50$, $n = 45$).

Distance offshore and migration path width

The offshore distribution of both northward and southward migrating groups each year is shown in Figure 3.14. There was a significant difference in the mean distance offshore of the northward migration by year (Table 3.5, $H = 9.68$, d.f. = 3, $p = 0.022$, $n = 360$) presumably arising from the distances recorded in 1988. The distance of migration waves offshore was significantly different (Table 3.6, $H = 25.85$, d.f. = 4, $p < 0.0001$, $n = 360$), with waves 3 and 4 being closer inshore. The densities recorded during these two waves were highest, and the apparent narrower width may have resulted from the missing of distant groups during periods of high density.

The southward migration in 1990 was significantly further offshore than any of the northward migrations (Figure 3.14, $H = 14.00$, d.f. = 4, $p = 0.037$, $n = 259$). This presumably reflects the funnelling of the northward migration stream against the coast, as well as avoidance of the Agulhas Current during the northward migration. The decline in the number of sightings closer inshore than the mode (Figure 3.14) possibly results from the whales avoiding shallow waters. However, closer groups pass through a narrower angle of vision than more distant ones, and so have a lower probability of being sighted (see chapter 4).

No correlations were found between the coastal distance of groups and sightability conditions (Figure 3.15, $r^2 = 1.52\%$, $p > 0.50$, $n = 360$), although no distant groups were recorded when sighting conditions were very poor. Consequently, periods of weather (sighting) conditions with sightability index < 2 have been considered as periods of no watch in abundance estimate analyses (chapter 5). No correlations were found between the coastal distance of groups and wind speed (Figure 3.16, $r^2 = 0.26\%$, $p > 0.50$, $n = 360$), and no differences were found between coastal distances recorded by hourly interval (Figure 3.17, $H = 8.47$, d.f. = 9, $p = 0.1758$, $n = 360$). However the lack of distant groups observed before 10h00 must be noted (Figure 3.17) and may be an artefact of the glare present early in the morning. Although Paterson and Paterson (1984) found glare to result in groups being missed in mid-morning, they later (Paterson and Paterson 1989) suggested this arose from insufficient data. Groups of northerly-migrating whales were distributed significantly closer

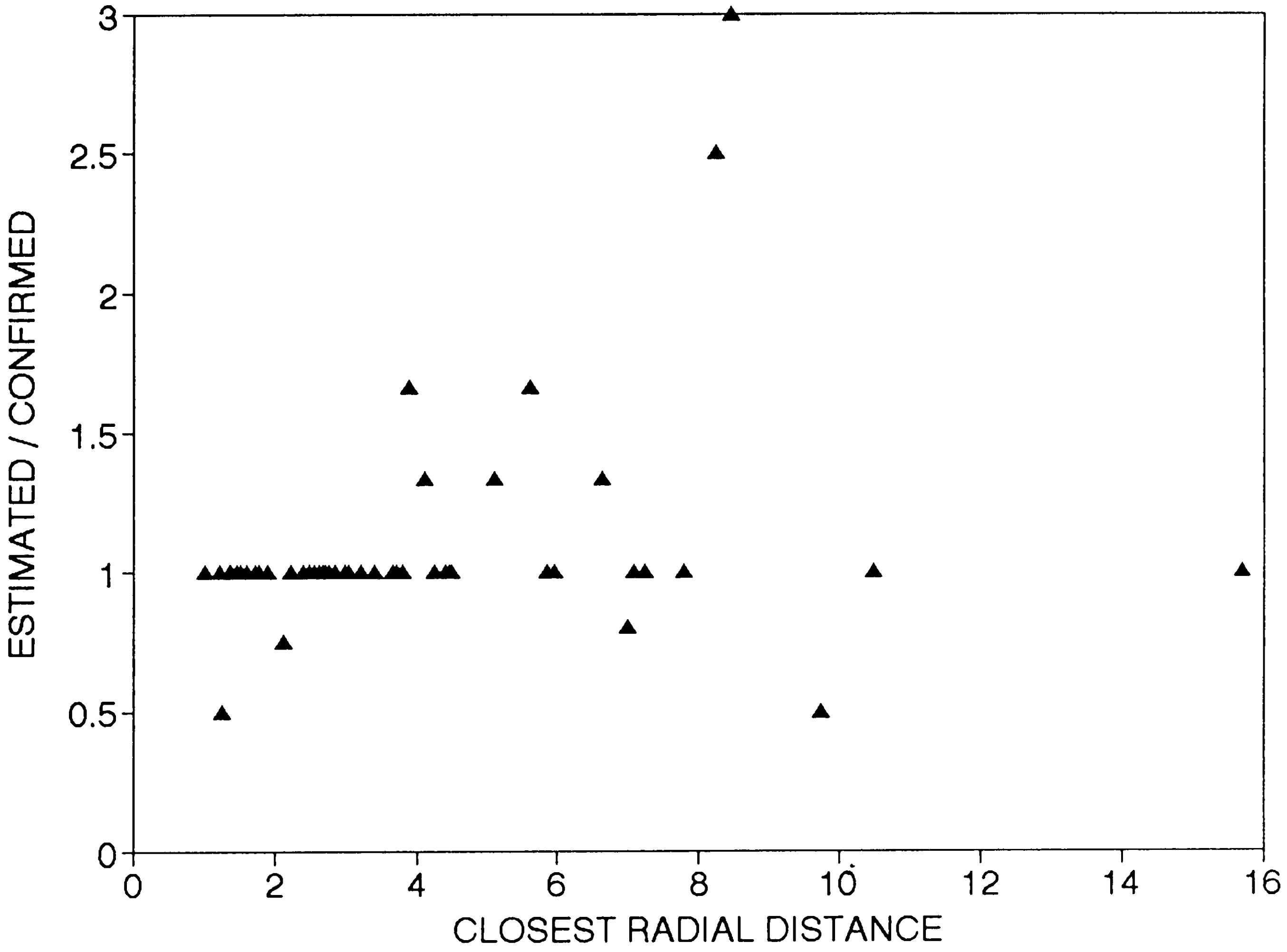


Figure 3.13 The ratio of estimated to confirmed group sizes off Cape Vidal at the closest radial distance at which the group was sighted, 1988-1991.

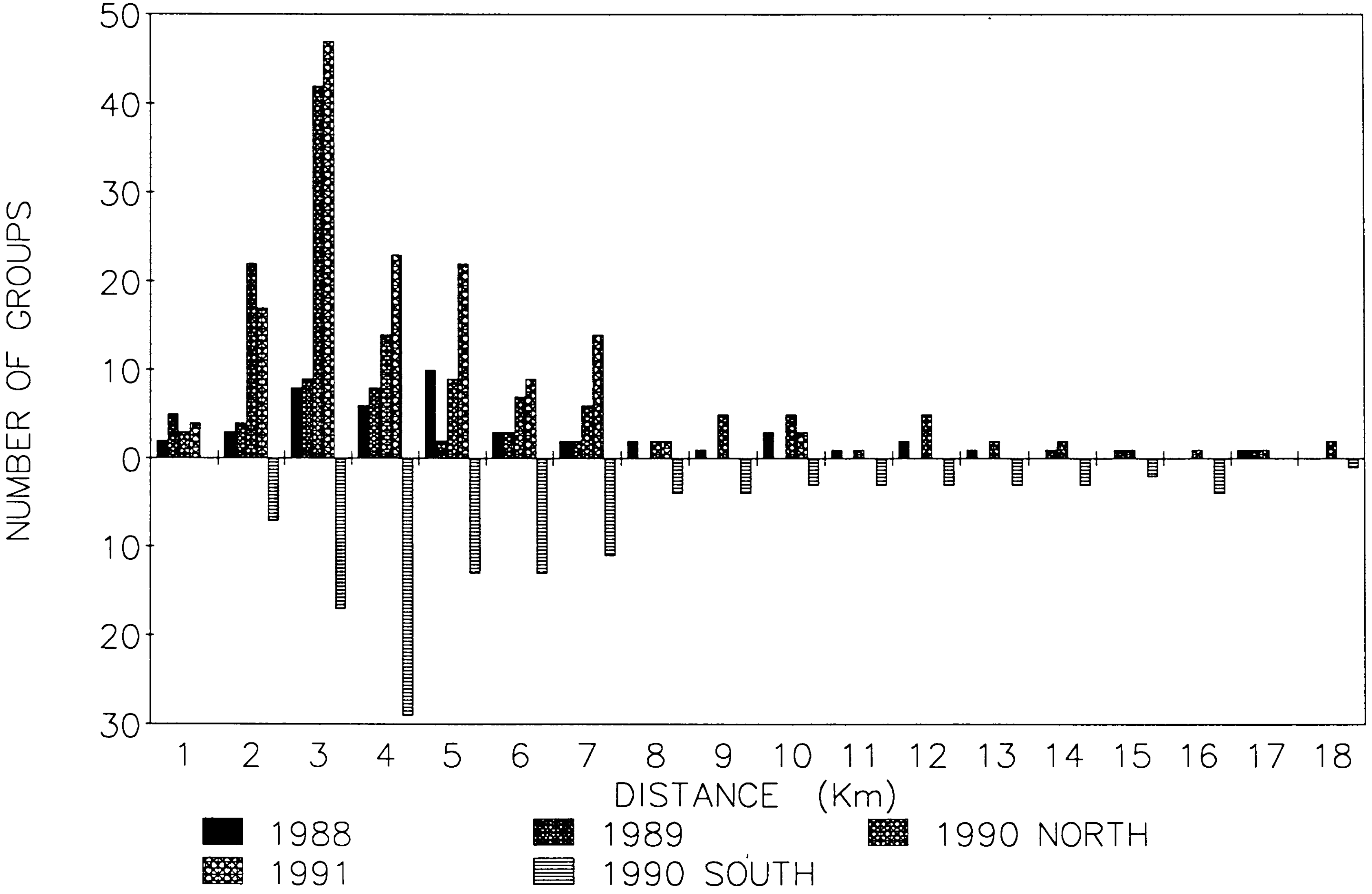


Figure 3.14 Perpendicular distances offshore of groups migrating past Cape Vidal each year.

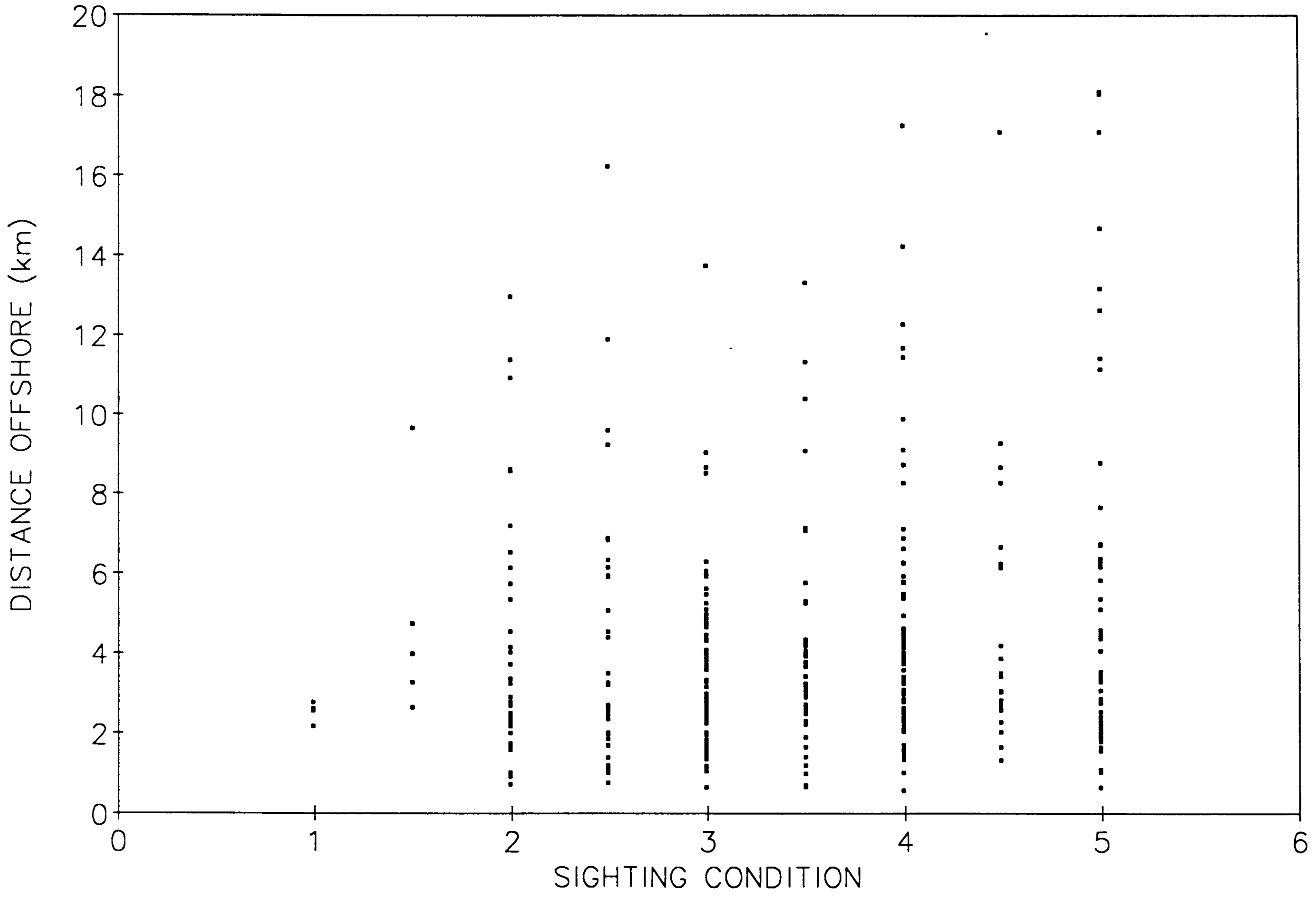


Figure 3.15 Perpendicular distances offshore of groups migrating northwards past Cape Vidal in different sighting conditions.

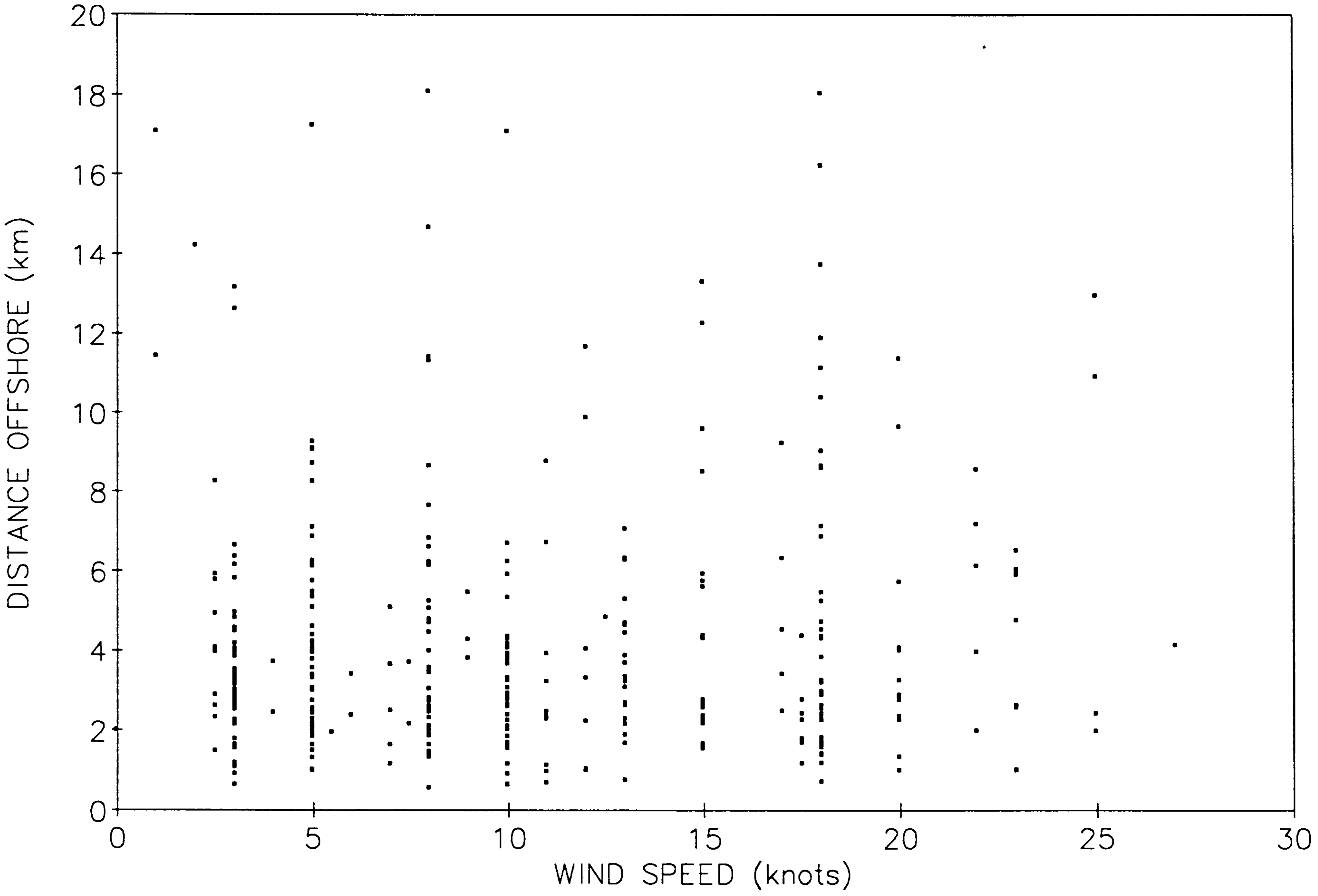


Figure 3.16 Perpendicular distances offshore of groups migrating northwards past Cape Vidal in different wind speeds.

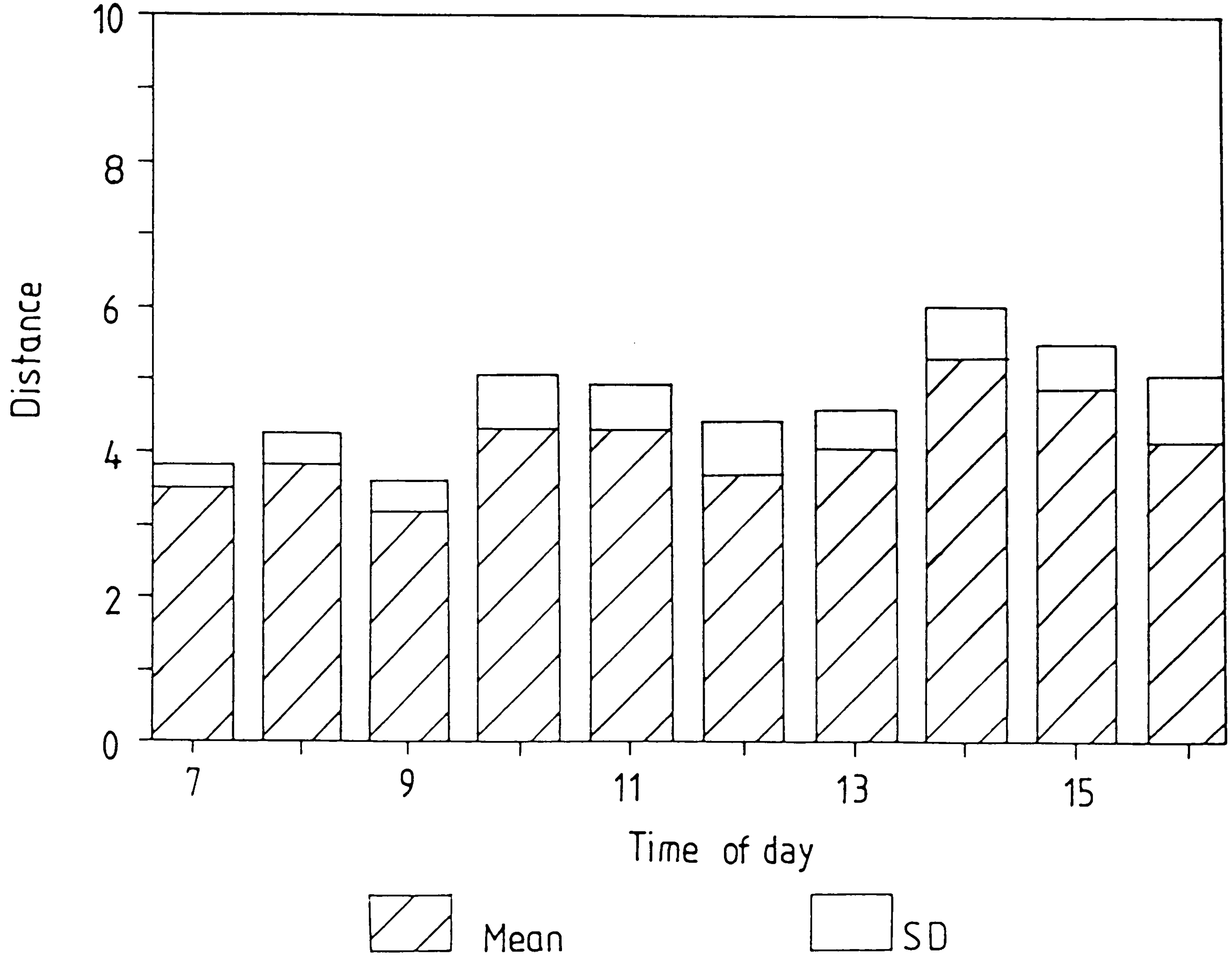


Figure 3.17 Mean perpendicular distances offshore of groups migrating northwards past Cape Vidal during hourly intervals.

inshore during south-westerly, southerly, or south -easterly winds than during winds blowing from the north-westerly, northerly or north easterly directions (Figure 3.18, H = 19.72, d.f. = 1, $p < 0.0001$, n = 360), although this could have resulted from the generally poorer sighting conditions associated with southerly winds.

A problem inherent in determining the distribution of groups with distance from the shore, is the fact that the groups may not be distributed randomly with respect to the observer. Consequently, the decline in sightings with the distance from the coast may represent either the true distribution of groups, or the decline in detectability of groups with distance, or a combination of both. Ideally an independent line transect survey should be undertaken to determine the true distribution of whales from the shore, but unfortunately the density of whales present was too low over the long duration of the survey to warrant a cost effective survey within the scope of this study. Not only would such a survey verify the distribution of groups, but it would also provide verification on group size estimation with distance from the coast. The related question of what proportion of the population is passing outside of observer's view would require even greater survey coverage.

Migration speed

Figure 3.19 shows the frequency of migration speeds of groups on both northward and southward migrations. There was a significant difference in the mean northward migration speed (Table 3.5) between years (one way ANOVA, F = 3.99, d.f. = 3;247, p = 0.0085, n = 251). No significant differences were found in northward migration speed by wave (Table 3.6) (F = 1.31, d.f. = 4;246, p = 0.265, n = 251), although Table 3.6 shows a progressive increase in speed from wave 1 to 5, or between northward and southward migration speeds recorded in 1990 (F = 1.463, d.f. = 1;186, $p > 0.05$, n = 187).

No significant difference was found between mean speeds by hourly interval (Figure 3.20, F = 0.67, d.f. = 9;241, p = 0.7355, n = 251) or by wind direction (Figure 3.21, F = 0.100, d.f = 1;249, p =0.7554, n = 251), and no correlation was found between migration speeds and wind speeds (Figure 3.22, r^2 = 1.35%, $p > 0.50$, n = 251) or weather (sighting) conditions (Figure 3.23, r^2 = 1.25%, $p > 0.50$, n = 251).

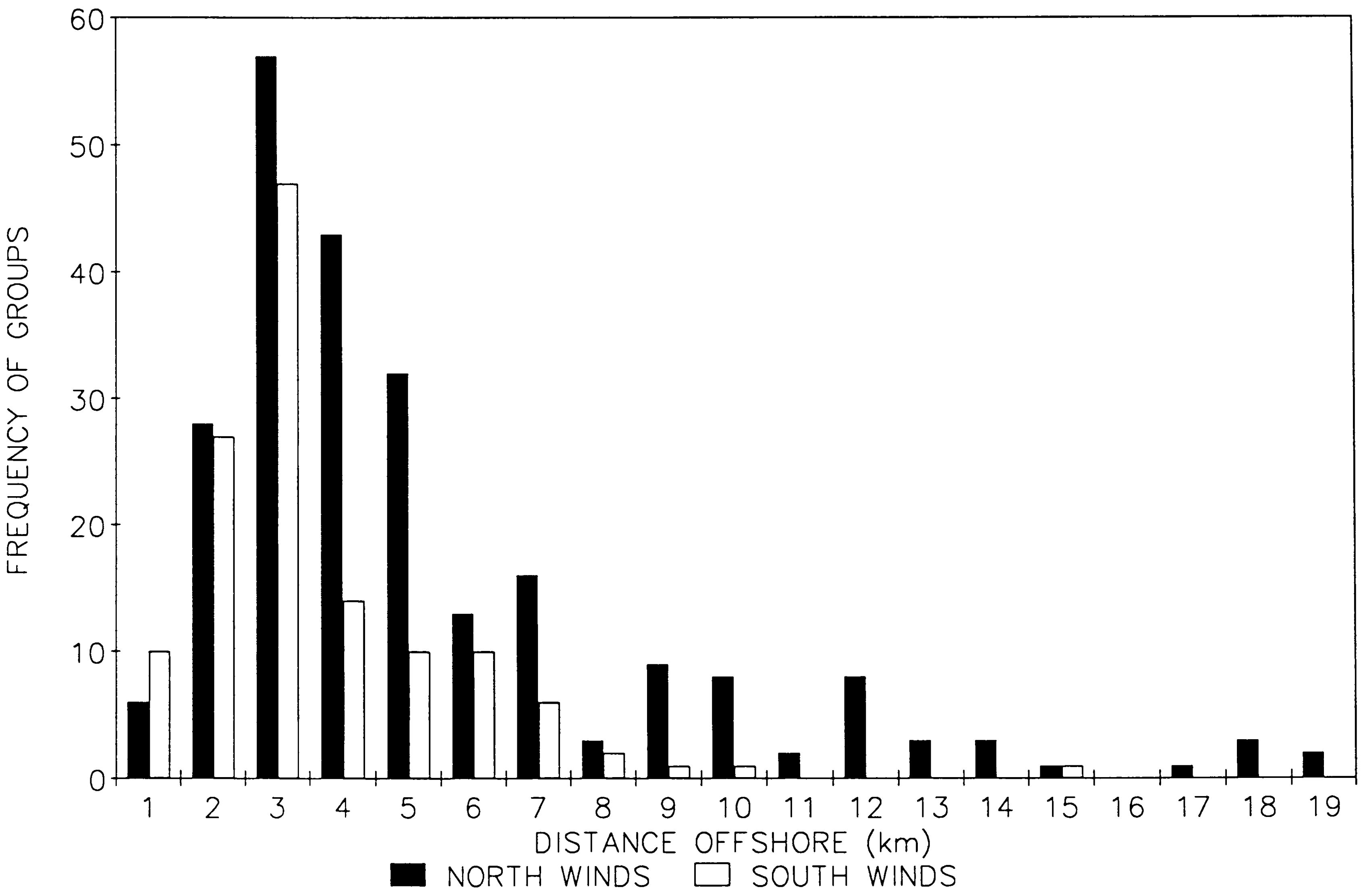


Figure 3.18 Distribution of perpendicular distances offshore for groups migrating northwards in northerly or southerly winds.

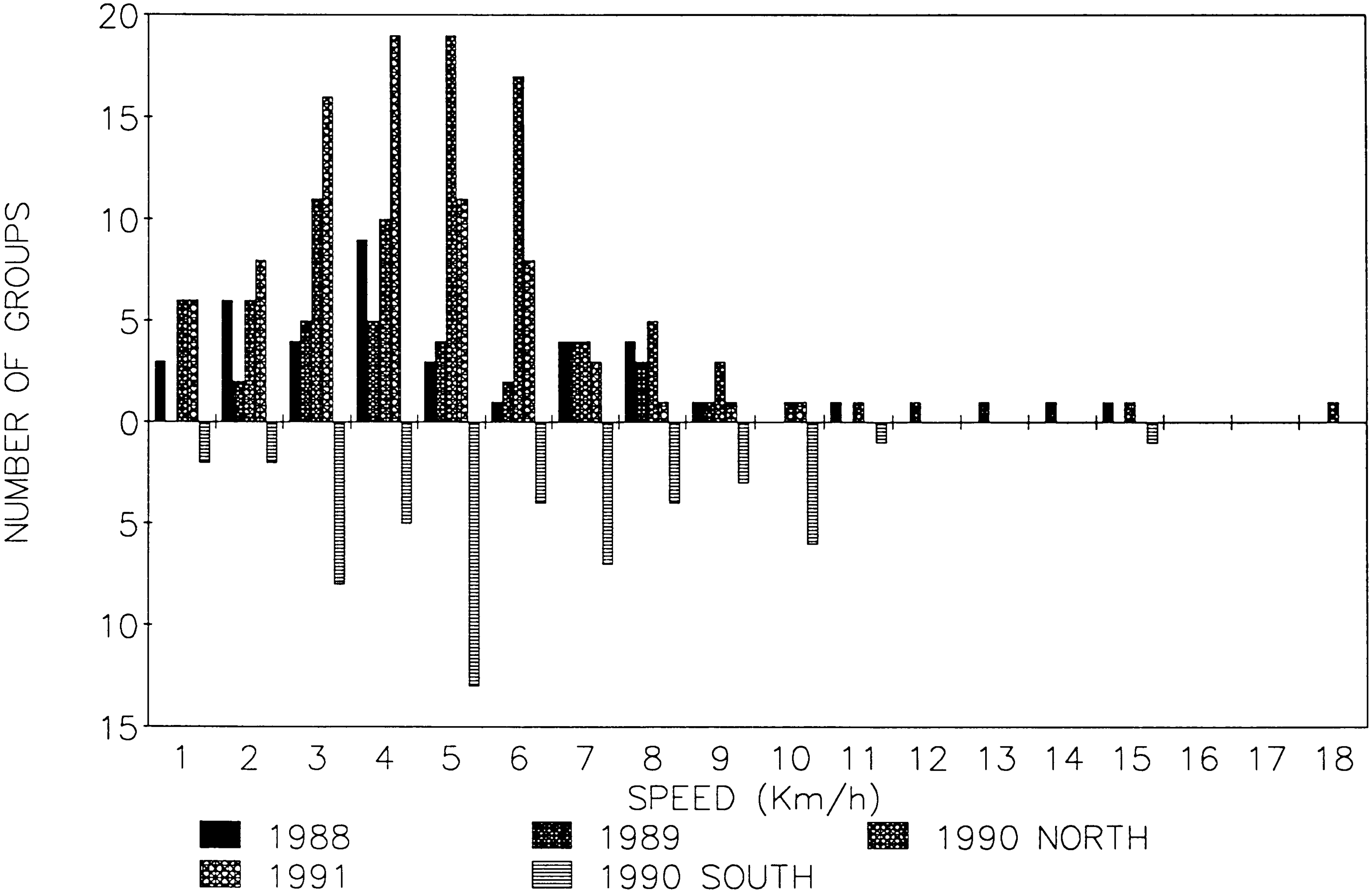


Figure 3.19 Distribution of swimming speeds for groups migrating past Cape Vidal each year between 1988 and 1991.

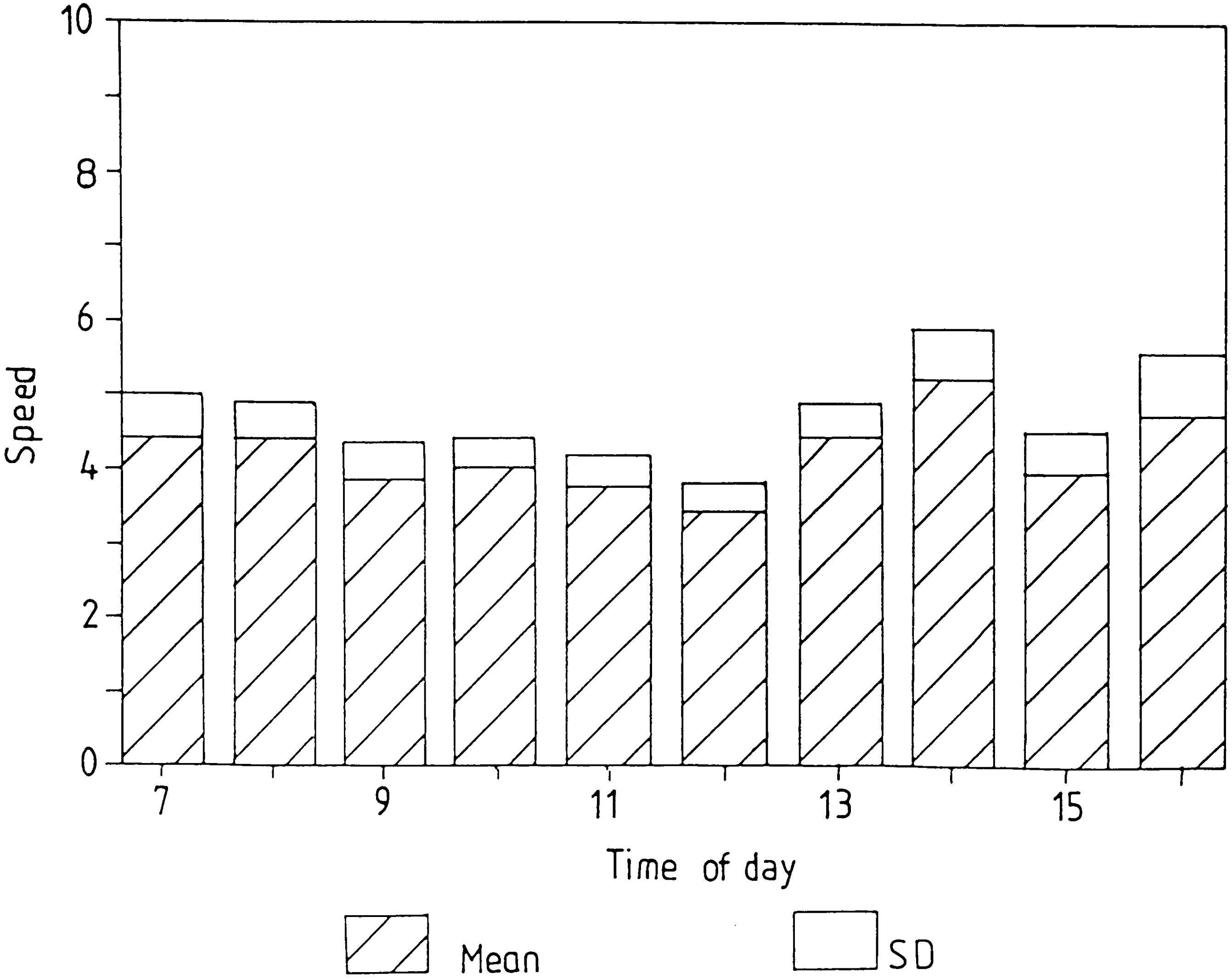


Figure 3.20 Mean swimming speeds of groups migrating northwards past Cape Vidal during hourly intervals.

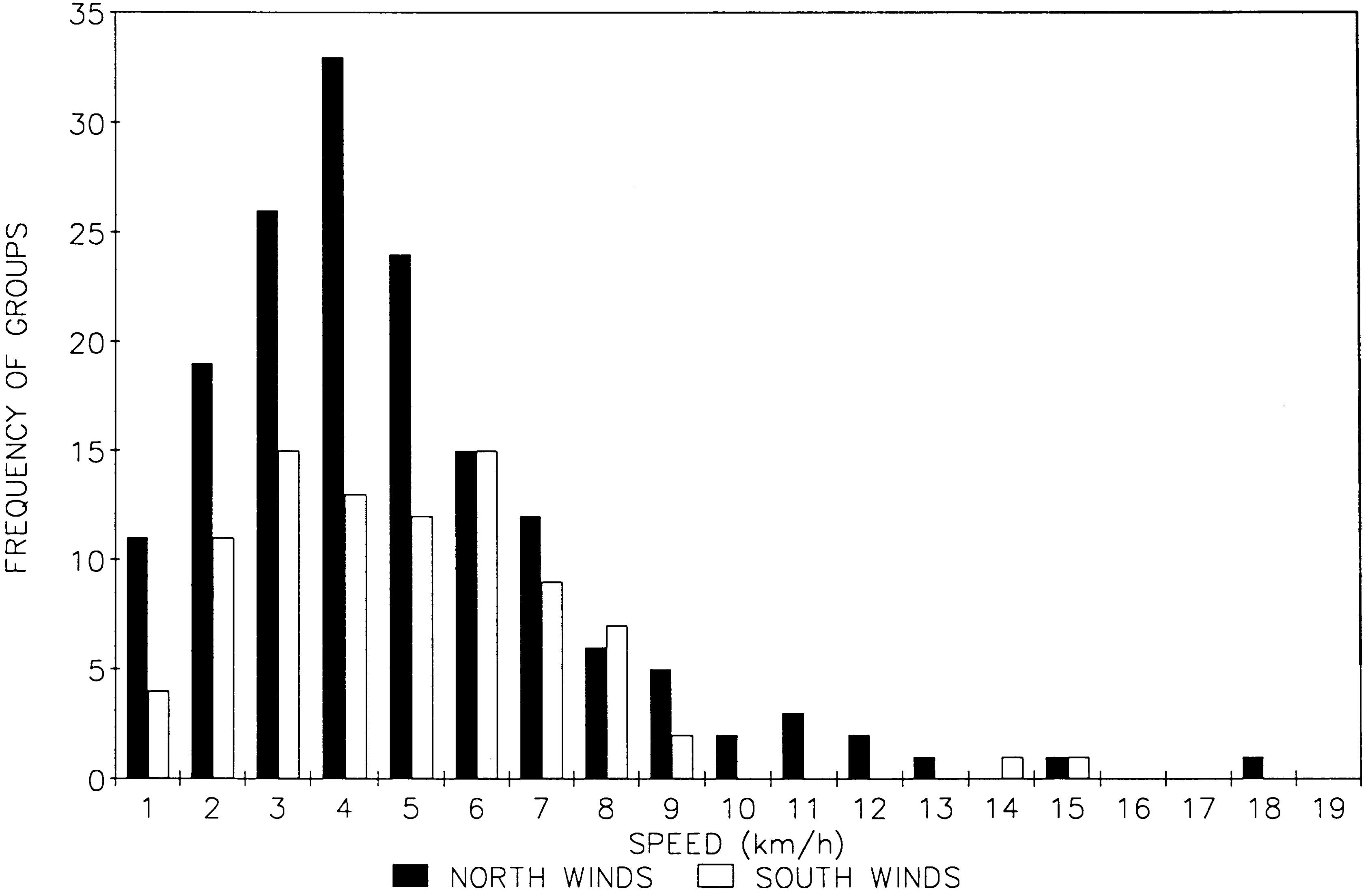


Figure 3.21 Distribution of swimming speeds for groups migrating northwards past Cape Vidal in northerly and southerly winds.

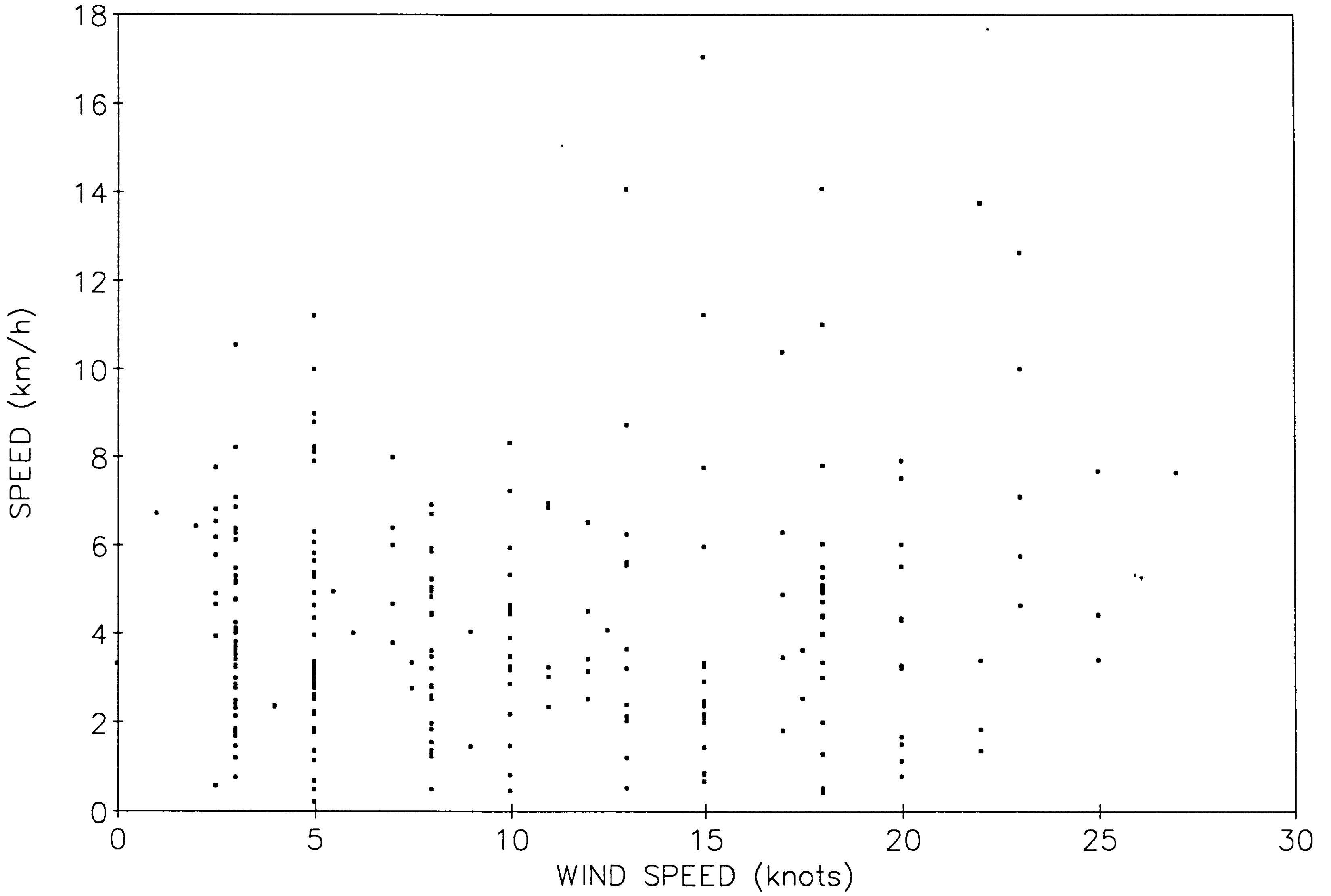


Figure 3.22 Swimming speeds of groups migrating northwards past Cape Vidal in different wind speeds.

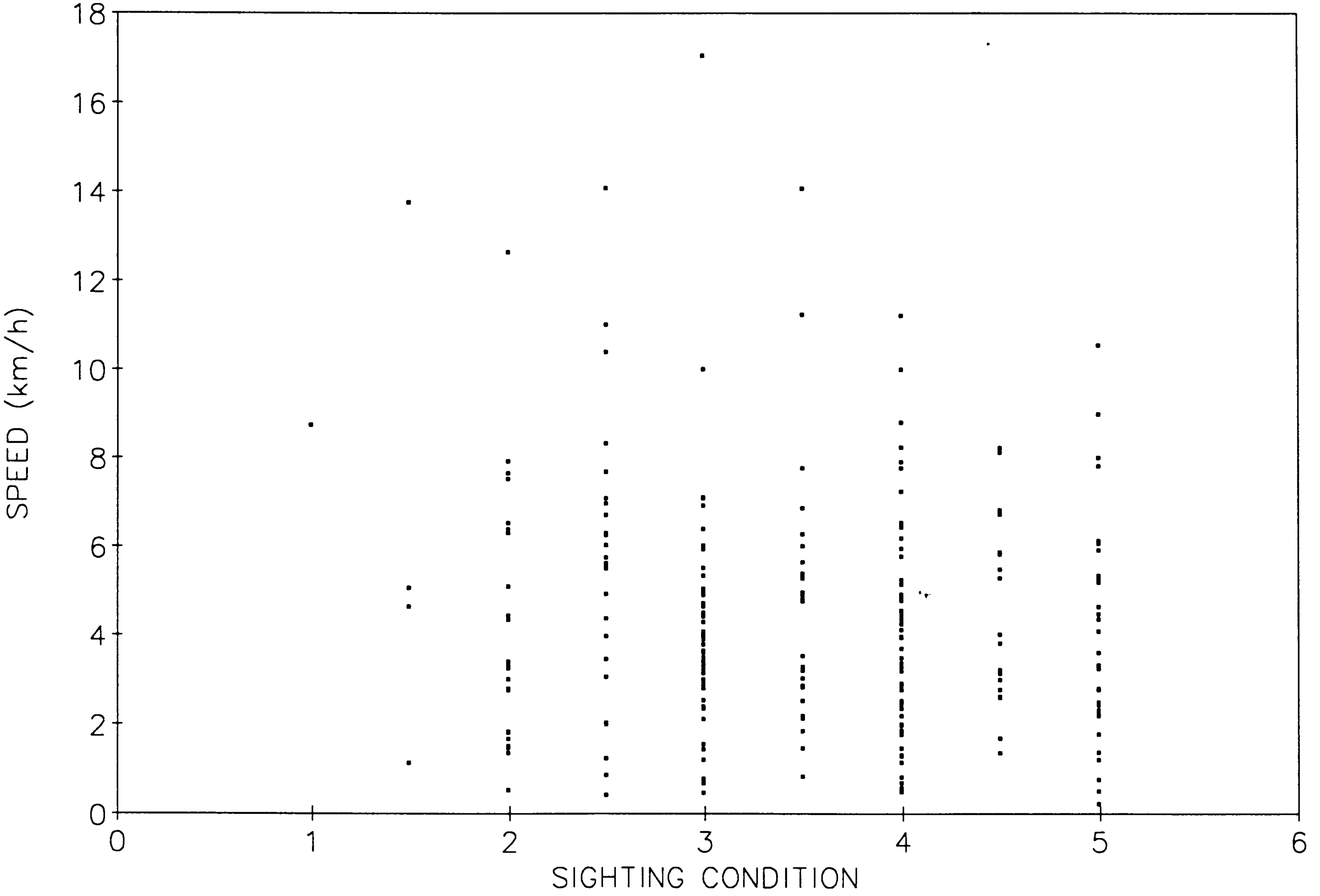


Figure 3.23 Swimming speeds of groups migrating northwards past Cape Vidal in different sighting conditions.

Migration direction

The frequencies of the headings of northward and southward (as reciprocal headings) migrating groups each year is shown in Figure 3.24. For the northward migration, no significant difference was found in migration headings by year (Table 3.5, F = 0.34, d.f. = 3;247, p =0.715, n = 251) or wave (Table 3.6, F = 1.25, d.f. = 4;246, p = 0.704, n = 251).

The coastline to the south of Cape Vidal lies at a bearing of approximately 20 degrees True, while to the north of Cape Vidal the coast lies at a bearing of about 10 degrees True. However, no difference was found between the mean northward migration heading recorded to north and south of Cape Vidal (Figure 3.25, F = 1.695, d.f. = 1;288, p = 1.939, n = 290). In both the northern and southern migrations, the mean headings (Table 3.5) lie between the bearings of the coastline, which suggests no convergence onto, or divergence from, the coastline during the northward or southward migration respectively. No differences were found between the heading of the northward migration by hourly interval (Figure 3.26, F = 0.71, d.f. = 9;241, p = 0.679, n = 251), or by weather (sighting) condition (Figure 3.27, F = 1.089, d.f. = 4;246, p = 0.382, n = 251), and no significant correlation was found between migration heading and wind speed (Figure 3.28, r^2 = 0.13%, p > 0.50, n = 251). No difference was found in heading by wind direction during the northward migration (Figure 3.29, F = 0.703, d.f. = 1;249, p = 0.4960, n = 251).

Migration dependent parameters

For the northward migration, no significant differences were found for migration speed by group size (Figure 3.30, F = 0.920, d.f = 5;245, p = 0.506, n = 251), or migration heading by group size (Figure 3.31, F = 0.257, d.f. = 5;245, p = 0.800, n = 251), or with distance offshore by group size (Figure 3.12, H = 4.32, d.f. = 5;245, p = 0.669, n = 251) - although the latter conclusion assumes group size estimation is not affected by distance offshore.

No significant correlations with migration speed were found for distance offshore (Figure 3.32 r^2 = 0.52%, p > 0.50, n = 251), or heading (Figure 3.33, r^2 = 0.07%, p > 0.50, n = 251), although rapidly moving groups appeared to show less deviation from the mean migration direction than slower groups.

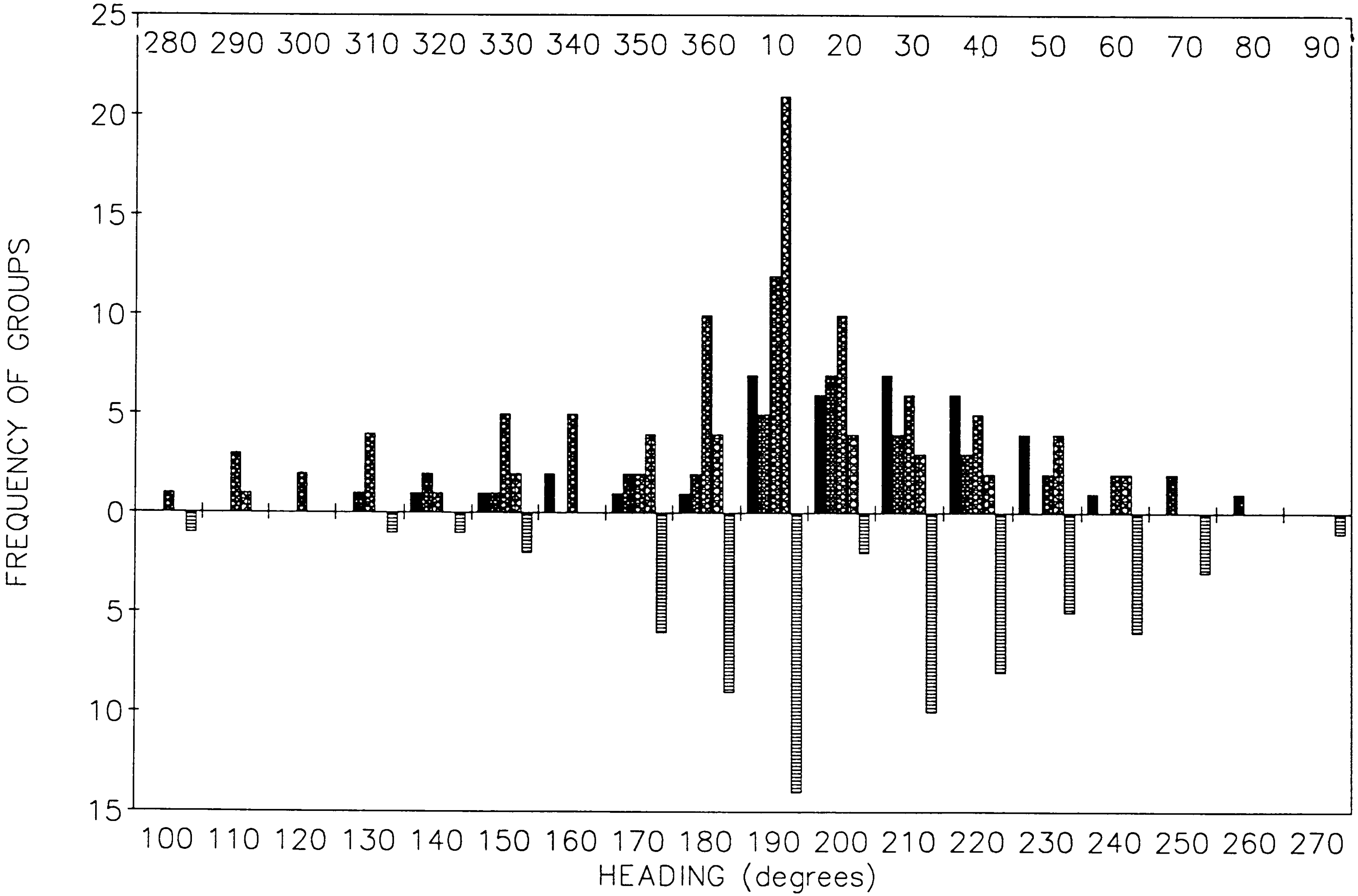


Figure 3.24 Distribution of headings of groups migrating northwards (1988-1991) and southwards (1990) past Cape Vidal each year.

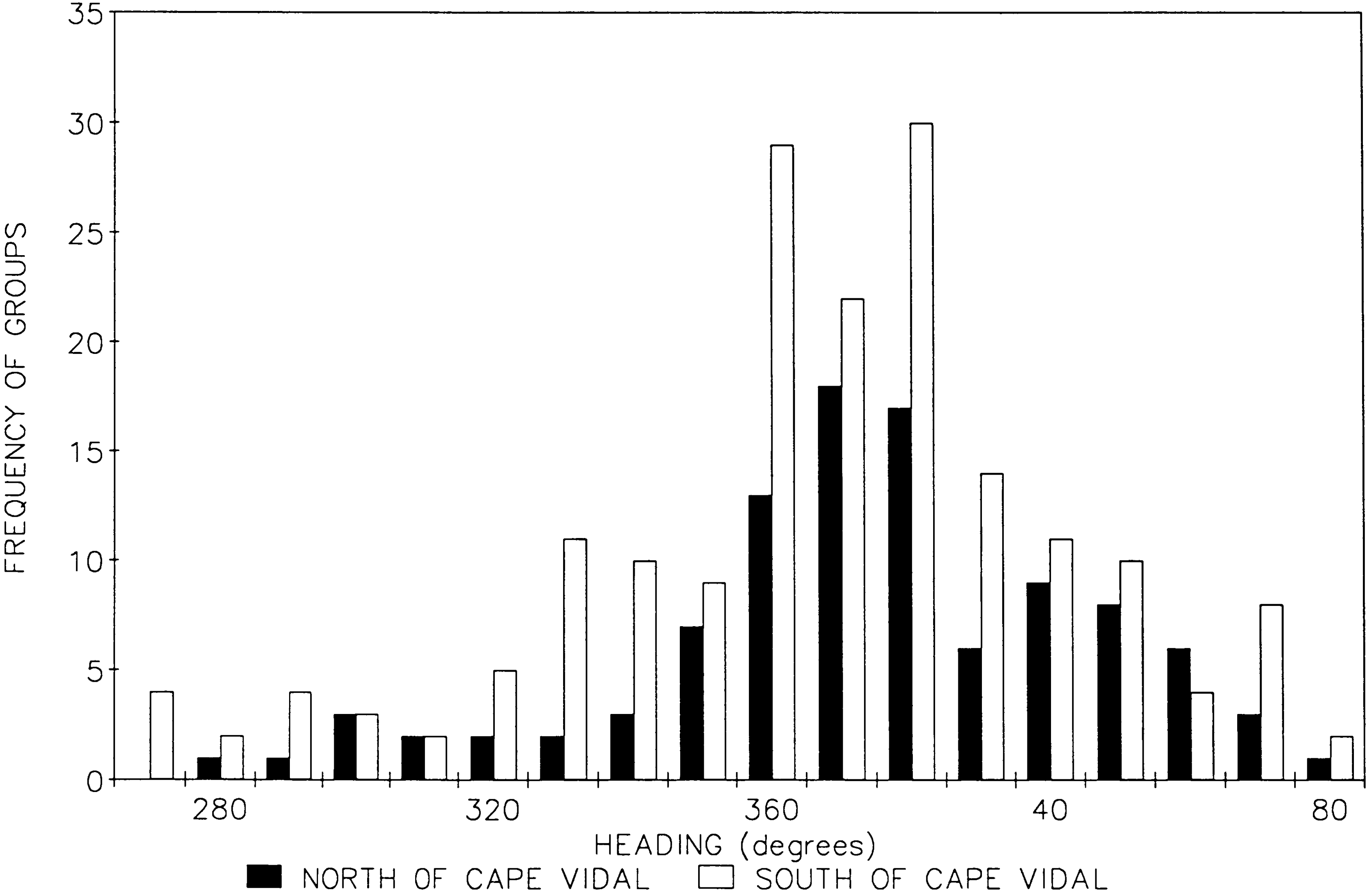


Figure 3.25 Distribution of migration headings of northward migrating animals to the north and south of Cape Vidal between 1988 and 1991.

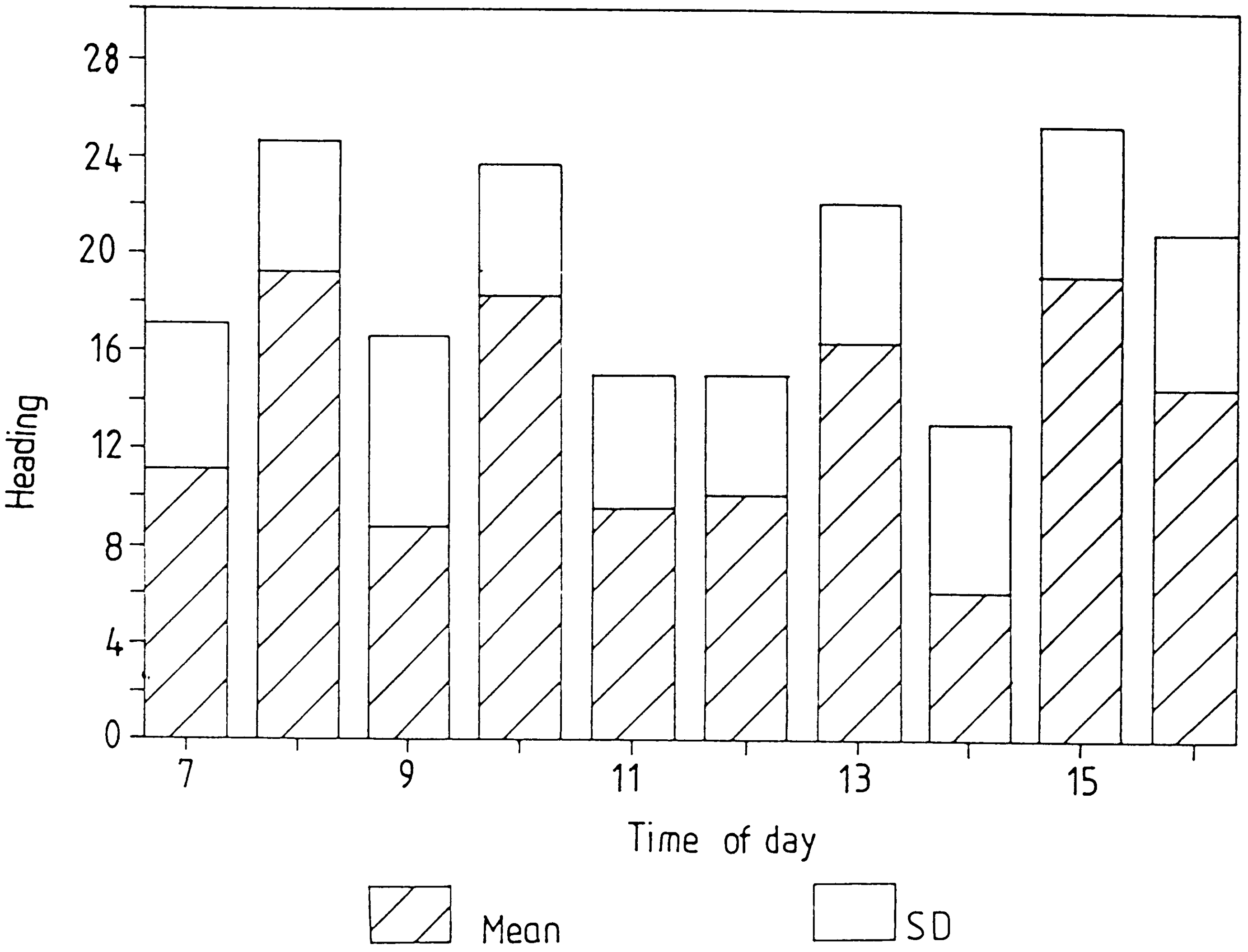


Figure 3.26 Mean migration headings of groups migrating northwards past Cape Vidal during hourly intervals.

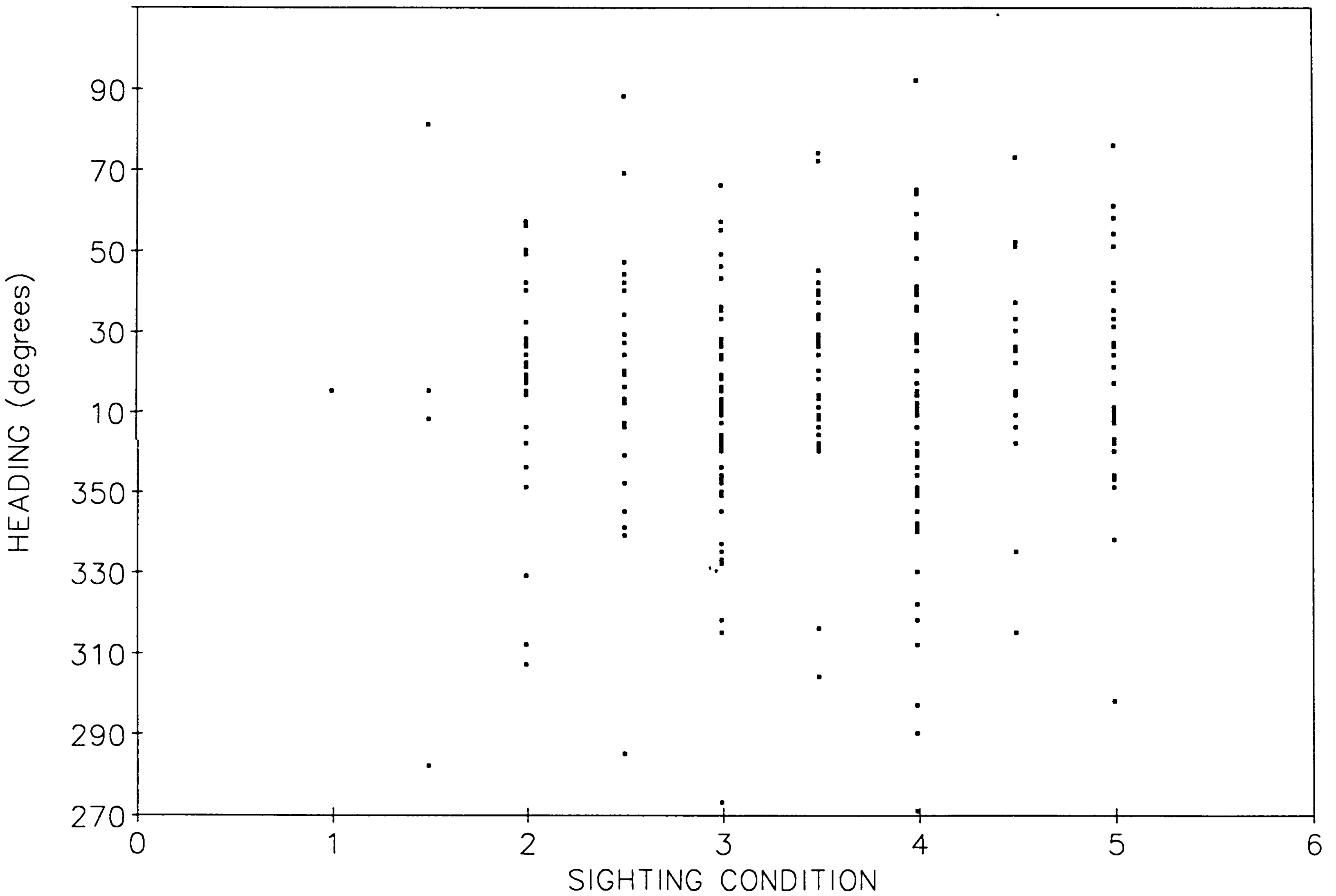


Figure 3.27 Migration headings of groups migrating northwards past Cape Vidal in different sighting conditions.

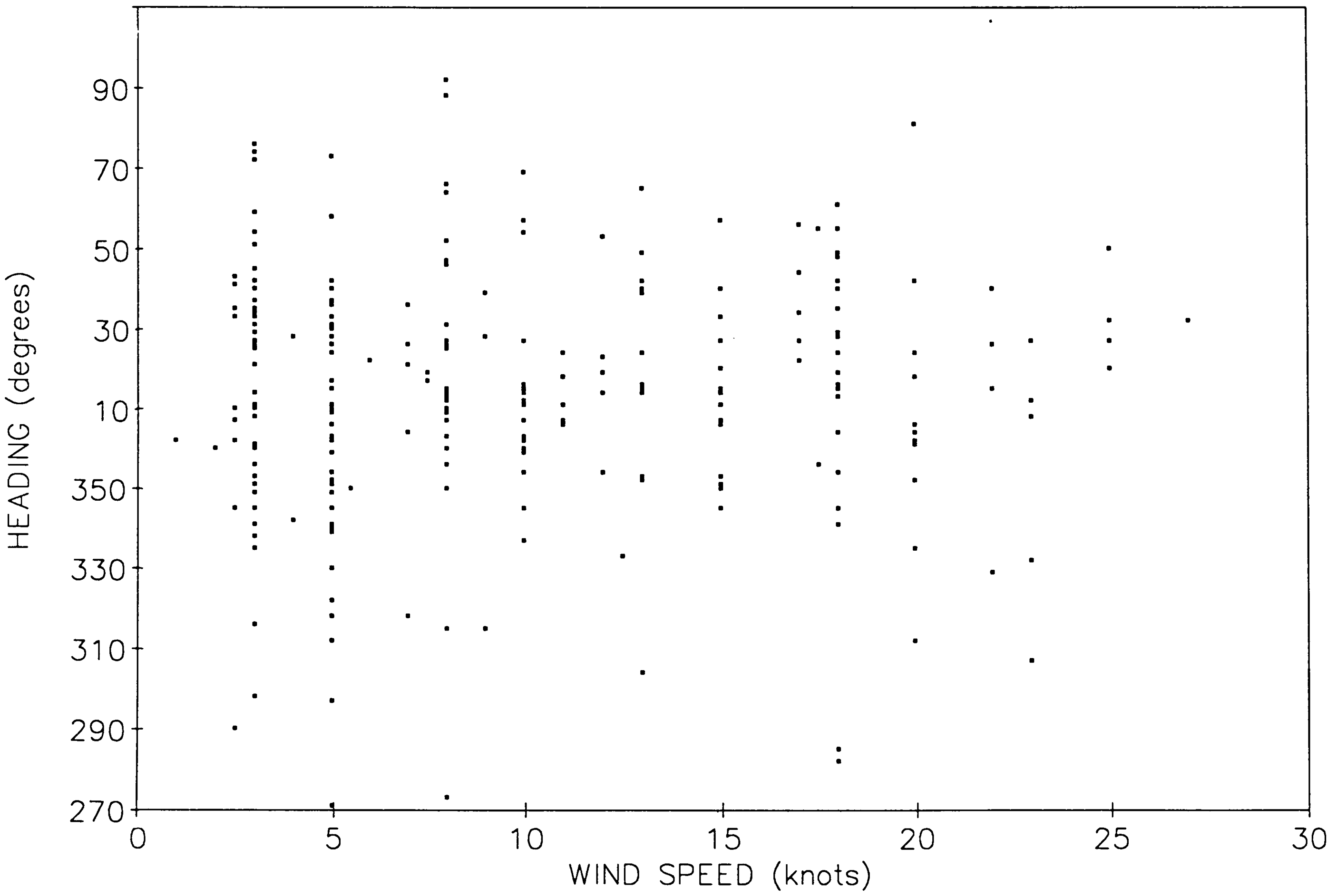


Figure 3.28 Migration headings of groups recorded migrating northwards past Cape Vidal in different wind speeds.

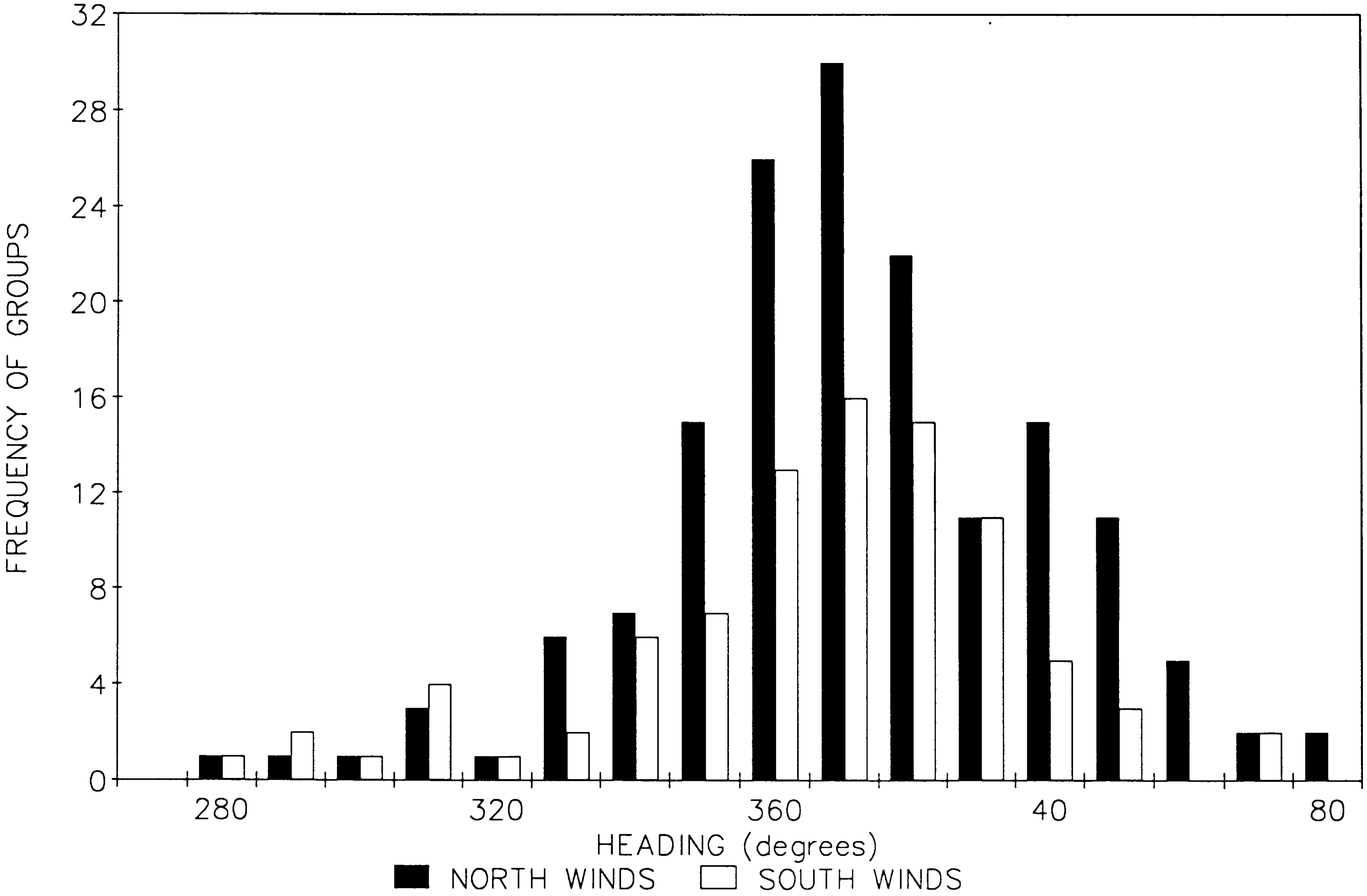


Figure 3.29 The distribution of migration headings of groups migrating northwards past Cape Vidal in northerly and southerly winds.

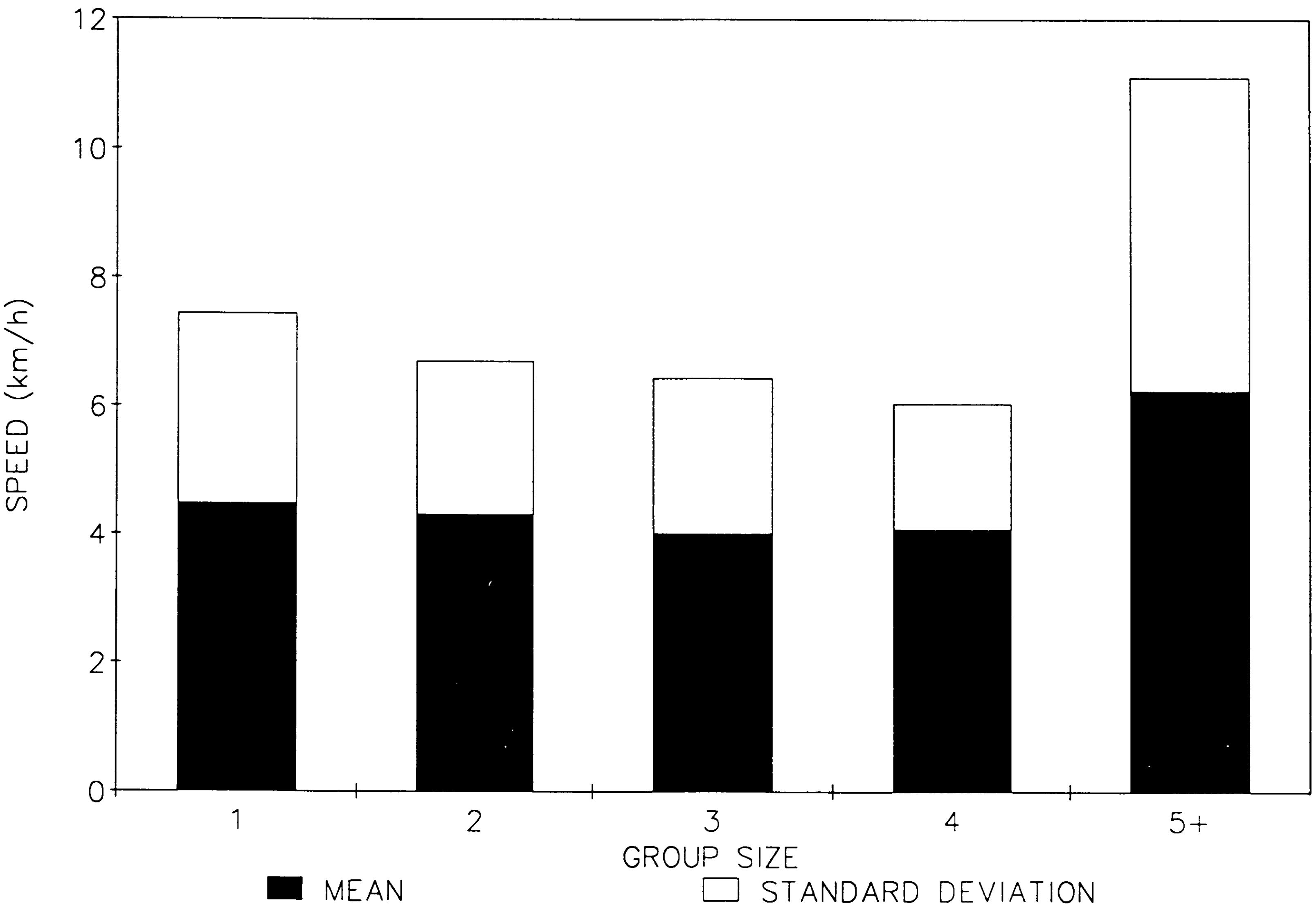


Figure 3.30 Mean migration speeds of different sized groups recorded migrating northwards past Cape Vidal between 1988 and 1991.

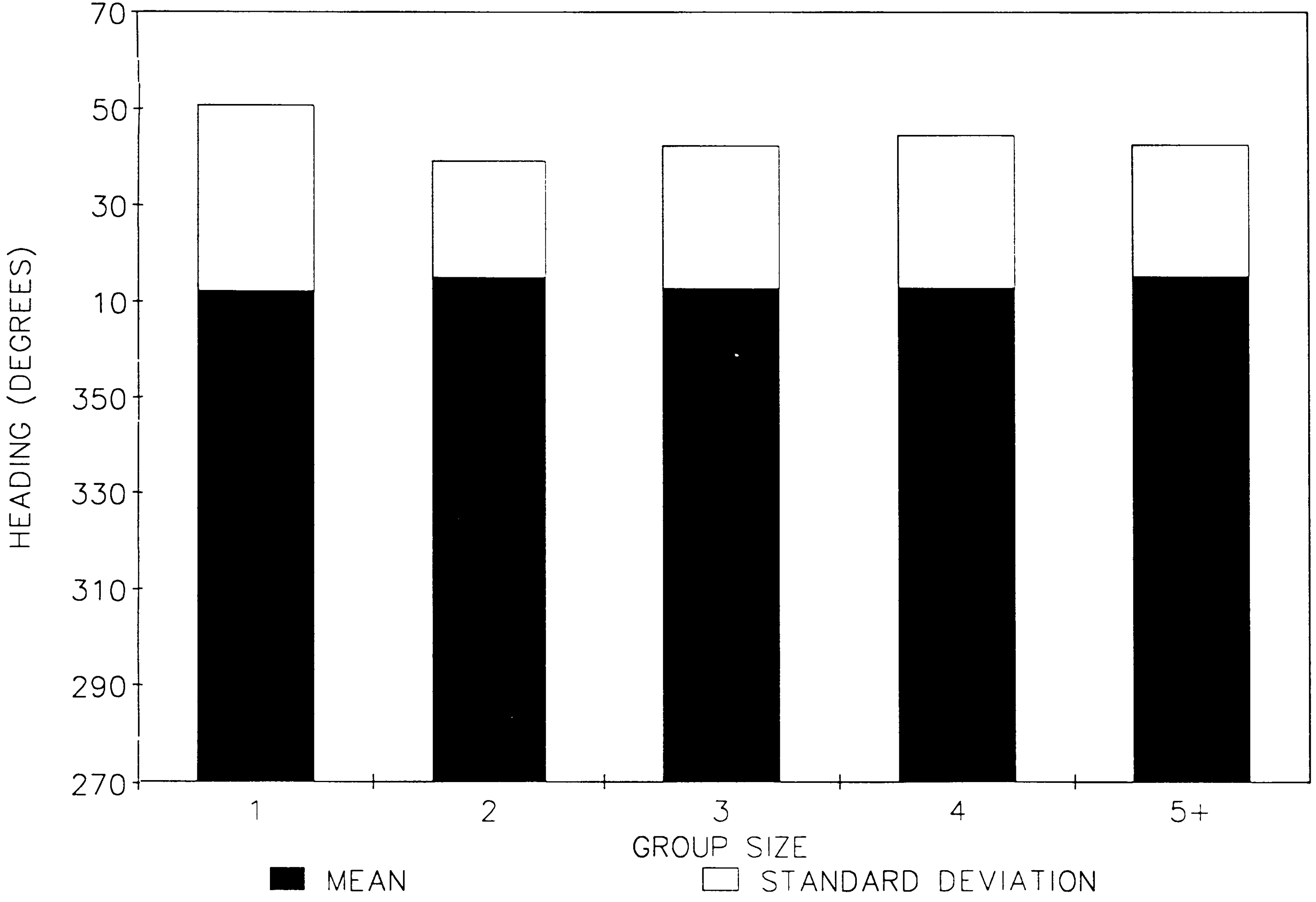


Figure 3.31 Mean migration heading of different sized groups migrating northwards past Cape Vidal between 1988 and 1991.

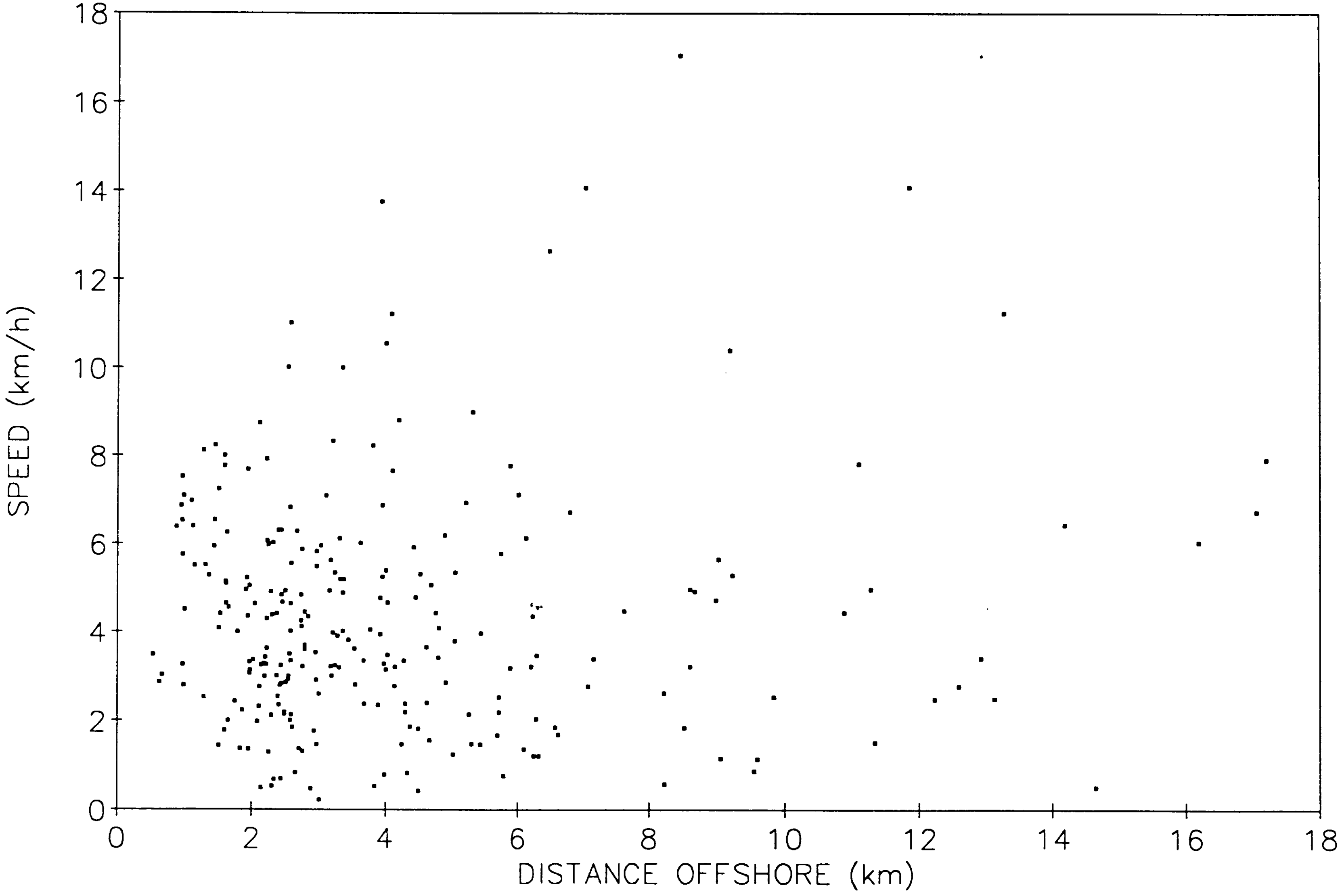


Figure 3.32 Relationship between migration speed of groups and distances offshore at which they were recorded northward migration only.

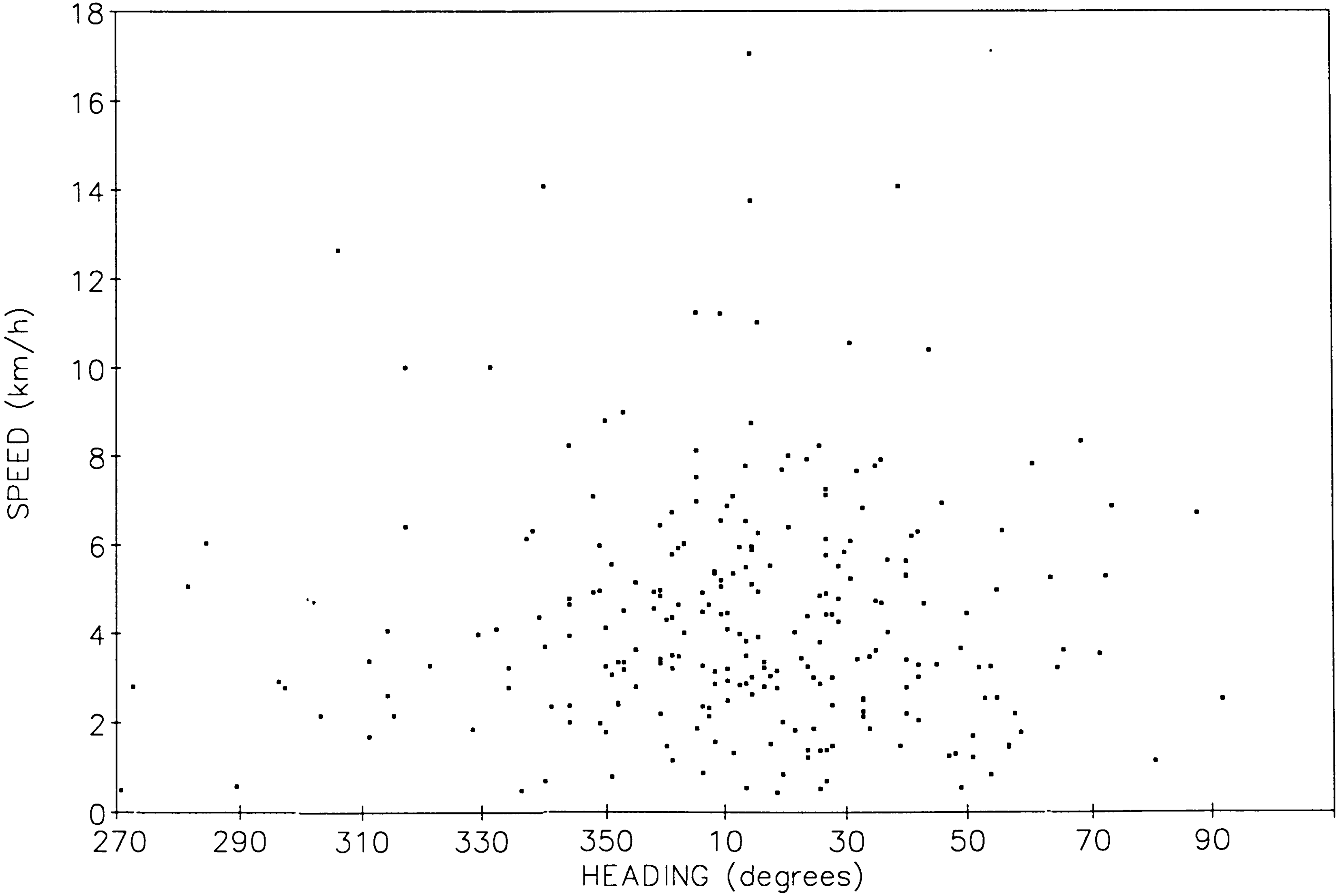


Figure 3.33 Relationship between migration speed of groups and the migration heading at which they were recorded (northward migration only).

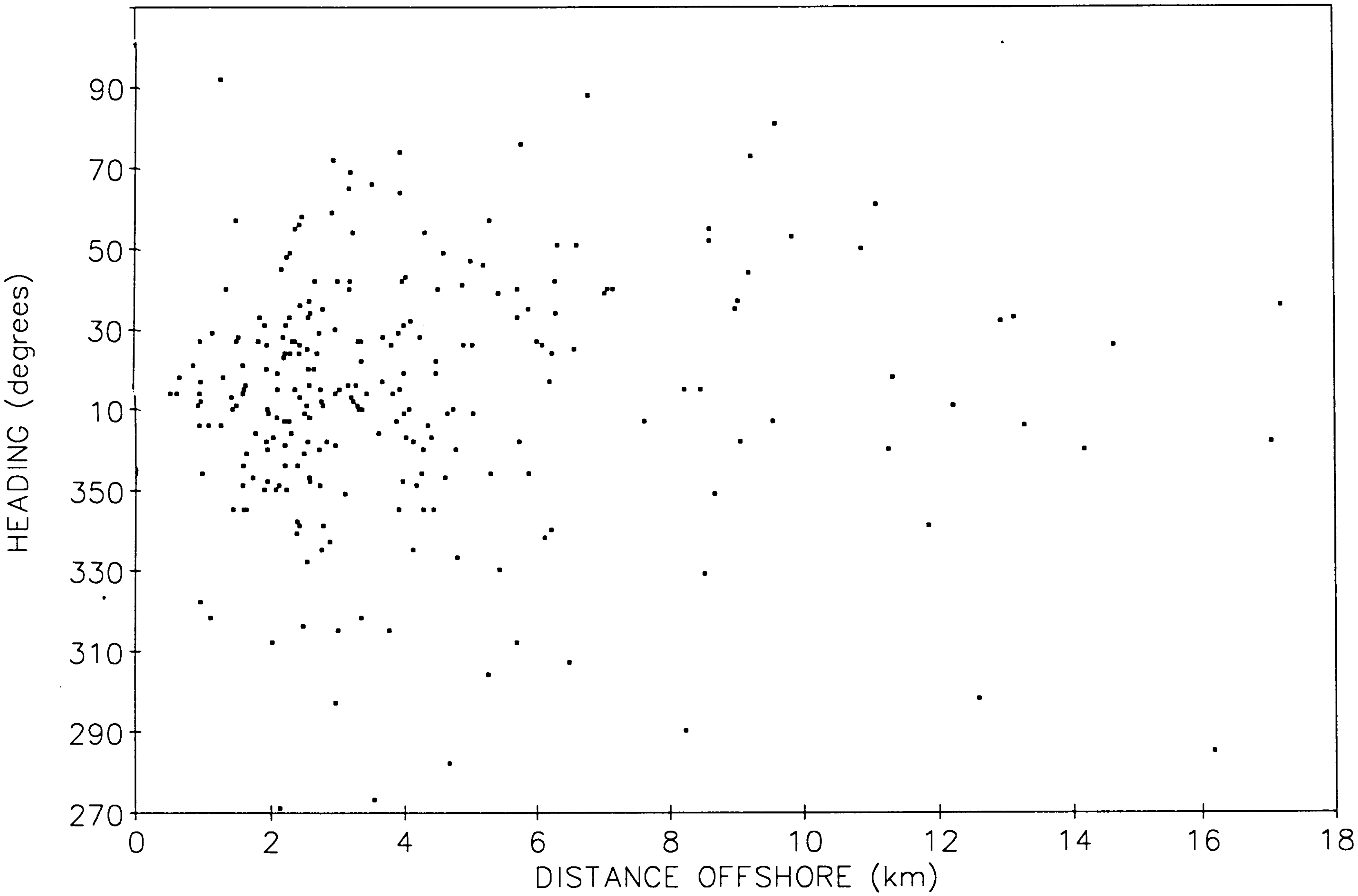


Figure 3.34 Relationship between migration headings (degrees) of groups and the distances offshore at which they were recorded (northward migration only).

No correlation was found between the distance offshore of groups and their heading (Figure 3.34, $r^2 = 0.01\%$, $p = 0.50$, $n = 251$).

Multivariate analyses

Results of the multiple regression of group size against independent variables of time of day, migration speed and bearing, distance offshore, migration wave, wind speed and direction and weather (sighting) conditions are shown in Table 3.7.

Table 3.7 Results of the multiple regression of group size against independent variables of time of day, migration speed and bearing, distance offshore, migration wave, wind speed and direction and weather (sighting) conditions.

Dependent Variable	Group Size					
Multiple r	0.2026					
Multiple r^2	0.0410					
Std error of est.	1.0502					
Analysis of Variance						
	SS	df	Mean square		F ratio	p
Regression	11.378	8	1.4223		1.290	0.2495
residual	265.80	241	1.1029			
intercept	3.62537					
Variable	Coeff	Std Err	Std Reg Coeff	t	p	tolerance
Time of day	0.152E-03	0.418E-03	0.02	0.36	0.72	0.8880
Distance	-0.0214	0.0225	-0.06	-0.95	0.34	0.9156
Wave	-0.0297	0.0563	-0.03	-0.53	0.60	0.9640
Speed	-0.0075	0.0263	-0.02	-0.29	0.77	0.9651
Heading	0.0011	0.0022	0.03	0.50	0.62	0.9860
Wind speed	-0.0365	0.0143	-0.22	-2.56	0.01	0.5219
Weather	-0.2285	0.0965	-0.21	-2.37	0.02	0.5111
Wind direction	-0.2018	0.1424	-0.09	-1.42	0.16	0.8910

Although wind speed and weather (sighting) conditions appeared to have the highest influence on group size (or group size estimation), none of the independent variables tested had a significant effect on group size.

Table 3.8 shows the results of the multiple regression analyses of migration speed against the independent variables of time of day, group size, migration heading, distance offshore, migration wave, wind speed and weather (sighting) conditions. Migration wave was identified as having the greatest effect on migration speed (although this was insignificant at the 5% level).

Table 3.8 Results of the multiple regression of migration speed against independent variables of time of day, group size, migration bearing, distance offshore, migration wave, wind speed and direction and weather (sighting) conditions.

Dependent Variable	Speed					
Multiple r	0.1876					
Multiple r^2	0.0352					
Std error of est.	2.5697					
Analysis of Variance						
	SS	df	Mean square		F ratio	p
Regression	58.0713	8	7.2589		1.099	0.3643
residual	1591.37	241	6.6032			
intercept	3.51981					
Variable	Coeff	Std Err	Std Reg Coeff	t	p	tolerance
Time of day	0.1150E-03	0.1024E-02	0.01	0.11	0.91	0.8876
Group size	-0.0451	0.1576	-0.02	-0.29	0.77	0.9593
Wave	0.2416	0.1368	0.11	1.77	0.08	0.9753
Distance	0.0457	0.0551	0.05	0.83	0.41	0.9147
Heading	-0.0025	0.0054	-0.03	-0.46	0.65	0.9858
Wind speed	0.0292	0.0353	0.07	0.83	0.41	0.5096
Weather	-0.0203	0.2386	-0.08	-0.84	0.40	0.5009
Wind direction	0.3734	0.3491	0.07	1.07	0.29	0.8879

The results of multiple regression of distance offshore against independent variables of time of day, group size, migration speed and heading, migration wave, wind speed and direction and weather (sighting) conditions are shown in Table 3.9. Wind direction had a significant effect on the distance offshore at which the group was migrating (standardised regression coefficient =-0.22, t = -3.43, p = 0.00, n = 251), although the effect of poor sighting conditions usually encountered in southerly winds may well have biased detection of distant groups. As found in the univariate analyses, time of day was an important although insignificant (at the 5% level) contribution to distance offshore, possibly through glare compromising the detection of offshore groups early in the mornings.

Table 3.9 Results of the multiple regression of distance offshore of migrating group against independent variables of time of day, migration speed and bearing, group size, migration wave, wind speed and direction and weather (sighting) conditions.

Dependent variable	Distance Offshore					
Multiple r	0.2964					
Multiple r^2	0.0879					
Std error of est.	2.9981					
Analysis of Variance						
	SS	df	Mean square		F ratio	p
Regression	208.66	8	26.08		2.902	0.0042
residual	2166.21	241	8.98			
intercept	1.93469					
Variable	Coeff	Std Err	Std Reg Coeff	t	p	tolerance
Time of day	0.0028	0.0012	0.15	2.39	0.02	0.9085
Group size	-0.1747	0.1835	-0.06	-0.95	0.34	0.9626
Wave	0.2542	0.1598	0.10	1.59	0.11	0.9730
Speed	0.0622	0.0750	0.05	0.83	0.41	0.9675
Heading	0.0012	0.0063	0.01	0.18	0.85	0.9851
Wind speed	0.0325	0.0412	0.07	0.79	0.43	0.5094
Weather	0.2741	0.2782	0.09	0.99	0.33	0.5015
Wind direction	-1.3656	0.3987	-0.22	-3.43	0.00	0.9267

Table 3.10 shows the results of multiple regression analyses of migration heading against independent variables of time of day, group size, migration speed and bearing, distance offshore, wind speed and direction, and weather (sighting) conditions. None of the independent variables tested showed significant contribution (at the 5% level) to migration heading.

Table 3.10 Results of the multiple regression of migration heading against independent variables of time of day, group size, migration bearing, distance offshore, migration wave, wind speed and direction and weather (sighting) conditions.

Dependent Variable	Heading					
Multiple r	0.1226					
Multiple r^2	0.0150					
Std error of est.	30.457					
Analysis of Variance						
	SS	df	Mean square		F ratio	p
Regression	3451.89	8	431.48		0.459	0.8837
residual	226337.16	241	939.15			
intercept	87.6050					
Variable	Coeff	Std Err	Std Reg Coeff	t	p	tolerance
Time of day	0.0017	0.0122	0.01	0.14	0.89	0.8876
Group size	0.9432	1.8787	0.036	0.50	0.62	0.9600
Wave	1.2302	1.6405	0.05	0.75	0.45	0.9651
Speed	-0.3515	0.7679	-0.03	-0.46	0.65	0.9656
Distance	0.1207	0.6584	0.01	1.18	0.85	0.9123
Wind speed	0.4861	0.4209	0.10	1.15	0.25	0.5110
Weather	2.8872	2.8432	0.09	1.02	0.31	0.5016
Wind direction	-3.6109	4.1668	-0.06	-0.87	0.39	0.8864

DISCUSSION

Although not recorded, the surface activity of groups of humpback whales migrating northwards against the southerly-flowing Agulhas Current appeared more pronounced than groups migrating southward with the current. Both this more extrovert behaviour and the better prevailing weather conditions suggest that the northward migration is the optimal of the two to monitor. Furthermore, the northward migration is slightly closer inshore than its southward counterpart, thus facilitating monitoring.

The seasonality of humpback whales on the Natal whaling grounds (some 300 km to the south of Cape Vidal) has been noted historically from both catches and sightings. Olsen (1914), Harmer (1928, 1931), Matthews (1938) and Bannister and Gambell (1965) showed a bimodal seasonality off the Natal coast (with peaks of abundance in July and September) as the whales presumably migrated northwards and southwards through the whaling ground.

The seasonality recorded during 1990 shows similar results, although on a far more refined scale. As found by Paterson and Paterson (1989) off the east coast of Australia, the southward migration lacked the sharp peak found in the northward migration, and Paterson and Paterson (1989) note that Chittleborough (1965) documented a similar trend during the 1961 migration.

Despite the majority of whales migrating southwards after the end of August in 1990, 31 % of northward-migrating individuals did so after 9 August. Both Chittleborough (1953, 1965) and Paterson and Paterson (1989) found northward-migrating individuals as late as October, and Paterson and Paterson (1989) and Paterson (1991) note that in 1987 over 15% of the northward migration occurred after late August. Incidental sightings of humpback whales have been reported migrating southwards off the northern Natal coast as late as January. While it may appear that such individuals do not migrate south to feed during summer (as suggested by Dawbin 1956), the southernmost extension of the northern limit of the pack ice (and presumably the feeding grounds) occur in February (Matthews 1938, Omura 1953), and these individuals may migrate south late in the summer. Chittleborough (1965), Chapman (1974) and Paterson and Paterson (1984) state that the presence of individuals in tropical and temperate waters so late in the season, reflects late migrations rather than failure to migrate south.

The co-incident timing of the migrations between years is somewhat surprising, given the approximately 2000 n. mile distance between the Antarctic feeding grounds and northern Natal. No waves in the migrations were reported by authors analysing catches or sightings in the Natal whaling grounds by month, day - decade or week (Olsen 1914, Harmer 1931, Matthews 1938, Bannister and Gambell 1965, and Findlay unpub.), although it must be noted that even a time division of a week would not be sufficiently refined for such waves to be detected. Despite the daily counts recorded by Bryden *et al* (1990) appearing to be composed of waves, these waves were not co-incident in timing between years. Although Dawbin (1956) found some annual differences in the timing of the northward migration through the Cook Strait, New Zealand, Chittleborough (1965) speculated that this resulted from differences in Antarctic oceanographic conditions and food availability between years causing differences in the timing of the initiation of the migration, and not differences in migration rates.

Dawbin (1966) noted that the migration was strongly linked to the reproductive cycle. Chittleborough (1965) and Dawbin (1966) showed that during the migrations, whales of certain age or reproductive classes travelled ahead of others, and found that lactating females were in the vanguard of the northward migration, followed by immature whales, mature males and resting females, and lastly pregnant females. On the return migration newly pregnant females were the first to leave the breeding grounds, followed by males and immature whales and lastly newly-lactating females. Dawbin (1966) noted that consequently, pregnant females spend approximately two months longer on the feeding grounds than lactating females. The waves recorded off the northern Natal coast might represent reproductive or age class segregation, although this is impossible to determine without some measure of the age or reproductive status of the individuals in each wave. A two-year reproductive cycle would further imply that the waves do not comprise the same individuals between years, but individuals of the same reproductive status.

Dawbin (1966) suggested that photoperiod was the likely initiating factor for the northward migration, and that once the migration had started it continued at a relatively constant rate without further environmental stimuli. However, the differences in migration timing recorded by Dawbin (1956), which Chittleborough (1965) ascribed to timing of the commencement of the migration, suggests there is either some variation in migration rate between years, or some difference in timing of commencement between years. The co-incident timing of the waves of migration found here suggests that the rate of migration is environmentally regulated.

Group size

The group sizes recorded were similar to those recorded off the east Australian coast by Bryden (1985) and (Bryden *et al.* 1990). Bryden (1985) defined a group as an aggregation of whales within an area of 1 square km, and found group sizes to range between one and five with a modal group size of two, although no confirmation of group sizes was undertaken. Bryden *et al.* (1990) suggested that up to 30 minutes observation of a group was required before group size could be determined, and found no difference between estimated and confirmed group sizes in a small sample of confirmed group sizes. However, as found in this study, their estimates of confirmed groups do not appear to be a representative sample of the groups present, and single whales appear over-represented in the unconfirmed group size estimates. Bryden (1985) and Bryden *et al.* (1990) note that the potential error in the population estimate arising from the error in group size estimates would be small due to the small group sizes recorded. However Antarctic minke whales are also found most often in small groups (eg. 2.41 in Area IV; Best and Butterworth 1980) and in surveys carried out in passing mode (equivalent to a shore-based survey), group size can be underestimated by an average of 35 % (Butterworth 1987). No group sizes were presented by Paterson and Paterson (1984, 1989) or by Paterson (1991) and they do not discuss the accuracy of group size estimation.

Offshore distance and migration path width

Paterson and Paterson (1984, 1989), Bryden (1985) and Bryden *et al.* (1990) state that it is unlikely that humpback whales will be seen at distances greater than 10 km from the coast, despite the horizon being further than this. Paterson and Paterson (1984) suggest that the number of whales passing beyond 10 km from the shore is small, while Bryden (1985) undertook independent aerial surveys to assess the distribution of whales with respect to the coast, and found 96% of whales to be within 10 km of observers on headlands. However, Chittleborough (1965) notes that the main stream of humpback whales migrating along the Australian coast passes within 18.5 km of the shore, and that few whales were seen or captured more than 37 km from the coast.

Although the fact that the northward migration in 1990 was closer to the shore than southward migration may reflect avoidance of the strong southerly Agulhas Current (and simultaneous utilisation of the northward inshore counter-current) by northward moving whales, and the more offshore utilisation of the Agulhas Current by southward migrating whales, the main core of the Agulhas Current lies offshore of the visibility limit of observers. Dawbin (1956, 1966) found that the course followed by migrating humpback whales showed no relationship to water depth or proximity to the coastline. Although Pearce (1977) noted little meandering of the Agulhas Current in the region of Cape Vidal, Schumann (1987) found longshore wind to be the dominant influence on local currents at Richards Bay, and it is unfortunate that no *in situ* measurements of current speed or direction have been carried out, as local currents may influence both the migration stream width and intensity.

Migration speed

The migration speeds recorded are comparable to instantaneous speeds recorded by Chittleborough (1953) off the west coast of Australia from aerial observations. He found individuals moved at speeds of between 4.8 and 14.2 km per hour, with a mean of 8.7 km/h. Chittleborough (1965) found integrated (over time) migration speeds of between 5.18 and 6.66 km per hour for animals marked and recovered in Australian waters, while Robins (in Dawbin 1956) reported a mark return where the individual must have migrated at a mean speed of 4 km per hour over six days. Katona and Beard (1991) found two photo-identified individuals in the western North Atlantic Ocean to have minimum migration speeds of 3.29 km/hr and 2.28 km/hr over 34 and 43 days respectively. It must be noted however that these integrated speeds assume no deviation from the shortest migration route and are assumed constant, so that they may be lower than instantaneous migration speeds. In contrast to these integrated migration speeds, Chittleborough (1965) reports a mark recovery where the animal had remained in the same area (Norfolk Island) for 10 days in the middle of the migration (July), and concludes that some whales may spend some days in one locality before continuing on their migration. Dawbin (1956) calculated the migration rate of humpback whales off New Zealand from timing of migration peaks as 2.4 km per hour and suggests that frequent periods of rest or other activity must occur during the migration. However, these peaks were measured in different seasons, and Dawbin notes that timing of components of the migration varies between seasons.

Despite the considerable variation in migration speeds reported both in the literature and recorded at Cape Vidal, no correlation was found between speeds and the environmental parameters, including time of day, measured. Although humpback whales migrate rapidly at certain times, the report of an individual marked and caught in the same area some days later (Chittleborough 1965) suggest some degree of rest during the migration. Instantaneous migration speeds, such as these measured at Cape Vidal, must therefore be regarded with caution in the integration of migration rates.

In the determination of population size through shore-based surveys, daily densities recorded during daylight hours are extrapolated up to a 24 hour period (Reilly *et al.* 1983, Bryden *et al.* 1990). This however, assumes that the diel migration rate is constant. Reilly *et al.* (1980, 1983) attempted to measure night-time migration speeds of gray whales using image-intensifying scopes, but noted their inadequacy for this type of work, due to the distance of groups from the shore. Rugh (1984) found gray whales off Unimak Pass, Alaska, slowed at night to 73 % of their daytime migration speed. Swartz *et al.* (1987) radio-tagged 20 gray whales off the coast of California in 1985 and 1986, and found no significant difference between rates of movement during the day and night, and suggest that gray whale population sizes estimated from shore-based surveys do not need to be adjusted for different diel migration speeds. Buckland, Breiwick and Cattanach and Laake (1993) reanalysed the results of Swartz *et al.* (1987) by excluding whales that were only tracked during the day or night, (including two whales in the same group) and found a significant difference in day and night speeds, with speeds 10 % higher at night. However they note that of the remaining 15 whales, six were tracked off the Channel Islands where they tend to mill around more than during the migration off Monterey. No significant differences were found in the day : night migration speeds recorded in the remaining nine animals tracked off Monterey.

Although no direct evidence of diel differences in migration rates is available for humpback whales, Watkins, Moore, Wartzok, and Johnson (1981) showed that three radio-tracked humpback whales in Prince William Sound, Alaska (a feeding ground) had shorter dive times at night than during the day. Bryden (1985) projected whales from positions where they were seen during aerial surveys, past shore-based observation points at a speed of 6.5 km per hour, and found no difference between the number of projected passes and the number of observed passes, and so concluded that diel migration speeds were constant. Paterson and Paterson (1989) cite Bryden (1985) as evidence of constant diel migration rate.

Migration heading

Dawbin (1956, 1966) noted that the course followed by migrating humpback whales off New Zealand showed no relationship to water depth or proximity of the coastline, and that the orientation of the coastline appeared to be the most important factor in determining migration direction; while northward-migrating whales were concentrated by the north-easterly orientation of the east coast, southward-migrating whales diverged from it. Although some convergence onto the coast would be expected in the region of Cape Vidal during the northward migration, given the conformation of the coast, this could not be detected from the analysis of headings observed off Cape Vidal. However, it should be noted that the length of coast-line within the visibility limits is possibly too short to quantify any such convergence. Furthermore, the number of southbound whales recorded off Cape Vidal in 1990 suggests that the migration has not diverted from the coastline at this latitude, a fact substantiated by the southward migration headings being parallel to the coastline. Incidental sightings of southward-migrating humpback whales close inshore have been made well to the south of Cape Vidal, and it is possible that migration follows the southerly-flowing Agulhas Current until it diverges from the coast in the region of Algoa Bay.

No measurements of migration heading were presented by Paterson and Paterson (1984, 1989) or Paterson (1991). Bryden (1985) noted that the majority of whales observed travelled a direct course from south to north as they passed headlands, and he estimated the offshore distribution of whales passing headlands by projecting the positions of groups seen on aerial surveys northwards. The lack of difference in northward headings recorded to the north and south of Cape Vidal implies that whales migrate from headland to headland during the northward migration, rather following the coast at a set distance offshore.

CONCLUSION

It is imperative that migration characteristics are analysed at the outset of a shore-based monitoring programme, particularly before making a choice of the optimal period for undertaking such monitoring. Failure to note differences in the characteristics of the migration stream may have consequences in the estimation of abundance, and the comparison of abundance estimates between years, particularly where such differences are in parameters which are dependent on environmental conditions which may change between years or seasons.

The use of multiple regression in predictive analyses have shown that migration-dependent parameters (group size, migration speed, heading and distance offshore) were largely unaffected by environmental or other migration-dependent parameters, although the interaction of real (eg. the animals moved further offshore in the late afternoon) and detection (eg. the whales were not detected offshore in morning due to environmental conditions (glare) needs further research, especially regarding the real distribution of whales with respect to the coast.

The measurement of migration characteristics has played a critical role in this study, in both the estimation of the proportion of the population missed by observers (chapter 4), and in the counting of groups not seen to cross the midline (chapter 5). This is the first use of these techniques in humpback whale population estimation based on shore-based visual studies.

CHAPTER 4

ASSESSMENT OF HETEROGENEITY IN SIGHTING PROBABILITIES OF HUMPBACK WHALES IN SHORE-BASED SURVEYS AT CAPE VIDAL, SOUTH AFRICA.

INTRODUCTION

Shore-based surveys have been undertaken for a number of migrating whale species, including bowhead whales (*Balaena mysticetus)* (Zeh, Ko, Krogman, and Sonntag, 1986a, 1986b, Krogman, Rugh, Sonntag, Zeh and Ko 1989, Gentleman and Zeh 1987, and Zeh, George, Raftery and Carrol 1991), gray whales (*Eschrichtius robustus*) off the Californian and Alaskan coasts (Reilly, Rice and Wolman 1980,1983, Reilly 1984, Rugh and Braham 1979, Rugh 1984, Breiwick, Rugh, Withrow, Dahlheim and Buckland 1988, Rugh, Ferrero and Dahlheim 1990), and humpback whales (*Megaptera novaeangliae*) off the east coast of Australia (Paterson and Paterson 1984, 1989, Paterson 1991, Bryden 1985, Bryden, Kirkwood and Slade 1990).

However, some groups of whales within the survey area may be missed due to heterogeneity in sighting probabilities with distance from the observer or under different weather conditions (Reilly 1984, Rugh 1984, Hiby and Hammond 1989, Rugh *et al.* 1990, Zeh *et al.* 1991). Detection probabilities may be further influenced by group size and the extent and duration of visible surface active behaviour. Zeh *et al.* (1986a) found the density of passing groups to have no effect on the probability of missing a whale group.

Detection probabilities have been determined in a number of shore-based visual surveys of both gray whales and bowhead whales, using modified mark-recapture methodology. Breiwick *et al.* (1988) used Chapman's (1951, in Seber 1982) modification of the Petersen estimate to calculate the proportion of gray whales missed by observers off California, while Rugh (1984) found that 19 % of gray whale groups within visibility range were missed by observers at Unimak Pass, Alaska. Rugh *et al.* (1990) estimated that 21 % of groups of gray whales were missed by observers off Central California, using a Petersen estimate. Zeh *et al.* (1986a, b) and Krogman *et al.* (1989) have used removal sampling (Seber 1982, Hiby and Hammond 1989) to estimate the proportion of bowhead whales missed by observers passing Point Barrow, Alaska, and found that numbers of observers, observer height and ice conditions affected detection probabilities. Gentleman and Zeh (1987) used a combination of visual and acoustic data in a simple mark recapture model to estimate the number of bowhead whales passing Point Barrow.

All shore-based visual surveys of humpback whales to date have assumed that all individuals within a 10 km visual strip were sighted (Bryden 1985, Paterson and Paterson 1984, 1989, Bryden *et al.* 1990, Paterson 1991). In this paper an attempt is made to assess the proportion of groups missed by shore-based surveys, using two independent observer stations.

METHODS

Field observations

Shore-based surveys of northward migrating humpback whales were carried out at Cape Vidal on the northern Natal coast, South Africa, over the periods 4 July to 22 July 1988, 27 June to 22 July 1989, 2 June to 28 October 1990, and 17 June to 6 August 1991. Results obtained in 1988 and 1989 suggested groups were being missed by observers, so the period 1 to 22 July 1990 and the entire 1991 survey were carried out as independent observer (IO) surveys. The 1990 survey was carried out with one team of observers, while three observation teams undertook the 1991 survey.

During IO surveys, observations were carried out independently from two similar timber towers (termed north and south towers) atop an approximately 56 m high vegetated sand dune situated on a slight headland less than 100 m from the waters edge. South tower, 61.5 m above sea level, has been used for all surveys since 1988, while north tower, 60.3 m above sea level and 22 m to the north of south tower, was used for IO surveys only. The distance to the horizon was approximately 23 km from both towers. South tower had an unobstructed view from 25 to 210 degrees True, while north tower had an unobstructed view from 355 to 185 degrees True. Both towers therefore had a field of view of 185-190 degrees, of which 160 degrees was shared (Figure 4.1). The towers were visually and acoustically isolated from each other by vegetation.

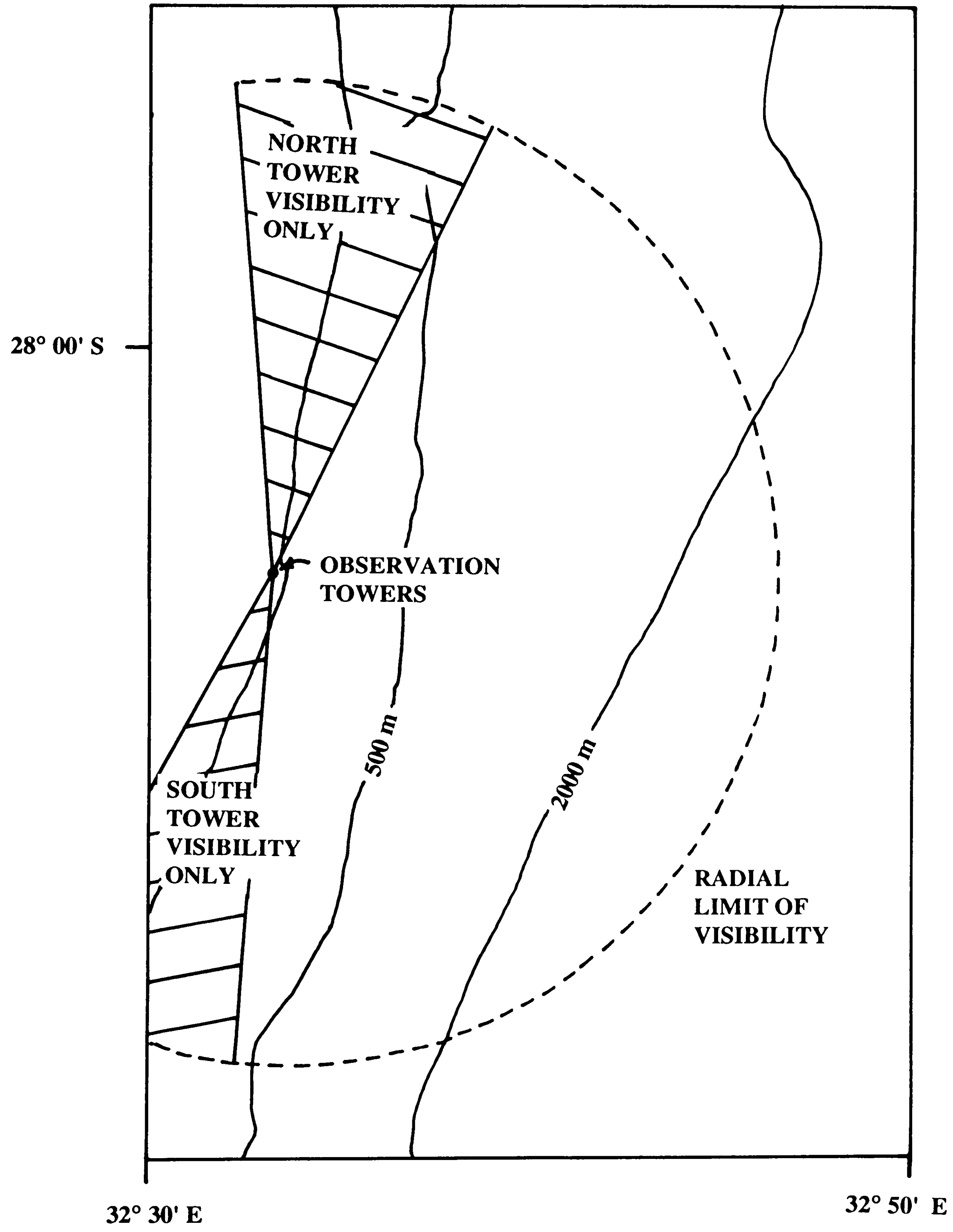


Figure 4.1 Plan of the study area showing visibility limits from each of the north and south towers.

Observations were undertaken from 07h00 to 17h00 each day, except during inclement weather (rain, wind speeds of over 25 knots, or visibility of less than 5 km). Observations were undertaken by two observers per tower at all times, and whenever possible one observer on each tower had previous cetacean survey experience. Generally one observer searched the area with 7x35 wide angle binoculars, while the other searched with the naked eye, with roles being changed every 15 minutes. No observer did more than 5 hours observation (split into three- and two-hour sessions) each day. An observer activity record was kept at all times during observation, on which any change of observer activity was noted. As far as possible observers were assigned to the same tower for all their observation duties, although rotation of one pair of observers between towers was carried out to allow all observers to participate in boat duties.

Wind speed and direction, cloud cover, swell height (number of formed waves off the beach in front of the towers), sea surface state (Beaufort scale), visibility (measured through the theodolite as the limit of visibility on the midline), and a general index of sightability (ranging from 1 (very poor) to 5 (excellent) taking all other factors into consideration), were recorded on a weather form each hour by each tower, as were the number of boats and ships within visibility.

Once sighted, groups of whales were tracked using Wild T1 or T1A theodolites, orientated on a reference object at the start of each day. Measurements of the angle between the vertical and the whales, and the angle between true north and the whales (both to the nearest 10 seconds), provided the distance and bearing respectively of the whales from the tower. Successive timed measurements (to the nearest three seconds) of vertical and horizontal angles of a group's surfacing provided a series of fixes of the migration track of the group (timepieces were synchronised on the two towers). Each fix was plotted onto a chart at the time of measurement, which not only allowed for immediate checking of fix errors, and discrimination of closely-migrating groups, but also provided observers with some idea of where the group would surface next.

Group size was estimated at each fix, so that some refinement in group size resulted during the tracking of a group. A subsample of estimates of group sizes made from the tower was confirmed through interception of groups by ski-boat (exemption for this work was granted in terms of the Sea Fishery Act (number 58 of 1973) and the Fishery Act (number 12 of 1988). In order to overcome the problem of the presence of the boat cueing observers on the other tower to the presence of the whale, both towers independently reported times and positions of all groups of whales sighted by radio to tertiary observers, who only intercepted groups they deemed to be duplicates.

Field data were entered into data retrieval files on completion of the field season. An application programme was written in BASIC to convert angles of fixes to cartesian coordinates (taking both the curved surface of the earth and refraction into consideration), thus providing successive positions of a migration track (Appendix I). Further algorithms calculated the migration heading, speed and distance offshore of each group. Migration headings were calculated between the first and last definite fix of each track, while speeds were calculated from the distance and time elapsed between the first and last definite fixes. The distance of the track from the shore was calculated as the mean of the distances of all definite fixes to the shore directly to the west of them. Migration speeds and headings were only calculated for tracks on which more than two theodolite fixes were taken. Overall mean speeds and headings were used for other groups.

Mean daily sightability conditions were calculated from the hourly sighting conditions recorded on each tower.

A difficulty in recognition of some duplicate sightings arises from the fact that the group may well have moved some distance between the times it was detected by each tower. Such duplicates are almost impossible to recognise in the field, although other duplicate sightings were easily recognisable and scored as "field duplicates" at the end of each day's observation.

In order to provide a more objective method of matching sightings, a further BASIC application programme was written to recognise duplicate sightings from the time groups crossed the midline of the observation area, and the distance from the shore at which the midline was crossed. Groups that were not observed to cross the midline were projected northwards or southwards to the midline at their calculated migration speed and heading. The time of the expected crossing was calculated from this projection. Symmetric upper and lower bounds were chosen around the migration speed (see below), and projection of the group at these speeds provided an interval around the time of crossing the midline. Where the lower bound was less than the lowest recorded speed of 0.5 km/h, 0.5 km/h was taken as the lower bound. The crossing time of each sighting made on a particular day from south tower was compared with the crossing time of each of the sightings made by north tower on the same day. In order for groups to be duplicates, the crossing time from either tower had to fall within the time interval of the other tower, and the crossing distance from the shore for either tower had to fall within less than two km of the other.

A modified version of the duplicate recognition programme was first run on the sightings from each tower to recognise internal duplicates (single groups recorded as two (or more) sightings by the same tower). This programme compared crossing times and positions of each sighting from a tower against those for all other sightings from the same tower on the same day. Modifications ensured that identical sightings (the same sighting number) and sightings that were observed within ten minutes of each other, were not recognised as duplicates; it was assumed that observers would only have recorded two or more groups within ten minutes of each other if they were certain that the groups were separate). Sightings that were recognised as duplicates by this modified programme were deemed as internal duplicates, and their migration tracks were merged into a single track for final duplicate recognition analyses.

Determination of the time interval around the crossing time was undertaken by running the programme on all sightings using each of 1, 2, 3, 4, 5 and 6 km/hr as the symmetrical bounds around the migration speed. The number of field duplicates recognised by the programme in each run, was compared to the total number of field duplicates recorded. The lowest speed bound at which 95 % of the field duplicates were recognised, was selected for final duplicate recognition analyses.

Counts of sightings made from the north (nn) and south (ns) towers, and the incidence of duplicate sightings (m) made by both towers were tallied each day. In order for the group to be included in the day's tally, it must have crossed the midline of the observation area within the period of observation. The Petersen estimate

$$N = nn.ns/m \qquad (1)$$

provides an estimate of the population given that the proportion of marked individuals in the second sample is a true reflection of the proportion of marked individuals in the population. Chapman (1951, in Seber 1982) noted that the Petersen estimate of N is biased for small samples and modified the estimate to

$$N = ((ns + 1)(nn + 1)/(m + 1)) - 1 \qquad (2)$$

The use of this method is comparable to Gentleman and Zeh's (1987) method of comparison of visual and acoustic data, in that it actually compares samples of tracks rather than groups, and consequently includes additional variance, arising from the uncertainty of linking sightings into tracks.

The proportions of tracks seen by the south tower (ps) and north tower (pn) of the total present are given by

$$ps = m/nn \qquad (3)$$

and

$$pn = m/ns \qquad (4)$$

respectively.

The estimated sampling variances are given by

$$\frac{(nn+1)\,(ns+1)\,(nn+m)\,(ns+m)}{(m+1)^2\,(m+2)} \quad \text{for N,} \qquad (5)$$

$$(1-m/ns)(m/nn)(1-m/nn)/(nn-1) \quad \text{for ps} \qquad (6)$$

and

$$(1-m/nn)(m/ns)(1-m/ns)/(ns-1) \quad \text{for pn} \qquad (7)$$

Seber (1982) notes the assumptions need to be met for N to be estimated accurately. These include :-

i) The population is closed.

As the two samples are taken almost instantaneously, emigration from (including mortality), or immigration to, the population in the true sense is zero. However, splitting or merging of groups within the observation area is equivalent to emigration or immigration respectively, as a group of whales is the unit being sampled. Groups which were seen to have joined or split were entered into the database as single or multiple groups depending on where in the visual survey area the split or merge occurred.

A further violation of this assumption may arise if observers use different criteria in defining groups from each tower. Bryden *et al.* (1990) defined a group of humpback whales as all individuals within 1 km^2, while Rugh *et al.* (1990) defined a group of gray whales as an aggregation of animals within one half body length of each other. In this study individuals within five body lengths of each other have been recorded as a group.

ii) All animals have the same probability of being caught in the first sample, and the second sample is a simple random sample.

Heterogeneity in the sighting probability could arise from four factors; whale behaviour, distance from the observer, sighting conditions, and group size. These heterogeneities result in the detection of groups from the north and south towers being conditionally independent rather than unconditionally independent (Schweder 1990), in that more detectable whales tend to be seen by both towers, while less detectable whales tend to be missed by both towers.

This problem can be partly circumvented through stratification of data into intervals of more equal sighting probabilities, although there is an obvious compromise between the integration of sighting probability over a range and a reduction in sample size. Analyses were carried out on both unstratified and stratified data. Data were stratified into (a) three mean daily sighting conditions (<3 (poor), 3-4 (fair), and greater than 4 (good)), and (b) three distance intervals from the shore (<3, 3-6, and greater than 6 km from the shore). The distance intervals were chosen so that each had a roughly similar sample size. Further stratification (by both behaviour and group size) was precluded by (a) the difficulty in applying objective behavioural criteria, (b) the fact that duplicate sightings could be recorded as different group sizes by the two towers, and (c) the relatively small numbers of sightings overall.

iii) Marking does not affect the catchability of the animal.

This assumption could be violated by one tower cueing the other tower to the presence of a group, although the independent surveys carried out from these two towers ensure that this assumption is not violated.

iv) Marks are not lost between the two samples, and all marks are reported on recovery in the second sample.

These assumptions are met if all, and only, duplicate sightings are recognised as such.

RESULTS

A total of 154.8 and 360.8 hours of independent observer surveys were carried out in 1990 and 1991 respectively (Figure 4.2). The mean daily sightability conditions recorded as the average of each tower are shown in Figure 4.3 by year.

The duplicate recognition programme was run on all sightings made during each of the 1990 and 1991 surveys (regardless of whether the group crossed the midline or not), using speed bounds of 1, 2, 3, 4, 5 and 6 km/hr. The number of field duplicates, and total number of duplicates found by the programme are shown in Figures 4.4(a) and 4.4(b) for 1990 and 1991 respectively. From these, five km/h was selected as a suitable speed bound for both years, as at this speed over 95 % of "field duplicates" were recognised by the programme in both years' data.

During independent-observer periods, totals of 46 and 47 groups were observed to cross (or were projected across) the midline during observation periods by the north and south towers respectively in 1990, of which 33 groups were seen by both towers. During independent - observer surveys in 1991, totals of 132 and 159 groups were observed to cross (or projected across) the midline by the north and south towers respectively, of which 96 groups were seen by both towers. There was a 17 % disparity in the total number of groups sighted from each tower in 1991, although it must be noted that no such disparity was recorded in 1990. This disparity was recorded throughout the 1991 survey and not just by one set of observers, and possibly reflects both south tower having a better view to the south (from where the whales are migrating) and glare to the north, although this does not explain why this disparity was not noted in 1990. The number of groups recorded by the two towers to cross the midline of the observation area during observation times each day and the associated number of duplicate sightings during the 1990 and 1991 surveys are shown in Figures 4.5(a) and 4.5(b) respectively. Estimates of the population within visible limits (N) and the proportions missed by each tower (pn and ps) arising from both stratified and unstratified results of both the 1990 and 1991 surveys are shown in Tables 4.1(a) and 4.1(b) respectively.

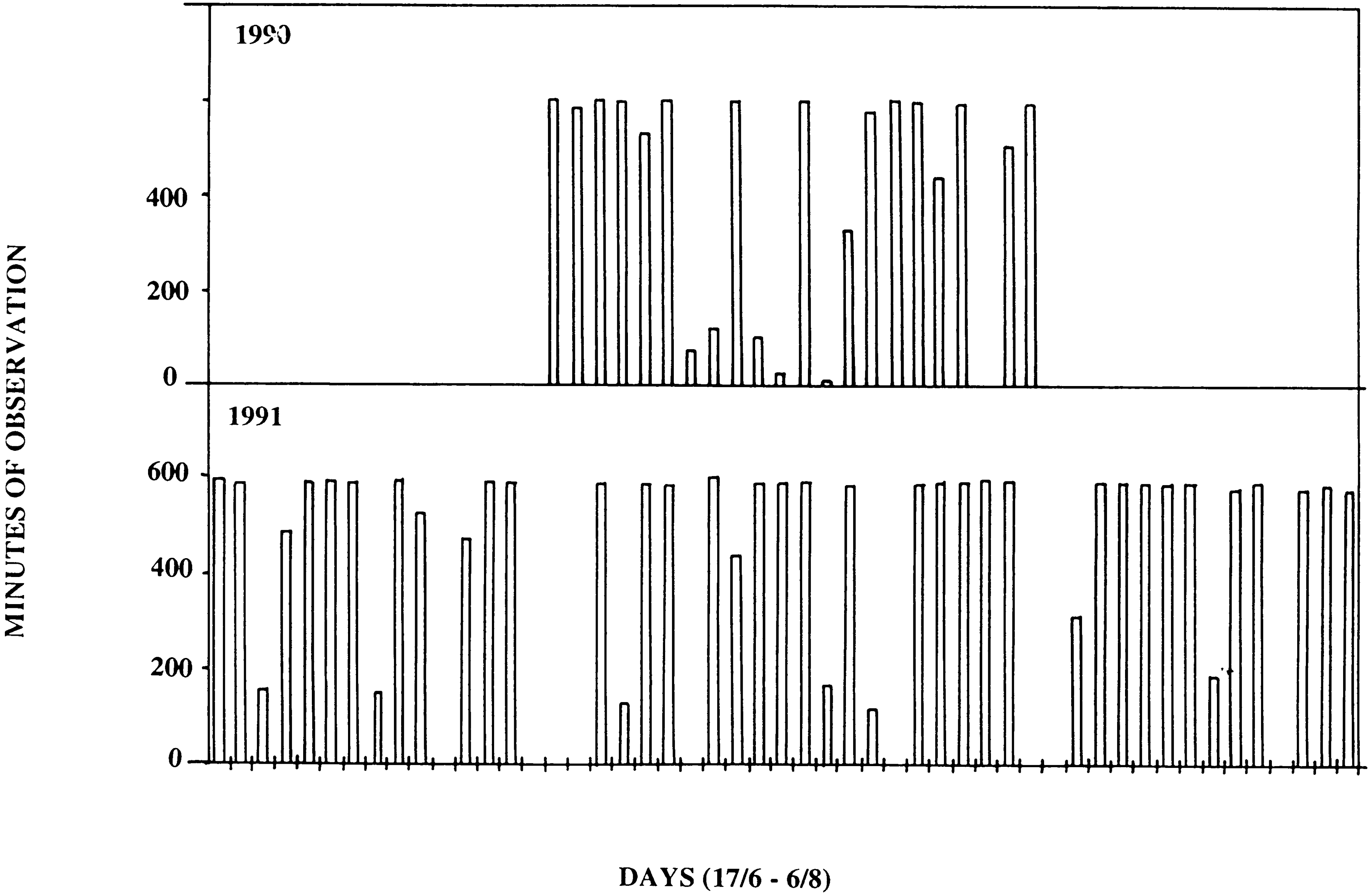


Figure 4.2 Distribution of search effort carried out in independent observer surveys in 1990 and 1991.

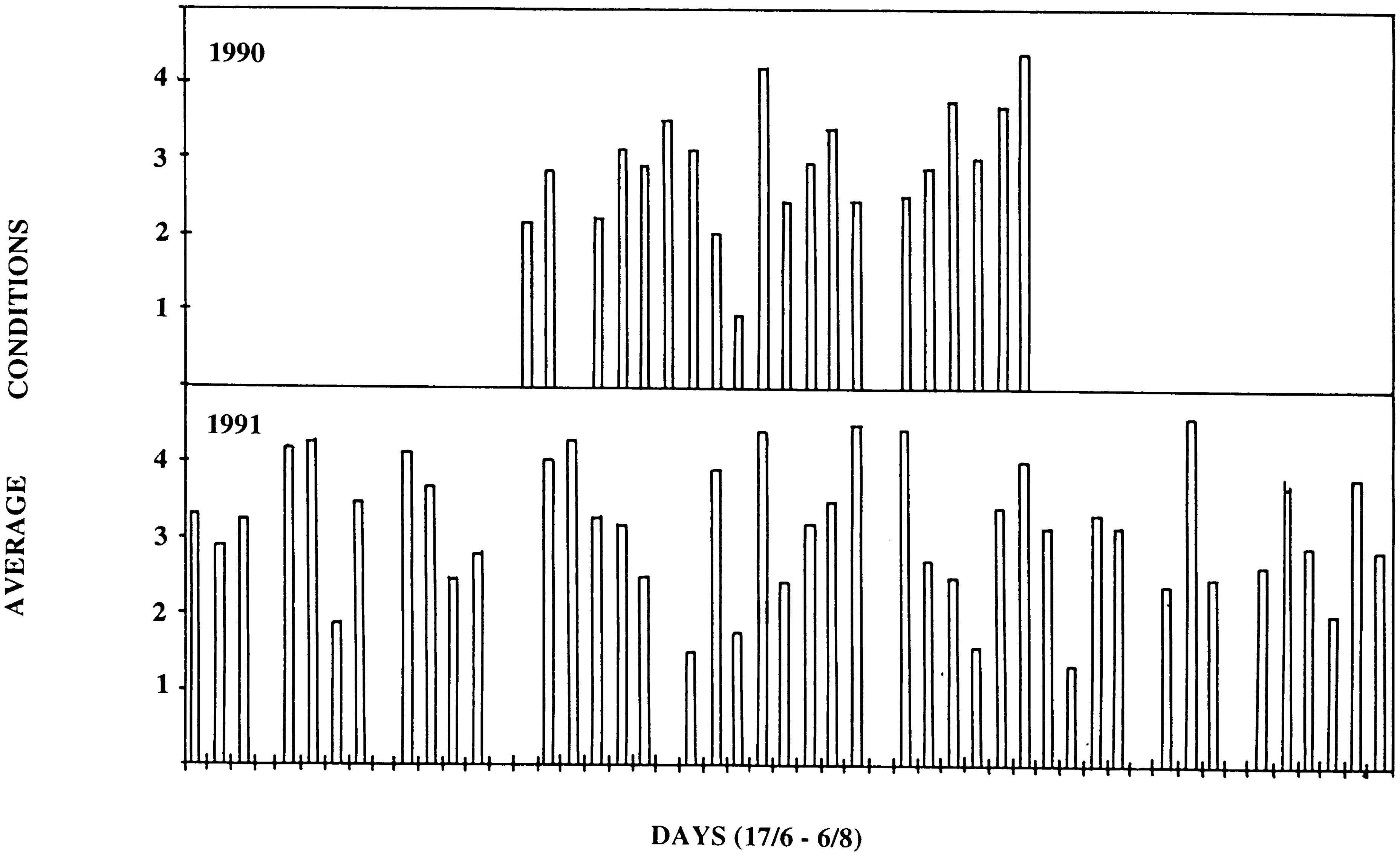


Figure 4.3 Mean daily sighting conditions recorded by the north and south towers in independent observer surveys in 1990 and 1991.

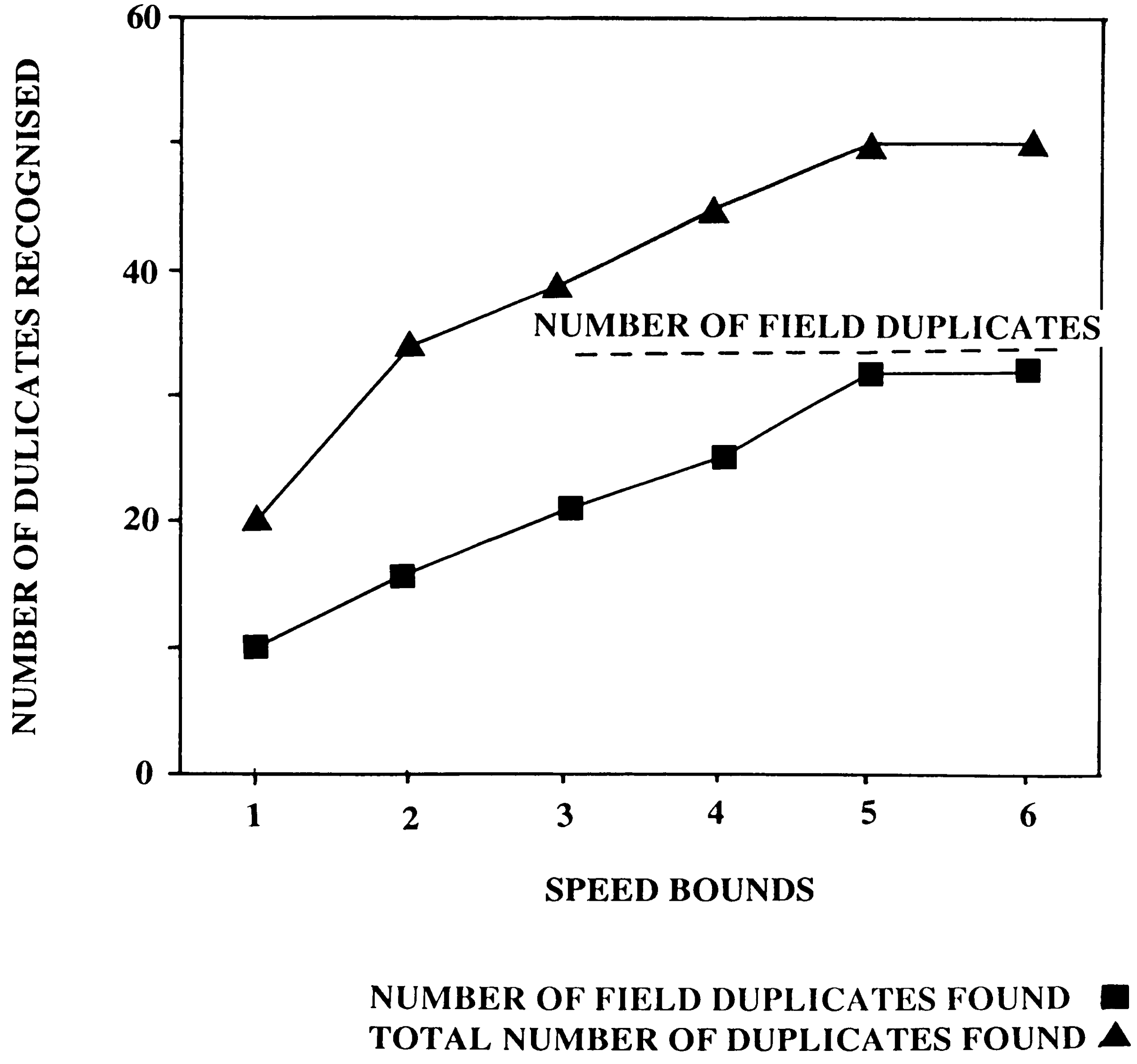


Figure 4.4(a) The number of duplicates and field duplicates found in the 1990 data by the matching programme at migration speed bounds at which the programme was run.

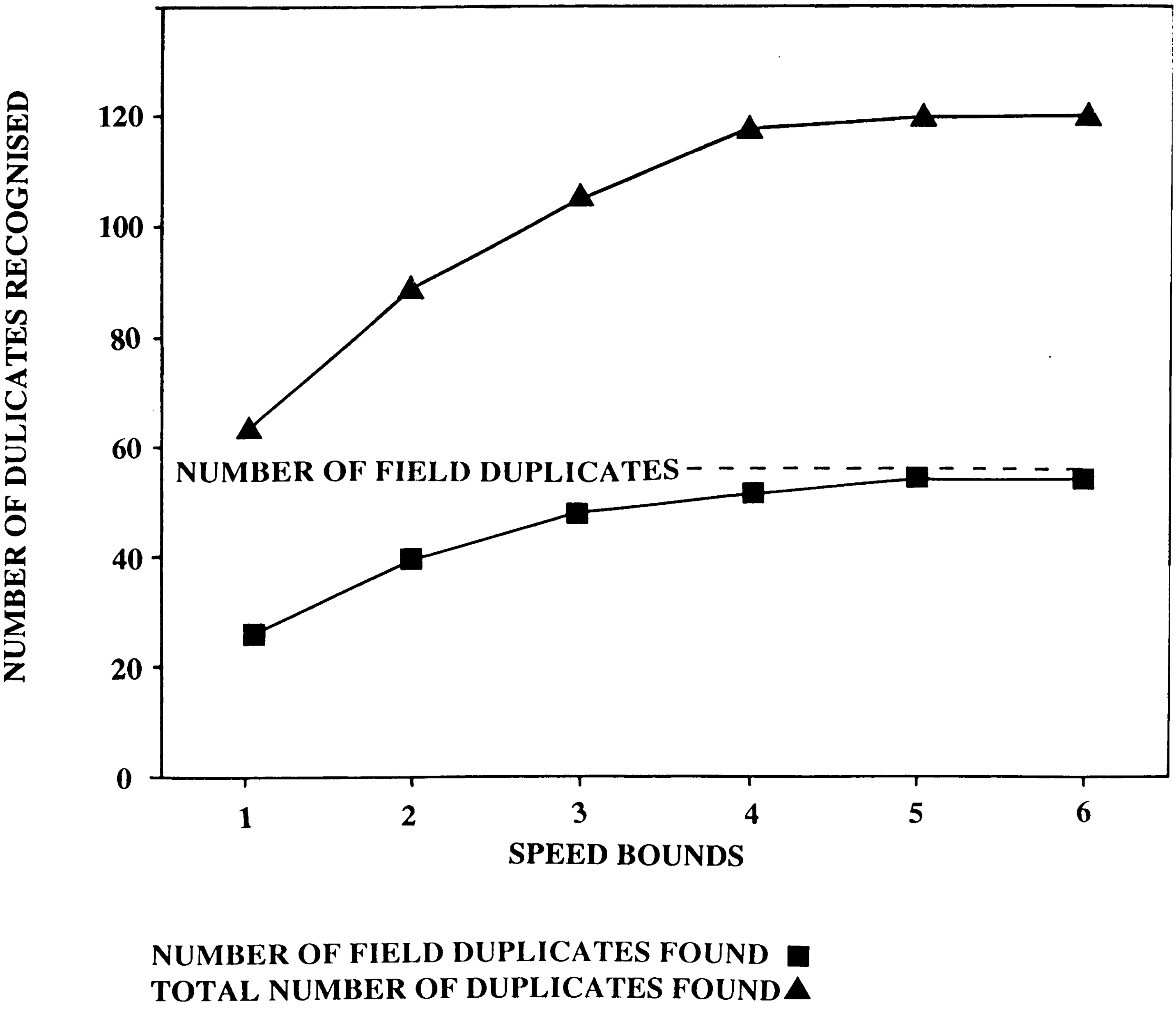


Figure 4.4(b) The number of duplicates and field duplicates found in the 1991 data by the matching programme at migration speed bounds at which the programme was run.

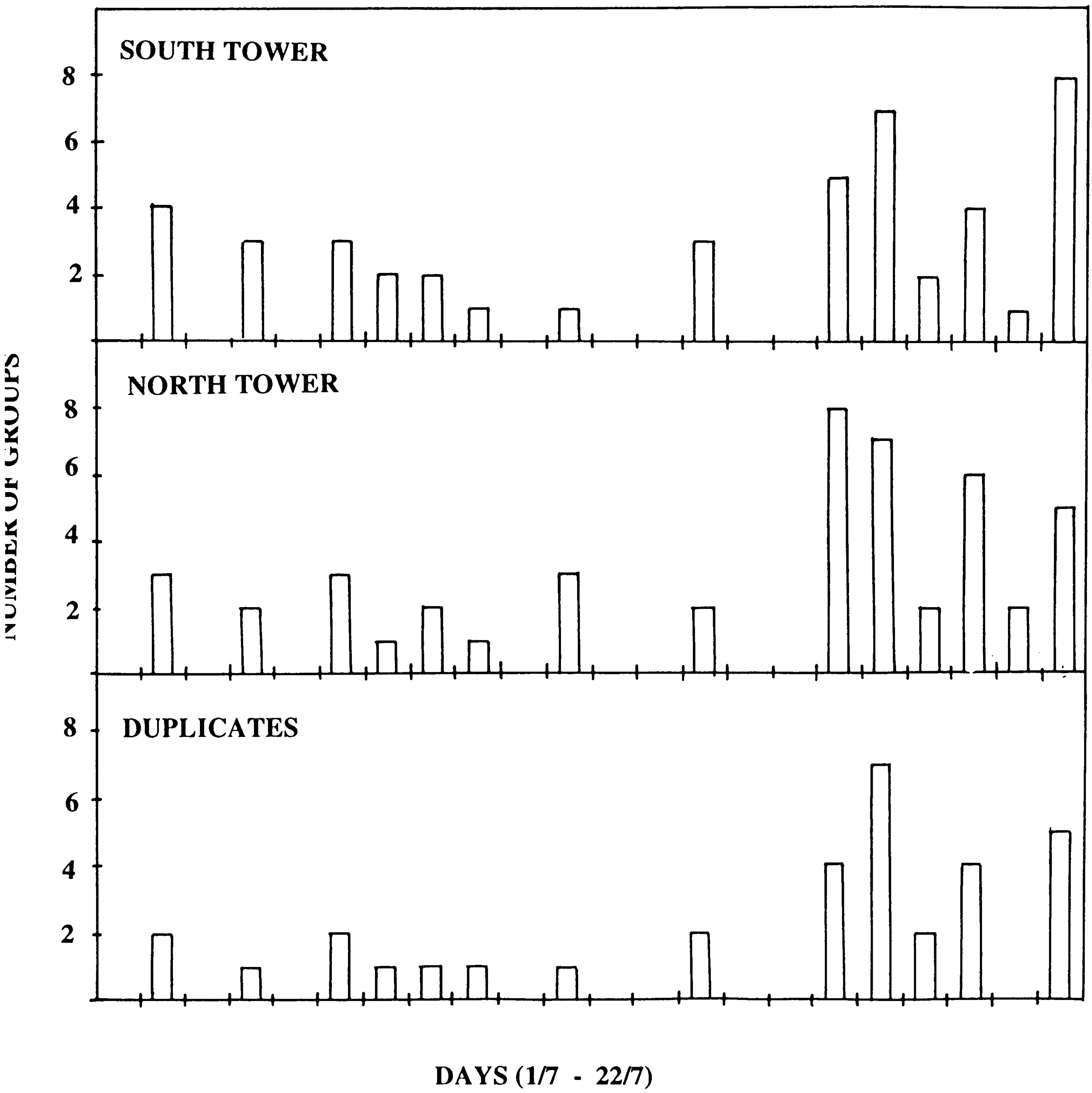


Figure 4.5(a) The number of independent sightings made by north and south towers and duplicate sightings made by both towers in independent observer surveys at Cape Vidal in 1990.

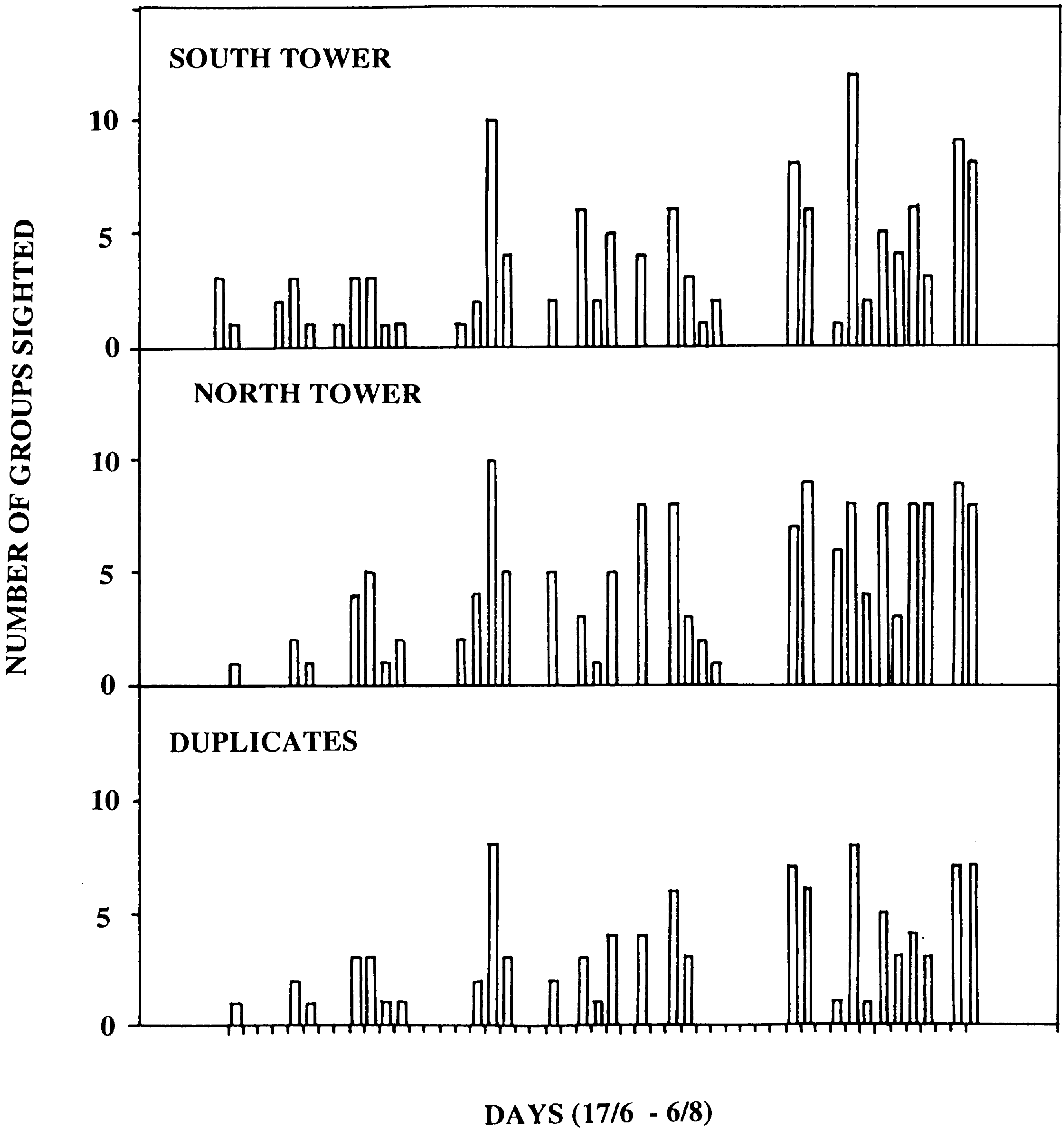


Figure 4.5(b) The number of independent sightings made by north and south towers and duplicate sightings made by both towers in independent observer surveys at Cape Vidal in 1991.

Table 4.1a. Independent sightings from the north and south towers, and duplicate sightings from both towers during independent observer surveys carried out at Cape Vidal in 1990 and 1991. Results are presented as both unstratified (UNSTR.) and stratified. Stratified results were divided into three distance intervals (NEAR = <3 km, MID = 3-6 and DIST > 6 km) from the shore, and three sighting condition intervals (POOR, FAIR and GOOD).

YEAR	STRAT.	NORTH	SOUTH	DUPL.	POP.	sd
1990	UNSTR.	46	47	33	65.35	3.19
1990	NEAR	28	30	20	41.81	2.72
	MID	10	10	10	10.00	0.00
	DIST	8	7	3	17.00	4.24
	TOTAL				68.81	
1990	GOOD	9	8	6	11.86	1.17
	FAIR	14	15	10	20.82	1.82
	POOR	23	24	17	32.33	2.02
	TOTAL				65.01	
1991	UNSTR.	132	159	96	218.38	7.23
1991	NEAR	42	69	29	99.33	7.49
	MID	59	66	51	76.31	1.83
	DIST	31	24	16	46.06	4.30
	TOTAL				221.70	
1991	POOR	34	46	23	67.54	5.38
	FAIR	60	75	47	95.58	3.87
	GOOD	38	38	26	55.33	3.28
	TOTAL				218.46	
1991	P/N	11	20	9	24.20	2.24
	P/M	13	18	10	23.18	2.10
	P/D	10	8	4	18.80	3.98
	F/N	19	32	12	49.77	6.25
	F/M	29	31	26	34.56	0.84
	F/D	12	12	9	15.90	1.18
	G/N	12	17	8	25.00	3.22
	G/M	17	17	15	19.25	0.55
	G/D	9	4	3	11.50	1.94
	TOTAL				222.16	
90/91	UNSTR.	178	206	129	284.02	7.95
90/91	NEAR	70	99	49	141.00	7.65
	MID	69	76	61	85.94	1.63
	DIST	39	31	19	63.00	6.05
	TOTAL				289.94	
90/91	GOOD	47	46	32	67.36	3.58
	FAIR	74	90	57	116.67	4.39
	POOR	57	70	40	99.44	5.45
	TOTAL				283.47	
90/91	P/N	25	37	20	46.05	2.94
	P/M	17	22	14	26.60	1.66
	P/D	15	11	6	26.43	4.69
	F/N	26	41	17	62.00	6.31
	F/M	33	36	30	39.58	0.86
	F/D	15	13	10	19.36	1.52
	G/N	19	21	12	32.85	3.42
	G/M	19	19	17	21.22	0.51
	G/D	9	6	3	16.50	3.97
	TOTAL				290.59	

Table 4.1b. The probabilities of sighting groups from the north (pn) and south (ps) towers, during independent observer surveys carried out at Cape Vidal in 1990 and 1991. Results are presented as both unstratified (UNSTR.) and stratified. Stratified results were divided into three distance (NEAR = 0-3 km, MID = 3-6 and DIST > 6 km) from the shore, and three sighting condition intervals (POOR, FAIR and GOOD).

YEAR	STRATIFICATION.	Pn	sd	Ps	sd
1990	UNSTR.	0.67	0.04	0.72	0.04
	NEAR	0.70	0.05	0.72	0.05
	MID	1.00	0	1.00	0
	DIST	0.47	0.16	0.41	0.14
	GOOD	0.76	0.09	0.67	0.08
	FAIR	0.67	0.07	0.72	0.07
	POOR	0.71	0.05	0.74	0.05
1991	UNSTR.	0.60	0.02	0.73	0.02
	NEAR	0.42	0.03	0.69	0.05
	MID	0.77	0.02	0.86	0.02
	DIST	0.67	0.07	0.52	0.05
	POOR	0.50	0.04	0.68	0.06
	FAIR	0.63	0.03	0.78	0.03
	GOOD	0.69	0.04	0.69	0.04
	P/N	0.45	0.05	0.83	0.07
	P/M	0.56	0.06	0.78	0.08
	P/D	0.53	0.15	0.43	0.12
	F/N	0.38	0.05	0.64	0.09
	F/M	0.84	0.02	0.90	0.02
	F/D	0.75	0.07	0.75	0.07
	G/N	0.48	0.07	0.68	0.10
	G/M	0.88	0.03	0.88	0.03
	G/D	0.78	0.20	0.35	0.08
90/91	UNSTR.	0.63	0.02	0.73	0.02
	NEAR	0.50	0.03	0.70	0.04
	MID	0.80	0.02	0.88	0.02
	DIST	0.62	0.06	0.49	0.05
	GOOD	0.70	0.04	0.68	0.04
	FAIR	0.63	0.02	0.77	0.03
	POOR	0.57	0.03	0.70	0.04
	P/N	0.54	0.04	0.80	0.06
	P/M	0.64	0.04	0.83	0.06
	P/D	0.57	0.12	0.42	0.09
	F/N	0.42	0.05	0.66	0.07
	F/M	0.83	0.02	0.91	0.02
	F/D	0.77	0.07	0.67	0.06
	G/N	0.58	0.07	0.64	0.07
	G/M	0.90	0.02	0.90	0.02
	G/D	0.55	0.18	0.36	0.12

Combined 1990 and 1991 sightings have been stratified by two of the four factors which influence the detectability of a group, distance from the shore and sighting conditions. Resulting sighting probabilities are presented in Figure 4.5. Sighting probabilities were highest in the mid-distance interval, with lower probabilities recorded in both the nearshore and offshore distance intervals. The low nearshore sighting probabilities may well result from the nearshore groups passing through a narrower visual cone than the mid-distance groups, and from the tendency for observers to search more offshore. The low offshore sighting probabilities result from both a) distant groups being less conspicuous than close groups, and b) distant groups making a shorter passage through the field of view than mid-distant groups, as the limit of visibility within the field of view is in fact a semi-circle.

Stratification of the combined 1990 and 1991 data by sighting conditions showed the south tower to have fairly constant sighting probabilities in all conditions (Figure 4.6). North tower, however, showed a slight decrease in sighting probability as sighting conditions deteriorated. This disparity between towers may arise from south tower having a better view of the nearshore region to the south, where the majority of sightings was made during inclement weather. This is further evident when the data are stratified by both distance and sighting conditions, when the nearshore sighting probabilities from the south tower were highest during poor sighting conditions.

Comparison of the results from the two towers suggests that the south tower has higher probabilities of sighting groups in the nearshore and intermediate distance intervals and a lower probability of sighting distant groups than the north tower. Hiby and Hammond (1989) note that problems arise in independent observer trials when observers allocate effort to different regions or distance intervals. The differences in sighting probabilities recorded suggest that the south tower observers spent more effort searching the nearshore region than north tower observers. Although both towers have an equal nearshore area within view, the north tower nearshore view largely lay to the north, while the south tower nearshore view lay to the south. Observers possibly spent more effort searching to the south, the direction from which whales migrate at this time of the year, and consequently south tower observers may have spent more effort searching the nearshore distance interval. Furthermore, glare to the north in the morning may have discouraged north tower observers from searching the nearshore region.

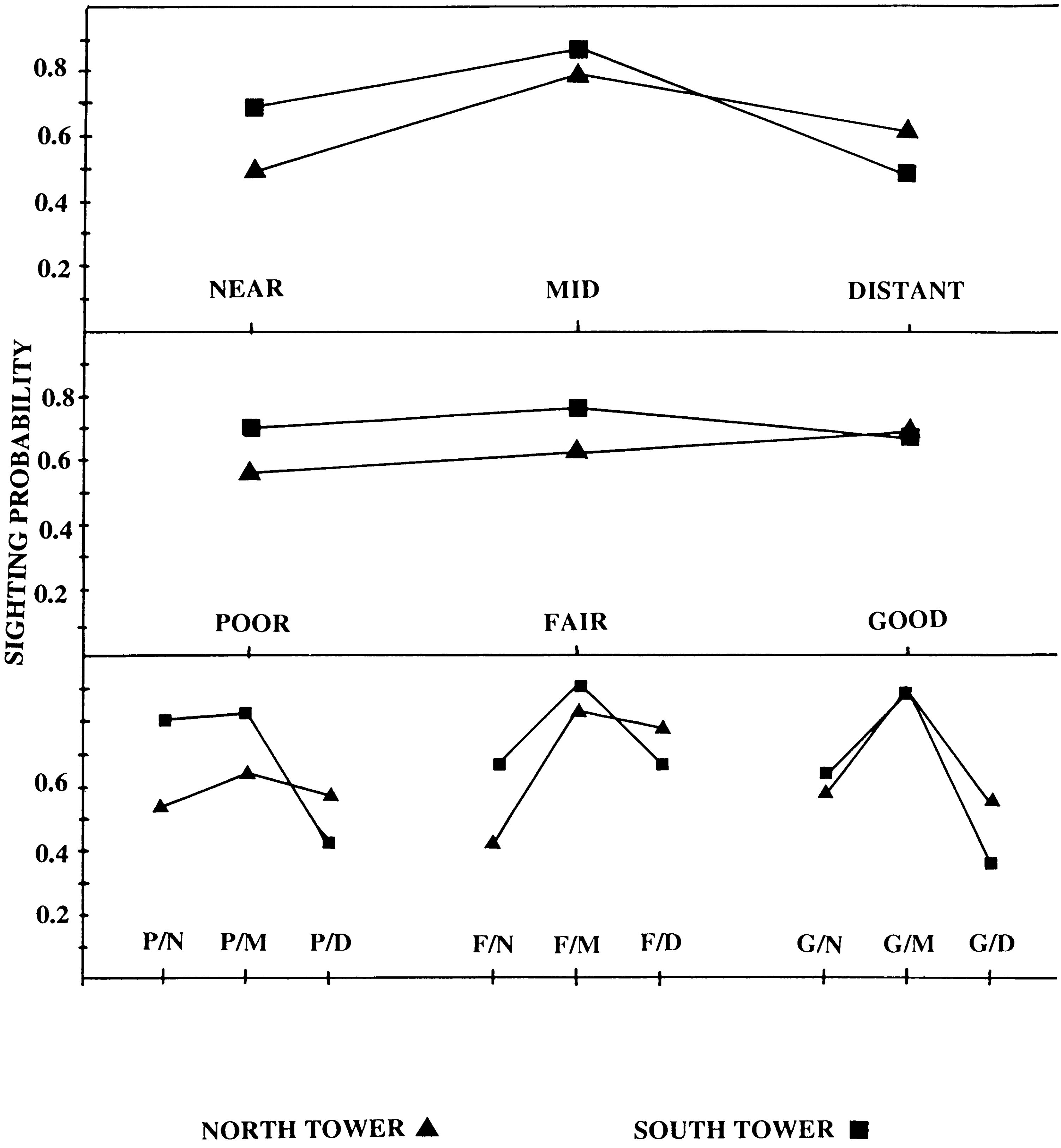


Figure 4.6 Sighting probabilities calculated from results of independent observer surveys at Cape Vidal in 1990 and 1991.

Stratification by group size is more difficult in that groups may be estimated as different sizes from the two towers. Nevertheless, the percentage of groups of one, two and more than two whales that were sighted as duplicates (Table 4.2) show smaller groups to have a higher probability of being missed than larger groups on both towers. However group size estimates were refined at each fix, and results from chapter 3 have shown that the sizes of groups for which less than two fixes were taken were often underestimated. As groups with few fixes may have lower sighting probabilities, the sighting probabilities of small groups (which include a component of underestimated larger groups) may also be biased downwards.

Table 4.2. The proportion of duplicates among groups of different sizes as seen from north and from south tower.

TOWER		GROUP SIZE		
		1	2	>2
NORTH	ALL	55	54	23
	DUPL.	33	41	22
	%	60	75	95
SOUTH	ALL	71	62	26
	DUPL.	40	37	19
	%	56	59	73

The fourth factor affecting sighting probability is whale behaviour. The extent and duration of surface-active behaviour, particularly breaching or tail slapping which produces splashes, plays a large role in the conspicuousness of the group. However, the quantification of whale behaviour (or cue patterns) is compounded by three factors, namely :-

1) objectively sampling cue patterns and assigning behaviours to strata is difficult.

2) the cue patterns produced by a single group may not be constant throughout the visible period and thus a group's detection probability could vary with time.

3) the cues have different detection probabilities with distance from the observer, or under different sighting conditions.

Accurate quantification of group behaviour would essentially require cue-counting, as undertaken on some IDCR minke whale assessment cruises (Ward and Hiby 1987), throughout the period the group is within visible limits.

Such cue-counting would be impractical at Cape Vidal, given that a number of groups may pass through the survey period at one time, so that it would seriously interfere with searching effort.

DISCUSSION

Land-based visual surveys of humpback whales off the east coast of Australia (Bryden 1985, Bryden *et al.* 1990, Paterson and Paterson 1984, 1989, Paterson 1991) have assumed that all whales within a 10 km wide strip from the shore, were detected. Although Bryden *et al.* (1990) make no estimation of the population size, they noted that weather and sea surface conditions affected the sightability of the whales, and assumed the proportions sighted each year were similar because weather conditions were similar between years.

Rugh *et al.* (1990) found that 21 % of gray whales within the study area were missed by observers, although they suggest this was biased downwards by excessive matching during peak density periods when a greater number of duplicates could be scored. They conclude that estimates of gray whale population size made through land-based visual surveys without taking the proportion missed into consideration, will underestimate the population. Rugh (1984) estimated that 19 % of gray whales were missed by observers at Unimak Pass, Alaska. Krogman *et al.* (1989) found 30 % of bowhead whales to be missed by observers at their primary observation site at Pt. Barrow, Alaska. Rugh and Dahlheim (1990) suggest that the higher proportion of bowhead whales missed compared to gray whales results from the lower elevation of the observation sites from which bowhead whales are surveyed, as well as the longer dive profiles of bowhead whales and the ice conditions through which they migrate.

Hiby and Hammond (1989) note that one of the major differences between shore-based surveys and random shipboard surveys is that the distribution of whales cannot be considered uniform with respect to the observer in shore-based surveys. The distribution of groups with distance from the shore in all surveys at Cape Vidal between 1988 and 1991 (Figure 4.7) shows the modal distance offshore to be in the region of 2-3 km, with lower densities recorded inshore of this. Given the expectation that sighting probability should decline progressively with distance from the coast, the distribution inshore of the mode could be assumed to reflect some avoidance of the extreme inshore region by the whales. However, results show that the sighting probability does not decline with distance from the shore, as originally expected, but in fact increases from the nearshore (< 3 km) to the intermediate (3-6 km) distance interval before declining again offshore. Rugh *et al.* (1990) found that gray whale sighting probabilities were lower in both close-to-the-shore and offshore intervals, than in intermediate distance intervals and ascribed this to the smaller sighting cues provided by offshore groups and to the narrow angular viewing area through which inshore whales must pass. However, distant groups not only provide smaller sighting cues than closer groups, but given that the outer limit of visibility is in fact a radius from the observer, they must pass through less of the survey area than closer groups. Therefore some difference in sighting probabilities must result regardless of any difference in other detection probabilities with distance from the observer.

Although increased sighting probabilities as sighting conditions improved would be expected, the results show a fairly constant and only a slight increase in probabilities from the south and north towers respectively. This may well result from increased surface activity by the whales with increasing sea state or wind speeds, as there appeared to be an increase in breaching behaviour in northerly winds during the northward migration at Cape Vidal, and little surface - active behaviour was apparent when the sea state was very calm (Findlay, pers. obs.). Best (1982) notes the difficulty in sighting minke whales in Antarctic waters when conditions are calm.

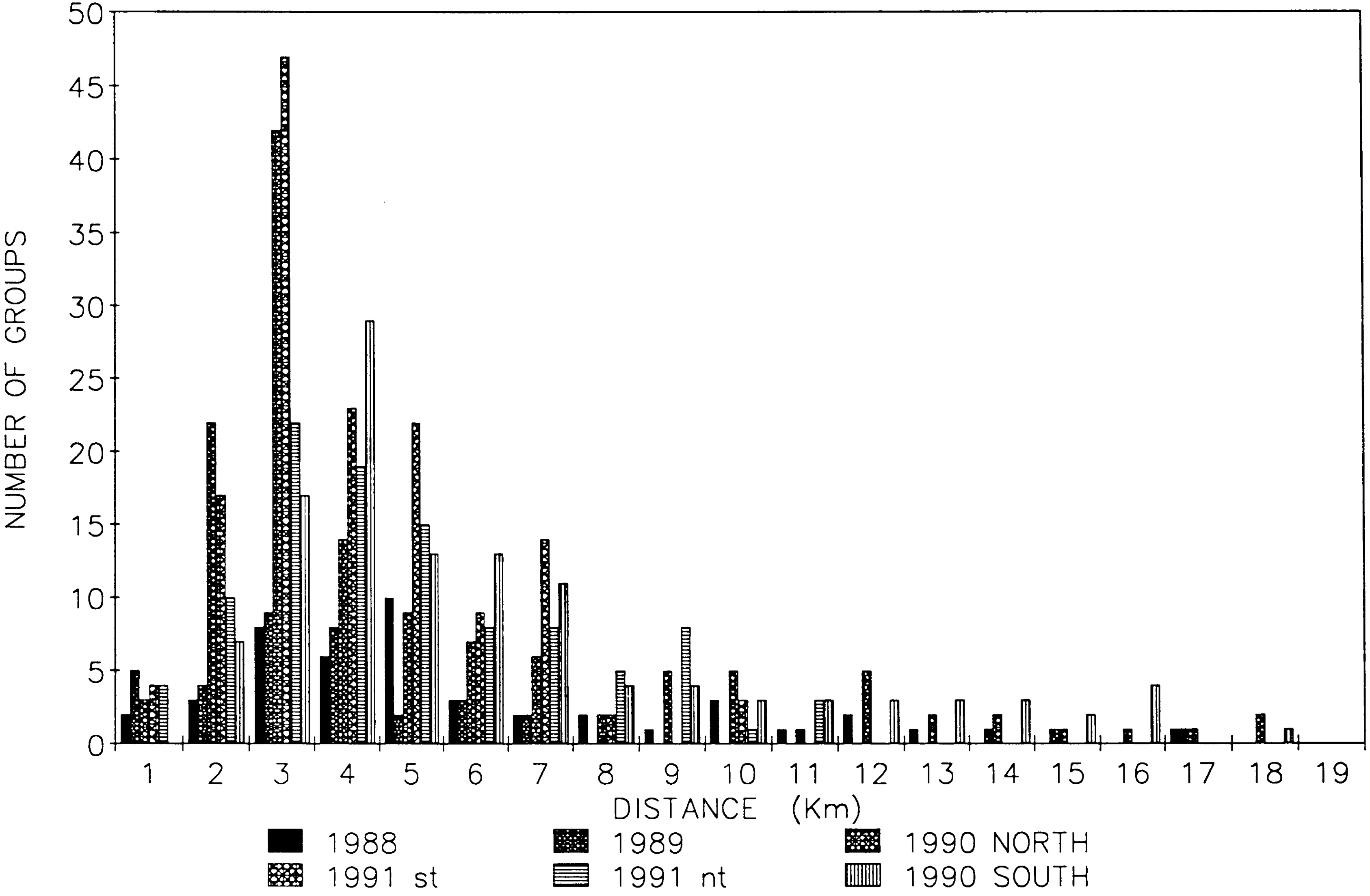


Figure 4.7 The distribution of groups with distance from the coast in surveys off Cape Vidal between 1988 and 1991.

The use of mark-recapture methodology to determine sighting probabilities requires that all groups must have equal probabilities of being sampled at either or both the first and second sampling events (Seber 1982). Heterogeneity in sighting probabilities results in the sighting of a group from the two platforms being conditionally independent rather than unconditionally independent (Schweder 1990). Stratification of data into intervals of more equal sighting probabilities reduces the conditional independence, although it does not circumvent the problem entirely, as sample size limitations necessitate stratification over a probability range. All four factors affecting sighting probabilities (whale behaviour, distance from the observer, sighting conditions, and group size) need to be taken into consideration when estimating population sizes. Each of these factors is compounded by the others. For example, under equal sighting conditions, a surface active, small and distant group may be more conspicuous than an inactive, larger group closer inshore. The conflict between stratification and sample size could be overcome through stratification by only one combined detection-probability factor, based on the conspicuousness of the group and taking all four factors into consideration. However, quantification of behaviour is difficult, time-consuming and subjective, especially so in humpback whales where a wide range of behaviours is evident during the migration.

The determination of population increase rates through comparison of inter-year counts requires that an equal proportion of the population is sighted each year. Failure to take sighting probabilities into consideration will reduce precision if such probabilities are not constant between years, and could introduce bias if there is a trend with time in any of the probabilities. Although sighting heterogeneity arising from whale behaviour has not been taken into consideration in this study, and thus the proportion missed is underestimated, whale behaviour is assumed to be constant between years, so that the resultant population estimates could potentially be used to examine trends.

CHAPTER 5

ESTIMATES OF THE NUMBERS OF HUMPBACK WHALES OBSERVED MIGRATING PAST CAPE VIDAL, SOUTH AFRICA, 1988-1991.

INTRODUCTION

An estimate of the pre-exploitation size of the southern hemisphere humpback whale population is between 90 000 and 100 000 with the Area III stock probably numbering less than 25 000 individuals (Chapman 1974). Catches of southern hemisphere humpback whales since the beginning of the century were heavy, and can be divided into three phases (Tonnesen and Johnsen 1982). The first of these, the pre-1917 coastal fisheries, was largely centred in the Falkland Dependencies (1904/1905 to 1916) and off the coast of southern Africa (1908 to 1917), with smaller fisheries in Australia and New Zealand (1912 to 1916). The second era, the Antarctic pelagic fishery, arose in the summer of 1923/1924, but by 1938 catches were regulated, and from 1953/1954 to 1962/1963 humpback whaling in the southern ocean was limited to four days per year. The third era, the post 1942 coastal fishery was largely centred in Australian and New Zealand waters. Humpback whaling officially ceased in the southern hemisphere in October 1963 and catches in these three eras amounted to approximately 43 000, 28 000, and 22 000 humpback whales respectively (Committee for Whaling Statistics, 1942-1964, Omura 1973, Chittleborough 1965), although catch statistics for the first era must be considered unreliable, and few records were reported for the second era prior to 1930.

Chittleborough (1965) estimated the population size of humpback whales in the southern hemisphere after 1938-1939 as approximately 22 000 to 34 000 individuals, and by application of Mackintosh's (1951 in Chittleborough 1965) relative abundance estimates, the Area III population would have comprised 4 400 to 6 800 individuals at this time. Winn and Reichley (1985) tabulated an African east coast population size of 340 individuals at the end of exploitation, although the source data for this estimate is not given.

Catches of humpback whales in Mozambique coastal waters between 1910 and 1915 (3157 whales), and south of Madagascar between 1937 and 1938 (2975 whales) and between 1949 and 1950 (2044 whales) (Committee for Whaling Statistics 1942-64) identified these areas as the principal breeding ground(s) in the western Indian Ocean, although the degree of interchange of individuals between these grounds is unknown. Although no links have been established between the Mozambique ground and an Antarctic feeding ground, the whales migrating to and from this breeding ground utilise Natal coastal waters as a migratory corridor (Olsen 1914), a factor which resulted in them being vulnerable to shore-based catches.

Increasing numbers of incidental sightings on the South African east coast between 1983 and 1987 suggested that the population utilising this migratory corridor was staging a recovery. The orientation of the northern Natal coastline to the general direction of the migration during the northward migration, compels whales to move in a north easterly direction in a narrow migration stream parallel to the coast, and the proximity of this migration stream to the coastline results in the migrating population being ideally suited to shore-based visual monitoring of its population size and demographic trends. Similar shore-based monitoring of migrating whales has been used to estimate the sizes of a number of stocks, including Californian gray whales (Rugh and Braham 1979, Reilly, Rice and Wolman 1980, 1983, Reilly 1984, Rugh 1984, Rugh, Ferrero and Dahlheim 1990, Buckland, Breiwick, Cattanach, and Laake 1993), bowhead whales (Zeh, Ko, Krogman and Sonntag 1986a, 1986b, Gentleman and Zeh 1987, Krogman, Rugh, Sonntag, Zeh and Ko 1989) and Australian humpback whales (Paterson and Paterson 1984, 1989, Bryden 1985, Bryden, Kirkwood and Slade 1990, Paterson 1991).

Reviews of the methodology used in shore-based visual surveys have been provided by Reilly *et al.* (1983), Reilly (1984), and Hiby and Hammond (1989). In this chapter counts of humpback whales at Cape Vidal, northern Natal, South Africa, between 1988 and 1991 are used to obtain an estimate of the size of the population passing within view of the coast.

METHODS AND MATERIALS

Field methods

Shore-based visual monitoring of humpback whale migrations has been undertaken between 1988 and 1991, at Cape Vidal (28° 07' S 32° 33' E) on the northern Natal coast. Observations were carried out for either ten or five hours per day (Table 5.1). The ten-hour observation periods were carried out continuously from 07h00 to 17h00 (weather permitting), while the five hour periods were carried out as two 2.5 - hour shifts, one each in the morning and afternoon (weather permitting). Observations were discontinued when part of the survey region was obscured by rain, when the wind speed was greater than 25 knots, or visibility was less than 5 km. As results obtained in the 1988 and 1989 surveys suggested a proportion of groups was being missed by observers, independent-observer surveys were carried out during July 1990, and for the entire 1991 survey (see chapter 4).

Table 5.1. Duration of surveys and observation regimes carried out at Cape Vidal between 1988 and 1991. (Independent obs. = Independent observations carried out from two towers.)

YEAR	DATES	OBSERVATION REGIME
1988	4 July-22 July	10 hours per day
1989	27 June - 22 July	10 hours per day
1990	2 June - 30 June	5 hours per day
1990	1 July - 22 July	10 hours per day (Independent obs.)
1990	23 July - 15 Sept.	5 hours per day
1990	16 Sept. - 15 Oct.	10 hours per day
1990	15 Oct. - 28 Oct.	5 hours per day
1991	17 June - 6 Aug.	10 hours per day (Independent obs.)

Observations were carried out from an approximately 60 m high vantage point on a headland. A timber tower erected in 1988 (designated the south tower) provided a 185 degree field of view from a height of 61.5 m. The horizon was approximately 23 km distant, although whales were not sighted further than 20 km from the tower. A second timber tower (designated the north tower) was erected 22 m to the north of the south tower at the start of the 1990 survey, and provided a vantage point 60.3 m above sea level and with a 190 degree field of view. The two towers were visually and acoustically isolated from each other by coastal dune forest.

Observations were carried out by two observers on each tower at all times, and both observers searched the entire field of view. When possible, at least one of each pair of observers had some previous experience in sighting and identifying whales. Generally one observer searched with 7 x 35 wide angle binoculars, while the other searched with the naked eye, and roles were changed approximately every 15 minutes. Once sighted, whales were tracked by using a Wild T1 or T1A theodolite to take fixes of horizontal and vertical angles of successive bouts of surface-active behaviour. During tracking, one observer took fixes while the second recorded these on data forms so that searching of the field of view was reduced during tracking. Positions of whales were also plotted onto charts which permitted error-checking of fixes, discrimination between closely migrating groups, and also provided some reference point as to where the whales would next surface. Angles were measured to the nearest 20 seconds in 1988 and 3 seconds in subsequent years, and time was measured to the nearest second, with timepieces being synchronised on both towers.

Both search effort and weather records were kept during all observation periods. The times of all changes of search activity (eg. start searching, sighting confirmation) were noted on the search effort record. Weather conditions (wind speed and direction, cloud cover, sea surface state (Beaufort), swell, visibility (measured as the limit of visibility through the theodolite), and a subjective index of "sightability" (taking all weather conditions into consideration) were noted at hourly intervals, along with the number of boats and ships within visibility limits.

Group sizes were estimated during each fix, and thus a series of fixes produced a refinement of the estimated group size. Group size estimates were confirmed through interception by ski-boat, although this was subject to ski-boat availability and weather conditions (see chapter 3). Exemption for this work was granted in terms of the South African Sea Fishery Act (no. 58 of 1973) and the Fishery Act (no. 12 of 1988). To avoid the boat providing a cue to the presence of whales during independent-observer surveys, both towers independently reported all groups to tertiary observers by radio, who only intercepted sightings they deemed as duplicates.

Analyses

Analysis of field counts

Results were entered into a computer database and analysed on completion of the field season. Each sighting was analysed by a BASIC application programme which translated horizontal and vertical angles into distances and bearings from the observer, and subsequently to co-ordinates on a cartesian plane, taking both the curvature of the earth and a refraction correction factor into consideration. The algorithm is given in Appendix I. Furthermore, this programme calculated the migration speed and heading of each group of which more than two fixes were taken, from the position and time difference between the first and last definite fix. Distance offshore of each group was calculated as the distance between the mean position of the group and the shore directly to the west of it.

Due to observations only being possible during daylight hours, daily densities had to be calculated by extrapolating from the number of groups sighted during periods of watch each day. Consequently to be included in the calculations of daily density, groups must have crossed the midline of the observation area within the period of observation. Groups that were not seen to have crossed the midline of the observation area, were projected forwards or backwards at their measured speed and bearing, and the time of the projected crossing was calculated. Such groups were included in the daily density if the time of their projected cross fell within an observation period. Groups of less than three fixes that were not seen to cross the midline were similarly projected but at the mean migration speed and direction of that year, while groups of indeterminate direction were apportioned to the total on a *pro rata* basis of groups scored to cross (or projected to cross) northwards or southwards of all groups seen on that day.

Mean daily sighting conditions were calculated from hourly sighting conditions recorded on the south tower.

Verification analyses

Five aspects require quantification to obtain accurate estimates of population size from shore counts of migrating whales (Reilly *et al.* 1983, Reilly 1984 and Hiby and Hammond 1989, Buckland *et al.* 1993). These are :-

1. The proportion of the population passing beyond observer visibility limits must be estimated through an independent survey run concurrently with the shore-based survey.

2. Whales passing the observation region before or after the survey also have no probability of being detected, and must be taken into consideration.

3. Detection probabilities vary with *inter alia,* distance and sighting conditions, and the consequent heterogeneity in sighting probabilities within the survey area must be taken into consideration. Although not noted by Reilly *et al.* (1983), Reilly (1984), Hiby and Hammond (1989) or Buckland *et al.* (1993) whale behaviour and group size may further compound detection probabilities. However, these detection probabilities would be extremely difficult to quantify.

4. Observer accuracy and precision must be constant throughout surveys.

5. Observations (outside of summer observations in polar regions) can only be conducted throughout daylight hours. Daily totals must therefore be extrapolated from daylight densities, and the assumption that the diel migration rate is constant must hold.

RESULTS

The total observation effort undertaken and number of sightings made each year are presented in Table 5.2. All observation effort has been assumed to be of equal intensity, and times during which whales were tracked have been included as full observation effort. Any density dependent bias arising from this inclusion is thought to be negated by increased observer awareness during tracking. The distribution of daily observation effort undertaken each year is shown in Figures 5.1(a) and (b).

Table 5.2. Observation effort undertaken and number of humpback and other whales sighted in 1988, 1989, 1990 and 1991. The 1990 and 1991 data are presented separately for the north (nt) and south (st) towers. Other whales include minke and southern right whales.

YEAR	OBSERVATION EFFORT	WHALES OBSERVED Groups (individuals)			
	Hours	Humpback	Other (R = southern right whale; M = minke whale)		Unidentified
			R	M	
1988	166	46 (115)	0 (0)	0(0)	17 (31)
1989	199.5	44 (91)	1 (2)	0 (0)	14 (20)
1990 nt	155.9	57 (120)	0 (0)	1 (1)	21 (34)
1990 st	618.25	291 (525)	3 (6)	2 (4)	89 (119)
1991 nt	361	139 (264)	1 (1)	0 (0)	51 (70)
1991 st	363	126 (254)	1 (1)	2 (3)	105 (154)

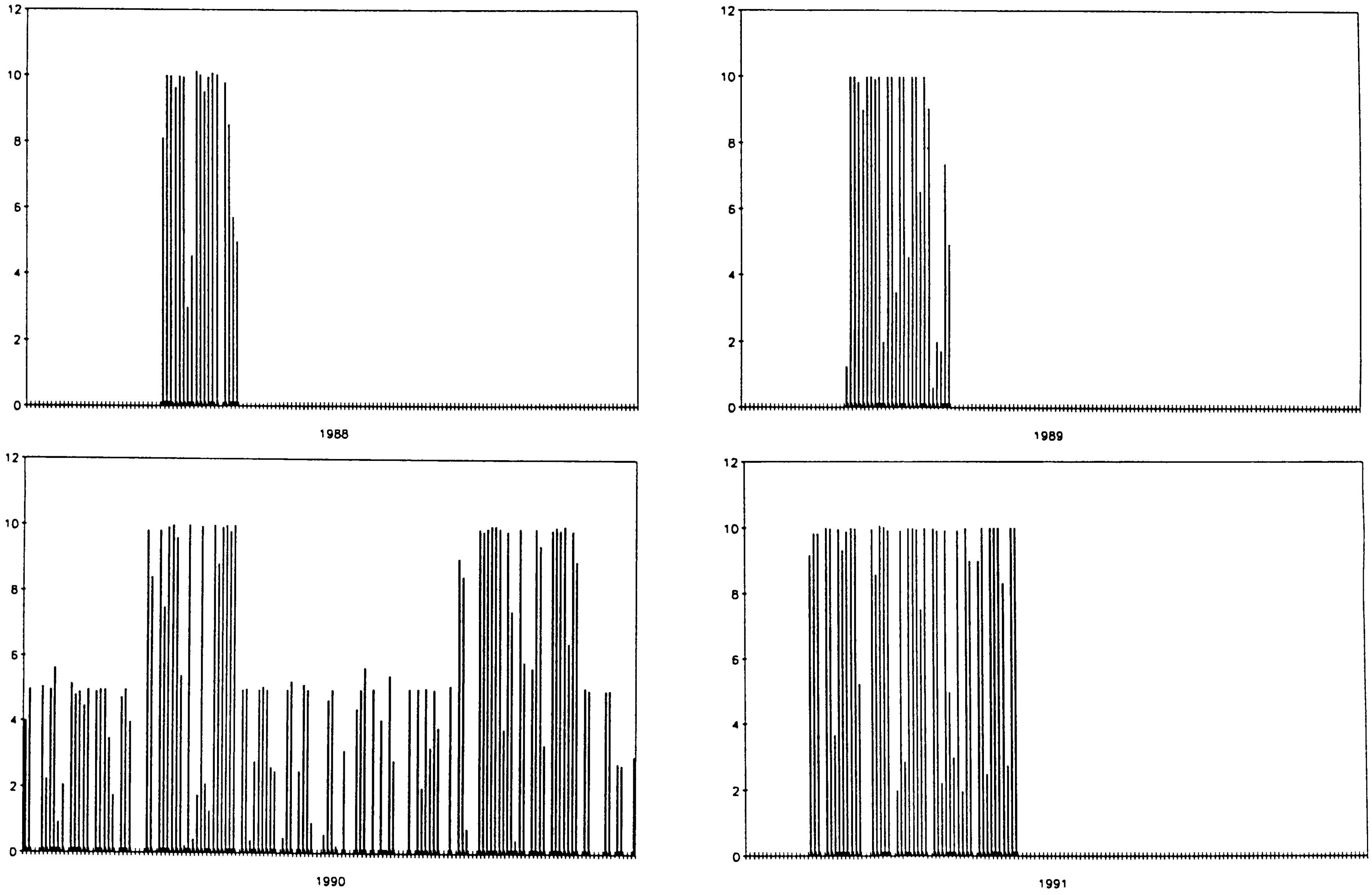


Figure 5.1(a) Daily observation effort (hours) carried out from the south tower at Cape Vidal between 2 June and 28 October in 1988, 1989, 1990 and 1991.

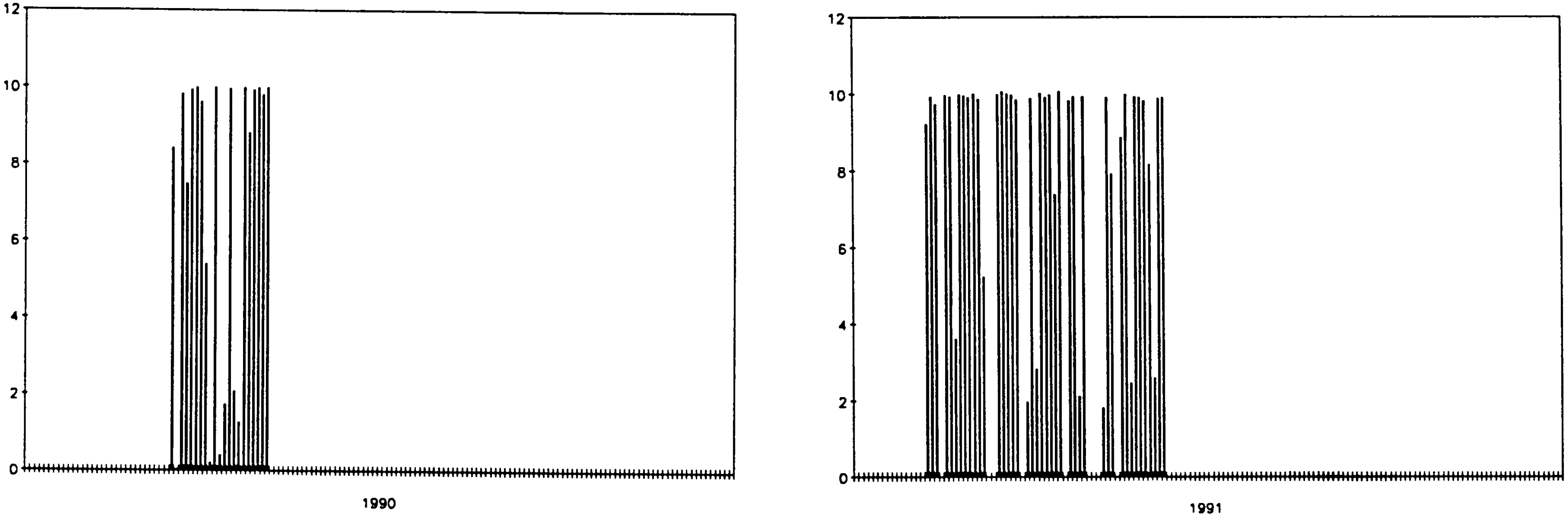


Figure 5.1(b) Daily observation effort (hours) carried out from the north tower at Cape Vidal between 2 June and 28 October in 1990 and 1991.

Totals of the number of groups ($n_{d,i}$) crossing the midline of the survey area each day (d) in each of three perpendicular distance intervals (i) were tallied.

$n_{d,i}$ for i = 1 (0-2.99 km from the coast)
2 (3.0-5.99 km from the coast)
3 (> 6.0 km from the coast

The proportions of groups missed by observers in each of the three perpendicular distance intervals (i) in three weather condition strata (w) were calculated in chapter 4.

$p_{w,i}$ for w = 1 (poor weather conditions) and i = 1, 2, 3 (as defined above)
2 (fair weather conditions) and i = 1, 2, 3 (as defined above)
3 (good weather conditions) and i = 1, 2, 3 (as defined above)

Daily tallies of the number of groups seen in each distance interval were adjusted for proportions missed in each distance interval under the weather condition of the day to produce adjusted tallies in each distance interval ($a_{d,i}$)

$$a_{d,i} = n_{d,i}(1 + p_{w(d),i}) \qquad (1)$$

Adjusted counts in each of the three distance intervals were summed and divided by the observation effort of that day (e_d) to give estimated densities (J_d)of groups per hour

$$J_d = \left(\sum_{i=1}^{3} (a_{i,d})\right) / e_d \qquad (2)$$

Estimated densities of groups crossing the midline per hour of observation were multiplied by 24 to produce daily densities (D_d).

$$D_d = J_d \cdot 24 \qquad (3)$$

Extrapolation of hourly densities to daily densities assumes that the migration rate is constant throughout the day. The frequencies of migration speeds recorded each year (Figure 5.2) compare favourably with migration speeds recorded over larger distances and longer time periods through mark returns (Chittleborough 1953, 1965, Dawbin 1956). Furthermore, no significant difference was found between the mean migration speed recorded each hour during the day (chapter 3). The assumption of a constant migration rate at day and night therefore seems reasonable.

Densities of individuals per day (I_d)were calculated as the product of daily group densities and the mean group size observed in that year (s).

$$I_d = D_d.s \qquad (4)$$

No difference was found between group sizes estimated from the tower and confirmed through interception (chapter 3), although there was some underestimation of the size of groups on which two or fewer fixes were taken. Consequently, only groups on which more than two fixes were taken were included in the estimation of mean group size. The frequencies of such groups recorded in the northward migration in all years and in the southward migration in 1990 are shown in Figure 5.3 along with the associated mean group sizes. Although a significant difference was found between mean group sizes recorded between years, no difference was found in mean group size by migration wave (chapter 3). Consequently the mean group size recorded each year has been used in calculating the daily densities of individuals for that year.

The number of whales observed migrating northwards past Cape Vidal (N) each year have been calculated through summation of the daily densities recorded for each day of each survey,

$$N = \sum_{d=1}^{h} (I_d) \qquad (5)$$

where h is the length of the survey in days.

The calculation of a cv for the 1991 south tower estimate has been carried out by bootstrapping each

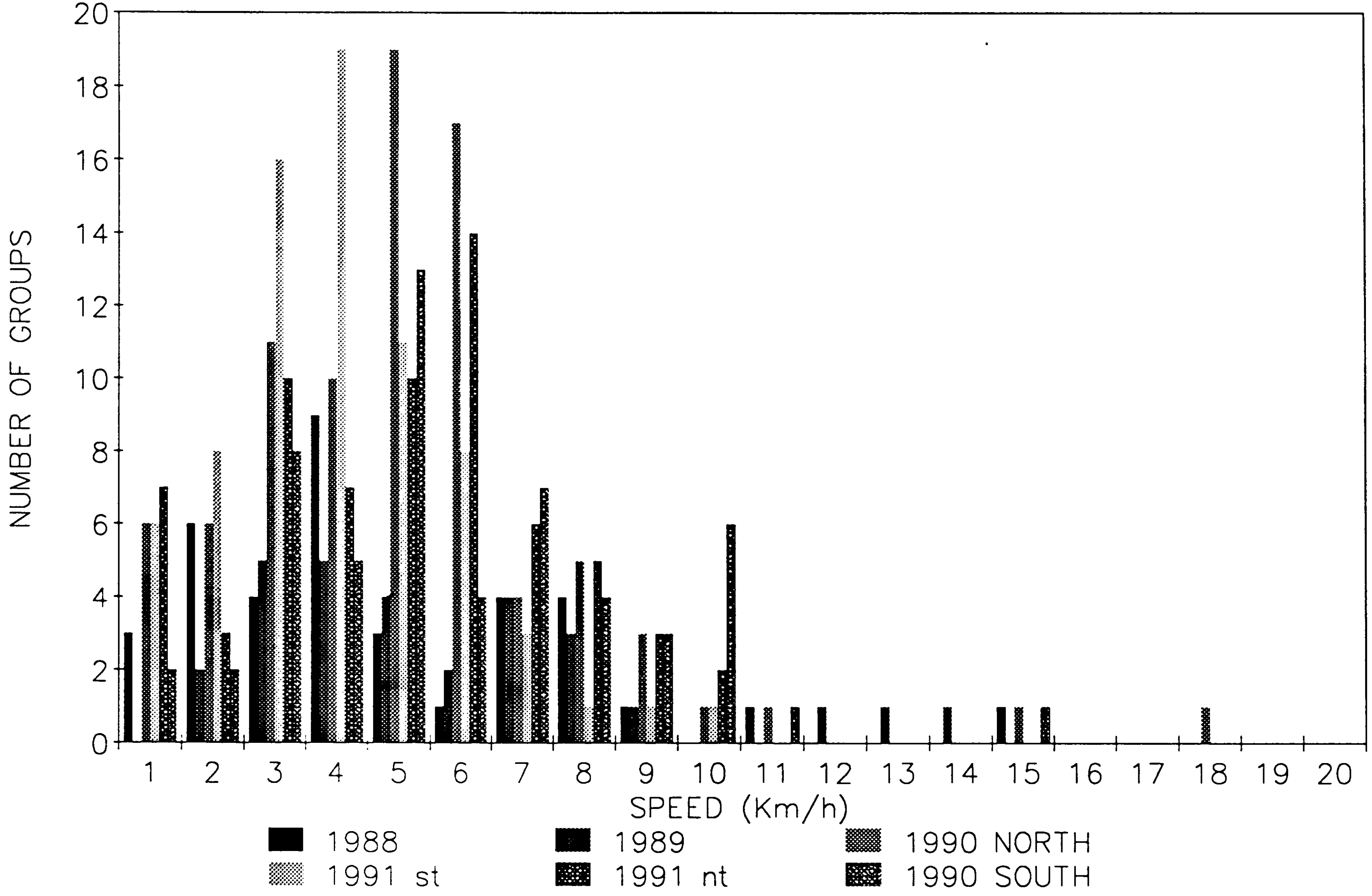


Figure 5.2 Distribution of swimming speeds for groups migrating past Cape Vidal each year between 1988 and 1991.

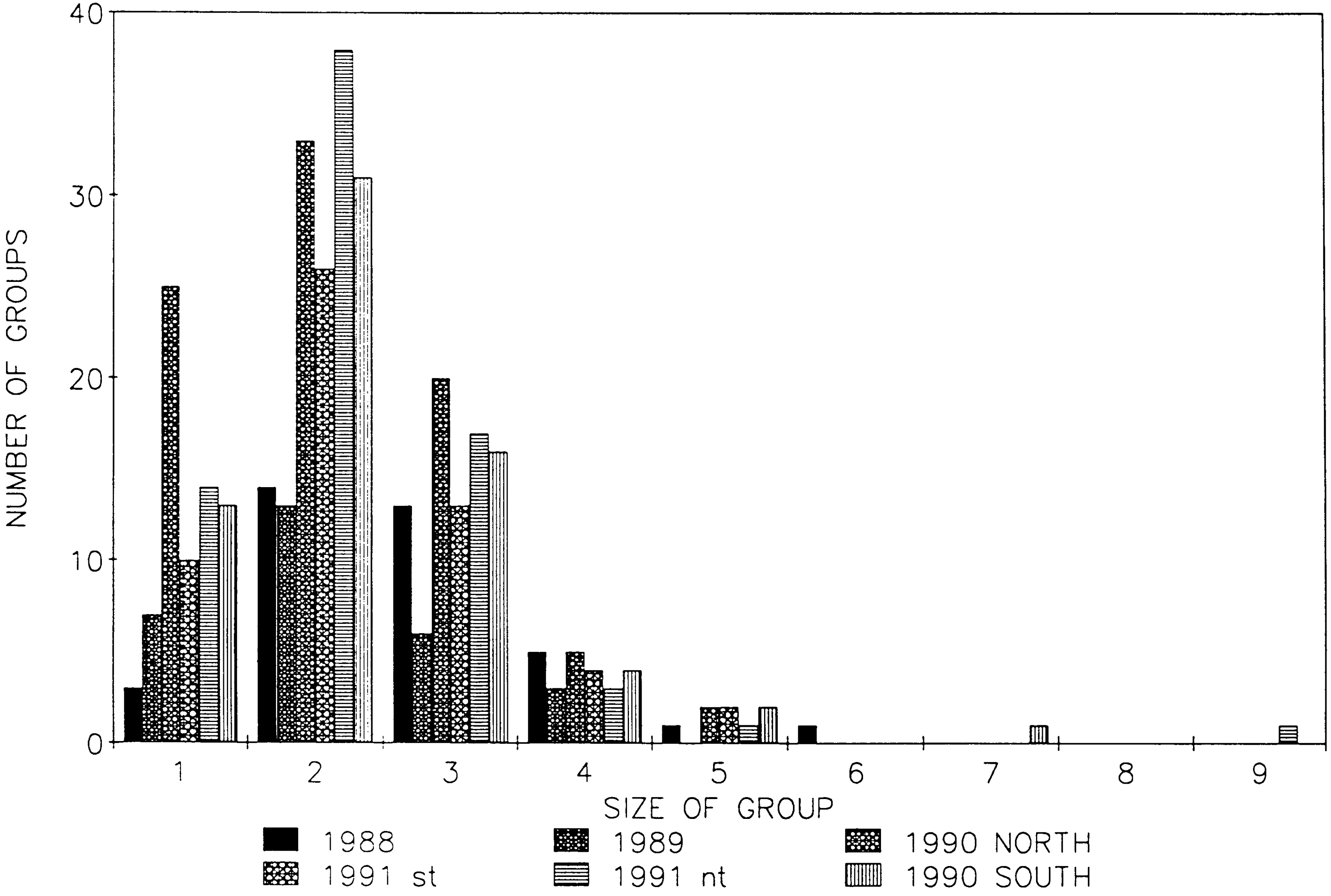


Figure 5.3 Frequencies of the sizes of groups recorded migrating past Cape Vidal between 1988 and 1991.

individual day's data (number of groups seen by each tower and by both towers in each of three distance bins, observation effort, and number of groups of which more than two fixes were taken and the total number of whales in these groups) to create a series of 51 pseudo-samples used in equations 1-5 to calculate a pseudo-estimate of the abundance. This was iterated 200 times and the mean and standard deviation of the 200 abundance pseudo-estimations were used to calculate the cv. This assumed that the daily density of migrating whales was constant throughout the survey period, an assumption violated by the wave nature of the migration. Consequently, further bootstrapping was done from both the 51 day data set and using four separate periods (17 June to 30 June, 1 July to 10 July, 11 July to 19 July and 20 July to 6 August) to take into consideration different densities in the migration waves. Cv's from the other three years were not calculated due to the lack of, or incomplete, twin tower data collected during these years.

To extrapolate the summation of daily densities into a total population estimate, two further sources of bias must be considered :-

1. The population estimate must include the proportion of the population passing outside the visibility limits of the observers.

This proportion would best be quantified through an independent aerial survey run concurrently with shore-based observations. However the low densities of groups sighted off Cape Vidal and the duration of the migration at present preclude a cost-effective aerial survey.

The distribution of whales sighted with distance from the coast each year (Figure 5.4) shows whales to be visible at up to 18 km from the coast, with the mode of the northward migration at 2-4 km, although the proportions missed by observers are not included here. Findlay (unpubl.) analysed the distribution of 22 groups of humpback whales sighted on the Durban whaling ground by spotter aircraft between 1972 and 1975. Although the positions of a high proportion of groups sighted would have been beyond the vision of shore-based observers at Durban, projection of all these groups in a northward direction resulted in their striking the coast to the south of Cape Vidal. The oceanography off Cape Vidal is dominated by both the strong southerly flowing Agulhas Current and a narrow continental shelf. Although no direct current measurements have been recorded

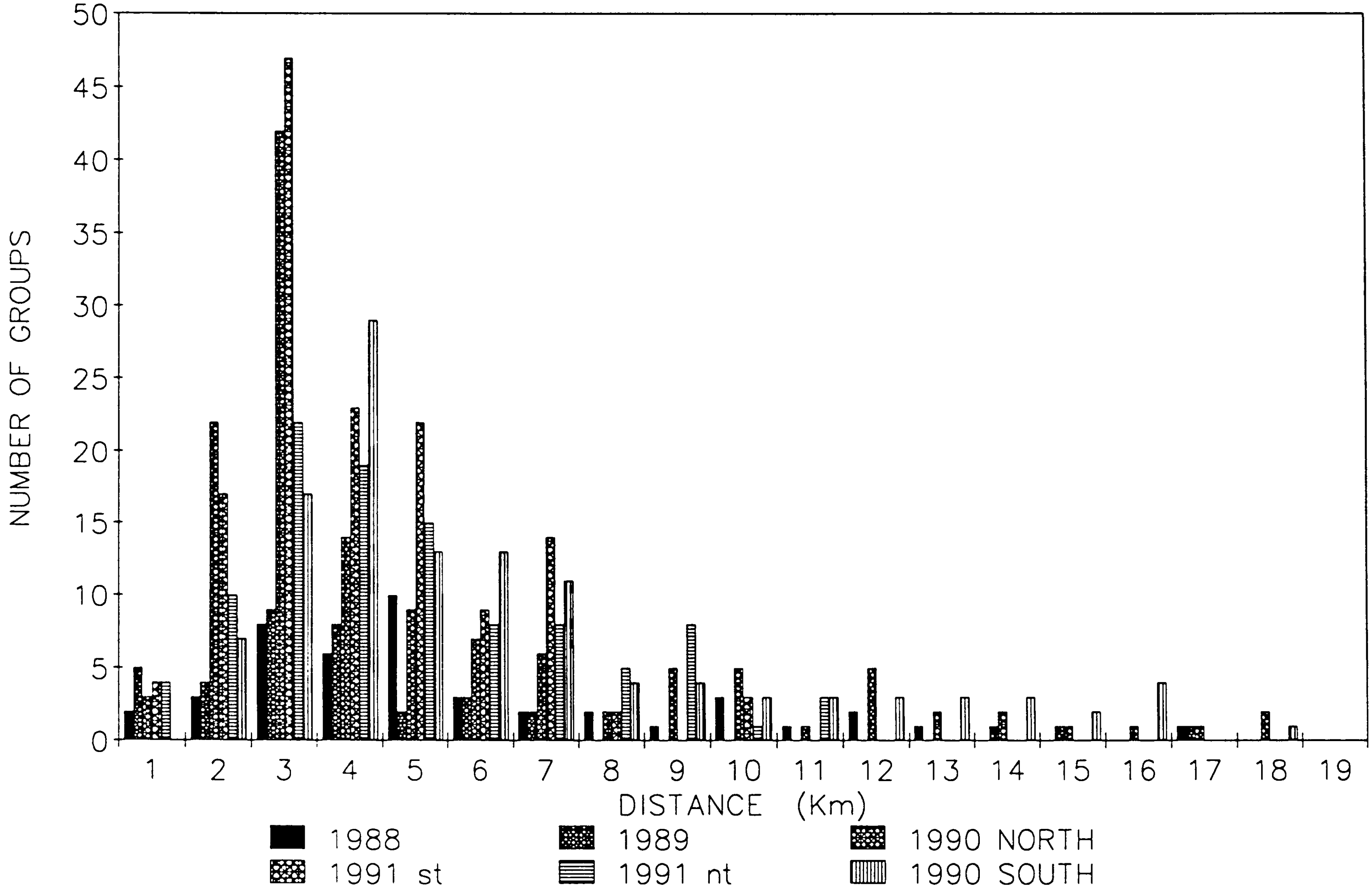


Figure 5.4 The distribution of groups with distance from the coast in surveys off Cape Vidal between 1988 and 1991.

at Cape Vidal, the nearshore edge of the Agulhas Current (corresponding to the 1 $m.s^{-1}$ isotach) can be within 10 km from the coast at Richards Bay, approximately 100 km south of Cape Vidal (Pearce 1977). Furthermore, a northward flowing counter-current exists inshore of the Agulhas Current. The northward migration in 1990 was significantly closer inshore than its southward counterpart (see chapter 3), a factor which possibly results from an avoidance of the offshore Agulhas Current during the northward migration. Although most of the whales would be expected to migrate inshore of the southerly flowing Agulhas Current, the proportion of the population passing beyond the limit of visibility is at present unknown.

2. The population estimate must include the proportion of the population passing outside of the survey period.

The daily densities of northward and southward migrating groups recorded each year are shown in Figures 5.5(a) to (c). Hiby and Hammond (1989) note that in land-based surveys of gray whales (Reilly *et al* 1983, Rugh 1984, Buckland *et al.* 1993), the tails of the migration were estimated by extrapolation of a predictive model fitted to the daily densities recorded. A similar approach was adopted by Bryden *et al.* (1990) who used both normal and gamma density functions to model the northward migration of humpback whales off the east coast of Australia. The northward migration off Cape Vidal seems to be composed of a sequence of waves each year, with peak densities evident over the periods 4-10 July, 15-18 July and 23-27 July (chapter 3), and it is possible that these waves represent the segregation of the migration into different age or reproductive classes as found by Dawbin (1966) and Chittleborough (1965). Although a probability distribution could be fitted to such waves, it would be unlikely that extrapolation of such a distribution would approximate the tails of the migration.

Figures 5.5(a) and (b) show the peak of the northward migration to occur in late July, which suggests that the pilot studies undertaken in 1988 and 1989 missed the peak migration period. Groups were sighted migrating northwards as late as October during the 1990 survey, and it is assumed that the northward migration is complete by the end of this month, although southward migrating groups have been noted (as incidental sightings) as late as December. The direction of the migration in 1990 changed from northward to southward between 5 and 25 August (chapter 3), although 32 % of the 1990 northward migration occurred after 7 August (the termination date of the 1991 survey). Paterson and Paterson (1989) note that approximately 15% of northward migrating groups observed off southern Queensland on the east coast of Australia occurred after late August. Four percent of the 1990 nOrthward migration occurred before 17 June (the commencement of the 1991 survey), of which 3.2 % passed on 16 June.

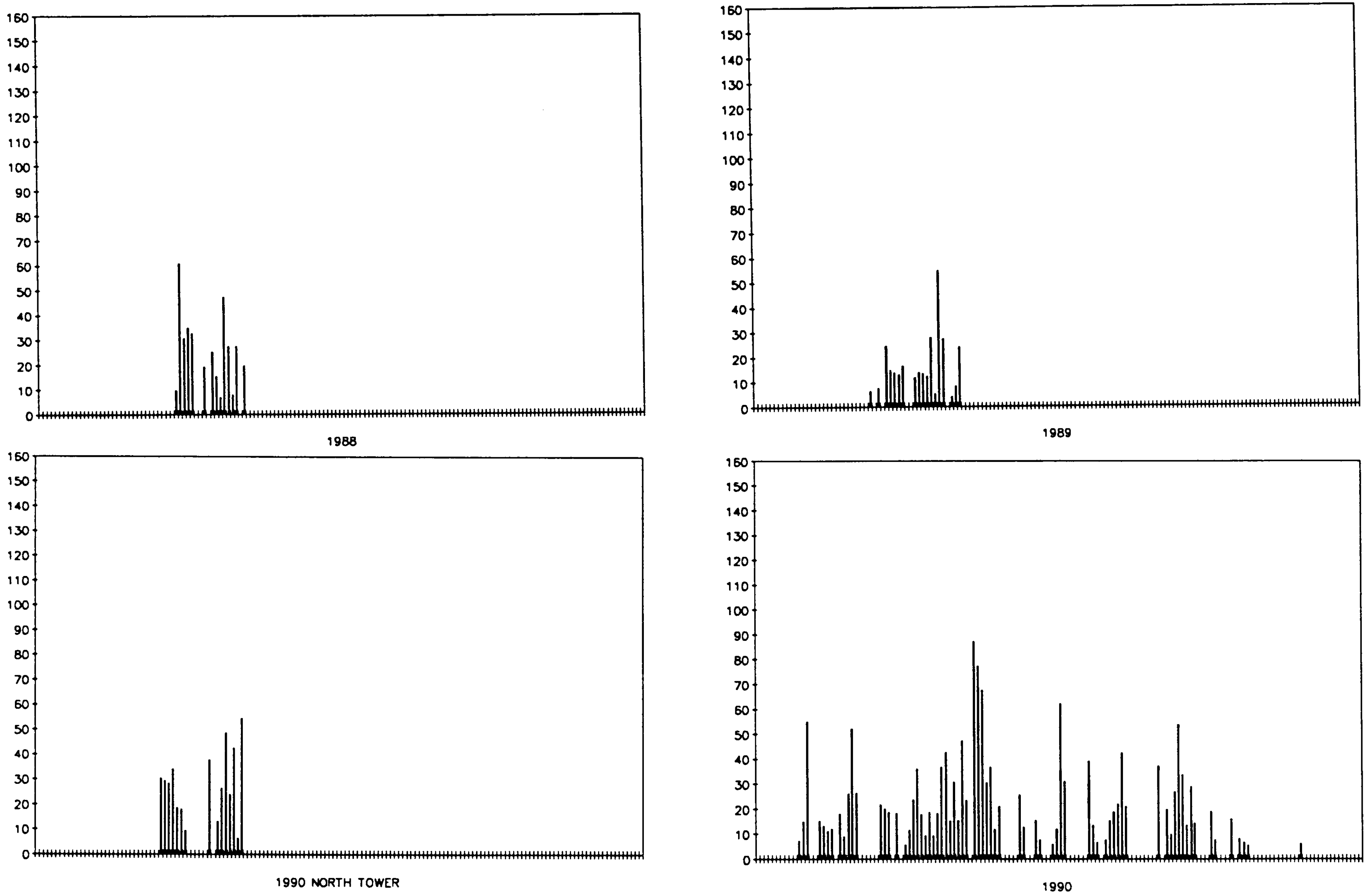


Figure 5.5(a) Daily densities of northward migrating humpback whales passing Cape Vidal between 2 June and 28 October as estimated from the south tower in 1988, 1989 and the north and south towers in 1990.

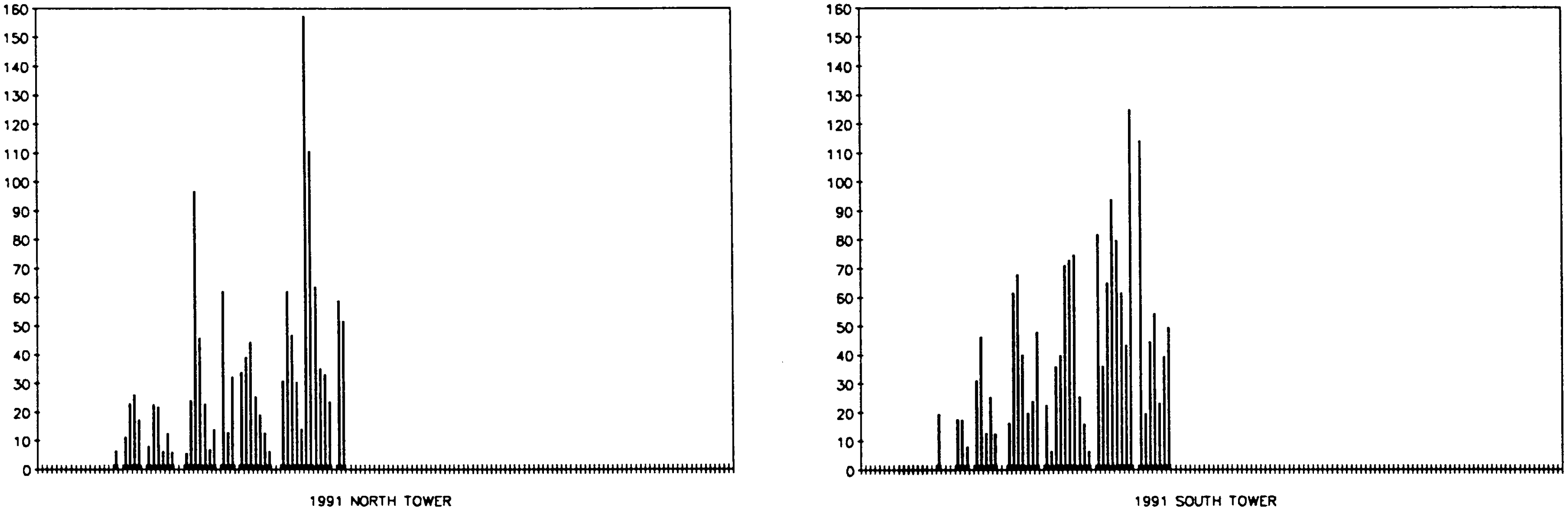


Figure 5.5(b) Daily densities of northward migrating humpback whales passing Cape Vidal as estimated the north and south towers between 2 June and 28 October in 1991.

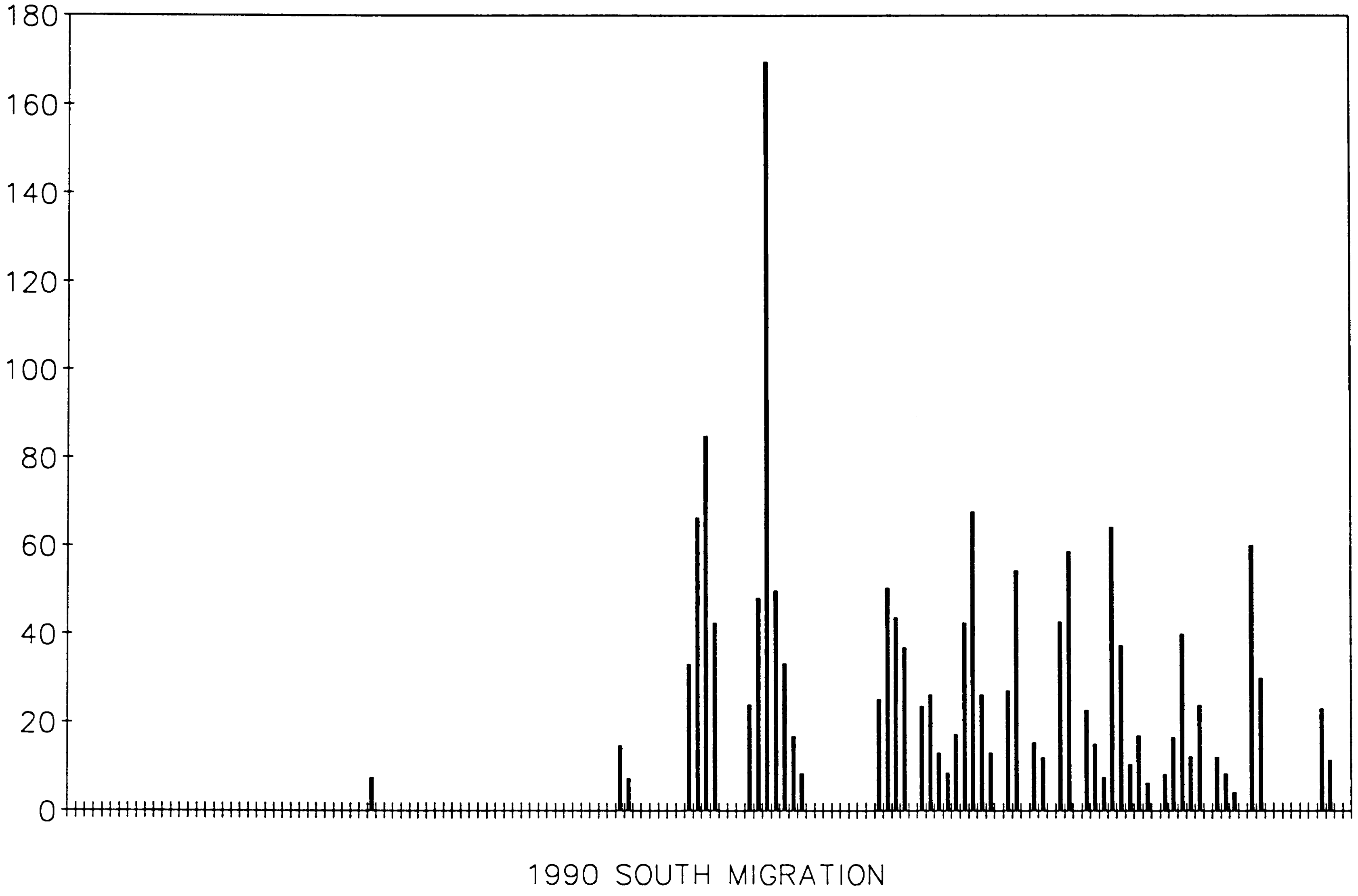


Figure 5.5(c) Daily densities of southward migrating humpback whales passing Cape Vidal as estimated from the south tower between 2 June and 28 October in 1990.

Table 5.3 shows the estimated number of whales passing Cape Vidal in each survey and in co-incident time periods between years. The pseudo-estimate of the 1991 abundance calculated from bootstrapping of the 51 day dataset without stratification was 1 463 with an associated cv of 0.114 (Table 5.4), while the pseudo-estimate from the bootstrapping of the stratified data was 1 687 with an associated cv of 0.122 (Table 5.5). The mean of these two pseudo-estimates is a slight underestimates of the actual abundance estimate (1 777).

Table 5.3. Estimated numbers of humpback whales passing Cape Vidal on the northward and southward migration during five survey periods each year.

SURVEY	PERIOD				
	1	2	3	4	5
NORTH					
1988 st	368	-	-	-	-
1989 st	288	296	302	-	-
1990 st	378	420	420	1000	1711
1991 st	717	734	831	1777	
1990 nt	365	425	-	-	-
1991 nt	502	507	555	1392	-
SOUTH					
1990 st	-	-	-	-	1647

SURVEY PERIODS 1 = 4/7-22/7; 2 = 1/7-22/7; 3 = 27/6-22/7; 4 = 17/6-6/8; 5 = 2/6-28/10.

st = south tower; nt = north tower.

Table 5.4. Results of bootstrapping of the 1991 51-day data set. ITN = iteration number, GRPS = number of groups, INDIV = number of individuals.

ITN.	GRPS.	INDIV.	ITN.	GRPS.	INDIV.	ITN.	GRPS.	INDIV.	ITN.	GRPS.	INDIV.
1	893.2	1889.1	51	659.6	1440.8	101	747.1	1593.8	151	601.2	1271.3
2	990.7	2136.2	52	828.4	1734.9	102	740.8	1582.6	152	757.7	1481.8
3	676.2	1360.6	53	788.9	1691.8	103	664.9	1486.8	153	692.5	1409.7
4	793.9	1713.8	54	834.2	1766.6	104	769.1	1565.3	154	773.8	1661.2
5	817.2	1797.9	55	748.1	1577.2	105	758.3	1623.0	155	748.1	1515.4
6	807.4	1797.8	56	731.9	1543.2	106	766.4	1596.6	156	735.1	1583.3
7	671.4	1392.4	57	665.1	1366.6	107	819.2	1721.3	157	733.6	1506.7
8	714.2	1530.3	58	801.2	1657.1	108	830.2	1812.3	158	814.0	1682.3
9	754.7	1464.5	59	785.1	1663.1	109	702.9	1500.0	159	684.4	1327.9
10	789.0	1569.3	60	792.5	1633.9	110	784.3	1687.8	160	778.5	1829.0
11	791.3	1661.7	61	617.4	1213.5	111	743.1	1505.8	161	790.4	1743.2
12	746.8	1526.5	62	816.4	1652.0	112	810.3	1698.7	162	779.3	1653.3
13	771.1	1625.9	63	697.6	1403.6	113	921.7	1968.6	163	725.1	1514.5
14	771.2	1542.4	64	693.6	1524.2	114	653.8	1361.3	164	718.5	1489.5
15	723.5	1531.6	65	772.0	1690.6	115	772.8	1584.3	165	792.3	1527.3
16	850.9	1826.3	66	760.7	1494.5	116	796.1	1723.1	166	720.4	1430.7
17	917.1	2071.2	67	710.4	1479.4	117	816.7	1703.6	167	739.7	1446.8
18	655.9	1387.3	68	697.3	1448.3	118	761.8	1628.7	168	697.4	1444.7
19	777.9	1649.8	69	741.6	1532.6	119	650.2	1403.5	169	802.1	1764.7
20	866.1	1880.9	70	800.7	1601.4	120	839.1	1874.1	170	646.7	1435.9
21	770.9	1613.6	71	708.0	1559.4	121	748.5	1569.5	171	730.9	1519.6
22	712.0	1531.8	72	811.8	1703.9	122	684.2	1368.4	172	883.5	1845.7
23	890.1	1976.8	73	709.4	1502.8	123	747.1	1543.4	173	840.0	1735.3
24	657.8	1412.4	74	624.8	1305.6	124	671.1	1488.1	174	635.8	1323.9
25	745.5	1530.2	75	826.0	1759.2	125	661.4	1369.4	175	765.5	1645.4
26	654.4	1390.7	76	719.7	1521.5	126	661.0	1382.0	176	812.9	1748.8
27	693.0	1530.7	77	693.6	1424.7	127	750.3	1512.1	177	548.2	1174.8
28	799.5	1644.1	78	795.5	1760.1	128	732.0	1567.1	178	725.3	1627.5
29	791.5	1775.7	79	741.3	1673.0	129	780.4	1570.2	179	719.7	1510.5
30	898.5	1881.7	80	633.7	1259.3	130	811.0	1612.7	180	659.0	1377.9
31	690.8	1390.5	81	692.5	1480.2	131	886.8	1857.0	181	665.4	1304.5
32	758.5	1587.8	82	896.9	1944.8	132	696.6	1527.5	182	704.6	1356.3
33	716.4	1416.0	83	720.5	1527.8	133	658.0	1385.3	183	849.2	1762.9
34	800.9	1700.8	84	751.5	1551.2	134	681.6	1425.3	184	691.5	1421.9
35	697.5	1488.5	85	807.7	1748.3	135	776.9	1589.2	185	600.4	1243.0
36	694.3	1414.6	86	614.8	1262.9	136	749.6	1538.6	186	701.6	1539.4
37	669.5	1452.0	87	618.8	1237.5	137	788.3	1612.7	187	679.1	1409.1
38	742.4	1539.8	88	723.8	1447.5	138	909.6	1808.2	188	783.6	1658.9
39	760.9	1712.0	89	804.0	1587.9	139	772.8	1612.7	189	779.6	1583.6
40	794.4	1744.0	90	821.6	1676.7	140	843.0	1729.3	190	786.5	1633.5
41	832.0	1832.4	91	717.9	1478.0	141	730.4	1610.6	191	731.6	1591.9
42	732.0	1474.4	92	789.1	1676.7	142	698.0	1414.2	192	646.2	1340.5
43	736.9	1533.7	93	813.2	1789.0	143	720.4	1402.4	193	741.9	1392.1
44	769.0	1616.0	94	692.1	1446.1	144	568.2	1091.5	194	645.7	1337.6
45	801.2	1727.0	95	721.2	1554.1	145	804.3	1681.0	195	809.6	1677.8
46	681.2	1454.9	96	696.3	1392.6	146	1005.2	2174.4	196	775.0	1685.2
47	668.3	1396.4	97	808.8	1653.9	147	676.4	1382.7	197	709.2	1494.1
48	910.8	1926.7	98	698.0	1428.2	148	698.4	1456.5	198	698.4	1447.3
49	956.1	2017.3	99	811.6	1672.6	149	671.4	1531.7	199	762.2	1636.0
50	676.1	1523.5	100	578.1	1224.6	150	772.4	1589.2	200	672.8	1462.6
MEAN = 1463											
CV = 0.114											

Table 5.5. Results of bootstrapping of the 1991 data set, stratified by the four periods (17 June to 30 June, 1 July to 10 July, 11 July to 19 July and 20 July to 6 August). ITN = iteration number, GRPS = number of groups, INDIV = number of individuals.

ITN.	GRPS.	INDIV.	ITN.	GRPS.	INDIV.	ITN.	GRPS.	INDIV.	ITN.	GRPS.	INDIV.
1	769.8	1600.4	51	775.8	1646.4	101	750.0	1565.6	151	846.7	1742.8
2	678.8	1427.5	52	585.1	1178.6	102	824.5	1816.1	152	811.4	1714.0
3	765.4	1586.8	53	862.1	1915.8	103	770.4	1549.9	153	757.8	1567.8
4	679.1	1478.1	54	798.0	1663.3	104	869.1	1862.4	154	643.5	1355.7
5	681.0	1362.0	55	874.9	1846.9	105	808.3	1616.5	155	796.5	1601.7
6	782.4	1651.8	56	760.6	1661.0	106	601.0	1159.0	156	812.7	1737.0
7	769.1	1579.9	57	595.5	1149.1	107	727.9	1514.0	157	789.3	1616.1
8	749.2	1585.6	58	774.0	1597.1	108	769.8	1805.3	158	610.7	1213.4
9	766.5	1622.1	59	709.4	1399.8	109	750.0	1554.4	159	715.6	1468.8
10	663.4	1384.8	60	869.0	1870.3	110	866.2	1783.9	160	746.2	1637.8
11	701.0	1527.1	61	637.8	1456.5	111	694.5	1419.2	161	703.2	1520.7
12	837.4	1773.3	62	692.2	1504.5	112	696.7	1534.6	162	820.2	1795.6
13	725.1	1490.8	63	793.0	1575.5	113	736.4	1492.5	163	706.8	1554.9
14	762.5	1478.5	64	760.0	1581.8	114	717.1	1520.2	164	630.5	1342.2
15	689.5	1463.1	65	873.5	1900.7	115	753.4	1614.5	165	701.2	1570.2
16	708.3	1527.8	66	682.7	1373.6	116	610.5	1211.3	166	655.1	1383.0
17	783.9	1649.2	67	750.2	1582.0	117	802.0	1692.1	167	647.8	1286.9
18	751.8	1614.7	68	743.4	1583.3	118	792.0	1619.1	168	829.0	1879.1
19	685.8	1424.3	69	727.0	1649.8	119	790.8	1591.7	169	782.1	1774.7
20	735.9	1529.7	70	775.2	1653.0	120	654.4	1379.0	170	755.8	1585.2
21	957.4	2059.4	71	788.8	1577.6	121	671.9	1446.5	171	884.2	1923.9
22	936.8	2035.1	72	627.1	1238.1	122	690.7	1431.3	172	631.8	1238.4
23	583.0	1213.2	73	786.0	1646.0	123	830.0	1770.1	173	812.1	1790.9
24	751.9	1549.6	74	790.8	1642.5	124	844.0	1779.7	174	811.3	1867.1
25	733.4	1575.7	75	779.3	1575.2	125	730.1	1507.7	175	897.4	1893.2
26	675.7	1380.4	76	737.7	1528.2	126	785.2	1653.6	176	821.1	1765.3
27	694.8	1426.7	77	668.5	1284.8	127	747.7	1621.5	177	832.4	1803.6
28	680.5	1308.6	78	773.6	1684.8	128	771.2	1593.1	178	705.8	1494.1
29	710.7	1450.2	79	596.4	1192.8	129	886.5	1833.3	179	832.6	1804.0
30	762.6	1465.9	80	767.3	1603.4	130	775.4	1591.1	180	719.6	1485.3
31	734.1	1391.9	81	778.7	1574.3	131	757.2	1594.7	181	767.7	1569.2
32	679.8	1429.9	82	746.2	1517.9	132	769.0	1638.7	182	759.1	1544.4
33	749.6	1518.0	83	653.4	1339.0	133	793.1	1717.0	183	738.1	1583.0
34	590.9	1253.8	84	767.0	1517.7	134	774.4	1672.3	184	670.3	1387.8
35	788.7	1688.7	85	569.9	1056.7	135	892.1	1806.0	185	827.3	1712.9
36	684.3	1468.7	86	745.7	1527.9	136	927.5	2008.0	186	728.7	1535.5
37	835.3	1788.5	87	789.7	1722.9	137	688.3	1425.3	187	852.3	1806.6
38	768.5	1554.8	88	778.9	1584.3	138	774.2	1597.9	188	770.8	1639.3
39	815.0	1696.3	89	696.9	1426.9	139	833.4	1921.5	189	704.5	1484.1
40	758.9	1702.1	90	706.3	1440.8	140	822.8	1708.2	190	656.1	1354.3
41	737.6	1475.2	91	723.2	1474.1	141	708.9	1519.0	191	696.5	1346.6
42	785.8	1505.4	92	646.9	1311.8	142	673.1	1338.1	192	741.2	1554.2
43	728.2	1579.2	93	771.3	1560.4	143	611.4	1222.8	193	832.6	1817.6
44	865.9	1741.1	94	658.5	1300.8	144	576.3	1143.2	194	767.9	1634.3
45	788.1	1687.6	95	764.3	1652.6	145	793.2	1616.5	195	679.7	1409.3
46	958.9	2013.6	96	873.8	1784.7	146	683.6	1432.0	196	779.2	1604.8
47	663.4	1365.2	97	580.5	1197.3	147	796.8	1743.6	197	784.1	1672.2
48	695.6	1382.4	98	825.0	1774.8	148	791.6	1758.0	198	704.3	1495.6
49	812.5	1729.4	99	682.7	1374.9	149	615.9	1201.1	199	889.0	1847.2
50	812.3	1624.5	100	729.5	1450.0	150	626.3	1333.9	200	816.4	1686.6
MEAN = 1687											
CV = 0.122											

The data set for the 1990 northward migration is the only one covering the entire migration, and consequently the point estimate of 1711 is the only estimate where the tails of the migration do not need to be extrapolated. The numbers recorded in each of the other surveys could best be extrapolated to total population estimates using the proportion of the total 1990 population recorded outside the co-incident survey period during 1990. However, the first of the northward migration waves (4-10 July) was absent in 1990, possibly as a result of an oil spill across the migration path some 100 km to the south of Cape Vidal between 3 and 12 July. Paterson (1991), however, found the northward migration off the east coast of Australia to be late in 1990, and it is not known whether individuals from this missing wave passed through the survey area at some other time, whether they passed outside of the survey area, or whether they did not undertake the migration. As the period during which this wave is expected is included in each year's survey, the extrapolation from the 1990 data will overestimate the population each year, and so such extrapolations have not been carried out.

Because there were no independent-observer surveys during the southward migration, the total for the southward migration in 1990 has been corrected by the proportion-missed factor calculated from northward-migration surveys. However the northward-migrating groups appeared to spend longer on the surface than their southward-migrating counterparts (Findlay, pers. obs.) so a greater proportion of the southward migration may have been missed. Furthermore, the southward migration continues after the end of October, so that one tail of the migration may be missing.

Despite the fact that all the estimates in Table 5.3 are possible underestimates of the number of whales passing during that phase of the migration, estimates of the increase rate of the population can be determined from them if a constant proportion of the population is assumed to pass within temporal and spatial limits of the survey period each year (as done by Bryden *et al.* (1990) for Australian east coast humpback whales, and Zeh *et al.* (1991) for bowhead whales migrating past Pt. Barrow, Alaska).

Population increase rates calculated for the limited survey periods 4 to 22 July each year of 0.227 (95% confidence interval of ± 0.6038), and 26 June to 22 July in 1989, 1990 and 1991 of 0.505 (95% confidence interval of ± 1.298) (Figure 5.6) are well above maximum increase rates for humpback whales expected from modelling of demographic parameters assuming a two year calving interval, although the wide confidence intervals includes increase rates calculated for other populations. These high increase rates and wide confidence interval presumably arise from the limited time series of four years and the fact that these survey periods did not include the major northward migration peak in each year, and cannot be considered reliable. Zeh *et al.* (1991) note that one source of positive bias in estimated increase rates could result from increased efficiency of observers with time. However, a high percentage of the 1991 observers were naive which would bias the estimate downwards rather than upwards.

DISCUSSION

The coastal migratory habits of southern hemisphere humpback whales, a factor which made them particularly susceptible to shore-based whaling in temperate waters, now result in the species being well suited to shore-based monitoring. Similar shore-based monitoring has been undertaken to estimate the sizes of stocks of gray whales off the coast of California (reviewed by Reilly, 1984), bowhead whales off Pt. Barrow, Alaska (Zeh, Ko, Krogman and Sonntag 1986a, 1986b, Gentleman and Zeh 1987, Krogman, Rugh, Sonntag, Zeh and Ko 1989) and humpback whales off the east coast of Australia (Bryden 1985, Bryden *et al.* 1990, Paterson and Paterson 1984, 1989 and Paterson 1991). Hiby and Hammond (1989) have noted that certain of these surveys have been analogous to strip surveys, where all groups within a truncated visibility distance are assumed to be seen. They further note that both the proportion of the population passing offshore of the truncation distance and the proportion of groups missed by observers within the visible limits, need to be determined before the size of the total population can be estimated. The shore-based surveys of the east Australian component of the Area V humpback whale population (Bryden 1985, Bryden *et al.* 1990, Paterson and Paterson 1984, 1989, and Paterson 1991) have assumed that all groups within a 10 km visible limit have been sighted, and no heterogeneity of sighting probabilities has been taken into account, although Bryden *et al.* (1990) note that the proportions of fair and poor weather were similar between years. The mean migration distance offshore of Cape Vidal was found to differ significantly between years (chapter 3). Although such a difference is not assumed to change the proportion of the population passing within the range of visibility at Cape Vidal, it could be of consequence in making inter-year comparisons if the proportion missed with distance is not considered.

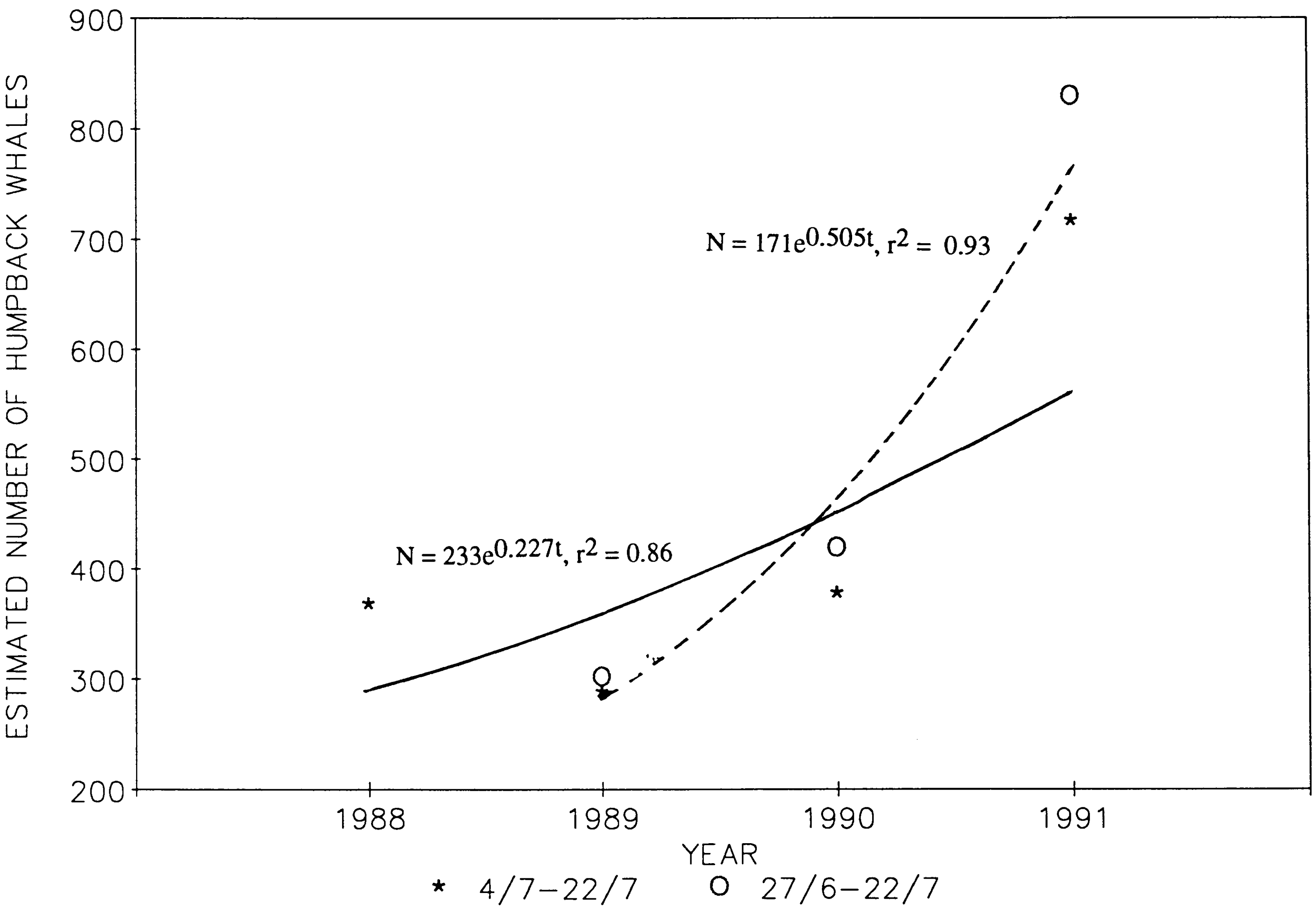


Figure 5.6. Estimates of the number of northward migrating humpback whales passing Cape Vidal during the periods 4 July to 22 July and 27 June to 22 July in 1988, 1989, 1990 and 1991.

The proportion of the population passing outside the observer's vision has been assumed to be negligible in all shore-based surveys of humpback whales on the Australian east coast. Bryden (1985) projected the positions of groups sighted during aerial surveys in a north - south direction, and found 96 % of all groups to pass within 10 km from observer platforms(situated on headlands) although Chittleborough (1965) notes that humpback whales were captured at up to 37 km from the east Australian coast.

Both the low densities of whales present and the lengthy duration of the northward migration preclude an independent survey to assess the distribution of whales off Cape Vidal. An indirect method of determining the proportion of the population passing offshore would be to compare the population estimate from sightings with one based on mark-recapture methodology, assuming that whales do not migrate consistently at the same distances offshore each year. Unfortunately the sample of photographed individuals is too small to make such a comparison. Findlay, Best, Peddemors and Gove (1992 - see chapter 6) estimated the size of the southern and central Mozambique population of humpback whales as 1954 individuals (cv = 0.38) from a line-transect survey in August and September 1991, and the numbers estimated to pass Cape Vidal during the northward migration of 1990, compare favourably with this estimate. However Findlay *et al.* (1992) note that this may be an underestimate of the Mozambique breeding ground population, given that the probability of seeing whales on the trackline was assumed to be 1 in this survey, that the proportion of the population not present on the ground at the time of the survey was unknown, and that the northern limit of the breeding ground was undetermined. The fact that the Mozambique population estimate is thought to underestimate the true population size, and that this estimate is comparable to the Cape Vidal estimate, suggests that the Cape Vidal estimate is also underestimated. However it is not possible to determine whether this underestimate is due to some proportion missed offshore, or to incomplete accounting for the heterogeneity of sighting probabilities. The relationship and extent of mixing between animals breeding off the coast of Mozambique and the coast of Madagascar is also unknown, although reports of incidental sightings off the coast of Madagascar suggest some recovery of this component of the population.

Humpback whaling ceased off the east African coast in October 1963, with an average of 36.9 (range of 27 to 49) animals taken in the Durban whaling grounds (some 300 km to the south of Cape Vidal) in a six month season each year between 1953 and 1963. Although the majority of the northward-migrating individuals would have passed inshore of the distribution of the catching effort at Durban as the main target species at this time occurred off the continental shelf, the limited offshore distribution in June and July noted by Findlay (unpubl.) (and the fact that catchers searched close inshore during poor weather) suggest that the population was small at that time. Furthermore, both the northward and southward migrations would have passed through the ground during the whaling season, so that the population was potentially exposed to two episodes of exploitation during each season.

Comparison of the 1953-1963 catches off Durban and the numbers estimated from Cape Vidal in 1990 implies that the Mozambique component of the Area III population has undergone considerable recovery since October 1963, although the four-year time period over which the surveys have been carried out is too short for accurate estimates of recovery rate at this stage. Significant recovery rates have been detected in three humpback whale stocks. The east Australian stock of the Area V population is estimated through similar shore-based visual monitoring to be increasing at annual rates of 0.144 (Bryden *et al.* 1990) and 0.097 (Paterson and Paterson 1989). The recovery rate of the Area IV population off the west coast of Australia has been estimated at 0.088 through aerial surveys (Bannister, Kirkwood and Wayte 1991), and the north west Atlantic Ocean population at 0.094 through photographic mark-recapture analyses (Katona and Beard 1990) and 0.138 through shipboard counts (Sigurjonsson and Gunnlaugsson 1990). Best (1993) however notes that the recovery rate estimates of 0.144 for the east Australian population and 0.138 for the north west Atlantic Ocean populations do not seem to be biologically feasible, given the likely gross recruitment rates for northern hemisphere humpback whales (Clapham and Mayo 1990).

CHAPTER 6

THE DISTRIBUTION AND ABUNDANCE OF HUMPBACK WHALES ON THEIR SOUTHERN AND CENTRAL MOZAMBIQUE BREEDING GROUNDS.

INTRODUCTION

The annual migration of humpback whales (*Megaptera novaeangliae*) from summer polar feeding grounds to winter breeding grounds in tropical and sub-tropical coastal waters has been well documented in both the Northern (Baker, Herman, Perry, Lawton, Straley, Wolman, Kaufman, Winn, Hall, Reinke and Ostman 1986; Katona and Beard 1990) and Southern Hemisphere (Olsen 1914; Kellogg 1929; Matthews 1938; Mackintosh 1942; 1966; Chittleborough 1965; Dawbin 1956; 1966). Mackintosh (1942) divided the Southern Ocean humpback whale population into five feeding stocks, each linked to a breeding ground (or grounds) in coastal tropical waters of the continent to the north of it. One such feeding ground off Queen Maud Land (10°-60° E) has been directly linked by two Discovery mark returns to the breeding ground off Madagascar (Rayner 1940), although Mackintosh (1942) also tentatively linked it to the west coast of Africa. Although no humpback mark returns have been recorded off the coast of the African mainland (as marking occurred well after the peak African catches), catch histories suggest that both the coastal waters of Mozambique and Madagascar are principal breeding grounds in the western Indian Ocean. A second feeding ground in the eastern Scotia Sea has been linked to breeding grounds off the African west coast (Kellogg 1929; Mackintosh 1942), but it must be noted that this is tenuously based on a similarity in catch histories.

Modern humpback whaling in southern Africa commenced in 1908 and between 1908 and 1917 about 25 000 humpbacks were estimated to have been taken on the southern African coast (Best, in press). The seasonality of catches by whaling stations at different latitudes has provided evidence of the migratory destinations of humpbacks on the African coast. A bimodal trend in seasonality suggests northward and southward migrations through the whaling ground, while a unimodal seasonality suggests that the northernmost or southernmost destination of the migration had been reached. On the west coast, Olsen (1914) found a bimodal seasonality in catches off the Cape (33°-34° S), and Harmer (1931) found bimodal seasonality of catches off Angola (6°-18° S), while unimodal seasonality was found by Harmer (1931) and Budker and Collignon (1952) off Gabon (0°-4° S).

On the east coast, bimodal seasonalities of catches (Olsen 1914; Matthews 1938) and sightings (Bannister and Gambell 1965) were evident off Durban (30° S), while Olsen (1914) and Angot (1951) found unimodal catch seasonalities off Inhambane, Mozambique (24°S) and southern Madagascar (15°-25° S) respectively. Thus there appears to be a large latitudinal difference in the position of the breeding grounds on the east and west coasts of southern Africa, presumably reflecting the southward movement of warm water by the Mozambique and Agulhas Currents on the east coast, and the northward extension of the cold Benguela system on the west coast.

Townsend's (1935) charts of the positions of 19th century open-boat whalers on the days on which humpback whales were caught, show high catches in the region of the town of Mozambique (12° S) and few or no catches elsewhere on the Mozambique coast. This is somewhat surprising given the coastal migration from the Antarctic feeding ground, and was taken by us to be an error on Townsend's part in plotting all whale catches from the coast of Mozambique in the region of the town of Mozambique. Wray and Martin (1983) refer to "Delagoa Bay" as a whaling ground for right and sperm whales in the early nineteenth century, and "Mozambique" as an ancillary nineteenth century whaling ground with seasonally abundant humpback whale stocks, but unreliable whaling. However only six humpback whale catches were included in the 27 Indian Ocean logbooks that they studied. Modern whaling occurred off the coast of Mozambique between 1910 and 1923, with a floating factory at Bazaruto Island in 1910, a land station operating at Linga-linga (Inhambane) between 1911 and 1915, two floating factories operating at Linga-linga in 1912 (and again in 1923), a land station operating in Delagoa Bay between 1912 and 1913, and floating factories operating at Quelimane in 1912 and at Angoche (16° S) between 1911 and 1912. The highest catches were recorded off Linga-linga, although Tonnessen and Johnsen (1982) noted that only 3360 whales were taken in the Mozambique whaling grounds in this era. Almost no information is available on the distribution of humpbacks on the Mozambique breeding grounds. Rorvik (1980) and da Silva (in litt.) record sightings of humpback whales made in Mozambique waters, but neither sets of data have associated effort and no distribution patterns can be determined.

This marked paucity of published information on the distribution of humpback whales on their breeding grounds is evident throughout the Southern Hemisphere. Although the localities of breeding grounds are inferred from historical catches and mark returns (see Kellogg 1929 and Mackintosh 1942) the distributions of whales on them are largely unknown. For instance, Dawbin and Gill (1991) state that the extent of the Area IV breeding ground is largely undetermined, and while Simmons and Marsh (1986) have identified the Great Barrier Reef as the breeding area of the Australian east coast population, Paterson (1991) states this may not be the sole destination of this stock. Simmons and Marsh (1986) found most humpbacks in the Great Barrier Reef lagoon to be within 10 km of islands or reefs, although they caution that this may reflect human usage in this area. In the Northern Hemisphere, Whitehead and Moore (1982) found humpback whales to be distributed in shallow waters of between 24° and 28° C on the West Indian breeding grounds, while Herman and Antinoja (1977) found humpback whales off Hawaii also to be distributed in waters of between 24° and 28°C and less than 100m deep.

Given the paucity of information on the winter distribution of East African humpback whales, a thirty-day cruise was undertaken in southern and central Mozambique coastal waters in August and September 1991 with the following objectives :-

1) To define the distribution of humpback whales over the continental shelf of southern Mozambique, and to identify the southern and northern limits of the breeding grounds.

2) To determine the abundance of humpback whales on the breeding grounds for comparison with abundance estimates obtained from shore-based monitoring of the migration at Cape Vidal, South Africa.

3) To obtain individual identification photographs for comparison with those taken off Cape Vidal and other east coast locations, Madagascar, the African west coast, and Antarctic waters.

4) To record songs as indicators of breeding behaviour, and for comparison with songs recorded at Cape Vidal in previous years (1988 to 1990), and off the west coast of South Africa.

5) To obtain skin biopsies for a genetic comparison with the African west coast population.

METHODS

Field methods

A 20m steel-hulled motor ketch, the *Zanj*, was chartered out of Richards Bay, northern Natal, for the period 15 August to 15 September 1991. Transit legs were steamed between Richards Bay and Maputo, and sawtooth search transects were undertaken between Maputo and Quelimane or 18° S (Figure 6.1). All transects were undertaken under motor. Chartering of the *Zanj* was largely carried out through funding from *Earthwatch*, and at any one time there were four or five *Earthwatch* volunteers on the cruise, each of whom spent ten days at sea. This necessitated the 30 day cruise being split into three legs (Maputo to Magaruque Island, Magaruque Island to 18° S and return, and Magaruque Island to Maputo) with *Earthwatch* volunteer changes being undertaken at Magaruque Island between each leg. Research carried out by *Earthwatch* was at all times overseen by three or four scientific staff.

The survey area was restricted to water depths of between 18.3 and 183m, and transects were designed to give equal coverage over the continental shelf on each leg between Maputo and 18° S within the one-month time frame. The cruise track was designed on an average of ten hours of steaming (at a speed of six knots), to obtain sixty miles of searching per day. The bearings of the transect legs from the coast were determined from the ratio of the length of coastline to be surveyed to the distance that could be steamed within the time constraints of the survey. No night steaming was planned, and each day's search was planned to commence at the final waypoint of the previous day. Although this was maintained as far as possible, some search effort was lost to inclement weather and adverse currents, and during closures on groups of whales by inflatable, or by the *Zanj*. These factors resulted in the final waypoint of each day seldom being reached, and in such cases the remaining search effort was forfeited, and night steaming was carried out to the first waypoint of the following day. Furthermore, the inability to anchor in deep water at night resulted in two offshore transects during the second leg of the cruise being shortened.

Observation effort was carried out from either a specially constructed barrel situated 10m above sea level on the main mast (type 1 effort), or, if inclement weather or volunteer reluctance prevented observation from the

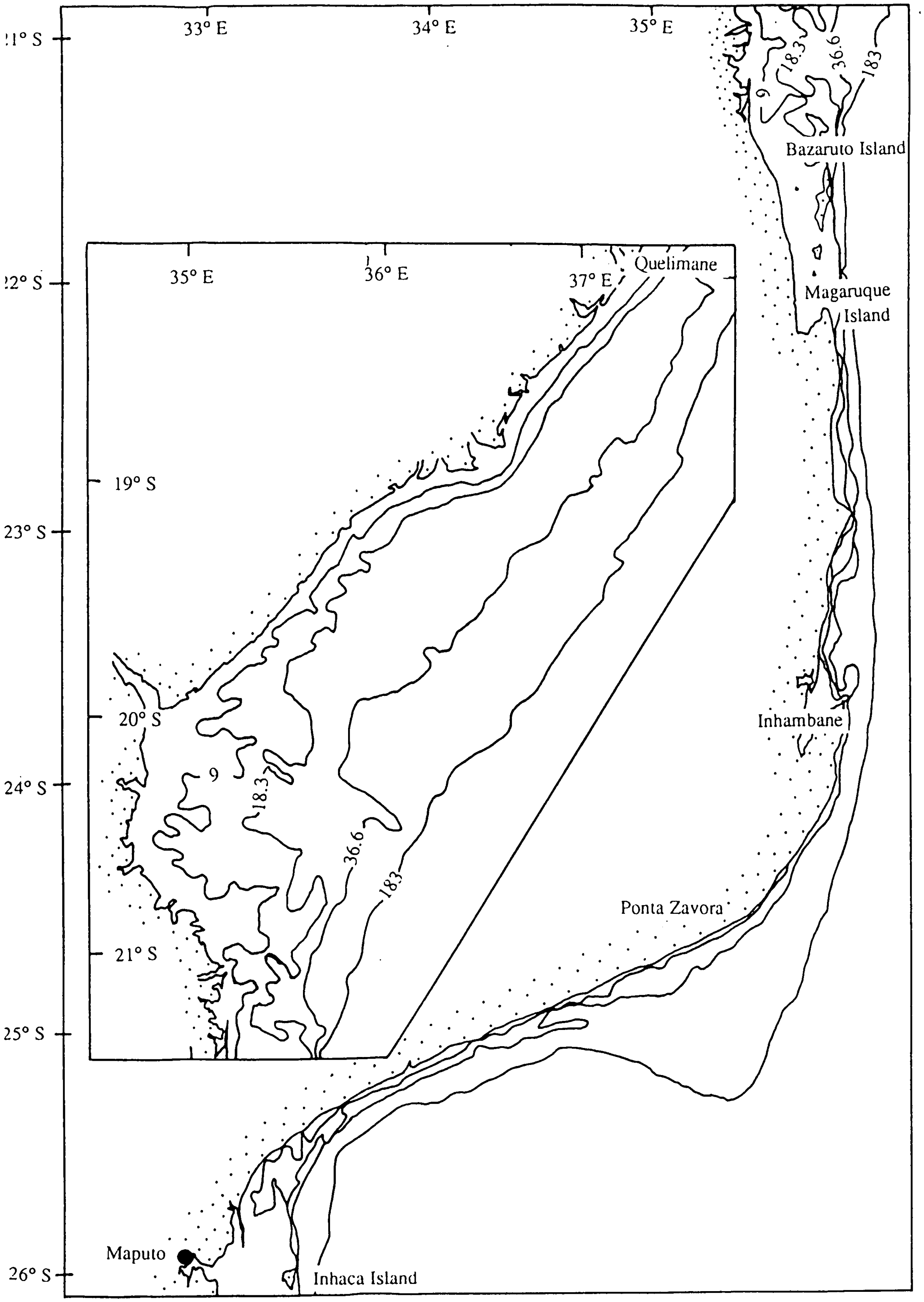


Figure 6.1 The study area off Mozambique showing localities referred to in the text.

barrel, from a vantage point on the coach-house roof, 3m above sea level (type 2 effort). All observations were carried out by two observers at a time (one *Earthwatch* volunteer and one scientist), and each observer undertook no more than five hours observation per day. Observations were carried out for 10 hours per day (07h00 to 17h00), with observers being rotated at 09h00, 12h00 and 15h00. During all observation effort, a scientist was on duty in the wheelhouse to record relevant data reported from the watch position by radio. Such data included the status of observer activity, hourly weather conditions, and data associated with each sighting. All sightings recorded outside periods of active searching were deemed secondary sightings.

The status of observer activity included commencement and termination of active searching, confirmation of group size and identity, and changes of observers, and was recorded on the search activity record, along with the time and position of their occurrence. Times and positions of any changes in course or speed of the vessel were also recorded. All position data were obtained from a GPS system. Weather conditions recorded included wind speed and direction, air temperatures, sea surface temperatures (measured in a bucket of seawater), sea surface state, visibility from watch position (estimated distance at which a humpback could be sighted) and sightability from watch position (the observer's estimate of sighting conditions taking all factors into consideration).

On making a sighting the observers immediately reported it to the recorder who logged observer activity as "group confirmation". Observers then measured the bearing of the sighting from the bow (on an angle board), and took one or more photographs of the group relative to the horizon for distance estimation (Gordon 1990), using a Minolta X500 camera and a 300mm lens of fixed focus and 400 ASA colour transparency film. Angle measurement, time of distance photograph, photograph film and frame number, group size estimates (as maximum, minimum and best estimate) and species identification were all reported to the scientist on wheelhouse watch, who recorded these along with date, time, position, and vessel heading.

At intervals throughout the cruise, a series of frames of ships and fishing vessels relative to the horizon was taken with the same camera and lens, and simultaneous readings of radial distance to the ship were made on the radar screen. A comparison between photographic and radar measurements was used to calibrate photographic measurements of the distance to whale sightings.

The decision to intercept the group was usually made by the scientist on bridge watch, and interceptions were carried out either with the *Zanj*, or the inflatable boat, depending on the weather and progress with the particular day's survey. Interceptions were undertaken to photograph individuals for identification purposes and for collection of skin biopsies for population identification purposes. Photographs were taken with a hand-held, motor-driven Minolta X500 camera with a 100-300mm zoom lens with 400 ASA black and white film. An attempt was made to photograph the ventral surface of the tail flukes and both left and right aspects of the dorsal fin of each animal in the group. Skin biopsies were collected using either a bolt fired from a crossbow or a modified immobilisation dart fired from a Paxarms gas immobilisation gun. Both types of projectile were designed to strike and bounce off the whale while retaining a piece of skin, and each had sufficient flotation to allow for subsequent retrieval from the surface of the water. Biopsies were stored in liquid nitrogen until returned to the laboratory. Data collected during interceptions were recorded by *Earthwatch* volunteers. Observers remained at the watch position during interceptions to direct the small boat or *Zanj* onto the whale group by radio. No active searching was undertaken during interceptions, and further groups seen during these times were recorded as secondary sightings. Only on resumption of steaming did the search effort recommence.

Acoustic watches were carried out on an opportunistic basis when the ship was at anchor, but usually prior to commencing steaming at the start of the day. Positions of acoustic watches are shown in Figures 6.2 and 6.3. Although it was originally intended to take directional fixes on singers using a rotational parabolic reflector, current drag on the reflector was too great for this to be practical. For the remainder of the cruise the hydrophone was deployed from a buoy to a depth of about 5 m. Problems with the hydrophone resulted in poor reception, and no acoustic watches were carried out during leg 3.

Analyses

Due to the high percentage of humpback whales in the identified sightings (99.7%), all unidentified whales were regarded as humpback whales, and analysed as such. Although minimum and maximum estimates of group size were also recorded, the best estimate of group size made in the field was used in analyses. Type 1 and type 2 effort (and corresponding sightings) were analysed separately, and all observation effort within each type was taken to be of equal intensity.

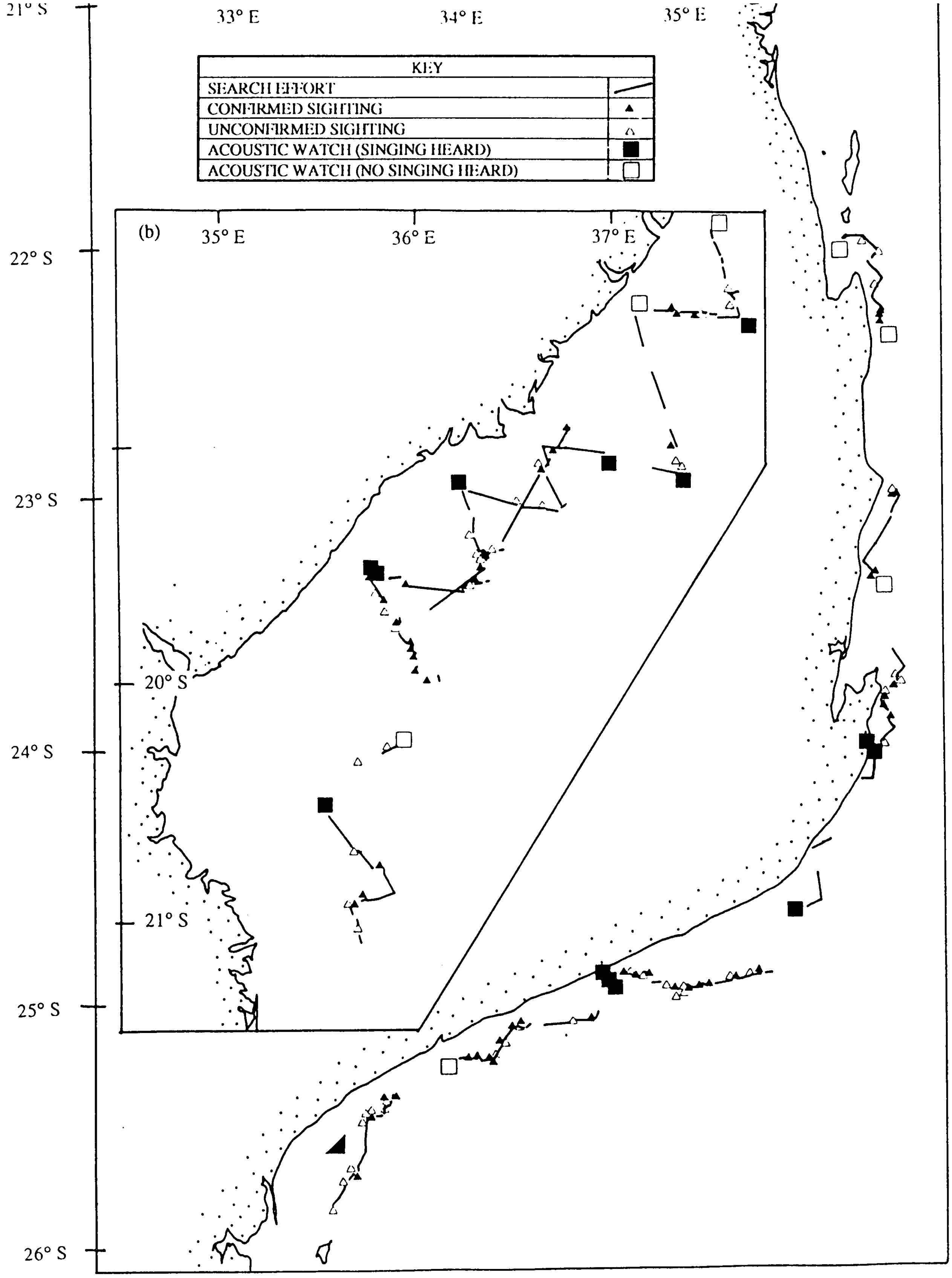


Figure 6.2. The distribution of search effort, acoustic watches and sightings made during the first (a) and second (b) legs of the survey off the coast of southern and central Mozambique.

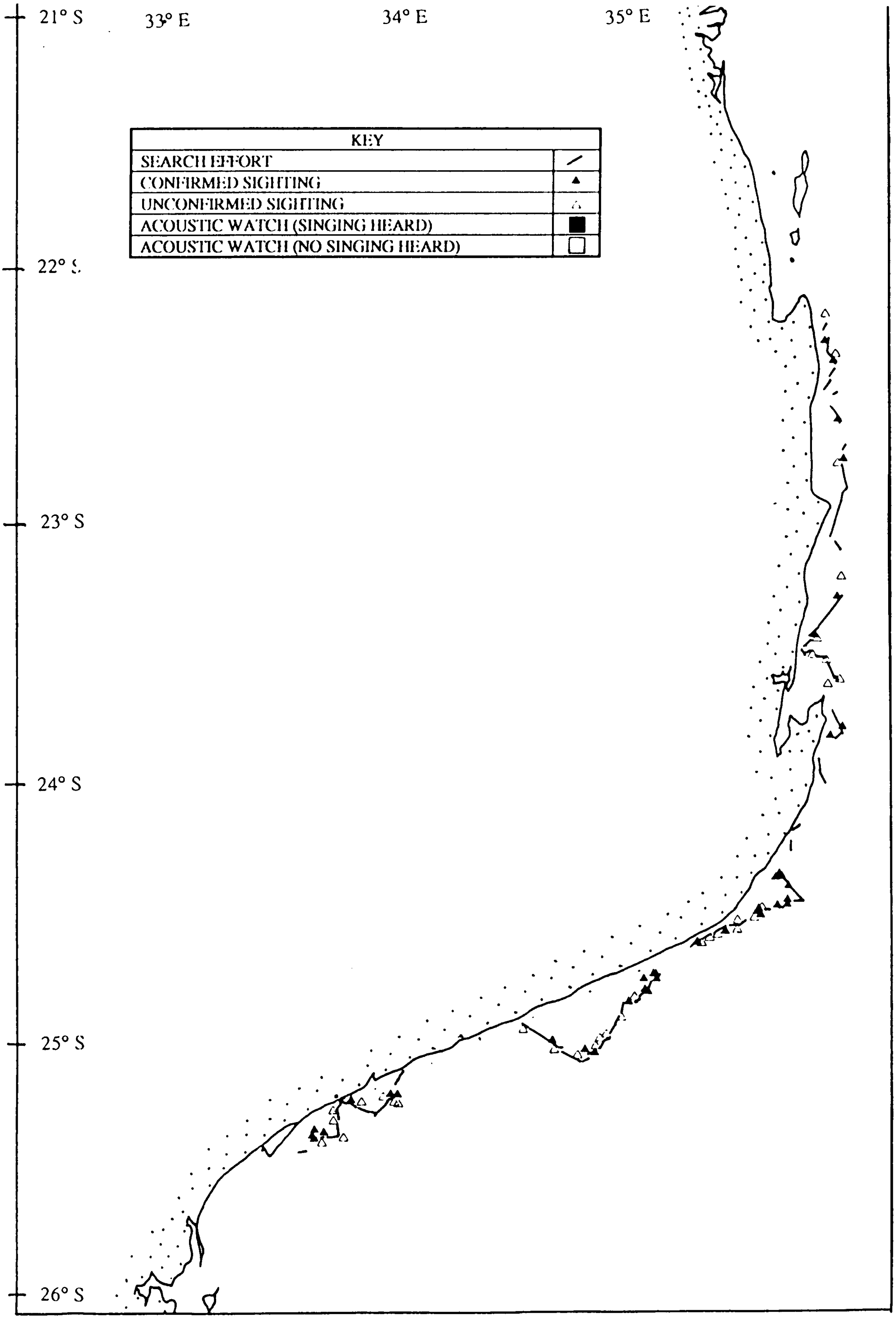


Figure 6.3. The distribution of search effort, and sightings made during the third leg of the survey off the coast of southern Mozambique.

Relative densities of whales were calculated by water depth (0-18.3, 18.3-36.6, and 36.6-183m depth intervals) measured from Admiralty charts, by longshore distance (measured as 10 minute intervals of longitude between 33 ° and 35° 30' E, or 10 minute intervals of latitude between 18° and 24° 30' S) and by sea surface temperature (20° C to 26.5° C in 0.5° C intervals). The observed number in each depth, longshore distance or temperature interval was compared to the expected number assuming equal density: the latter was calculated from the total number of whales sighted on each leg apportioned to the particular interval by the distance searched in that interval.

Distances from the yacht to each sighting were calculated using Gordon's (1990) photographic method, where distances between the horizon and the whale on an image taken with a known focal length lens can be used to calculate the angle between the vertical and the whale. Distances were measured on a binocular microscope, and yacht to whale distances were computed using a BASIC algorithm, incorporating a correction factor derived from the radar calibration experiments, refraction and the curvature of the earth.

Perpendicular distances of groups from the trackline were calculated for all sightings for which distances were available. The hazard -rate model (Buckland 1985),

$$g(y) = 1 - \exp[-(y/a)^{1-b}]$$

was fitted to the perpendicular distances grouped into 0.5 n. mile intervals to give the probability density function f(0) and its variance V[f(0)]. (The size of the intervals was chosen to provide sufficient data in each interval for a goodness-of-fit test). No measure of the detectability on the trackline, g(0), was made and it was assumed to be 1 (ie. that every whale on the trackline was seen). The abundance estimate (N) of whales in the area surveyed (A) was given by

$$N = [A.n.s.f(0)]/[2L.g(0)]$$

where n is the total number of groups sighted on primary effort, s is the mean group size of confirmed groups, and L is the length of the search track. (The mean group size was taken because there was no significant trend in school size with radial distance from the trackline, $y = 0.133x + 1.61$, $r = 0.01$, $p > 0.05$, where y = group size and x = perpendicular distance in n. miles.) The variance on this estimate (V(N)) was calculated using the delta method,

$$V(N) = [V[f(0)/[f(0)]^2 + V[s]/s^2 + V[n_i/l_i]/[n/L]^2].$$

V[ni/li] was the variance on daily sighting rates, where n_i and l_i were the number of sightings and the search effort of each day (i) respectively. Because of the disproportionate distribution of effort, population estimates were calculated for two strata, the area between Maputo and Magaruque (covered on legs 1 and 3) and the area to the north of Magaruque (covered on leg 2).

Identification photographs were processed and printed on return to the laboratory. Only within-cruise matching was undertaken. Only prints that were deemed sufficiently sharp enough for individuals to be recognised were used in analyses. Although the retention time of the sloughed skin (or moult) markings and dorsal fin scarification is unknown, the dorsal fin scarification is thought to be permanent enough for use over a one-month period.

RESULTS

Observation effort

A total of 630.0 miles was steamed on effort during the survey (Figures 6.2 and 6.3), of which 325.9 miles were undertaken as type 1 effort, with the remaining 304.1 miles as type 2 effort. The distribution of observation effort undertaken by water depth is presented in Table 6.1. The major portion of the area covered to the south of Magaruque Island (legs 1 and 3) was in water deeper than 36.6 m, while to the north of Magaruque Island (leg 2) much of the search effort was undertaken over the Sofala Bank in water depths of less than 36.6 m. On leg 2 the lack of suitable night anchorages near the 183m isobath, and the distances between the 183m isobath and suitable anchorages, resulted in less observation effort in the 36.6-183m interval than originally planned. On all legs the paucity of search effort in water depths of less than 18.3m results from the inability of the yacht to navigate in such shallow waters.

Table 6.1. Observation effort (nautical miles) and densities of humpback whales by water depth interval in southern Mozambique waters.

Depth	Type 1		Type 2	
	Effort	Density	Effort	Density
Leg 1 (14 - 24 August)				
0-18.3m	4.0	0.0	3.5	0.0
18.3-36.6m	9.3	0.537	12.7	0.0
36.6-183m	56.9	0.667	99.8	0.428
Leg 2 (26 August - 4 September)				
0-18.3m	0.3	0.0	1.1	0.0
18.3-36.6m	87.4	0.308	117.8	0.110
36.6-183m	29.2	0.274	23.5	0.213
Leg 3 (6 - 15 September)				
0-18.3m	3.2	0.625	5.9	0.0
18.3-36.6m	42.3	0.756	4.4	0.0
36.6-183m	93.3	0.461	35.4	0.226

Disproportionate search effort by longshore distance in certain areas (Table 6.2) arises from either inclement weather conditions reducing search effort, or the forfeiting of search effort due to time constraints and the trade-off between searching and closure with whales. The total lack of search effort between 21° S and 21° 50' S (the narrow continental shelf east of the Bazaruto archipelago) arises from inclement weather conditions during both transects through this area.

Search effort by sea surface temperature interval is shown in Table 6.3. The temperatures recorded during each leg largely reflect the latitudes in which the legs were undertaken, although it must be noted that major portions of both legs 1 and 3 were undertaken in the region between Ponta Zavora and Maputo which is inshore of the direct stream of the warm southerly flowing Mozambique Current.

Sightings

Totals of 64, 54 and 85 sightings of 92, 75 and 138 whales were made on legs 1, 2 and 3 of the survey respectively (Figures 6.2 and 6.3). During leg 1, 41 whales were sighted during type 1 effort, 42 whales were sighted during type 2 effort and 9 whales were sighted as secondary sightings when no search was being maintained. Thirty-five whales were sighted during type 1 effort during leg 2, while 18 whales were seen during type 2 effort. A further 22 whales were sighted as secondary sightings during this leg. Totals of 78 and 7 whales were sighted during type 1 and type 2 effort during leg 3 respectively. Fifty-three animals were sighted as secondary sightings during leg 3.

Apart from one sighting of a single minke whale (*Balaenoptera acutorostrata*) of the diminutive form (Best 1985), during the second leg of the survey (at 18° 23' S 37° 07' E), all the remaining (99.7%) identified sightings were humpback whales. One sighting recorded as a probable right whale during the first leg remained unidentified and was excluded from analyses.

Mean sizes of confirmed groups of humpback whales were estimated as 1.80 (sd ± 0.71), 1.92 (sd ± 0.75) and 2.16 (sd ± 1.24) on legs 1, 2 and 3 respectively. The sex or age composition of groups could not be determined, although individuals which were accompanied by a calf were assumed to be female. The compositions of groups containing a calf are shown in Table 6.4. The relatively high proportion of cow-calf groups on leg 2 to the north of Magaruque Island (14.8%, compared to 3.1 and 4.7 % on legs 1 and 3 respectively) suggests that this area may be a calving or nursery ground.

Table 6.2. Longshore observation effort (nautical miles) and densities recorded by 10 minute distance interval between 18° S and 24° 30' S off the coast of southern Mozambique.

Latitude	Type 1		Type 2	
	Effort	Density	Effort	Density
Leg 1				
21° 50'-60'	8.3	0.0		
22° 00'-10'	8.3	0.0	4.5	0.444
10'-20'			7.1	0.563
50'-60'	1.1	1.818		
23° 00'-10'			10.8	0.185
10'-20'			12.1	0.165
40'-50'			9.0	0.333
50'-60'			12.2	0.095
24° 00'-10'			10.5	0.095
10'-20'			6.7	0.0
20'-30'			6.1	0.0
Leg 2				
18° 00'-10'	7.0	0.287		
10'-20'	6.9	0.144		
20'-30'	28.7	0.714		
30'-40'	5.1	0.0		
40'-50'	7.7	0.129		
50'-60'	4.6	0.867	31.3	0.096
19° 00'-10'	12.1	0.0	30.3	0.129
10'-20'	7.4	0.135	19.2	0.0
20'-30'	9.4	0.532	8.0	0.625
30'-40'	21.6	0.185	11.0	0.00
40'-50'	4.7	0.851		
50'-60'	1.7	2.253		
20° 00'-10'			1.5	0.666
10'-20'			3.8	0.092
20'-30'			3.8	0.211
30'-40'			10.8	0.196
40'-50'			14.2	0.0
50'-60'			5.1	0.0
Leg 3				
22° 10'-20'	8.2	0.243		
20'-30'	10.1	0.0		
30'-40'	5.0	0.40		
40'-50'	5.8	0.172		
50'-60'	10.4	0.096		
23° 00'-10'	4.9	0.408		
10'-20'	3.8	0.263		
20'-30'	10.3	0.679		
30'-40'	12.2	0.238		
40'-50'			2.5	0.0
50'-60'			7.0	0.143
24° 00'-10'			6.4	0.0
10'-20'			3.5	0.571
20'-30'			4.5	0.222

Table 6.2 (cont.) Longshore observation effort (nautical miles) and densities by 10 minute distance interval between 33° E and 35° 30' E off the coast of southern Mozambique.

Longitude	Type 1		Type 2	
	Effort	Density	Effort	Density
Leg 1				
33° 00'-10'	7.7	0.779	10.0	0.00
10'-20'	8.1	1.358		
20'-30'				
30'-40'			2.9	1.304
40'-50'	10.1	0.792		
50'-60'	2.0	0.0	3.0	1.333
34° 00'-10'	7.2	0.138	0.3	0.0
10'-20'	5.0	0.277		
20'-30'	3.0	2.333		
30'-40'	3.5	1.428		
40'-50'	6.0	0.500		
50'-60'	4.5	0.444	3.1	0.654
35° 00'-10'	0.8	0.00		
10'-20'	10.5	0.0	1.2	0.0
Leg 3				
33° 00'-10'	3.1	0.967		
10'-20'	7.7	0.649	8.5	
20'-30'			10.5	
34° 00'-10'			10.8	0.277
10'-20'	9.4	0.319	0.9	0.0
20'-30'	11.8	0.593		
30'-40'	6.3	1.111		
40'-50'	4.4	1.818		
50'-60'	7.1	0.985		
35° 00'-10'	2.9	3.103		
10'-20'	7.4	0.675		

Table 6.3. Observation effort (nautical miles) and densities by sea surface temperature interval (in degrees Centigrade) off the coast of southern Mozambique.

Temperature (°C)	Type 1		Type 2	
	Effort	Density	Effort	Density
Leg 1				
20-20.5				
20.5-21	5.0	1.6	9.3	0.0
21-21.5	11.2	0.714	8.9	0.112
21.5-22	7.25	0.827	26.8	0.621
22-22.5	2.95	1.695	9.8	1.320
22.5-23	19.8	0.505	14.9	0.268
23-23.5	11.8	0.00	14.0	0.642
23.5-24	0.2	0.00	9.5	0.0
24-24.5	12.8	0.312	7.9	0.253
24.5-25			11.7	0.171
25-25.5			2.3	1.740
25.5-26				
Leg 2				
23-23.5			20.4	0.147
23.5-24	3.8	0.526	6.6	0.0
24-24.5	14.9	0.268	34.6	0.144
24.5-25	35.2	0.227	60.6	0.148
25-25.5	29.6	0.439	14.0	0.071
25.5-26	28.8	0.382	3.1	0.0
26-26.5	3.0	0.0		
Leg 3				
21-21.5	2.4	0.0		
21.5-22	7.4	1.081	5.9	0.0
22-22.5	9.3	1.860	10.3	0.097
22.5-23	25.7	1.170	18.7	0.267
23-23.5	61.2	0.333	1.3	0.0
23.5-24	29.8	0.300	1.5	0.0
24-24.5	2.0	0.0	8.0	0.0
24.5-25	1.0	3.0		

Table 6.4. Composition of groups which included calves.

Date	Group composition
Leg 1	
20-8-91	1 Ad + 1 Ca
20-8-91	1 Ad + 1 Ca
Leg 2	
27-8-91	1 Ad + 1 Ca
29-8-91	2 Ad + 1 Ca
29-8-91	1 Ad + 1 Ca
31-8-91	1 Ad + 1 Ca
01-9-91	2 Ad + 1 Ca
01-9-91	1 Ad + 1 Ca
01-9-91	1 Ad + 1 Ca
03-9-91	1 Ad + 1 Ca
Leg 3	
08-9-91	1 Ad + 1 Ca
09-9-91	1 Ad + 1 Ca
10-9-91	2 Ad + 1 Ca
10-9-91	3 Ad + 1 Ca

Absolute densities

The relationship between photographically-determined distances to ships and radar measured distances is shown in Figure 6.4. Distances measured photographically were slight, but insignificant, underestimates (Chi-square = 0.845, df = 1, $p > 0.25$) of the radar distances, possibly due to the rolling of the vessel placing photographers in the barrel at a slightly lower height than the 10 metres used in calculations. Distances to 37 groups of whales were obtained from photographs, and these were corrected for the error calculated from the radar calibrations ($y = 0.177 + 0.897x$, $r = 0.81$, $p < 0.05$, where x = radar distance, y = photo distance). Figure 6.5 shows the position of these 37 groups relative to the vessel at the time of sighting, and some rounding of angles is evident towards the trackline. Figure 6.3 suggests that most whales were detected at over 1 n. mile from the vessel and this has been ascribed to detectability rather than vessel avoidance.

Frequencies of perpendicular distances of these groups to the trackline are shown in Figure 6.6. The hazard-rate model fitted to these data resulted in a detection function given by the parameters in Table 6.5, and an estimated effective track half-width of 1.62 miles. Population sizes and associated standard errors of 925 (533) and 1,029 (540) were estimated (from parameters shown in Table 6.6) for the southern and northern strata of

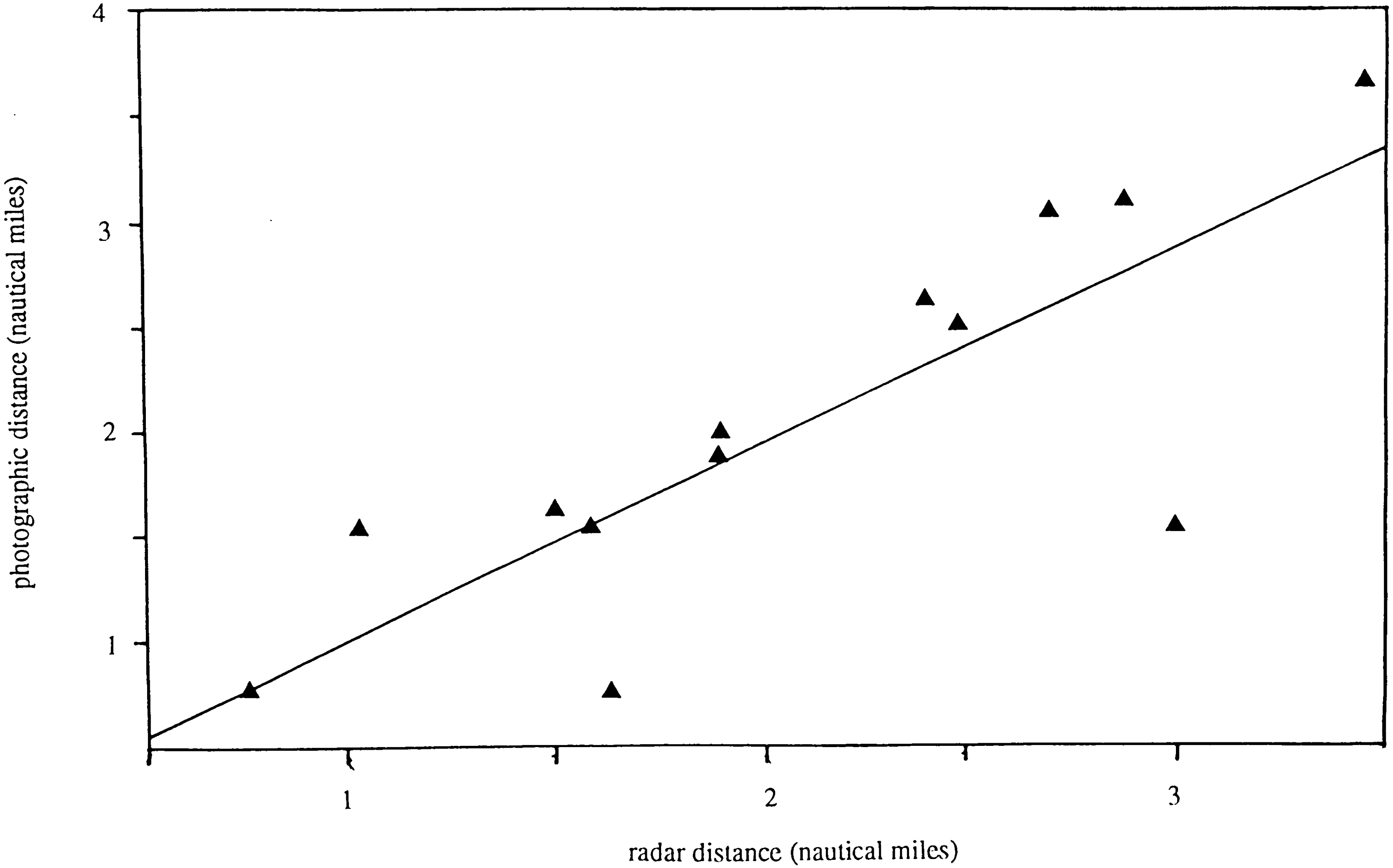


Figure 6.4. The relationship between photographically and radar determined distances from the yacht of ships and fishing vessels photographed during the cruise.

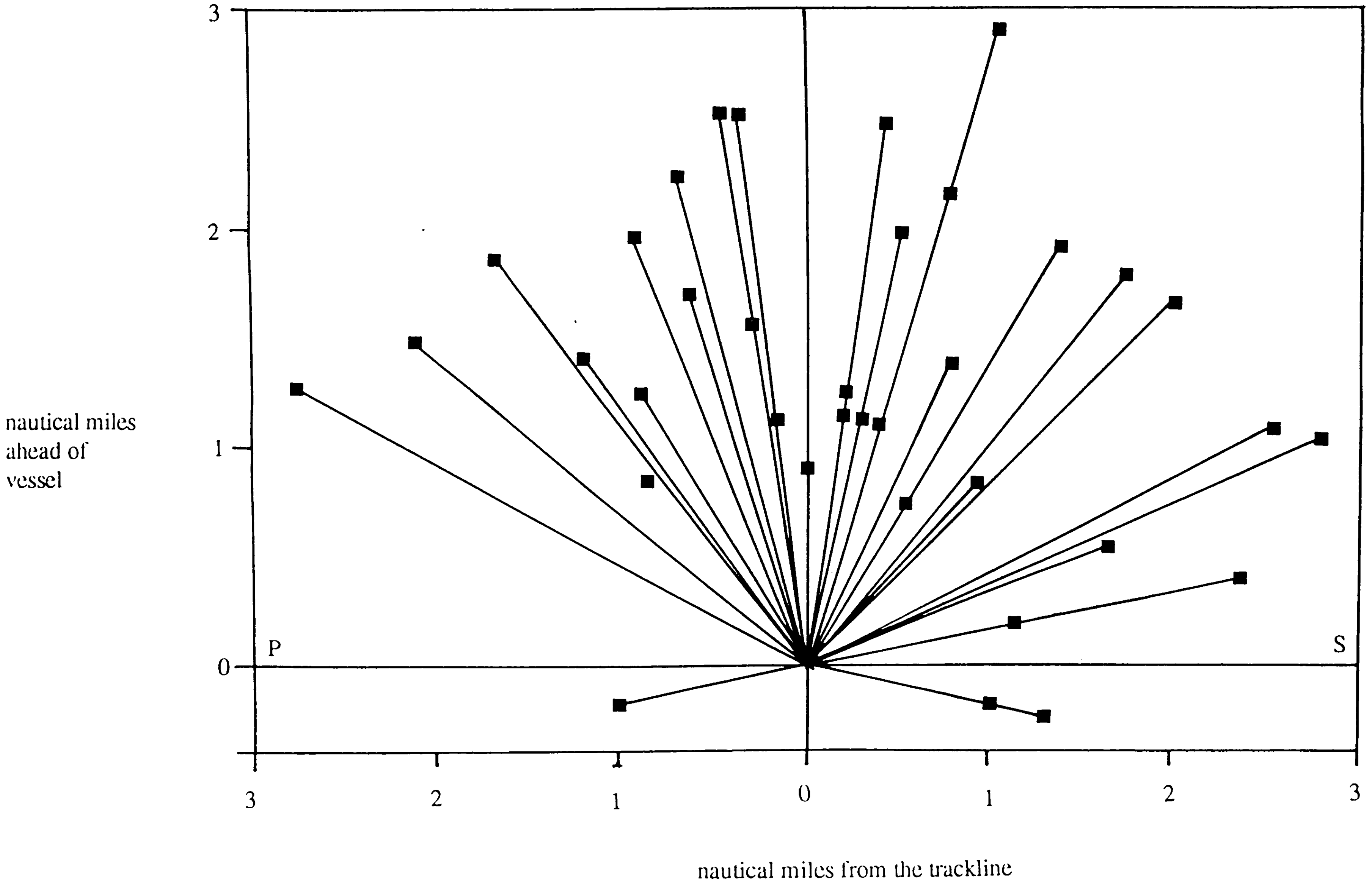


Figure 6.5. Positions of 37 sightings of whales for which photographic distances were obtained in relation to the survey vessel.

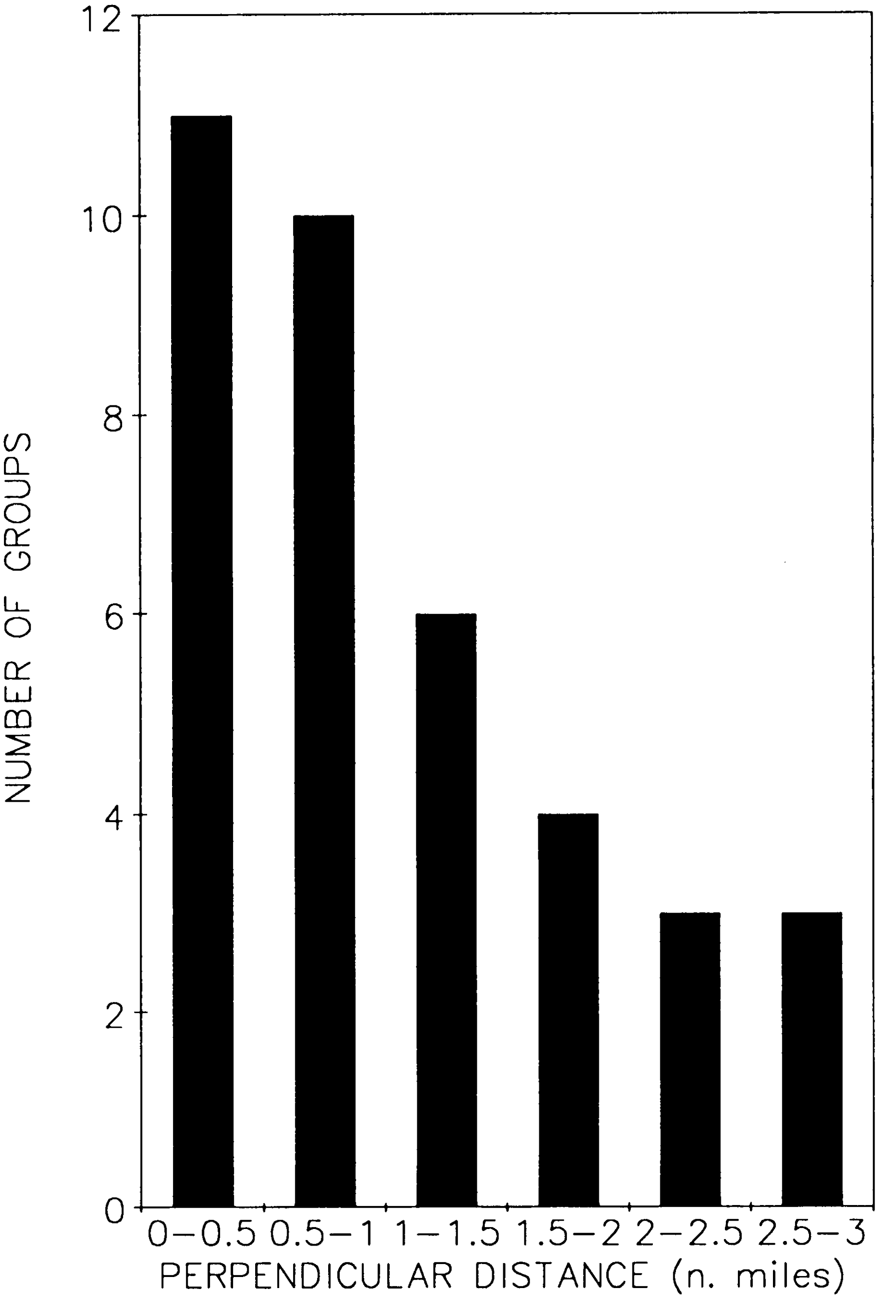


Figure 6.6. Frequencies of perpendicular distances from the trackline of 37 sightings for which photographic distances were obtained.

breeding ground surveyed. In conclusion, a total population size of 1,954 (758) whales was estimated for the southern Mozambique breeding ground. The major source of the variance arose from the variation in school size recorded in confirmed groups.

Table 6.5. The fit of the hazard-rate model, $g(y) = 1 - \exp[-(y/a)^{1-b}$, to the sighting data.

Parameter	Estimate	Std. Error	CV
a	1.066	0.588	0.551
b	2.472	0.886	0.359

Table 6.6. Components of the population estimation equation and their standard errors.

Stratum	n[1]	s	f(0)	A	L	N
Leg 1	28	1.80	0.616	4011	70	1010
	(0.075)	(0.71)	(0.166)			(480)
Leg 3	50	2.16	0.616	4011	139	881
	(0.060)	(1.24)	(0.166)			(547)
South[2]	78	2.00	0.616	4011	209	925
	(0.059)	(1.04)	(0.166)			(533)
North	23	1.92	0.616	8580	116.9	1029
	(0.062)	(0.75)	(0.166)			(540)

1. Standard errors are of n_i/l_i.

2. Legs 1 and 3 combined.

Relative densities

The relative densities of whales sighted by depth interval are shown in Table 6.1. The observed and expected numbers of whales sighted in the 0-36.6 and 36.6-183m depth intervals are shown in Table 6.7. No difference was found in the observed and expected densities recorded on type 1 effort in legs 1 (Chi-square = 3.608, df = 1, $p > 0.05$), 2 (Chi-square = 0.158, df =1 $p > 0.5$) or 3 (Chi-square = 1.958, df = 1, $p > 0.10$). Whales sighted during type 2 effort on leg 1 were in deeper water than expected (Chi-square = 6.682, df = 1, $p < 0.0250$), but sightings during type 2 effort during legs 2 and 3 were too few for significant trends to be determined.

Table 6.7. Observed and expected numbers of whales sighted by depth interval and effort type in each of the survey legs in Mozambique waters..

Depth	Type 1			Type 2		
	exp	obs	χ^2 value	exp	obs	χ^2 value
Leg 1						
0-36.6m	7.8	3	3.608	5.9	0	6.682 *
36.6-183m	33.2	38		36.3	42	
Leg 2						
0-36.6m	25.4	27	0.158	15.1	13	-
36.6-183m	8.7	8		2.8	5	
Leg 3						
0-36.6m	25.6	34	1.958	1.6	0	-
36.6-183m	52.4	43		5.4	7	

* $p < 0.05$

Relative densities of whales sighted by longshore interval of 10 minutes of latitude or longitude are shown in Table 6.2. Table 6.8 shows the observed and expected numbers of whales sighted by degree of latitude or longitude. Greater numbers of whales were sighted between 33° E and 35° 30' E than expected during type 1 effort on both legs 1 (Chi-square = 7.12, df = 1, $p < 0.01$) and 3 (Chi-square = 33.04, df = 1, $p < 0.001$). Densities recorded during type 2 effort on leg 1 showed significantly greater numbers of whales were recorded between 33° and 35° 30' than expected (Chi-square = 6.630, df = 1, $p < 0.025$). Densities recorded in this region during type 2 effort on leg 3 were too low for trends to be established. No significant differences in densities by latitude were recorded during type 1 effort on leg 2 (Chi-square = 1.121, df = 1, $p > 0.25$), and numbers of whales recorded during the type 2 effort in this region were too few for trends to be established. The data recorded on leg 2 suggest therefore that the northernmost limit of the distribution was not determined.

Table 6.8. Expected and observed numbers of whales sighted by longshore interval, by 10 minute interval of either latitude or longitude in Mozambique waters.

Longshore interval	Type 1			Type 2		
	exp	obs	χ^2 value	exp	obs	χ^2 value
Leg 1						
21° 50'-23° 00' S	10.3	3	7.12 *	4.2	6	6.630 *
23° 00'-24° 00' S				16.0	14	
24° 00'-25° 00' S				8.5	1	
33° 00'-34° 00' E	10.1	17		9.5	19	
34° 00'-35° 00' E	14.1	20		3.0	2	
35° 00'-35° 30' E	6.1	1		0.7	0	
Leg 2						
18° 00'-19° 00' S	18.0	15	1.121	4.0	3	-
19° 00'-20° 00' S	15.8	19		8.9	9	
20° 00'-21° 00' S				5.0	5	
Leg 3						
21° 00'-23° 00' S	22.2	6	33.04 *			-
23° 00'-24° 00' S	17.5	14		1.4	1	
24° 00'-25° 00' S	4.5	3				
33° 00'-34° 00' E	6.0	8		1.8	3	
34° 00'-35° 00' E	17.5	26		1. 8	3	
35° 00'-35° 30' E	5.6	21				

* $p < 0.05$

Relative densities of whales sighted by temperature interval are shown in Table 6.3. The observed and expected numbers (assuming equal densities) of whales in each temperature interval (Table 6.9) show that during type 1 effort the whales were sighted in cooler waters than expected on legs 1 (Chi-square = 14.04, df = 3, $p < 0.005$) and 3 (Chi-square = 24.52, df = 2, $p < 0.001$). Densities recorded during type 2 effort on leg 1 showed a similar significant result (Chi-square = 12.78, df = 3, $p < 0.01$). Whales recorded during type 1 effort on leg 2 were distributed without regard to water temperature (Chi-square = 1.881, df = 1, $p > 0.10$). Once again data collected during type 2 effort during legs 2 and 3 were too few for a significant trend to be established.

Table 6.9. Observed and expected numbers of whales sighted by sea surface temperature interval (in degrees Centigrade) in Mozambique waters.

Temperature interval (° C)	Type 1			Type 2		
	exp	obs	χ^2 value	exp	obs	χ^2 value
Leg 1						
21-22	9.5	16	14.04 *	6.6	1	12.78 *
22-23	5.95	11		13.3	20	
23-24	18.0	10		10.5	11	
24-26	7.6	4		11.4	10	
Leg 2						
23-25	16.3	14	1.881	15.8	17	-
25-27	18.6	21		2.2	1	
Leg 3						
21-22	5.3	8	24.52 *	0.9	1	-
22-23	18.9	35		4.40	5	
23-25	50.9	29		1.6	1	

* $p < 0.05$

Interceptions.

A total of 38 groups of 97 humpback whales and one individual minke whale was intercepted by inflatable or the *Zanj*. Dorsal fins of 47 and 50 individual humpback whales were photographed from the left and right aspects, while the ventral surface of the flukes of 25 animals was photographed. However, only 35 individuals could be identified in 64 sharp photographs of the left dorsal fin aspect, 25 animals could be identified in 57 sharp photographs of the right dorsal fin aspect, and 21 animals could be identified from 36 sharp tail fluke photographs. Two resights were identified from left dorsal fin aspects and tail flukes, while three resights were identified from right dorsal fin aspects (Table 6.10). The movement patterns of two individuals were common in all three data sets and they are assumed to be the same individuals.

Eighteen biopsy attempts were carried out with the crossbow, six of which missed the whale, six of which did not retain a sample or broke up and sank, and six of which retained a skin sample. Of the 11 biopsies attempted with the Paxarms immobilisation gun, one misfired, four missed the whale, four were lost or did not retain a sample, while two were retrieved with skin samples. Most samples, however, were far smaller than intended.

Table 6.10. Movement of photographically identified individuals in southern and central Mozambique waters, August to September, 1991.

Date and time	Group composition	Position
Right dorsal fin		
(a)		
3/9/91 14h19	1 Ad + 1 juv	20° 50' S 35° 34 ' E
9/9/91 15h17	6 Ad + 1 "small"	24° 41' S 34° 59 ' E
(b)		
9-9-91 05h45	5 Ad	24° 28' S 35° 21 ' E
9-9-91 05h45	3 Ad	24° 28' S 35° 21 ' E
9-9-91 05h45	4 Ad	24° 28' S 35° 21 ' E
9-9-91 11h00	4 Ad + 1 juv	24° 35' S 35° 20 ' E
(c)		
9-9-91 05h45	3 Ad	24° 28' S 35° 21 ' E
9-9-91 12h30	4 Ad	24° 36' S 35° 15 ' E
Left dorsal fin		
(d)		
3-9-91 14h19	1 Ad + 1 juv	20° 50' S 35° 34 ' E
9-9-91 15h17	6 Ad + 1 "small"	24° 41' S 34° 59 ' E
(e)		
9-9-91 05h45	3 Ad	24° 28' S 35° 21 ' E
9-9-91 05h45	4 Ad	24° 28' S 35° 21 ' E
9-9-91 11h00	4 Ad + 1 juv	24° 35' S 35° 20 ' E
Tail fluke		
(f)		
3/9/91 14h19	1 Ad + 1 juv	20° 50' S 35° 34 ' E
9/9/91 15h17	6 Ad + 1 "small"	24° 41' S 34° 59 ' E
(g)		
9-9-91 05h45	5 Ad	24° 28' S 35° 21 ' E
9-9-91 05h45	3 Ad	24° 28' S 35° 21 ' E
9-9-91 11h00	4 Ad + 1 juv	24° 35' S 35° 20 ' E

Behavioural observations.

Unfortunately, direction of movement was recorded for very few groups. The direction of 12 groups was recorded during leg 1, six of which were moving north and six of which were moving south. Directions of 18 groups were recorded on leg 3, of which 13 were moving northwards and five of which were moving in a southerly or southeasterly direction. The direction of only three groups was recorded during leg 2, of which two were moving north and one was moving south.

Despite no dedicated behavioural observations being undertaken during the cruise, two surface active incidents involving resights of identified individuals deserve mention.

At 05h45 on 9/9/91 a group of five whales was intercepted by the inflatable boat at 24° 28' S; 35° 21' E. These were joined by a further two individuals to form a group of seven which moved eastwards and subsequently split into two groups of three and four each. The group of three turned northwards after the split, and a surface charge was observed between this group and a new group of unknown size. Although contact was not seen, one individual had fresh wounds thereafter. This behaviour resulted in one group of two whales which moved northwards and one group of two whales which moved eastwards. This was the only incident of aggressive behaviour observed during the entire cruise. A further group of an adult and a calf was seen during this time, but was not intercepted. Results of the photographic identifications show that one individual (identified in the field notes as having a white scar on its dorsal fin) was present in the group of five, the northward-moving group of three, and the eastward moving group of two. This individual was sighted, and intercepted, later in the day (at 11h00) in a group of two adult animals some 7 miles to the south. During the second closure, this group was joined by a further two adults and one juvenile. A second identified individual in the group of three (at 05h45) was sighted later (12h30) the same day in a group of four some 10 n. miles to the south east. These resighted individuals had minimum migration speeds of 1.48 and 1.33 knots respectively.

A group of one small and five (possibly six) large humpback whales was sighted moving rapidly northeast at 15h17 on 9/9/91 at 24° 41' S; 34° 21' E. One large individual had conspicuous white flanks on which a yellow - brown diatom film was evident. These individuals were intercepted by the *Zanj* and, despite being approached to a distance of less than 10m, tended to ignore the vessel. Furthermore, no interaction between the whales was observed and although no nuclear animal was identified it appeared as if all animals were chasing each other. They were followed for 50 minutes during which they remained swimming rapidly northwards. Unfortunately, no speeds or distances were recorded during this interception. Photographic identification results show that the white-flanked individual was photographed six days previously accompanied by a juvenile animal some 245 n. miles to the north. This animal had a minimum migration speed of 1.69 knots, although this must be an underestimate given the animal's northward heading when resighted.

Acoustic watches

Despite problems with the hydrophone reception, 20 acoustic watches amounting to 458 minutes were undertaken during the cruise and positions of these are shown in Figures 6.2 and 6.3. Singing whales were heard during 14 of these watches and recordings were made for 113 minutes. Singing whales were distributed from 25° S to 18° 23' S, although no singing was heard over the narrow portion of the shelf between 24° S and Magaruque Island. Despite no whales being heard during the single northernmost acoustic watch, whales were heard some 25 n. miles southeast of this location, suggesting that breeding behaviour occurs as far north as, and possibly further north than, the area surveyed.

DISCUSSION

The population estimate of 1 954 (cv 0.38) whales made during this survey is larger than population estimates of 1,711 and 1,647 made from counts of the northward or southward migration off Cape Vidal during 1990 (Findlay, Best and Borchers 1991; see chapter 5), although these have no associated cv's. However, the levels of statistical precision associated with the estimate suggests no significant difference between population estimates measured off Cape Vidal and on the Mozambique breeding grounds. Because the northern limit of the breeding ground and the proportion of the population present on the breeding ground were not determined during the survey, because g(0) was assumed to equal 1, and because the seaward limit of the distribution was assumed to be the 183m isobath, it is likely that the Mozambique estimate is biased downwards. One source of overestimation could have arisen from the movements of whales during the survey. The southern migration is thought (from the results of a shore based survey at Cape Vidal) to commence in late August, ie. during this survey. Although the southern migration might therefore be thought to affect results of leg 3 (as the ship might be following the migration), the recorded densities of groups suggest no difference in the sighting rates during legs 1 and 3 (Table 6.6).

Furthermore, a high proportion of groups recorded on leg 3 was moving in a northerly or northeasterly direction. It is therefore assumed that the incidence of duplicate sightings on leg 3 was fairly low.

On the other hand, estimates of population size arising from the shore-based counts at Cape Vidal may also be too low, as only groups visible from the shore are surveyed, and the proportion of groups missed may be underestimated (chapter 5). Although the width of the coastal migration is thought to lie inside the visibility limits from the shore, it is possible that a proportion of the population strikes the coast to the north of Cape Vidal. A proposal to survey the northward migration at Inhaca Island, off Maputo, has been suggested by DG and could provide some insight into this effect.

The higher densities than expected of whales recorded on legs 1 and 3 between Ponta Zavora and Maputo presumably result from both the orientation of the coast to the general migration direction and the wider continental shelf in this region compared to the region between Ponta Zavora and Magaruque Island. The narrow continental shelf region results in the strong southerly Mozambique Current flowing close inshore and it is possible that the whales find shelter from this on the wider shelf regions; this is confirmed by the fact that whales were distributed in cooler waters on legs 1 and 3 than expected (ie. inside the current). Furthermore, the localised distribution apparent in the region of, or offshore of, the shallow banks lying parallel to the coastline may have contributed to the higher density in this region. Both Rorvik (1980) and da Silva (in litt.) illustrate the majority of their sightings of humpback whales in the region between 34° 30' and 35° 30' E, but the lack of information on the distribution of survey effort makes the interpretation of their results impossible.

The high proportion of cow-calf groups seen to the north of Magaruque Island on the second leg of the cruise (14.8%) compares favourably with proportions of cow-calf pairs seen on other calving grounds (17% on Virgin Bank (Mattila and Clapham 1989)) and suggests that the northern area is a calving or nursery ground. Sheltered shallow-water distributions of cow-calf pairs have been found on a number of breeding grounds, including Silver Bank (Whitehead and Moore 1982), Hawaii (Herman and Antinoja 1977) and Virgin Bank (Mattila and Clapham 1989). Dawbin (1966) showed that the migration of female humpback whales in the Southern Hemisphere is segregated by reproductive status, and that females undertaking a calving (as opposed to a mating) migration, are the first to arrive and last to leave the breeding ground and could consequently migrate to lower latitudes than other whales. Matthews (1938) described a mean date of parturition for southern humpback whales of mid-August, so an increase in sightings of calves would be expected later in the season. However only a slightly higher proportion of cow-calf pair groups was sighted on the third leg (4.7%) than on the first leg (3.1%) suggesting that cow-calf pairs had not yet migrated southward by the third leg.

No difference in group size was recorded between the three legs (although the photographic identification data show some flexibility in group association). This flexibility however, arises largely from the two behavioural episodes noted on 9 September 1991. The composition of groups which contained a calf show that escorts were present on 31 % of occasions. This is considerably lower than the incidence of escorts in Hawaii, where Herman and Antinoja (1977) and Glockner-Ferrari and Ferrari (1984) found 78.9% and 72.2% respectively of cow-calf pairs to be accompanied by escorts. All escorts sexed in Hawaiian waters were found to be male whales (Glockner-Ferrari and Ferrari 1984), and although the function of the escort is unknown, Herman and Antinoja (1977) have suggested it is protective, while Tyack and Whitehead (1983) proposed that escorts are males waiting for the females to become receptive, and such a reproductive function would provide evidence for post-partum oestrus.

The distances moved by resighted individuals were 245, 10 and 7 n. miles, and minimum speeds of movement were 1.69, 1.48, and 1.33 knots. These speeds are within the ranges reported by other authors (Chittleborough 1953; 1965; Dawbin 1956; Glockner and Venus 1983; Tyack and Whitehead 1983) although it must be noted that a number of these reported speeds refer to actively migrating animals. Although no Discovery mark returns have been recorded on the coast of the African mainland, Olsen (1914) reports two incidents of humpback whale movement between Mozambique and Natal established from the recovery of lost harpoons, although he gives no exact dates or positions for such recoveries. The 245 n. mile movement of the one individual reported here is the first record of a resight reported on the African coast.

The distribution of humpback whales on the Mozambique breeding grounds extended further north than was expected from historical catches in modern whaling and from reports of incidental sightings made since the cessation of humpback whaling. Both relative densities recorded in the northern region of the survey and the distribution of singing whales suggested that the breeding grounds extend further north than 18° S. Although Townsend's (1935) charts illustrate numerous catches in the region of the town of Mozambique (15° S), catches by modern whalers were highest in the region of Inhambane (24° S), and catches in the regions of Quelimane (18° S) and Angoche (16° 30' S) were described by Tonnessen and Johnsen (1982) as being poor. Reeves, Leatherwood and Papastavrou (1990) note the presence of humpback whales in the northern Indian Ocean in the austral winter, but state that at present it is impossible to determine how far north the Area III humpback whales migrate in winter. The highest densities recorded on the cruise were south of 24° 30' S in the region between Maputo and Ponta Zavora. The region to the north of 18° S is characterised by archipelagos and shallow banks similar to those characteristic of the Maputo to Ponta Zavora region. These banks may be sheltered from the southerly flowing Mozambique Current, as with the region to the west of Ponta Zavora, and may be sought-after wintering regions. Future surveys of northern Mozambique waters should be undertaken to define the northern distribution limit of the breeding ground.

CHAPTER 7

PHOTO-IDENTIFICATION OF SOUTHERN AFRICAN HUMPBACK WHALES.

INTRODUCTION

Historical catches of humpback whales off the east coast of southern Africa identified the coastal waters of Mozambique and Madagascar as the principal breeding areas of the Area III population. Two mark-returns link the coastal waters of Madagascar with Antarctic Area III (Rayner 1940), and lost and recovered harpoons link the Durban whaling grounds and Mozambique waters (Olsen 1914). Apart from these historical records, no evidence of links between areas frequented by Area III humpback whales exists.

Humpback whales can be individually recognised through pigmentation patterns and scarification on the ventral surface of the tail (Katona, Baxter, Brazier, Kraus, Perkins and Whitehead 1979, Katona and Whitehead 1981), through scarification and colouration of the lateral flanks (Kaufman, Smultea, and Forestell 1987), and through the shape and scarification of the dorsal fin (Balcomb and Nichols 1978, Katona and Whitehead 1981, Clapham and Mayo 1990). Glockner-Ferrari and Ferrari (1984) utilised underwater photography of colouration and various body features to identify humpback whales in Hawaiian coastal waters. However, it is predominantly markings, scarification and pigmentation patterns on the ventral surface of the flukes that have been used to identify individual humpback whales (Anon. 1990). Photographic identification of the ventral surface of the tail flukes has been utilised in studies of migration links (Darling and Jurasz 1983, Baker, Herman, Perry, Lawton, Straley and Straley 1985, Darling and McSweeney 1985, Kaufman, Osmond, Ward and Forestell 1990, Stone, Florez-Gonzalez and Katona 1990, Darling and Cerchio 1993), calving intervals (Glockner-Ferrari and Ferrari 1990, Baker, Perry and Herman 1987, Clapham and Mayo 1990, Baker, Straley and Perry 1992) and population estimation through mark-recapture analyses (Whitehead 1982, Whitehead, Chu, Perkins, Bryant and Nichols 1983, Balcomb and Breiwick 1984, Perkins, Balcomb, Nichols, Hall, Smultea and Thumser 1985, Whitehead and Glass 1985, Balcomb, Katona and Hammond 1986, Baker and Herman 1987, Alvarez, Aguayo, Rueda and Urban 1990, Katona and Beard 1990, 1991 and Baker *et al.* 1992).

A photo-identification programme was initiated in 1988 (although it included photographs taken earlier) incorporating both of the African east and west coast migration streams and their associated tropical breeding, and Antarctic feeding grounds with the aim of establishing migration links between breeding grounds and the Antarctic feeding regions, and between the breeding grounds and migration streams on the east and west coasts. A further objective of compiling a photo-identification collection was to estimate population sizes through mark-recapture analyses, thereby providing confirmation of the population estimates obtained from shore-based monitoring at Cape Vidal, and during the line-transect survey of animals in Mozambique waters. However, the sample sizes obtained fall far short of sample sizes required for reasonably precise population estimation (Robson and Reiger 1964, in Seber 1982).

METHODS

Sources used to compile the photographic collection included :-

1. Animals photographed during interceptions of groups observed passing Cape Vidal during shore-based surveys between 1988 and 1992.

   Shore-based monitoring of the migrations of humpback whales was undertaken at Cape Vidal, northern Natal, each year between 1988 and 1991, although additional photographs collected in 1992 were included in the database to increases the sample size. An integral part of shore-based surveys was the interception of whales by ski-boat to confirm group size, and to photograph whales for individual identification purposes. Whales were intercepted using a 5.5 m ski-boat and were photographed by a principal photographer (and occasionally a secondary photographer using a personal camera). During 1989 and 1990 photography was carried out from a flying bridge, which gave the principal photographer a 3m elevation above the sea surface.

2. Animals photographed in the coastal waters of central and southern Mozambique during the 1991 line-transect survey of humpback whales within Mozambique waters.

   The distribution of survey effort, and techniques used, off the coast of Mozambique are presented in chapter 6.

In both of the above sources, whales were photographed using a hand-held, motor-driven Minolta x500 camera and 100-300 mm telephoto lens with 400 ASA black and white film, although during 1990 films were exposed and push-processed at 1600 ASA. Films from other field seasons were exposed and processed at 400 ASA. An attempt was made to photograph the left and right aspects of the dorsal fins and flanks, and ventral surfaces of the tail flukes of all animals intercepted.

3. Humpback whales photographed during other research cruises.

   A number of humpback whales, sighted during research cruises at Walters Shoal, in Antarctic Areas II and III, off the west coast of southern Africa, and in Madagascan waters, were photographed for identification purposes. The majority of these photographs was taken on colour positive film and was photographed onto 100 ASA black and white film using a film copy stand. A large number of such photographs was taken by personnel not involved in cetacean research.

4. Animals photographed by the public.

   An appeal was made through the press for clear photographs of humpback whales taken by the public for inclusion in the catalogue. However the response to this appeal was poor (one respondent), probably as a result of South African legislation prohibiting a boat approaching a whale closer than 300 m.

All negatives were inspected on a light table, and images of suitable quality were printed onto 12.5 x 17.5 cm paper. In a number of cases, further underexposed prints were made where these enhanced mark detection. As researchers did not keep track of individual whales during the interception, it was often impossible to match the aspects of any particular individual. Consequently, photographs were divided into left dorsal fin, right dorsal fin, tail fluke and "other" aspect categories. Each photographed aspect of an individual was catalogued on a separate card, and all clear photographs of the particular aspect were fixed to the same card, so that any card could have a number of views of one aspect of a particular individual. Photographs of the dorsal surface of the tail flukes have been included when no ventral aspect photograph was available, and when the trailing-edge of the tail was sufficiently serrated to provide identification. Three photographs of flippers are included in the other aspect category.

All cards within any particular aspect category were compared against all other cards in the same category. Where there was more than one photograph on a card, all photographs were used in making the comparison. The matching process was carried out twice by KPF, with over six months between the two matching attempts.

RESULTS

Totals of 107, 106, 62 and 3 individuals were identifiable from left dorsal, right dorsal, tail fluke and other aspects respectively (Table 7.1). Particularly evident in this table is the low incidence of fluke (as compared to dorsal fin) images from Cape Vidal, reflecting the infrequency of fluking during the migration past Cape Vidal. This factor has necessitated accent being placed on dorsal fin rather than fluke characteristics.

Table 7.2 shows the relative proportions of Mizroch, Beard and Lynde's (1990) generic fluke patterns (Figure 7.2) found in the east and west coast samples. No difference was found in the incidences of "barnacle marked" (small circular scars resulting from barnacles - Plate 7.1) in the sample of tail flukes between the east and west coasts ($\chi^2 = 0.7913$, d.f. = 1, $p > 0.05$). Although the incidence of "tooth-raked" (long parallel scars possibly resulting from killer whales, *Orcinus orca* - Plate 7.2) tail flukes in the samples off the two coasts appeared different, the sample size was too small to test this difference statistically.

Table 7.1 The numbers of humpback whales identified through photography of tail flukes, and left and right dorsal aspects between 1983 and 1992. The locations of photographs include Cape Vidal (CV), Mozambique (MOZ), Madagascar (MD), Antarctic Area II (AII), Antarctic Area III (AIII), Walters Shoal (WS), the South African east coast excluding Cape Vidal (EC), and the South African west coast (WC). Locations are charted in Figure 7.1.

TAIL FLUKES									
YEAR	LOCATION								
	CV	MOZ	MD	AII	AIII	WS	EC	WC	TOTAL
1983								2	2
1984								2	2
1985							2		2
1986				1					1
1987									0
1988	4					1		3	8
1989	5		1					1	7
1990	7							2	9
1991	2	21	1						24
1992	5							2	7
TOTAL	23	21	2	1	0	1	2	12	62
LEFT DORSAL ASPECT									
YEAR	LOCATION								
	CV	MOZ	MD	AII	AIII	WS	EC	WC	TOTAL
1983								1	1
1984									0
1985									0
1986									0
1987									0
1988	10								10
1989	20								20
1990	25								25
1991	7	31	1						39
1992	10							2	12
TOTAL	72	31	1	0	0	0	0	3	107
RIGHT DORSAL ASPECT									
YEAR	LOCATION								
	CV	MOZ	MD	AII	AIII	WS	EC	WC	TOTAL
1983								1	1
1984									0
1985								2	2
1986									0
1987									0
1988	8							1	9
1989	23							1	24
1990	27								27
1991	5	25	1						31
1992	10							2	12
TOTAL	73	25	1	0	0	0	2	5	106

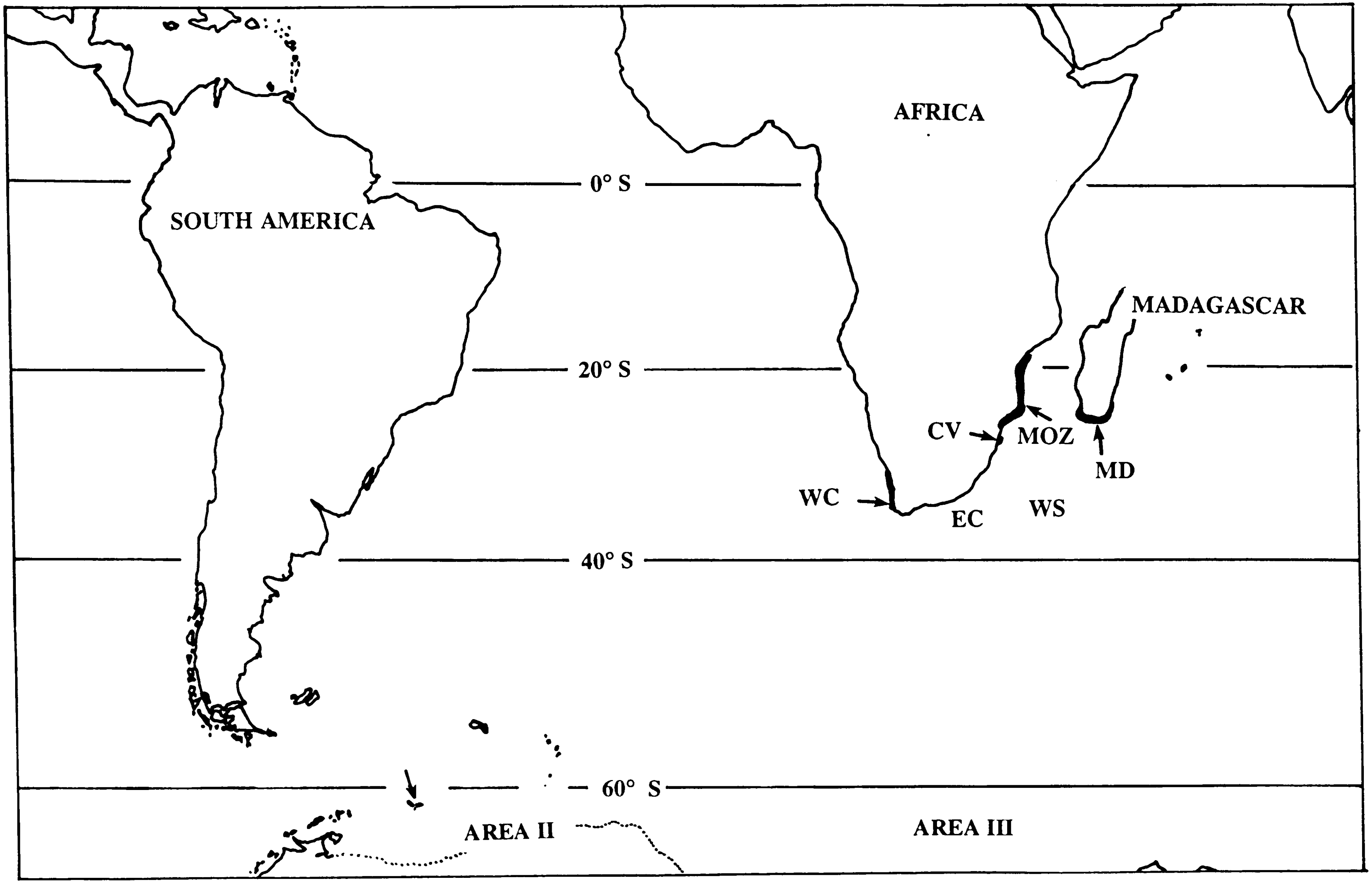


Figure 7.1. Localities of humpback whales photographed for identification purposes in this study. Cape Vidal (CV), Mozambique (MOZ), Madagascar (MD), Antarctic Area II (AII), Antarctic Area III (AIII), Walters Shoal (WS), the South African east coast excluding Cape Vidal (EC), and the South African west coast (WC).

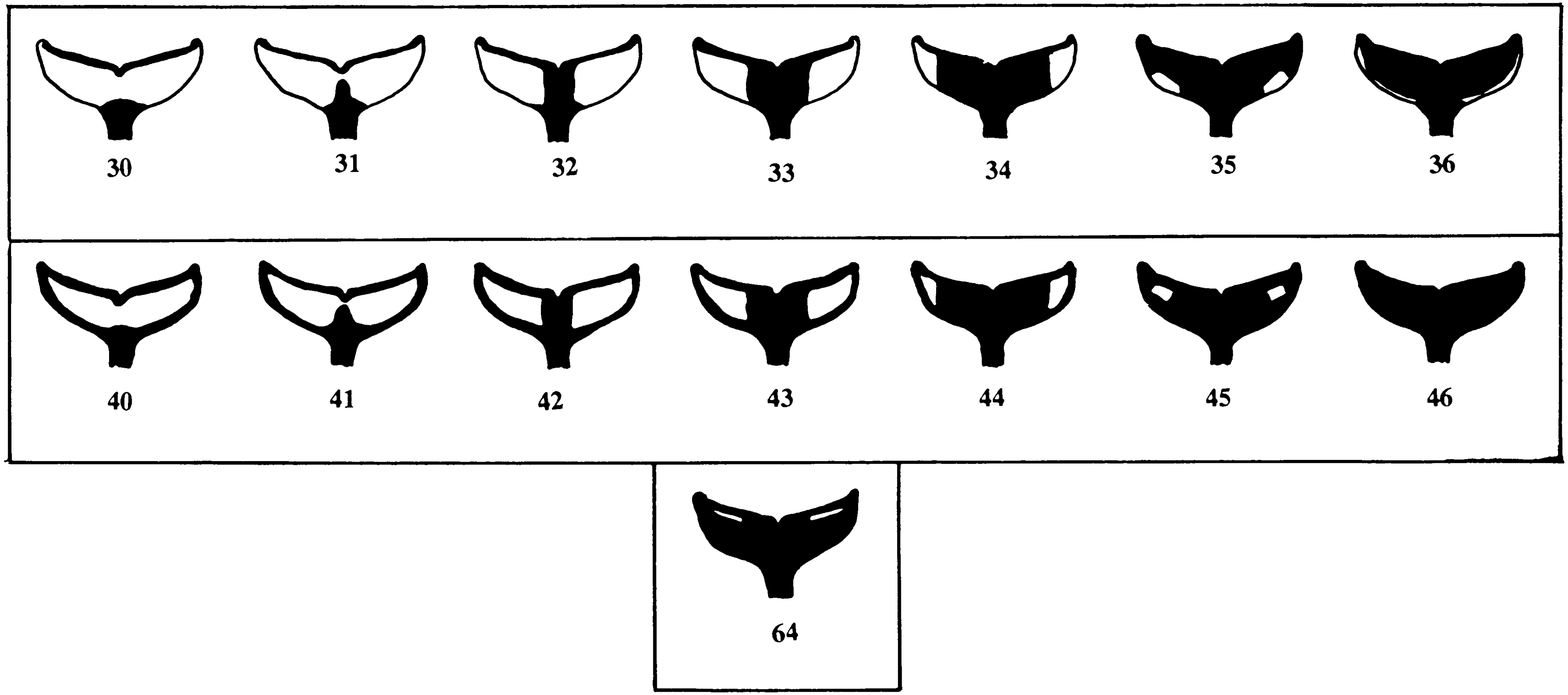


Figure 7.2 Tail fluke patterns described by Mizroch, Beard and Lynde (1990) found in the sample of tail flukes photographed in this study.

Table 7.2. Comparison of the of fluke patterns present in the samples of flukes from the east and west coasts. Photographs in which part of the fluke have been obscured have not been included in this table.

Pattern	West coast	East coast
Fluke Pattern[a]		
30	1	5
31	1	2
32	1	2
33	1	3
35	0	1
40	1	10
41	0	3
42	2	5
43	0	3
45	2	0
46	1	2
64	1	2
Total	11	38
Scarification		
"Barnacle scar"	5	23
"Tooth rake"	5	0

a: (Figure 7.2, after Mizroch, Beard and Lynde 1990)

The only definite resighted individuals (repeat photographs of an individual taken during a different interception) of dorsal fins and tail flukes were three intra-season resighted individuals made during the 1991 survey in Mozambique waters and reported in Chapter 6 (Table 6.10, Plates 7.3 to 7.9). Three "possible" resighted individuals were found in the left dorsal aspect category (Table 7.3, Plates 7.10, 7.11, and 7.12), although some speculation exists as to the validity of these. No "possible" resighted individuals were found in the right dorsal or tail fluke aspect categories. Kaufman *et al.* (1987) note that, with the exception of "damaged or highly anomalous dorsal fins", differences in dorsal fin shapes are difficult to discriminate. Plate 7.13 shows two images of an animal taken from slightly different angles, and the difference in orientation of marks is clearly evident. A further compounding factor in matching individuals from dorsum scarring, is the extent of what appears to be desquamation, in the photographs from both Cape Vidal and Mozambique (Plate 7.14). Sears, Williamson, Wenzel, Berube, Gendron and Jones (1990) note that desquamation caused some errors in the matching of blue whales from dorsum pigmentation.

Table 7.3 Dates and positions of marking and possible resightings of individuals from the left dorsal aspect.

IND.	MARKED		RECAPTURED		POP. ESTIMATE	
	DATE	POSITION	DATE	POSITION	ESTIMATE	CV
a	14-07-89	Cape Vidal	23-08-91	22° 55' S 35° 55 E	335	0.68
b	14-07-88	Cape Vidal	08-07-89	Cape Vidal	114	0.58
c	16-07-89	Cape Vidal	20-07-90	Cape Vidal	272	0.71

Position of Cape Vidal is 28° 07' S 32° 33' E.

Bell (1974) stated that the probability of zero marked individuals in the second sample (P) could be calculated as

$$P = (N - n1)!(N - n2)!/[N!(N - n1 - n2)!] \quad (1)$$

where N = the size of the population and $n1$ and $n2$ the size of the first and second sample respectively. For example, assuming a population size of 1711 animals in 1990 (from shore-based counts), no immigration or emigration between 1989 and 1990, and no mark loss between samples, the probabilities of zero recaptures from the 1989 and 1990 left and right dorsal aspect samples are

$(1711 - 20)!(1711 - 28)!/[1711!(1711 - 20 - 28)!]$ for the left

and

$(1711 - 23)!(1711 - 27)!/[1711!(1711 - 23 - 27)!]$ for the right.

As these are the largest inter-season samples it can be seen that the probabilities of making any matches are extremely low. Robson and Reiger (1964, in Seber 1982) give mark and recapture samples sizes required for estimation of the population size with 50, 25 and 10 % precision, and the sample sizes obtained here are too low for confirmation of the population size measured through shore-based surveys.

Hammond (1986) provides a comprehensive review of mark-recapture techniques for estimating the size (N) of a whale population. Included in these techniques is the Petersen estimator

$$N = n1.n2/m \qquad (2)$$

where n1 and n2 are the sample sizes of the first and second samples respectively, and m the number of individuals common to both samples. The Petersen estimator requires the following assumptions to be met (Seber 1982).

1. The population, N, is closed (so that no immigration, emigration, deaths or births occur between samples).

2. All individuals have the same probability of being caught in the first sample.

3. Marking does not affect the catchability of the individual.

4. The second sample is a simple random sample.

5. No marks are shed between samples.

6. All marks are reported in the second sample.

Chapman (1951, in Seber 1982) found the Petersen estimator to be biased for small samples, and modified it to

$$N = (n1+1)(n2+1)/m+1)$$

with an estimate of its variance given by

$$\text{var } N = (n1+1)(N2+1)(n1-m)(n2-m)/(m+1)^2(m+2).$$

Assuming a closed population, and that the possible resightings recorded from the left dorsal aspect are definite resighted individuals, then Chapman's (1951) modified estimator, results in population estimates and associated cv's as shown in Table 7.3. These are clearly underestimates of the east coast population sizes as recorded from both shore-based and line transect surveys, and certainly cannot be considered valid given the extremely small sample of resighted individuals.

The lack of resightings off Cape Vidal within one season (compared to the resightings off Mozambique) may be indicative of the lack of milling off Cape Vidal during the migration. However, interceptions were only carried out during peak migration periods when the frequency of milling would be expected to be low.

DISCUSSION

The majority of mark-recapture analyses on photo-identified humpback whales has been carried out using pigmentation patterns and scarification of the ventral surface of the tail flukes (Anon. 1990), presumably because the information content of these markings is high. As found off the east coast of Australia by Bryden (1982, in Kaufman *et al.* 1990), the incidence of fluking behaviour during the migration off Cape Vidal appeared relatively low compared to fluking on the breeding grounds. Although lateral flank pigmentation has been used to identify humpback whales in Australia where a high proportion of the whales has white-marked flanks (Kaufman *et al.* 1987), the proportion of white-flanked animals in southern African waters is far lower, so that this technique could not be used in this study.

Dorsal fin and dorsum scarring appears to have been poorly utilised as a recognition feature for humpback whales, compared to ventral fluke markings. Although it has been suggested by Katona and Whitehead (1981) as a suitable identification characteristic, they note that variation is less distinctive than in tail flukes, and cite a personal communication of C. Mayo, that dorsal fin scarring has been seen to change between years. Clapham and Mayo (1990) note however that variation in the shape, size and scarring of the dorsal fin is almost as useful as ventral fluke markings in identifying individuals over long periods. Clapham (in litt.) states that dorsal fin scars can range from major to minor, with the former stable over long periods, although the latter may fade or merge with new scars, and that it may be difficult to identify certain individuals if they were only seen once every few years. Glockner-Ferrari and Ferrari (1990) recognised individual humpback whales over a twelve year period, from "body pattern identification", although it must be noted that features used in identification included pigmentation patterns of the flippers, throat grooves, abdomen, flanks and flukes, spatial-numerical patterns of the lip grooves, as well as the shape of the dorsal fin. Schilling, Seipt, Weinrich, Frohock, Kuhlberg and Clapham

(1992) evaluated the feasibility of using dorsal fin marks and shape to identify sei whales, and noted that not all individuals were identifiable, and that changes in mark patterns could make inter-season recognition difficult. Chu and Nieukirk (1978) note that dorsum scaring of humpback whales may change over time, and suggest that a study of such changes would be beneficial. Clapham (in litt.) states that no information on the permanence of dorsum scarification has been published. The permanence of marks can be estimated through double marking experiments, where two different types of marks are utilised to determine mark loss rates (eg. as carried out for southern right whales by Payne, Brazier, Dorsey, Perkins, Rowntree, and Titus 1983). Hammond (1986) recommends that a comprehensive double mark study be undertaken on humpback whales (using dorsal fins and ventral fluke markings) to determine the permanence of ventral fluke markings, although here it is recommended that the relative stability of ventral fluke patterns be used to identify permanence of dorsum markings.

The majority of mark-recapture analyses carried out on humpback whales in the western North Atlantic Ocean have utilised the Petersen estimator (Whitehead 1982, Whitehead, Chu, Perkins, Bryant and Nichols 1983, Balcomb and Breiwick 1984, Perkins *et al.* 1985, Whitehead and Glass 1986, Balcomb, Katona and Hammond 1986, Baker and Herman 1987, Alvarez, Aguayo, Rueda and Urban 1990, Katona and Beard 1990, 1991, Baker *et al.* 1992). Hammond (1986) notes that births and deaths in the population will result in a poor approximation to population closure, although if only mortality occurs between the two samples then the Petersen estimator is valid for the first sample. If only birth or recruitment occur between samples then the estimate is valid at the time of the second sample. Hammond (1986) has shown that given a population N at the time of the first sample, an average probability of survival of α and a recruitment rate of β then the Petersen estimate N is biased by β/α at the first sample and by $1/\alpha$ at the second sample, $N(\alpha+\beta)$. Using Chittleborough's (1965) mortality rates Whitehead (1982) suggests the size of the population at the second sample is overestimated by over 10t %, where t is the number of years between samples.

Whitehead (1982), Hammond and Larsen (1985), Whitehead and Glass (1986) and Baker and Herman (1987) have used the Jolly Seber method (Jolly 1965, Seber 1965, both in Seber 1982) to estimate humpback whale populations. This method is based on two equations, the estimate of the number of marked animals in the population at each sample, and a general form of the Petersen estimator. The method makes fewer assumptions and gives estimates with wider confidence intervals, than the Petersen estimator which results in more precise estimates, although requires stricter assumptions to be met.

Despite the majority of mark-recapture estimates being determined through recognition of ventral fluke patterns, violations of assumptions may be present in both methods. Hammond (1986) lists three components to equal probability of natural making of cetaceans, namely :-

- all individuals must have an equal probability of being sighted, prior to marking.

This does not appear to hold true at Cape Vidal, where the interception of groups is dependent on it being sighted from the shore, and the sightability of groups is affected by distance offshore, sighting conditions, and possibly by group size and behaviour. However provided these are random effects (so that the same whales do not have the same probability of sighting each year), then the second sample will still be a random sample of those photographed on the first occasion.

- all individuals must have an equal probability of being photographed once sighted.

Hammond (1986) and Perkins, Balcomb, Nichols, Hall, Smultea, and Thumser (1985) have noted that heterogeneities in marking (or recapture) probabilities may arise through different frequencies of fluking behaviour by different age or sex classes of the population. Kenney and Winn (1987) found seasonal differences in the incidence of fluking of humpback whales, with fluking being more common in the late season. The relative infrequency of fluking overall at Cape Vidal has been mentioned already, and additionally there appeared to be considerable variation in the frequency of fluking, even within members of the same group. Such heterogeneity would violate the second and fourth assumption in the Petersen and the first assumption of the Jolly Seber methods. Although unlike fluking, all individuals have to surface to breathe, so that dorsal fins are exposed for photography, some individuals are elusive during interceptions (KPF pers. obs.) so that heterogeneity in capture probabilities may occur. Nevertheless, such heterogeneity is likely to be less than that for fluking.

- all photographed individuals must have an equal probability of being recognised from the photograph.

Two factors to be considered here are the quality of the photograph, including for example glare and focus, and the extent of marking possessed by the individual. Although Hammond (1986) states that poor photographs and individuals with indistinct marking may be ignored as if never photographed, the latter will result in an underestimate of the population (in that the technique would only estimate the population of suitably marked individuals).

It has not been possible to estimate the size of the east coast humpback whale population or to determine the inter-relationships between the Mozambique and Madagascan breeding grounds, between these grounds and Cape Vidal, and between the western Indian Ocean and the Antarctic feeding areas through photo- identification. This is largely as a result of the small sample size of photographs, which has stemmed from the inaccessibility of certain of these migratory destinations (Mozambique in years other than 1991, Madagascar in all years, and Antarctic Area III in all years), and the lack of boat time for interceptions off Cape Vidal in certain years (particularly in 1991). Given that larger samples could be obtained, the technique could provide a third population estimate, against which the population estimates obtained in chapters 5 and 6 could be evaluated. However, the expense and effort required to obtain a large sample of resighted individuals may well preclude the use of this method off the east coast of southern Africa.

Furthermore, prior to using dorsal fin shape and dorsum scarring for mark-recapture estimate, it is recommended that the permanence of dorsal marking be assessed through double marking (dorsal fin and tail fluke photo-identification) as suggested by Hammond (1986).

CHAPTER 8

SUMMER INCIDENCE OF TWO HUMPBACK WHALE CALVES IN SOUTHERN AFRICAN WATERS.

INTRODUCTION

The migrations of Southern Hemisphere humpback whales (*Megaptera novaeangliae*) from austral summer regions where they feed almost exclusively on krill (*Euphausia superba*), to winter breeding grounds in temperate and tropical waters have been documented by numerous authors (Risting 1912, Olsen 1914, Hinton 1925, Harmer 1928, 1931, Kellogg 1929, Matthews 1938, Rayner 1940, Mackintosh 1942, Chittleborough 1953, 1958, 1965, and Dawbin 1956, 1966). Both conception and birth occur on the northern winter ground and gestation is approximately 11 months, during which the pregnant female makes a summer migration to the southern feeding ground. The duration of lactation of 11 months includes a second summer migration to the feeding ground, and weaning occurs during the following northward migration, although solid food may be ingested by the calf prior to this (Dawbin 1956, Chittleborough 1965). Olsen (1914) noted that juvenile humpback whales could be found year-round off the west coast of South Africa.

MATERIALS AND METHODS

An emaciated male humpback whale was found stranded dead at the Berg river mouth (32° 40' S; 18° 03' E) on 8 February 1982 and was assigned a reference number of PBB 82/5. A female humpback whale was found ensnared and dead in the buoy - line of a rock lobster trap approximately 5 n. miles south west of Saldanha Bay (33° 01' S; 17° 58' E) on 14 December 1990, and was assigned a reference number of PBB 90/40. Although cut adrift at the time, it was retrieved at sea the following day and towed to a slipway at Saldanha Bay harbour where it was examined a day later. The examination of both included *inter alia* external morphometric measurements, examination of the skin for ectoparasites and epizooites, and collection of a sub-sample of stomach contents.

RESULTS

The lengths of PBB 82/5 and PBB 90/40 were 6.45 and 6.15 m respectively. From analysis of foetal length data, Matthews (1938) found the modal date of mating of southern humpback whales to occur in September, with the birth of a 4.5 - 5.0 m calf occurring eleven months later. Chittleborough (1954) found a gestation period of 11.5 months, with conception occurring in August and the birth of a 4.2m calf the following July or August. Comparison of the 6.45 m and 6.15 m lengths with growth data presented by Matthews (1938) and Chittleborough (1958, 1965) suggests that PBB 82/5 and PBB 90/40 were approximately 6 1/2 and 4 1/2 months old respectively. Although Matthews (1938) states that a sudden spurt of baleen growth occurs at weaning when the individual is between 7 and 8 m, or about five months old, he provides no evidence for this; the shortest baleen he figures is 18 cm long from a 7.25 m long individual. Furthermore, Matthews (op cit) based his time of weaning on this sudden spurt in the growth of baleen. Chittleborough (1958,1965) however, found that many sexually mature, non - pregnant females with no evidence of recent parturition, were lactating off the west Australian coast in June and July and suggests weaning occurs approximately 10.5 to 11 months after birth, when the calf might be 8.7 to 8.9 m long. Furthermore, Chittleborough (1958) found no increase in the baleen length at 7 to 8 m in body length (although he too provides no supporting data). The length of the longest baleen plates of PBB 82/5 (18.5 cm) and PBB 90/40 (16.9 cm) seem to fit Matthew's (1938) expected lengths for a 6.45 or 6.15 m calf if no spurt in baleen growth occurs. Olsen (1914) reports baleen lengths of 7 cm on a calf of 6.5 m, but it was not clear how his measurements were taken.

No contents were found in the stomach of PBB 82/5 apart from a "reddish-brown" liquid. The only prey recorded in the stomach of PBB 90/40 was young adults of the stomatopod species, *Pterygosquilla armata capensis.* Griffiths and Blaine (1988) found this to be the only stomatopod species occurring to the west of Cape Point, with the distribution off the west coast corresponding to terrigenous mud beds. Although predominantly a benthic species, the occurrence of *P. armata capensis* in stomachs of pelagic predators such as jackass penguins, cormorants and snoek, (Rand 1960a, 1960b, Nepgen 1979, Dudley 1987 in Griffiths and Blaine 1988) implies some pelagic swarming behaviour.

Ectoparasites and epizooites of both PBB 82/5 and PBB 90/40 included coronulid barnacles (up to about 3 cm in diameter) and cyamid whale lice. Scarff (1986) notes that little is known of the natural history of *Coronula diadema* or *C. reginae*, although it is generally believed that the life span is a year or less. Angot (1951 in Scarff 1986) reported large (2.5 to 5 cm) *C. diadema* on humpback whales taken off Madagascar between mid-June and mid-August, which by September had dropped off and been replaced by larvae, so that by October small sessile barnacles were attached. According to Olsen (1914) humpback whales moving past Benguela (southern Angola) in June/July were densely covered with barnacles, but those migrating in October were almost clean or carrying only very small barnacles. The 2 to 3 cm coronulid barnacles found on these individuals in December and February suggest infestation took place to the north some months before their death.

DISCUSSION

The December occurrence of humpback whales off the South African west coast is considerably later than the peak seasonal abundance measured in October by Olsen (1914). However, reports of humpback whales off the African west coast in summer months include numerous catches off Walvis Bay in January recorded by Townsend (1935), reports of Keeler (in Best and Shaughnessy 1979) of "a great many humpback whales" off Hollams Bird Island, Namibia in January 1829, reports by Olsen (1914) that immature animals could be found off Saldanha bay in summer months, and incidental sightings off the south western Cape coast in December, January and February in recent years (Findlay unpubl.)

The relatively low incidence of food in stomachs of humpback whales on breeding grounds and the decrease in blubber thickness as the breeding season progresses suggest that little or no feeding occurs during the breeding migration compared to the feeding migration in Antarctic waters (Olsen 1914, Matthews 1938, Chittleborough 1965, Dawbin 1956, Bannister and Baker 1967). Matthews (1938) reported two humpback whales taken off Saldanha Bay (one in June and one in September) which had recently fed on fish, while Olsen (1914) presented a photograph of a stomach of a humpback whale filled with small fishes taken at Saldanha Bay. These reports and a sighting of humpback whales feeding off Port Nolloth in May 1992 (Mr M.A. Meyer pers. comm.) (albeit all in winter) suggest that humpback whales may well feed opportunistically in the Benguela system during migrations. Dawbin (1956) noted that there is some evidence that a small number of humpback whales remain in New Zealand waters during summer, feeding on *Munidia gregaria* rather than completing the migration to the Antarctic feeding grounds. Paterson and Paterson (1984) found humpback whales off the Queensland coast of Australia as late in the year as December, and agree with the suggestions of Chapman (1974) and Chittleborough (1965) that such animals probably undertake late migrations, rather than no migrations at all. Although the presence of PBB 82/5 in temperate waters in February suggests that this animal did not make the feeding migration, its emaciated state and the fact that it was stranded makes interpretation difficult.

Baraff and Weinrich (1993) found that North Atlantic humpback whales can wean their calves in autumn while still on the high latitude feeding grounds, prior to the breeding migration, although Chittleborough (1965) speculated that after 6 months southern hemisphere humpback calves may supplement their diet with euphausids. It is assumed that PBB 90/40 was supplementing its milk diet, rather than having weaned (although there was no indication of fatty milk-like fluid in the stomach). This record not only provides evidence of a calf feeding on solid food at an estimated 4 1/2 months of age, but also of summer feeding in temperate waters as found by Dawbin (1956). It is also the first record of stomatopod remains in a whale stomach (Manning *in litt*).

CHAPTER 9

CONCLUSIONS

The ultimate objective of the programme is to provide an abundance estimate for the population of humpback whales migrating along the east coast of South Africa, and to determine, if possible, the recovery rate of this population. Initial emphasis, however has been placed on describing the migration characteristics, determining the optimum period for measuring changes in annual abundance of the species off the northern Natal coastline, and identifying the tropical and polar destinations of this migration stream.

The close proximity of the migration to the coast suggested that shore-based visual monitoring would be the most suitable technique for estimating population sizes and associated annual changes in abundance, and to describe migration characteristics. Reviews of the methodology of shore-based visual surveys to estimate the size of whale populations have been provided by Reilly (1984) and Hiby and Hammond (1989), and such surveys have been used to estimate the population sizes of Californian gray whales (*Esrichtius robustus*) off the Californian and Alaskan coasts (see Reilly 1984), bowhead whales (*Balaena mysticetcus*) migrating past Pt. Barrow in Alaska (Krogman, Rugh, Sonntag, Zeh and Ko 1989, Zeh, George, Raftery and Carroll 1991) and the Australian east coast humpback whale stock (Bryden 1985, Bryden *et al.* 1990, Paterson and Paterson 1984, 1989 and Paterson 1991).

The characteristics of the migration measured by shore-based tracking, have been analysed in chapter 3. The measurements of such characteristics play an important role in the meeting of assumptions required in population estimation through shore-based surveys, and in comparing population estimates between years. Furthermore the projection of groups not seen to cross the midline of the observation area, across that midline, requires that the mean speed and direction of the migration be estimated.

Both migration characteristics and observation conditions are critical considerations in choosing the optimal period for monitoring annual changes in abundance. The 1990 surveys have shown that both of these factors are more favourable for monitoring during the northward migration than during the southward migration. One aspect in favour of monitoring the southern migration, however is the presence of calves in the migration from the breeding ground. Although Poole (1984) estimated the minimum production of gray whale calves from shore-based surveys of their northward migration off California, it is felt that there would be considerable underestimation of the number of calves seen from Cape Vidal. Interceptions by boat carried out during the survey however would access cow-calf groups, and could possibly over time, provide an estimate of calving intervals from photo-identification, as carried out by Glockner-Ferrari and Ferrari (1984), Perry, Baker and Herman (1990), Baker, Perry and Herman (1987) and Baker, Straley and Perry (1992). However this advantage is outweighed by the more optimal visual conditions and migration characteristics found during the northward migration, and the fact that the whales are not forced to converge on the coast during the southward migration.

The primary aim of this thesis, the estimation of the size of the migration of humpback whales off northern Natal, has been undertaken in chapter 5, and many of the parameters required in this estimation have been analysed in chapters 3 and 4. Reilly *et al.* (1983), Reilly (1984) and Hiby and Hammond (1989) note a number of verification analyses that must be carried out in estimating population sizes and changes in abundance from shore- based visual surveys, including :-

1) Not all individuals pass within visual limits of observers and the proportion of the population passing outside of this limit must be estimated.

The proportion of the population that passes Cape Vidal outside limits of visibility is at present unknown. Although it could be argued that the comparable estimates made off Cape Vidal and in Mozambique waters suggest a high proportion of animals pass within view at Cape Vidal, the northern limit of the Mozambique breeding ground was not covered and is at present unknown (Reeves, Leatherwood and Papastavrou 1990), the entire population may not have been present on the Mozambique breeding ground at the time of the survey, and g(0) was assumed to be 1 (all animals on the trackline were assumed to have been sighted), so that the population estimate obtained may well have underestimated the population. Unfortunately the project has had neither the staff nor the resources to undertake a cost-effective independent survey to determine the proportion of the Mozambique breeding ground population passing outside of the observers visibility limits. In any case the low density of groups passing Cape Vidal over an extended period, precludes the use of either a ship or aircraft for a cost-effective offshore survey at this time. Furthermore, the south-west to north-east orientation of the Mozambique coastline (along which the breeding grounds lie), results in some uncertainty as to how far offshore such an independent assessment needs to be undertaken. It is recommended that this independent assessment be taken co-incidentally with shore-based surveys as soon as densities allow. Such a survey would require offshore transects to be surveyed across the migration stream in the vicinity of and co-incident with the shore-based programme, to a distance offshore at which whales are no longer detected.

Butterworth, Borchers and Challis (unpub.) have estimated the southern ocean humpback whale population south of 60° S at 5500 (0.23) and 6900 (0.24) from the 1978/79-1983/84 and 1985/86-1990/91 circumpolar IDCR cruises respectively, although these estimates are being revised at present (Butterworth, pers. comm.). Extrapolation of these estimates to the area south of 30° S, based on Japanese Scouting Vessel data resulted in a circumpolar abundance estimate of 12 000 (0.41) individuals (Borchers 1992). The proportion of the Area III stock that undertakes the migration past Cape Vidal is almost totally unknown, as is the inter-relationship of this migration stream and migrations to the rest of the western Indian Ocean, and the assumption that equal proportions of the population are migrating past Cape Vidal each year may be violated. Furthermore Matthews (1938) notes the presence of humpback whales off South Georgia during winter, and suggests that not all animals make the migration to the breeding grounds each year.

2) Heterogeneities in sighting probabilities exist within the area monitored by observers, and groups missed by observers within their view must be taken into consideration.

Heterogeneity in sighting probability is caused by distance from the observer, weather conditions, whale behaviour and group size. As regards distance offshore, whales are seldom distributed randomly with respect to the observer in shore-based surveys. Consequently, the distribution of sightings with perpendicular distance from the observer may represent either the probability density function of sighting groups with distance, or the true distribution of whale groups. A problem inherent in the survey method is that as the limit of visibility is a radius, groups passing through the visible area at different perpendicular distances from the observers will have different sighting probabilities, regardless of any decline in sightability resulting from diminished cues from distant animals (Figure 9.1). The distribution of radial distances at which groups were sighted provides an unbiased sighting probability function, if sightability conditions and the rate of cue production are constant with distance offshore. It does not, however, overcome the problem of the radial visibility limit, and the true offshore

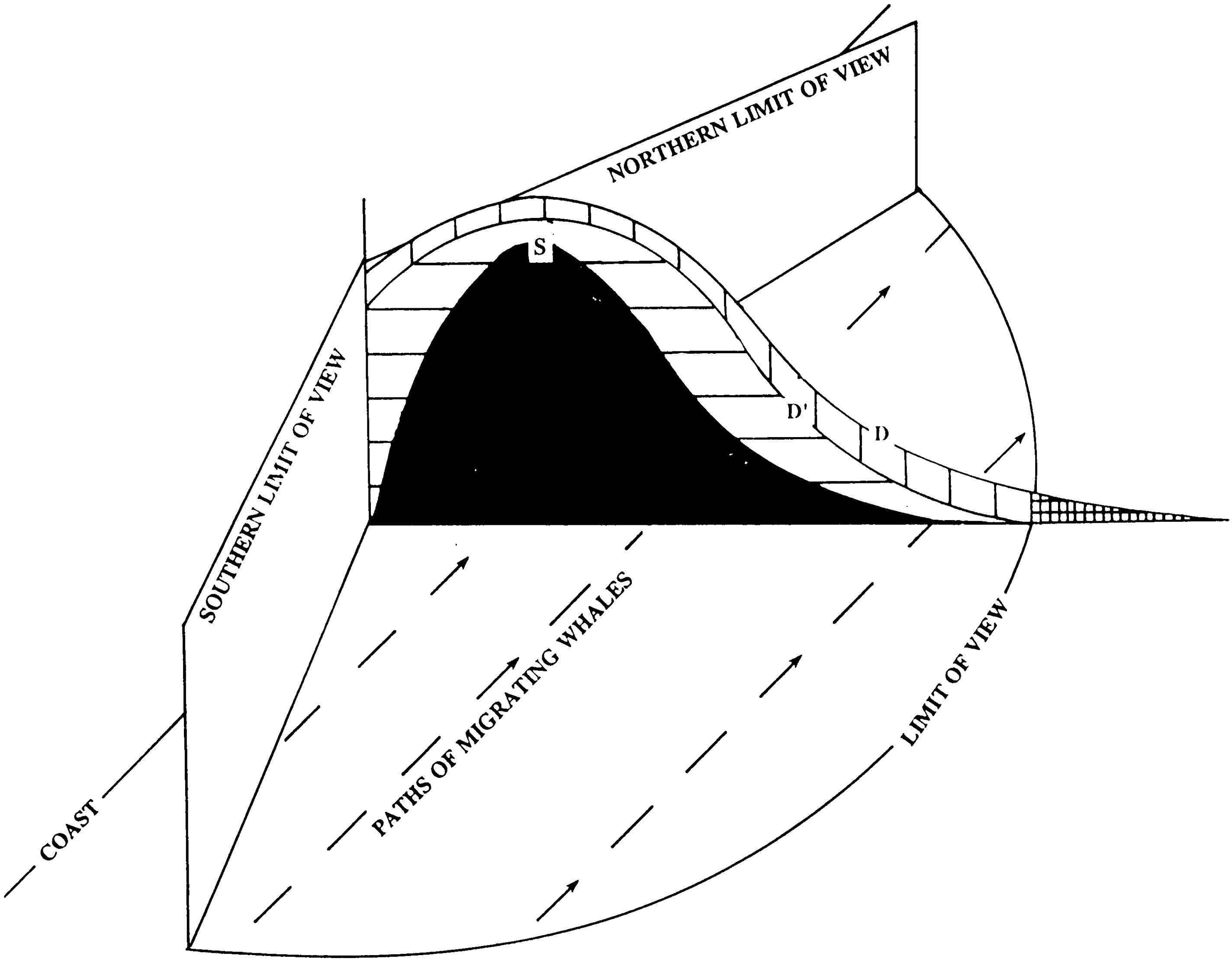


Figure 9.1 Diagrammatic representation of the distribution of whales from the coast and aspects pertaining to the offshore distribution which require consideration when estimating population sizes from shore-based surveys.

distribution can only be determined from an independent survey, where whales are distributed randomly with respect to the observer, and observer effort is distributed randomly offshore. Comparison of the true distribution of whales with the distribution seen by shore-based observers should provide a cross-check on the proportion of groups missed by observers, presently determined from independent observer surveys.

The proportion of groups missed by observers within the visible survey area, has been assessed in chapter 4, using mark-recapture methodology. This technique assumes that the total number of groups passing within the observer's view can be determined. However, two possible sources of error in this method are matching of duplicate groups, and the violation of the assumption of all groups having an equal probability of being sighted. There may be both time and position differences between the sighting of a group from each tower, and consequently groups are often impossible to match by eye. It is possible that the wide bounds, placed around migration speeds in the matching algorithm (chosen so that 95 % of field duplicates were found by the algorithm) may overestimate the number of groups seen by both towers, especially during peak migration periods. Rugh, Ferrero and Dahlheim (1990), for instance, note that the 21 % of gray whales missed by observers may be biased downwards owing to excessive matching resulting from wide allowances. As regards the violated probability assumption, not all heterogeneity in sighting probability could be accounted for by stratification, with unaccounted for heterogeneity arising from group size and behaviour. Both possible identified sources of error would bias the proportion missed downwards, and the population sizes calculated in chapter 5 could therefore be underestimates of the true population size.

The application of the combined 1990 and 1991 twin-tower results to the 1988 and 1989 surveys (and the 1990 survey outside of the July twin tower survey) when no independent surveys were undertaken, is deemed to be justified as it is not expected that the behaviour of the whales (that led to the unaccounted-for heterogeneity of sighting probabilities) would change significantly between years. Hiby and Hammond (1989) noted that the majority of shore-based surveys have been analogous to strip transects, where all animals within a certain truncation distance are assumed to have been seen, and that these counts have been adjusted for the proportion of the population passing beyond the truncation distance. This approach has been adopted in all the surveys off the east coast of Australia (Paterson and Paterson 1984, 1989, Bryden 1985, Bryden *et al.* 1990), although these authors have assumed that the proportion of the population passing offshore of the truncation distance is negligible. Although it could be argued that the resulting population estimate would be an underestimate of the true population size, sighting probabilities may well differ between years (through both different offshore distributions or weather conditions), resulting in fluctuations in yearly population estimates that may obscure demographic trends.

Figure 9.1 summarises the factors relating to offshore distribution that require consideration in determination of population estimates from shore-based surveys. The hypothetical distribution of all groups from the coastline is given by function D, and includes groups passing outside of the observer's view. The distribution of groups sighted with distance from the coast under mean sighting conditions (given by function S) must be adjusted to include the proportion of groups missed by observers within their view. The resulting function D' is assumed to approach D within the observers view, although D' may underestimate D through either overestimating matched groups or not fully accounting for heterogeneity in sighting probabilities. Both this function and the proportion of the population passing offshore of the observer's view require verification against the relative distribution of with distance offshore as determined by independent surveys.

3) All individuals in the population must undertake each migration along that coast once each year, and if the survey does not cover the entire migration period, the proportion of the population migrating outside of the survey period must be estimated.

The presence of waves in the migration each year suggest that densities of whales passing outside of the observation periods, may not be adequately predicted through mathematical modelling of the migration tails as carried out by Reilly *et al.* (1980, 1983). However, the migration waves themselves suggest some co- incident timing of the migration each year, which implies that the proportion of the migration passing outside the survey period may be constant each year.

An unknown factor is the proportion of the Area III population that is undertaking the migration past Cape Vidal each year. Area III humpback whales breed off the coasts of Madagascar and Mozambique, in waters to the south of Madagascar, off Indian Ocean Islands and possibly off the west coast of southern Africa. The inter-relationship of each of these grounds to the east coast migration stream is almost totally unknown, and in making between-year comparisons, it is assumed that a constant proportion migrates past Cape Vidal each year.

Furthermore, not only must the whole population pass through the study area during the migration, but individuals must only pass through the area once during each migration. For example, Matthews (1938) found that the humpback whales caught at Durban between the northward and southward migrations were immature animals and concluded that juvenile animals do not migrate as far north as mature animals. This aspect may have one of two consequences on counts made off Cape Vidal; firstly that juvenile animals do not migrate as far north as Cape Vidal, and are therefore under-represented in the Cape Vidal counts, or secondly that juvenile animals migrate to and remain in, the region of Cape Vidal between migrations, and are thus over-represented in the counts.

The fact that no intra-season matches were made in the identification photographs from Cape Vidal suggests that individuals migrate past only once during the northward migration. However no photographs were taken during August when milling in the area by immature animals may have occurred.

4) As visual surveys outside of polar regions in summer can only be undertaken during daylight hours, the numbers sighted during daylight hours must be extrapolated to night periods. Furthermore the migration continues during poor weather, when visual surveys are impossible, so that the whales passing during poor weather periods have to be extrapolated from numbers sighted during good weather.

These extrapolations usually assume that the migration speed is constant throughout a 24 hour day and under different weather conditions. No evidence of differences in diel migration speeds for humpback whales could be found in the literature, and measured migration speeds compared favourably to both instantaneous speeds and those integrated over longer distances that were reported in the literature. Consequently these have been assumed to be equal in this thesis. However it recommended that this aspect is verified through either a radio or satellite tagging programme or photo-identification of migrating animals in the future, as it is an extremely important parameter in population estimation.

A further factor arising from this extrapolation is that only animals that cross the midline of the observation area during observation effort must be considered, as inclusion of animals not seen to cross this midline will inflate the daily densities. Although Bryden *et al.* (1990) only counted groups which passed a point due east of the observation platform, it appears that no allowance was made for groups sighted which were not actually seen to have crossed this line. Paterson and Paterson (1989) appeared to have counted all animals sighted (irrespective of whether they crossed a midline) and note that sighting rates in the early hours of the day were inflated by animals which passed in the night, but were still in view at these times.

5) All observation effort must be of equal intensity.

Every attempt has been made to standardise survey effort between years by keeping the numbers of observers constant (an aspect which was not carried out in all the shore-based surveys of humpback whales off eastern Australia), by recommending standardised searching techniques, and in the latter two years by estimating observer efficiency under different conditions (through estimation of the proportions of the visible population missed by observers). Furthermore, whenever possible naive observers have been paired with experienced observers.

6) Group sizes and distance offshore must be accurately estimated.

One survey difficulty, which is not limited to shore-based surveys, is the determination of the position of the whale group with respect to the observer. The majority of shore-based surveys in which the offshore distribution of groups has been determined, have used the measurement of the angle of declination of the whale group from the horizon (or the angle of the sighting from the perpendicular) as seen by an elevated observer to calculate distance. The difficulty arises in the angle becoming progressively smaller with distance from the observer, and consequently distance estimates become less precise. Measurement of the angle of inclination has been carried out using reticule binoculars, as carried out during gray whale surveys (Reilly *et al.*. 1980, 1983) and on IDCR cruises (Hiby and Hammond 1989), or theodolites (Wursig, Cipriano and Wursig 1991) . More precise position fixing could be undertaken with baseline triangulation using two theodolites some distance apart (as carried out by Krogman, Rugh, Sonntag, Zeh and Ko 1989), although logistic considerations preclude the use of such a method at Cape Vidal, particularly in conjunction with twin-tower surveys.

Although the technique of measuring distances using a theodolite is more time consuming than binocular reticules, for instance, and thus can interfere with true searching effort, it has the advantage of being more accurate and provides simultaneous distance and angle measurement.

The subsample of 50 intercepted groups (in which the size was confirmed) represents the best information on group size available. However, the interception technique used required that the group be spotted by the shore-based observers prior to interception. The size frequencies of intercepted groups may therefore reflect more conspicuous groups, and so may not be a true distribution of group sizes. As noted by Bryden *et al.* (1990) the correct estimation of group size requires some time, and a further error in group size determination is the underestimation of groups of which few fixes are taken (which are not represented in the intercepted groups as the directing of the boat onto the group required that the group be kept in view for some time). As with the offshore distribution of groups, an independent verification of group size is required, in which all groups have an equal probability of being both sighted and estimated.

Paterson and Paterson (1984, 1989) give no information on the sizes of groups recorded by them, and no confirmation of group size was carried out by them. Although Bryden (1985) presented frequencies of observed group sizes, no confirmation was carried out. Bryden *et al.* (1990) confirmed the size of 16 groups, but as in this study these do not appear to be a representative sample of all groups. No distance-offshore measurements were made by Paterson and Paterson (1984, 1989), Bryden (1985), Bryden *et al.* (1990), or Paterson (1991), although Paterson (1991) recorded the migration paths of individuals in relation to offshore rocks.

The photo-identification component of the project was aimed at providing some information on the inter-relationship of the Cape Vidal migration stream with the Mozambique and Madagascan breeding grounds, and with Antarctic feeding grounds. However this component has been severely compromised by the small sample size of identified animals, particularly animals identified through tail flukes. As recommended by Chu and Nieukirk (1988), information on the retention of dorsal fin scars would be beneficial to this photo-identification study, given the low incidence of fluking off Cape Vidal. The limited sample of photo- identified individuals arises from inaccessibility of both breeding and feeding grounds, the low incidence of fluking behaviour recorded during the migration off Cape Vidal, and the lack of availability of a boat for interceptions off Cape Vidal in some years, particularly in 1991.

The best estimate of the African east coast component of the Area III population of humpback whales resulting from the surveys off Cape Vidal is the 1990 northward migration count (of 1711) as it included the entire migration. However this estimate can be applied only to the proportion of the Area III population which passes Cape Vidal within visibility limits of observers. Assuming that this proportion is representative of the population and that it does not change between years, annual changes in abundance should reflect demographic trends. Unfortunately the limited four-year time series of observations, and the fact that the 1988 and 1989 surveys missed the main migration peak, precluded any accurate estimation of demographic trends over the survey period. Winn and Reichley's (1985) post-exploitation population estimate of 340 for the Area III stock, Osumi and

Masaki's (1972) estimates of the Antarctic Area III stock between 1965/66 and 1970/71 (330-710 individuals, average 570) and annual catches of humpback whales off Durban in the final decade of humpback whaling, all suggest that the population has undergone considerable recovery in the last 28 years.

The 1991 survey of humpback whales in Mozambique waters provided a population estimate (1954, cv 0.38) that was comparable to estimates obtained off Cape Vidal, and described the distribution patterns of humpback whales on the southern and central Mozambique breeding grounds. The relative densities recorded and the distribution of songs suggest the continental shelf region (where the Mozambique Current is further offshore) to be the principal breeding areas. Although the population estimate is comparable to the estimate from Cape Vidal, it could well be an underestimate of the true population on the Mozambique breeding grounds as it assumed (i) that g(0) was 1 (that all groups on the trackline were sighted), and (ii) that all individuals were present on the breeding ground, a source of error noted by Herman and Antinoja (1977), Reilly (1984), and Butterworth, Borchers and Challis (unpubl). Furthermore, the northern limit of the breeding ground was not determined. This underestimate would suggest that a considerable portion of the population is passing offshore of observers at Cape Vidal.

Unfortunately the collection of photo-identified individuals was too small to provide an independent population estimate for comparison with those obtained from Cape Vidal and on the Mozambique breeding ground.

Given that the assumptions listed by Reilly *et al.* (1980, 1983) and Hiby and Hammond (1989) are met, and that the proportions of the population missed by, or offshore of, observers can be estimated, shore-based visual surveys provide a relatively inexpensive and straightforward technique for monitoring coastal migrating species. The technique is particularly advantageous for situations where the entire population is not present on feeding or breeding grounds at any one time, thus precluding censuses on these grounds. The technique could be adequately used to estimate changes in the abundance of humpback whales off the east coast of southern Africa, if the proportion of the population that migrates within view of Cape Vidal is constant each year, and there is no change in the ratio of day : night migration speeds between years. However, the estimation of the total size of this component of the population will require further information on migration destinations, offshore distribution of migrating animals, and nocturnal migration speeds. It is recommended that these aspects are investigated in a second phase of the project prior to the continuation of shore-based surveys. An interval of some years between periods of survey might also be advantageous in improving data contrast.

REFERENCES

Alvarez, C., Aguayo, A., Rueda, R., and Urban, J. 1990. A note on the stock size of humpback whales along the Pacific coast of Mexico. *Rep. int. Whal. Commn (special issue 12)*: 191 - 193.

Angot, M. 1951. Rapport scientifique sur les expeditions baleinieres autour de Madagascar (saisons 1949 et 1950). *Mem. Inst. Sci. Madagascar.* 6(2): 439-486.

Anon. 1990. Report of the workshop on individual recognition and the estimation of cetacean population parameters. *Rep. int. Whal. Commn (special issue 12)*: 3 - 17.

Baker, C. S. and Herman, L.M. 1987. Alternative population estimates of humpback whales (*Megaptera novaeangliae*) in Hawaiian waters. *Can. J. Zool.* 65: 2818 - 21.

Baker, C.S., Herman, L.M., Perry, A., Lawton, W.S., Straley, J.M., and Straley, J.H. 1985. Population characteristics and migration of summer and late season humpback whales (*Megaptera novaeangliae)* in southeastern Alaska. *Mar. Mammal Sci.* 1(4): 304-323.

Baker, C.S., Herman, L.M., Perry, A., Lawton, W.S., Straley, J.M., Wolman, A.A., Kaufman, G.D., Winn, H.E., Hall, J.D., Reinke, J.M. and Ostman, J. 1986. Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Mar. Ecol. Prog. Ser.* 31: 105 - 119.

Baker, C.S., Palumbi, S.R., Lambertsen, R.H., Weinrich, M.T., Calambokidis, J. and O'Brien, S.J. 1990. The influence of seasonal migration on the geographic distribution of mitochondrial DNA haplotypes in humpback whales. *Nature (Lond.)* 344: 238 - 240.

Baker, C.S., Perry, A. and Herman, L.M. 1987. Reproductive histories of female humpback whales (*Megaptera novaeangliae*) in the North Pacific. *Mar. Ecol. Prog. Ser.* 41: 103 - 114.

Baker, C.S., Slade, R.W., Bannister, J.L., Abernethy, R.B. Weinrich, M.T., Lien, J., Urban, R., Corkeron, P., Calambokidis, J., Vasquez, O. and Palumbi, S.R. (in prep) *Genetics.*

Baker, C.S., Straley, J.M. and Perry, A. 1992. Population characteristics of individually identified humpback whales in southeastern Alaska: Summer and fall 1986. *Fish. Bull. U.S.* 90: 429 - 437.

Balcomb, K.C. and Breiwick, J.M. 1984. Mark recapture analysis of western North Atlantic humpback whales using fluke photographs. *Rep int. Whal. Commn.* 34: 141.

Balcomb, K.C., Katona, S.K. and Hammond, P.S. 1986. Population estimates for the North Atlantic humpback whale using capture - recapture methods on photo-identified whales. *Rep. int. Whal. Commn* 36: 110.

Balcomb, K.C. and Nichols, G. 1978. Western North Atlantic humpback whales. *Rep. int. Whal Commn* 28: 159 - 164.

Bannister, J.L. and Baker, A. de C. 1967. Observations on food and feeding of baleen whales at Durban. *Norsk Hvalfangsttid.* 4: 78 - 82.

Bannister, J.L., and Gambell, R. 1965. The abundance of blue, fin, sei and other whales off Durban. *Norsk Hvalfangsttid.* 54: 45-60.

Bannister, J.L., Kirkwood, G.P. and Wayte, S.E. 1991. Increase in humpback whales off western Australia. *Rep. int. Whal. Commn.* 41: 461 - 465.

Baraff, L. and Weinrich, M.T. 1993. Separation of humpback whale mothers and calves on a feeding ground in early autumn. *Mar. Mamm. Sci.* 9(4): 431-434.

Bell, G. 1974. Population estimates from recapture studies in which no recaptures have been made. *Nature (Lond.)* 248: 616.

Best, P.B. 1982. Whales as target animals for sighting surveys. *Rep. int. Whal. Commn* 32: 551 - 553.

Best, P.B. 1985. External characteristics of southern minke whales and the existence of a diminutive form. *Sci. Rep. Whales Res. Inst., Tokyo.* 36: 1-33.

Best, P.B. 1993. Increase rates in severely depleted stocks of baleen whales. *ICES J. Mar. Sci.* 50: 169 - 186.

Best, P.B. in press. A review of the catch statistics for modern whaling in Southern Africa, 1908 - 1930. *Rep. int Whal. Commn 44.*

Best, P.B. and Butterworth, D.S. 1980. Report of the Southern Hemisphere minke whale assessment cruise, 1978/79. *Rep. int. Whal. Commn* 30: 257 - 283.

Best, P.B. and Ross, G.J.B. 1989. Whales and Whaling. pp. 315-338. *In* Payne, A.I.L. and Crawford, R.J.M. (eds) Oceans of Life off Southern Africa. Vlaeberg Publishers, Cape Town.

Best, P.B. and Shaughnessy, P.D. 1979. An independent account of Captain Benjamin Morrell's sealing voyage to the south-west coast of Africa in the *Antarctic*, 1828/29. *Fish. Bull. S. Afr.* 12: 1 - 19.

BMDP Statistical Software Inc., 1440 Sepulveda Blvd., Los Angeles, California, 90025, USA.

Borchers, D.L. 1992. SC/43/Mi34. Revised southern hemisphere whale abundance estimates south of 30° derived from IWC/IDCR survey and Japanese scouting vessel data (addendum to SC/42/SHMi18). *Rep. int. Whal. Commn* 42 : 756.

Breiwick, J., Rugh, D., Withrow, D., Dahlheim, M. and Buckland, S. 1988. Preliminary population estimate of gray whales during the 1987 - 88 southward migration. Document SC/38/PS14 submitted to the Scientific Committee of the International Whaling Commission 1988.

Brown S.G. 1957. Whales observed in the Indian Ocean. *Mar. Obsr* 27: 157 - 165.

Brown, S.G. 1977. Whale marking: a short review. *In* M.Angel (ed.) *A Voyage of Discovery: George Deacon 70th Anniversary Volume.* Pergamon Press, Oxford.: 569 - 581.

Bryden, M. M. 1985. Studies of humpback whales (*Megaptera novaeangliae*), Area V. pp. 115 - 123. In: Ling J.K. and Bryden M. M. (eds.) *Studies of sea mammals in south latitudes.* South Australian Museum, Adelaide, pp: 115 -123.

Bryden, M.M., Kirkwood, G.P. and Slade, R.W. 1990. Humpback whales, Area V. An increase in numbers off Australia's east coast. pp. 271 - 277. *In*: Kerry K.R. and Hempel, G. (eds.) *Antarctic ecosystems. Ecological change and conservation.* Springer - Verlag Berlin Heidelberg, 327 pp.

Buckland, S.T. 1985. Perpendicular distance models for line transect sampling. *Biometrics* 41: 177-195.

Buckland, S.T, Breiwick, J.M., Cattanach, K.L. and Laake, J.L. 1993. Estimated population size of the California gray whale. *Mar. Mammal Sci.* 9(3) : 235-249.

Budker, P. 1954. Whaling in French oversea territories. *Norsk Hvalfangsttid.* 43: 320 - 325.

Budker, P., and Collignon, J. 1952. Trois campagnes baleinieres au Gabon: 1949-1950-1951. *Bull. Inst. Etud. centrafr.* 3: 75-100.

Butterworth, D.S. 1987. An initial analysis of experiments carried out on the 1984/85 IWC/IDCR Antarctic Minke whale assessment cruise to compare closing and passing mode procedures in respect to minke whale density estimation. *Rep. int. Whal. Commn* 37: 391 - 392.

Butterworth, D.S., Borchers, D.L., and Chalis, S. (unpublished). Updates of abundance estimates for Southern Hemisphere blue, fin sei and humpback whales incorporating data from the second circumpolar set of IDCR cruises. Document SC/44/SHB19 submitted to the Scientific Committee of the International Whaling Commission 1992.

Calambokidis, J., Cubbage, J.C., Steiger, G.H., Balcomb, K.C. and Bloedel, P. 1990. Population estimate of humpback whales in the Gulf of the Farallones, California. *Rep. int. Whal.Commn (special issue 12)*: 325 - 333.

Chapman, D.G. 1974. Status of Antarctic rorqual whale stocks. pp. 218 - 238. *In* Schevill, W.E. (ed.) *The whale problem, a status report.* Harvard University Press, Massachusetts.

Chittleborough, R.G. 1953. Aerial observations on the humpback whale, *Megaptera nodosa* (Bonnaterre), with notes on other species. *Austr. J. mar. Freshw. Res.* 4: 219 - 26.

Chittleborough, R.G. 1954. Studies on the ovaries of the humpback whale, *Megaptera nodosa* (Bonnaterre), on the Western Australian coast. *Austr. J. mar. Freshw. Res.* 5: 35 - 63.

Chittleborough, R.G. 1958. Breeding cycle of the female humpback whale, *Megaptera nodosa* (Bonnaterre). *Austr. J. mar. Freshw. Res.* 9: 1-18.

Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. mar. Freshw. Res.* 16: 33 - 128.

Chu, K. and Nieukirk, S. 1987. Dorsal fin scars as indicators of age, sex, and social status in humpback whales (*Megaptera novaeangliae*). *Can. J. Zool.* 66: 416 - 420.

Clapham, P.J. and Mattila, D.K. 1990. Humpback whale songs as indicators of migration routes. *Mar. Mamm. Sci.* 6(2): 155 - 160.

Clapham, P.J. and Mayo, C.A. 1990. Reproduction of humpback whales (*Megaptera novaeangliae*) observed in the Gulf of Maine. *Rep. int. Whal. Commn (special issue 12)*: 171 - 176.

Climate Diagnostics Bulletin, August 1990, Climate Analysis Center, U.S. Department of Commerce.

Committee for Whaling statistics, 1942 - 1964. Sandjeford, Norway.

Darling, J.D. and Cerchio, S. 1993. Movement of a humpback whale (*Megaptera novaeangliae*) between Japan and Hawaii. *Mar. Mamm. Sci.* 9(1): 84 - 88.

Darling, J.D. and Jurasz, C.M. 1983. Migratory destinations of North Pacific humpback whales (*Megaptera novaeangliae*). pp. 359 - 368. *In* Payne, R. (ed.) *Communication and behavior of whales.* AAAS Sel. Symp. No 76, Westview Press, Boulder. 643 pp.

Darling, J.D. and McSweeny, D.J. 1985. Observations on the migrations of North Pacific humpback whales (*Megaptera novaeangliae*). *Can. J. Zool.* 63: 308 - 314.

Dawbin, W.H. 1956. The migrations of humpback whales which pass the New Zealand coast. *Trans. R. Soc. N. Z.* 83: 147 - 196.

Dawbin, W.H. 1966. The seasonal migratory cycle of humpback whales. pp. 145 - 170. *In*: Norris K.S. (ed.) *Whales, dolphins and porpoises.* University of California Press, Berkely.

Dawbin, W.H. and Eyre, E.J. 1991. Humpback whale songs along the coast of Western Australia and some comparison with east coast songs. *Mem. Qd Mus.* 30 (2): 249 - 254.

Dawbin, W.H. and Gill, P.C. 1991. Humpback whale survey along the west coast of Australia: a comparison of visual and acoustic observations. *Mem. Qd Mus.* 30(2): 255-257.

Donovan, G. 1991. A review of IWC stock boundaries. *Rep. int. Whal. Commn. (special issue 13)*: 39 - 68.

Findlay, K.P. 1989. The distribution and seasonal abundance of cetaceans off the coast of South Africa and South West Africa - Namibia. MSc thesis submitted to University of Pretoria, Pretoria.

Findlay, K.P., Best, P.B. and Borchers D.L. 1991. Shore-based monitoring of humpback whale migrations in the western Indian Ocean. Document SC/43/PS/14 submitted to the Scientific Committee of the International Whaling Commission 1991.

Findlay, K.P., Best, P.B., Peddemors , V. and Gove, D. 1992. The distribution and abundance of humpback whales on their southern Mozambique breeding grounds. Document SC/43/SHB5 Submitted to the Scientific Committee of the International Whaling Commission, Glasgow, Scotland 1992.

Gentleman, R. and Zeh, J.E. 1987. A statistical model for estimating the number of bowhead whales, *Balaena mysticetus,* passing a census point from combined visual and acoustic data. *Rep. int. Whal. Commn* 37: 313 - 327.

Glockner, D.A. 1983. Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment. pp. 447 - 464. *In* Payne, R. (ed.) *Communication and behavior of whales.* AAAS Sel. Symp. No 76, Westview Press, Boulder. 643 pp.

Glockner, D.A. and Venus, S.C. 1983. Identification, growth rate and behaviour of the humpback whale (*Megaptera novaeangliae*) cows and calves in the waters off Maui, Hawaii, 1977-79. pp. 223-258. *In* Payne, R. (ed.) *Communication and behavior of whales.* AAAS Sel. Symp. No 76, Westview Press, Boulder. 643 pp.

Glockner-Ferrari, D. and Ferrari, M. 1984. Reproduction in humpback whales, *Megaptera novaeangliae,* in Hawaiian waters. *Rep. int. Whal. Commn (special issue 6)*: 237 - 242.

Glockner-Ferrari, D. and Ferrari, M. 1990. Reproduction in the humpback whale (*Megaptera novaeangliae*) in Hawaiian waters, 1975 - 1988: The life history, reproductive rates, and behaviour of known individuals identified through surface and underwater photography. *Rep. int. Whal. Commn (special issue 12)*: 161 - 169.

Goodall, T.B. 1913. With the whalers at Durban, and a few notes on the anatomy of the humpback whale (*Megaptera boops*). *Zoologist*, 4th Ser. 17: 201 -211.

Gordon, J.C.D. 1990. A simple photographic technique for measuring whales at sea. *Rep. int. Whal. Commn* 40: 581-588.

Griffiths, C.L. and Blaine, M.J. 1988. Distribution, population structure and biology of stomatopod crustacea off the west coast of South Africa. *S. Afr. J. mar. Sci.* 7: 45 - 50.

Grady, D. 1982. The Perano whalers of Cook Strait 1911 - 1964. A.H. and A.W. Reed Ltd. Wellington. xv + 238 pp.

Grundlingh, M.L. 1977. Drift observations from NIMBUS VI satellite-tracked bouys in the southwestern Indian Ocean. *Deep Sea Res.* 24: 903-923.

Hammond, P. S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. *Rep. int. Whal. Commn* (special issue 6): 253 - 282.

Hammond, P.S. and Larsen, F. 1985. Some notes on estimating population size of West Greenland humpbacks using mark - recapture. *Rep. int. Whal. Commn* 35: 129.

Harmer, S.F. 1928. History of whaling. *Proc. Linn. Soc. Lond.* (1927 - 28): 51 - 59.

Harmer, S.F. 1931. Southern Whaling. *Proc. Linn. Soc. Lond.* 142(1929 -30): 85-163.

Harris, T. F. W. 1978. Review of coastal currents in southern African waters. *Rep. S. Afr. natn. scient. Progrms.* 30: 103 pp.

Helweg, D.A., Herman, L.M., Yamamoto, S., and Forestell, P.H. 1990. Comparison of songs of humpback whales (*Megaptera novaeangliae*) recorded in Japan, Hawaii, and Mexico during the winter of 1989. *Sci. Rep. Cetacean Res.* 1: 1 - 20.

Herman, L.M. and Antinoja, R.C. 1977. Humpback whales in Hawaiian breeding waters: population and pod characteristics. *Sci. Rep. Whales Res. Inst., Tokyo* 29: 59-85.

Heydorn, A.E.F., with Bang, N.D., Pearce, A.F., Flemming, B.W., Carter, R.A., Schleyer, M.H., Berry, P.F., Hughes, G.R., Bass, A.J., Wallace, J.H., Van der Elst, R.P., Crawford, R.J.M. and Shelton, P.A. 1978. Ecology of the Agulhas Current region: an assessment of biological responses to environmental parameters in the south- west Indian Ocean. *Trans. R. Soc. S. Afr.* 43 (2): 151 - 190.

Hiby, A.R. and Hammond, P.S. 1989. Survey techniques for estimating abundance of cetaceans. *Rep. int. Whal. Commn (Special issue 11)*: 47 - 80.

Hinton, M.A.C. 1925. Report on the papers left by the late Major Barrett-Hamilton, relating to the whales of South Georgia. Crown Agents for the Colonies, London: 57 - 209.

Ivashin, M.V. 1970. Some results of whale-marking carried out from Soviet ships in the southern hemisphere. *Zool. Zh.* 50 (7): 1063 - 1078.

Katona, S.K. and Beard, J.A. 1990. Population size, migrations and feeding aggregations of the Humpback Whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Rep. int. Whal. Commn (Special issue 12)*: 295 - 306.

Katona, S.K. and Beard, J.A. 1991. Humpback whales (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Mem. Qd Mus.* 30 (2): 307 - 321.

Katona, S., Baxter, B., Kraus, B., Perkins, J. and Whitehead, H. 1979. Identification of humpback whales by fluke photographs. pp. 33-44. *In* Winn, H.E. and Olla, B.L. (eds), *Behaviour of marine animals, vol 3*, Plenum Press. New York.

Katona, S.K. and Whitehead, H.P. 1981. Identifying humpback whales using their natural markings. *Polar Rec.* 20 (128): 439 - 444.

Kaufman, G. D., Osmond, M.G., Ward, A.J. and Forestell, P.H. 1990. Photographic documentation of the migratory movement of a humpback whale (*Megaptera novaeangliae*) between East Australia and Antarctic Area V. *Rep. int. Whal. Commn (special issue 12)*: 265 - 268.

Kaufman, G.D., Smultea, M.A. and Forestell, .H. 1987. Use of lateral body pigmentation patterns for photographic identification of East Australia (Area V) humpback whales. *Cetus* 7: 5 - 13.

Kellogg, R. 1929. What is known of the migration of some of the whalebone whales. *Rep. Smithson Instn* 1928: 467 - 494.

Kenney, R.D. and Winn, H.E. 1987. Why some whales fluke: suggesting a novel hypothesis. *Cetus* 7 (2): 15 - 19.

Krogman, B., Rugh, D., Sonntag, R., Zeh, J. and Ko, D. 1989. Ice - based census of bowhead whales migrating past Piont Barrow, Alaska, 1978 - 83. *Mar. Mamm. Sci.* 5 (2): 116 - 138.

Lillie, D.G. 1915. Cetacea. British Antarctic ("Terra Nova") Expedition, 1910. *Zoology* 1 (3): 85 - 124.

Mackintosh, N.A. 1942. The southern stocks of whalebone whales. *"Discovery" Rep.* 22: 197 - 300.

Mackintosh, N.A. 1966. The stocks of whales. Fishing News (Books) Ltd. London. pp. 82-86.

Matthews, L.H. 1938. The humpback whale, *Megaptera nodosa. "Discovery" Rep.* 17: 7 - 92.

Mattila, D.K. and Clapham, P.J. 1989. Humpback whales, *Megaptera novaeangliae,* and other cetaceans on Virgin Bank and in the northern Leeward Islands, 1985 and 1986. *Can. J. Zool.* 67: 2201 - 2211.

Mizroch, S.A., Beard, J.A. and Lynde, M. 1990. Computer assisted photo-identification of humpback whales. *Rep. int. Whal. Commn (Special issue 12)*: 37-45.

Morch, J. A. 1911. On the natural history of whalebone whales. *Proc. Zool. Soc. Lond.*: 661 - 70.

Nepgen, C.S. De V. 1979. The food of the snoek *Thyristes atun. Fish. Bull. S. Afr.* 11: 39 - 42.

Nishiwaki, M. 1966. Distribution and migration of the larger cetaceans in the North Pacific as shown by Japanese whaling results. pp. 171 - 191. *In* Norris, K.S. *Whales, dolphins and porpoises*. University of California Press. Berkeley and Los Angeles. xv + 789 pp.

Olsen, O. 1914. Hvaler og hvalfangst i Sydafrika. *Bergens Mus. Arb. 1914 -15*, 5: 1 - 56.

Ommaney, F.D. 1933. Whaling in the Dominion of New Zealand. *"Discovery" Rep.* 7: 239 - 252.

Omura, H. 1953. Biological study on the humpback whales in the Antarctic whaling Areas IV and V. *Sci. Rep. Whal. Res. Inst., Tokyo.* 8: 81 - 101.

Omura, H. 1973. A review of pelagic whaling operations in the Antarctic based on the effort and catch data in 10^{o} squares of latitude and longitude. *Sci. Rep. Whales Res. Inst., Tokyo* 25: 105 - 203.

Ohsumi, S. and Masaki, Y. 1972. Status of stocks of baleen whales in the Antarctic. 1971/72. *Rep. int. Whal. Commn.* 22: 60-68.

PAN files. Cape Provincial Administration, Nature Conservation. Files held in Cape Archives, Cape Town, South Africa.

Paterson, R. 1991. The migrations of humpback whales, *Megaptera novaeangliae.* in east Australian waters. *Mem. Qd Mus.* 30 (2): 333 - 341.

Paterson, R. and Paterson P. 1984. A study of the past and present status of humpback whales in east Australian waters. *Biol. Conserv.* 29: 321 - 343.

Paterson, R. and P. Paterson 1989. The status of the recovering stock of humpback whales *Megaptera novaeangliae* in east Australian waters. *Biol. Conserv.* 47: 33 - 48.

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* Payne, R. (ed.). *Communication and behavior of whales.* AAAS Selected Symposium No 76, Westview Press, Boulder, Co.

Payne, R. and Guinee, L. 1983. Humpback whale (*Megaptera novaeangliae*) songs as an indicator of stocks. pp. 333 - 358. *In* Payne, R. (ed.) *Communication and behavior of whales.* AAAS Selected Symposium No 76, Westview Press, Boulder. 643 pp.

Payne, R. and McVay, S. 1971. Songs of humpback whales. *Science N.Y.* 173: 585 - 597.

Pearce, A.F. 1977. Some features of the upper 500 m of the Agulhas Current. *J. mar. Res.* 35 (4): 731 - 751.

Perkins, J.S., Balcomb, K.C., Nichols, G., Hall, A.T., Smultea, M. and Thumser, N. 1985. Status of the West Greenland humpback whale feeding aggregation, 1981 - 1983. *Rep. int. Whal. Commn* 35: 379 - 383.

Perry, A., Baker, C.S. and Herman, L.M. (1990) Population characteristics of individually identified humpback whales in the central and eastern North Pacific: a summary and critique. *Rep. int. Whal. Commn (special issue 12)*: 307-317.

Poole, M.M. 1984. Preliminary assessment of annual calf production in the gray whale, *Eschrichtius robustus*, from Pt Piedras Blancas, California. *Rep. int. Whal. Commn (special issue 6)*: 223 - 231.

Rand, R.W. 1960a. The biology of guano-producing seabirds. The distribution, abundance and feeding habits of the Cape Penguin, *Spheniscus demersus*, off the south-western coast of the Cape Province. *Investl Rep. Div. Fish. S. Afr.* 41: 28 pp.

Rand, R.W. 1960b. The biology of guano-producing seabirds. The distribution, abundance and feeding habits of the cormorants, *Phalacrocoracidae* off the south west coast of the Cape Province. *Investl Rep. Div. Fish. S. Afr.* 42: 32 pp.

Rayner, G.W. 1940. Whale marking: progress and results to December 1939. *"Discovery" Rep.* 19: 245-284.

Reeves, R.R., Leatherwood, S., and Papastavrou, V. 1990. Possible stock affinities of humpback whales in the Northern Indian Ocean. pp. 259 - 270. *In* Leatherwood, S. and Donovan, G.P. (eds) Cetaceans and cetacean research in the Indian Ocean Sanctuary. Nairobi. Kenya. UNEP Marine Mammal Technical Report (3) viii + 287 pp.

Reilly, S.B. 1984. Assessing gray whale abundance: a review. In: Jones, M.L., Swartz, S. and S. Leatherwood, S. (eds.) *The Gray Whale (*Eschrichtius robustus*)*. Academic Press, Orlando, Florida, pp: 203 - 223.

Reilly, S.B. Rice, D.W. and A.A. Wolman 1980. Preliminary population estimate for the California gray whale based upon Monterey shore censuses 1967/68 to 1978/79. *Rep. int. Whal. Commn* 30: 359 - 368.

Reilly, S.B. Rice, D.W. and A.A. Wolman 1983. Population assessment of the gray whale, *Eschrichtius robustus*, from California shore censuses, 1967 - 80. *Fish. Bull. U.S.* 81: 267 - 281.

Risting, S. 1912. Knolhvalen. *Norsk FiskTid.* 31: 437 - 49. (Translation in Hinton, M.A.C. 1925. Report on the papers left by the late Major Barrett-Hamilton, relating to the whales of South Georgia. Crown Agents for the Colonies, London: 57 - 209).

Rorvik, C.J. 1980. Whales and whaling off Mozambique. *Rep. int. Whal. Commn* 30: 223-225.

Rugh, D.J. 1984. Census of gray whales at Unimak Pass, Alaska: November - December 1977 - 79. pp. 225 - 248. *In*: Jones, M.L., Swartz, S. and Leatherwood, S. (eds.) *The Gray Whale (*Eschrichtius robustus*)* . Academic Press, Orlando, Florida,

Rugh, D.J. and Braham, H.W. 1979. California gray whale *Eschrichtius robustus* Fall migration through Unimak Pass, Alaska, 1977: A preliminary report. *Rep. int. Whal. Commn* 29: 315 - 320.

Rugh, D.J. and Dahlheim, M. 1990. A review of methods for counting gray whales from shore - based sites. Document SC/A90/G 4 submitted to the Scientific Committee of the International Whaling Commission.

Rugh, D.J., Ferrero, R.C. and Dahlheim, M.E. 1990. Inter - observer count discrepancies in a shore - based census of gray whales (*Eschrichtius robustus*). *Mar. Mamm. Sci.* 6 (2): 109 - 120.

Scarff, J.E. 1986. Occurrence of the barnacles *Coronula diadema, C. reginae, and Cetopirus complanatus* (Cirripedia) on right whales. *Sci. Rep. Whales Res. Inst., Tokyo* 37: 129 - 153.

Schilling, M.R., Seipt, I., Weinrich, M.T., Frohock, S.E., Kuhlberg, A.E. and Clapham, P.J. 1992. Behavior of individually- identified sei whales *Balaenoptera borealis* during an episodic influx into the southern Gulf of Maine in 1986. *Fish. Bull. U. S.* 90: 749 - 755.

Schumann, H.E. 1987. The coastal ocean off the east coast of South Africa. *Trans. R. Soc. S. Afr.* 46 (3): 215 - 229.

Schweder, T. 1990. Independent observer experiments to estimate the detection function in line transect surveys of whales. *Rep. int. Whal. commn* 40: 349 - 465.

Sears, R., Williamson, J.M., Wenzel, F.W., Berube, M., Gendron, D. and Jones, P. 1990. Photographic identification of the blue whale (*Balaenoptera musculus*) in the Gulf of St. Lawrence, Canada. *Rep. int. Whal. Commn (special issue 12)*: 335-342.

Seber, G.A.F. 1982. *The estimation of animal abundance.* (Second edition). Macmillan Publishing Co., Inc., New York. i - xvii + 654 pp.

Sigurjonsson, J. and Gunnlaugsson, T. 1990. Recent trends in abundance of blue (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*) off west and southwest Iceland, with a note on occurrence of other cetacean species. *Rep. int. Whal. Commn* 40: 537 - 551.

Simmons, M.L. and Marsh, H. 1986. Sightings of humpback whales in Great Barrier Reef waters. *Sci. Rep. Whales Res. Inst., Tokyo* 37: 31-46.

Slijper, E.J., Van Utrecht, W.L. and Naaktgeboren, C. 1964. Remarks on the distribution and migration of whales, based on observations from Netherlands ships. *Bijd. Dierk.* (34): 4 - 93.

Stone, G.S., Florez-Gonzalez, L., and Katona, S. 1990. Whale migration record. *Nature, Lond.* 346: 705.

Swartz, S.L., Jones, M.L., Goodyear, J., Withrow, D.E. and Miller, R.V. 1987. Radio-telemetric studies of gray whale migration along the California coast: a preliminary comparison of day and night migration rates. *Rep. int. Whal. Commn* 37: 295 - 299.

Tonnesen, J.N. and Johnsen, A.O. 1982. The history of modern whaling. University of California Press. Berkeley and Los Angeles, 798 pp.

Townsend, C.H. 1935. The distribution of certain whales as shown by logbook records of American whale ships. *Zoologica N.Y.* 19: 1-50.

Tyack, P. and Whitehead, H. 1983. Male competition in large groups of wintering humpback whales. *Behaviour* 83: 132-154.

Ward, A.J. and Hiby, A.R. 1987. Analysis of cue counting and blow rate estimation experiments carried out during the 1985/86 IWC/IDCR minke whale assessment cruise. *Rep. int. Whal. Commn* 37: 259-262.

Watkins, W.A., Moore, K.E., Wartzok, D. and Johnson, J.H. 1981. Radio tracking of finback (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales in Prince William Sound, Alaska. *Deep Sea Res.* 28A: 577 - 588.

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

Whitehead, H. 1985. Humpback whale songs from the North Indian Ocean. *Invest. Cetacea* 17: 157 - 162.

Whitehead, H., Chu, K., Perkins, J., Bryant, P. and and Nicols, G. 1983. Population size, stock identity, and distribution of the humpback whale off West Greenland - summer 1981. *Rep. int. Whal. Commn* 33: 497 - 501.

Whitehead, H. and Glass, C. 1985. The significance of the Southeast Shoal of the Grand Bank to humpback whales and other cetacean species. *Can. J. Zool.* 60: 2173 - 2179.

Whitehead, H. and Moore, M.J. 1982. Distribution and movements of West Indian humpback whales in winter. *Can. J. Zool.* 60: 2203 - 2211.

Winn, H.E., Bischoff, W.L. and Taruski, A.G. 1973. Cytological sexing of cetacea. *Mar. Biol.* 23: 343 - 346.

Winn, H.E. and Reichley, N. 1985. Humpback whale - *Megaptera novaeangliae*. *In*: Ridgway, S.H. and Harrison, R. (eds.) *Handbook of marine mammals. Vol 3: The Sirenians and Baleen Whales.* Academic Press, London. 362 pp.

Winn, H.E., Thompson, T.J., Cummings, W.C., Hain, J. Hudnall, J. Hays, H. and Steiner W.W. 1981. Song of the humpback whale - population comparisons. *Behav. Ecol. Sociobiol.* 8: 41 - 46.

Winn, L. K. and Winn, H.E. 1985. *Wings in the Sea. The Humpback Whale.* University Press of New England, Hanover and London. 115 p.

Wray, P. and Martin, K.R. 1983. Historical whaling records from the Western Indian Ocean. *Rep. int. Whal. Commn (special issue 5)*: 213 - 241.

Wursig, B., Cipriano, F. and Wursig, M. 1991. Dolphin movement patterns. Information from radio and theodolite tracking studies. pp. 79-111. *In* Pryor, K. and Norris, K.S. *Dolphin societies. Discoveries and Puzzles.* University of California Press, Los Angeles. 397 pp.

Zeh, J.E., Ko, D., Krogman, B.D. and Sonntag, R. 1986a. A multinomial model for estimating the size of a whale population from incomplete census data. *Biometrics* 42: 1 - 14.

Zeh, J.E., Ko, D., Krogman, B.D. and Sonntag, R. 1986b. Statistical considerations in estimating the number of bowhead whales, *Balaena mysticetus*, from ice - based visual census data. *Rep. int. Whal. Commn.* 36: 317 - 323.

Zeh, J.E., George, J.C., Raftery, A.D., and Carroll, G.M. 1991. Rates of increase, 1978 - 1988, of bowhead whales *Balaena mysticetus*, estimated from ice - based census data. *Mar. Mammal Sci.* 7 (2): 105 - 122.

APPENDIX I

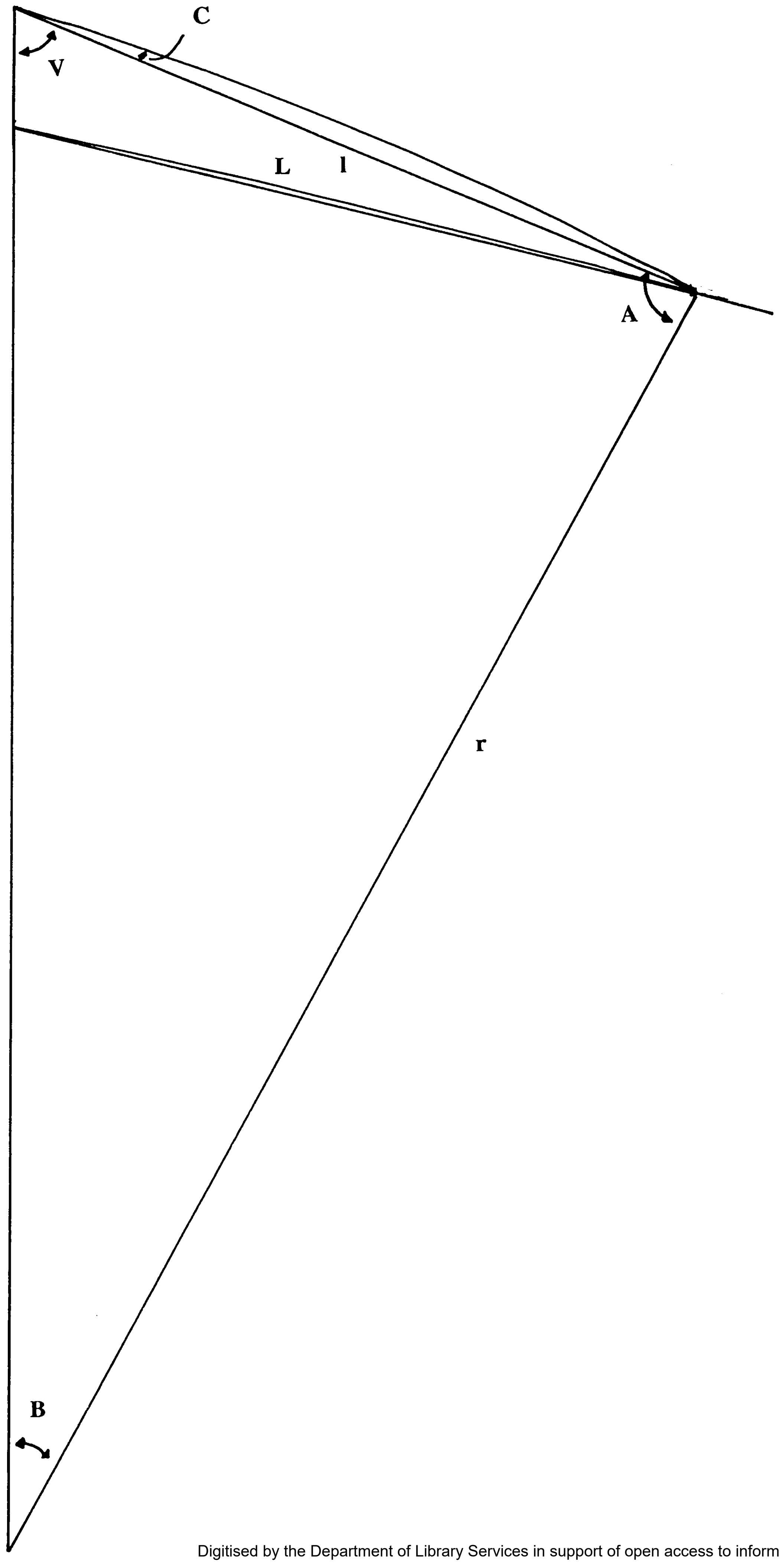
Algorithm to calculate XY co-ordinates of whales from the tower (0;0) using vertical and horizontal angles as measured by theodolite. The horizontal angle is measured from TrueNorth, while the vertical angle is measured from the vertical.

DECLARATIONS

H	horizontal angle
hd	degrees of horizontal angle
hm	minutes of horizontal angle
hs	seconds of horizontal angle
V	vertical angle
vd	degrees of vertical angle
vm	minutes of vertical angle
vs	seconds of vertical angle
cf	constant refraction correction factor (0.13)
r	radius of the earth (6378388 m)
h	height of tower
L	distance of whale from tower base measured over curved surface of earth (m)
l	distance of whale from observers measured through the air (m)
C	refraction correction angle
Vc	angle of declination corrected for refraction

```
$H = hd + (hm/60) - (hs/3600)$
$V = 180 - vd - (vm/60) - (vs/3600)$

FOR $K = 1$ TO 10

    $A = \arcsin \{[(r + h) * \sin V]/r\}$

    $B = 180 - (A+V)$

    $L = r*B$(radians)

    $l = L/\sin V$ (here L is assumed to be measured on a flat plane)

    $C = (l*cf)/2r$

    $V = 180 - vd - (vm/60) - (vs/3600)$

    $Vc = V - C$

    IF $K = 1$ THEN NEXT K ELSE $TOTAL = TOTAL + L$

NEXT K

$D = TOTAL/9$
```

The XY co-ordinates can then be calculated from D and H.


C
V
h
L
l
A
r
B

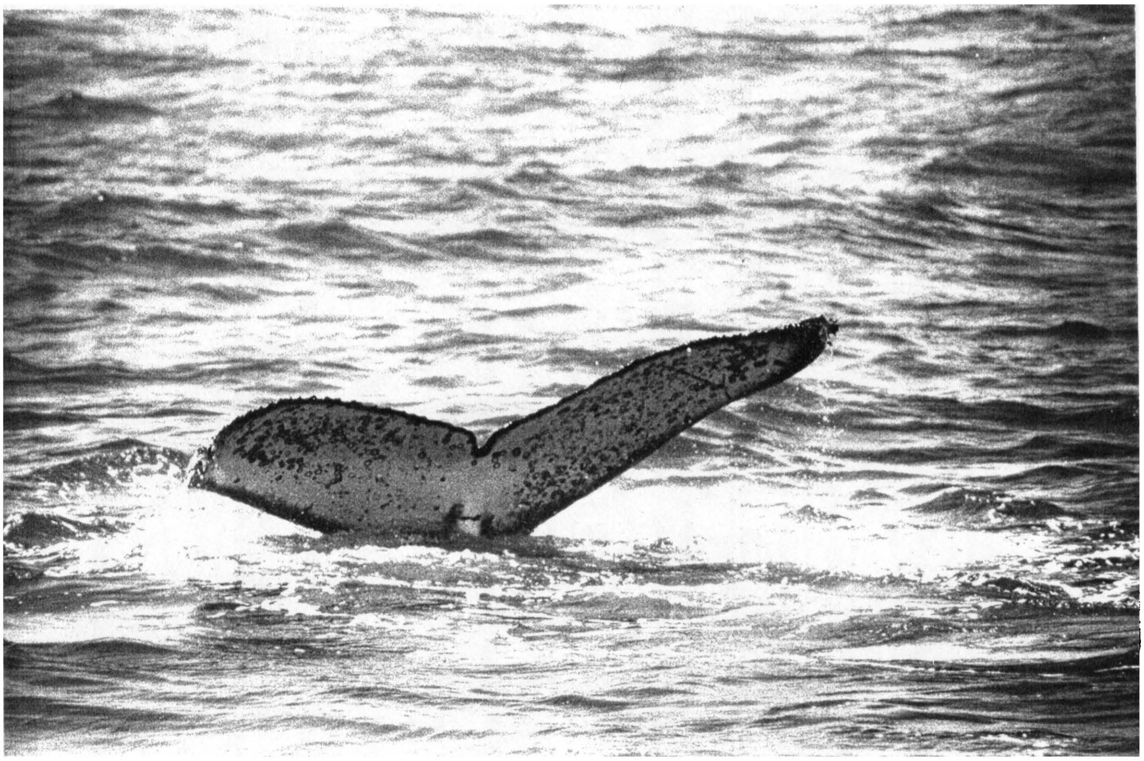


Plate 7.1 Barnacle markings on the ventral surface of the tail flukes of a humpback whale off the African east coast.

Plate 7.2 Tooth rakings (probably by killer whales *Orcinus orca*) on the ventral surface of tail flukes of a humpback whale off the African west coast.

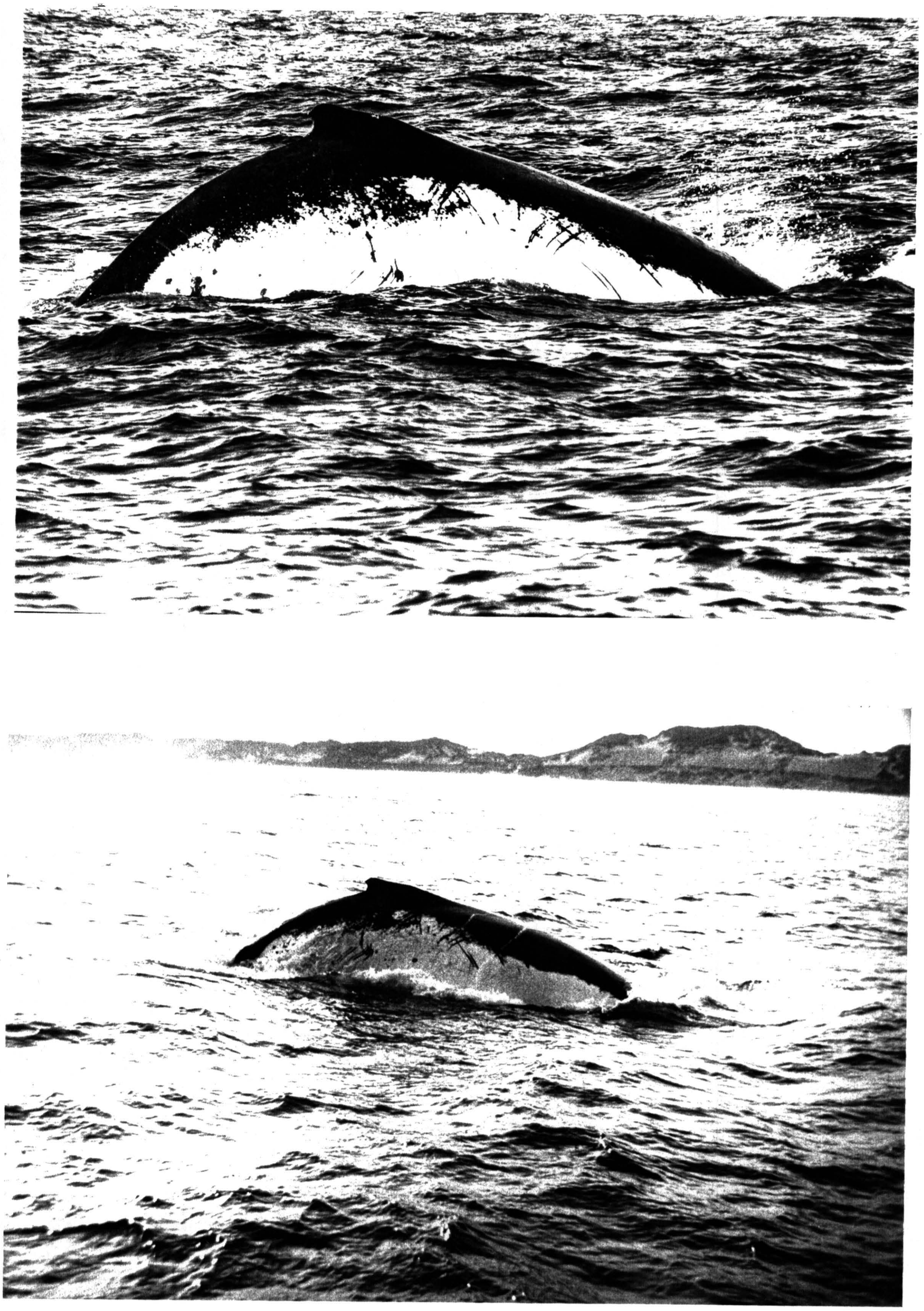


Plate 7.3 A humpback whale resighted within Mozambique waters in 1991 from the right dorsal aspect (resighting (a) in Table 6.10).

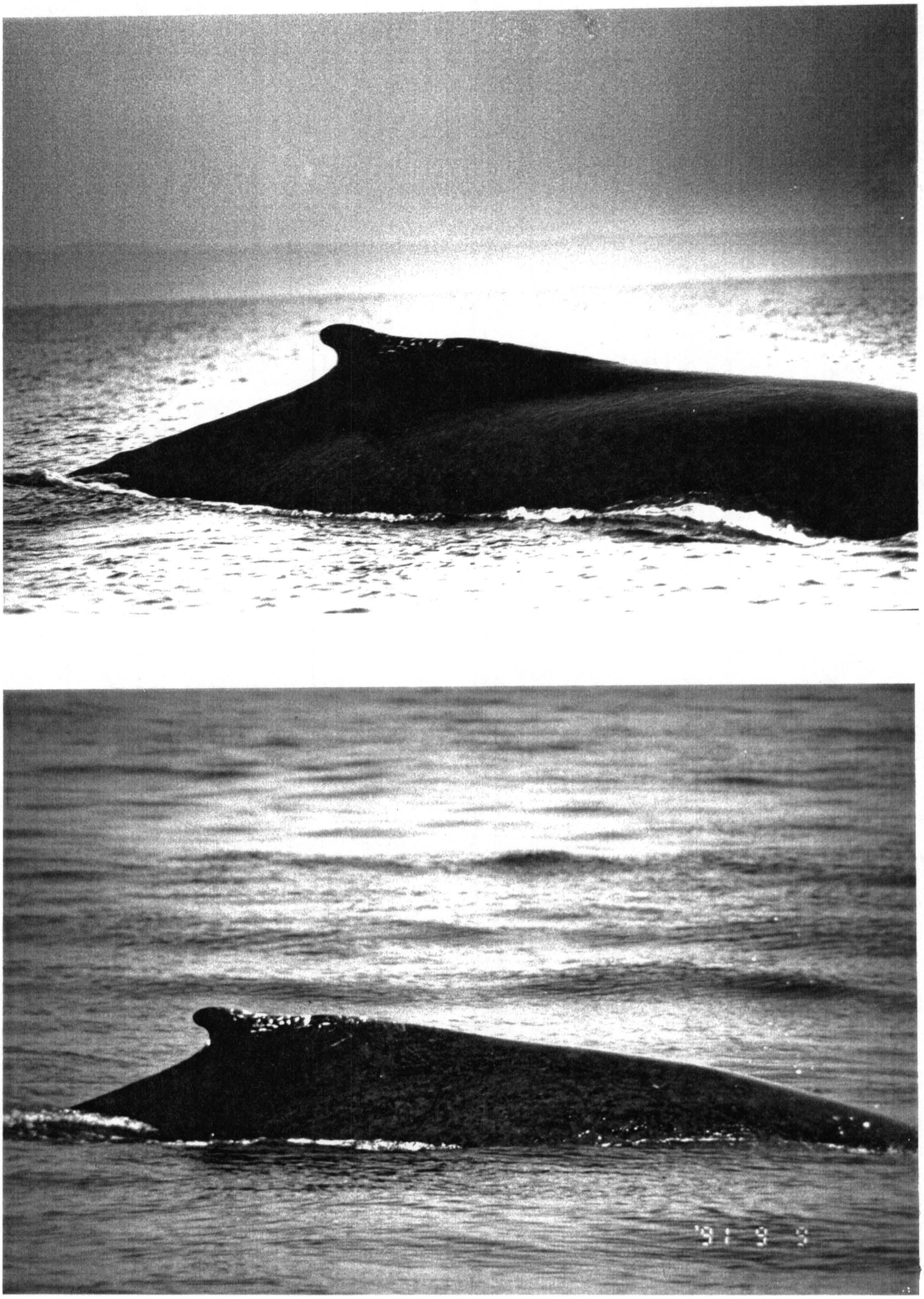


Plate 7.4 An individual humpback whale resighted within Mozambique waters in 1991 from the right dorsal aspect (resighting (b) in Table 6.10).

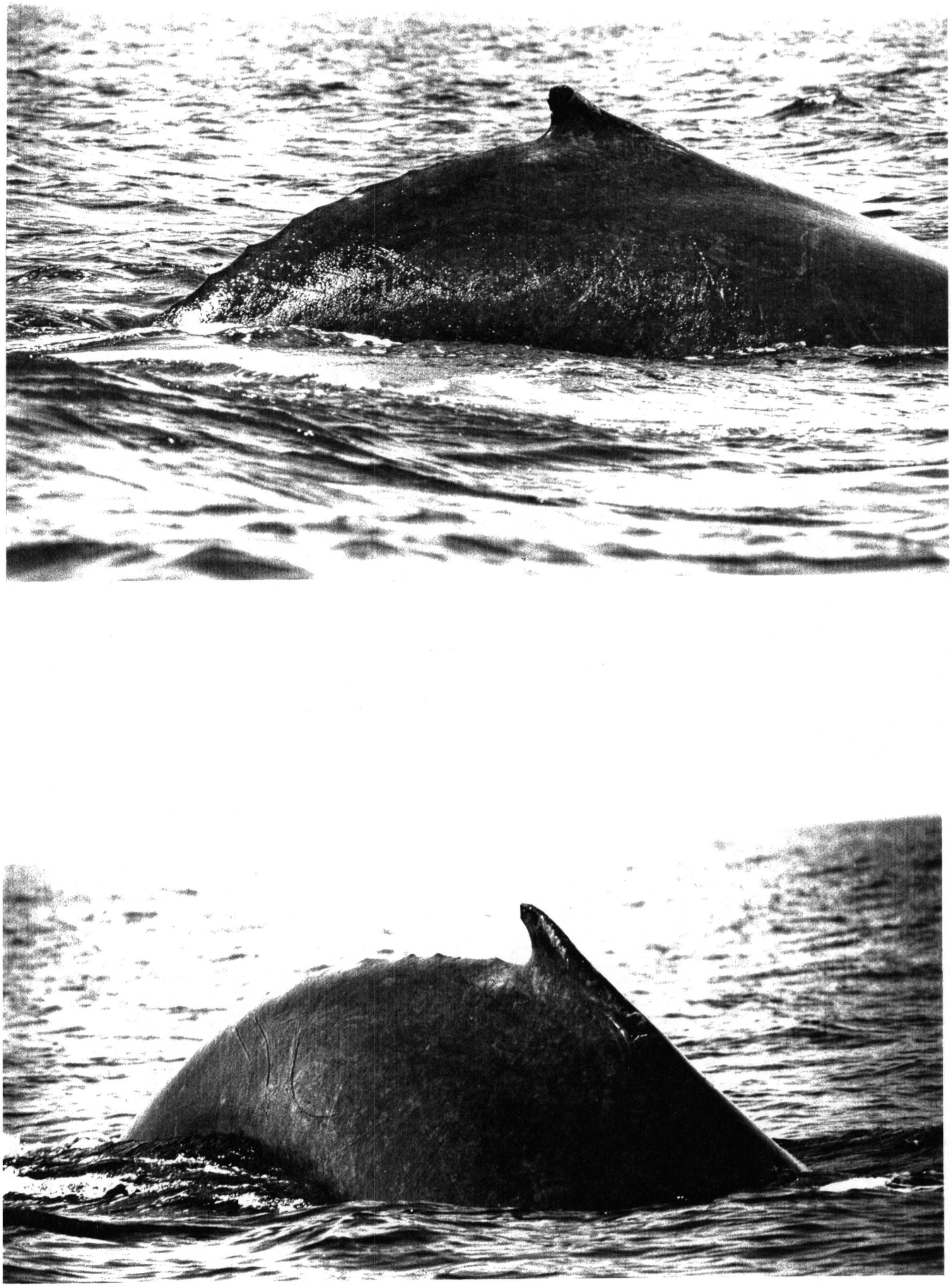


Plate 7.5 An individual humpback whale resighted within Mozambique waters in 1991 from the right dorsal aspect (resighting (c) in Table 6.10).

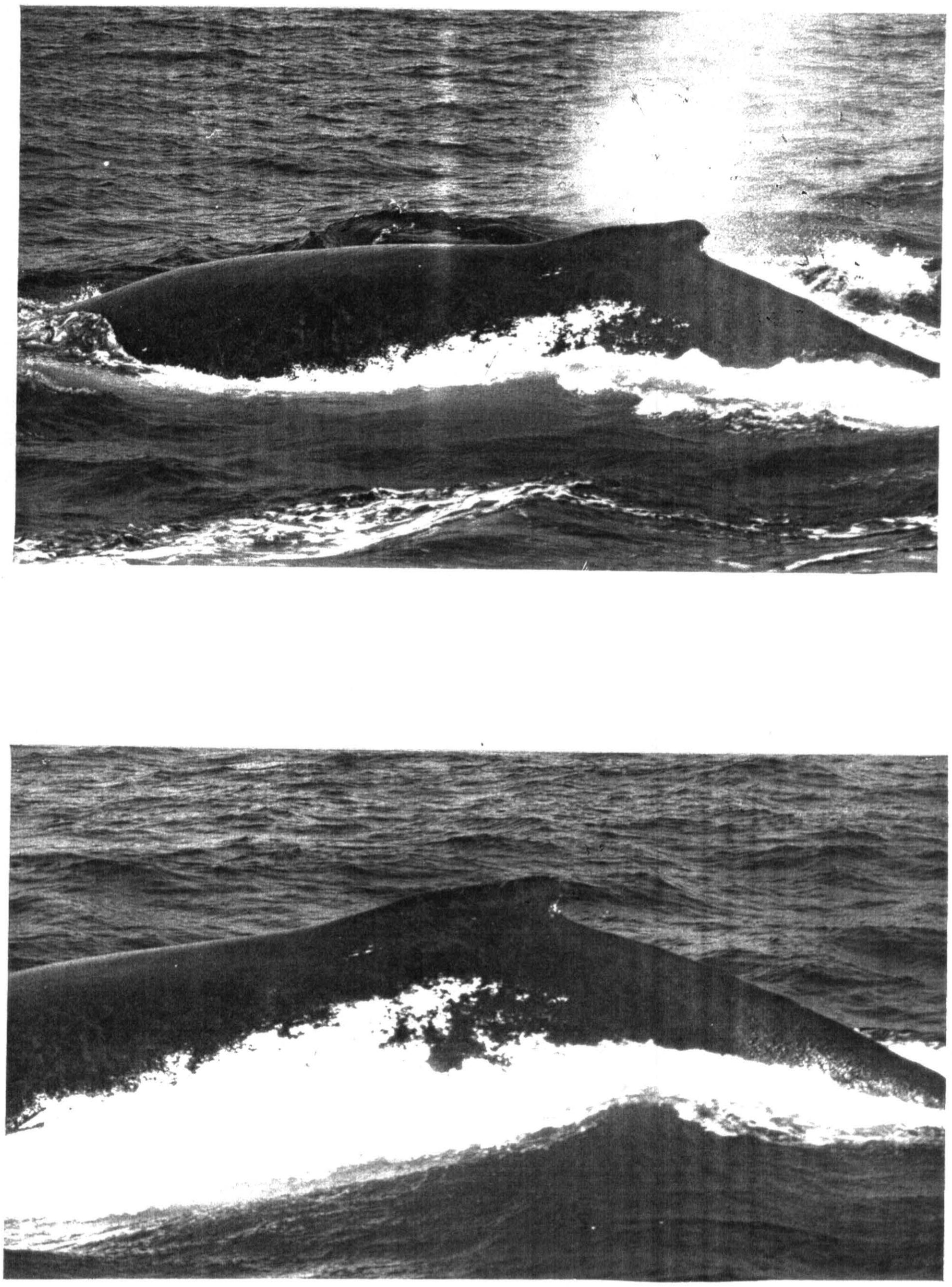
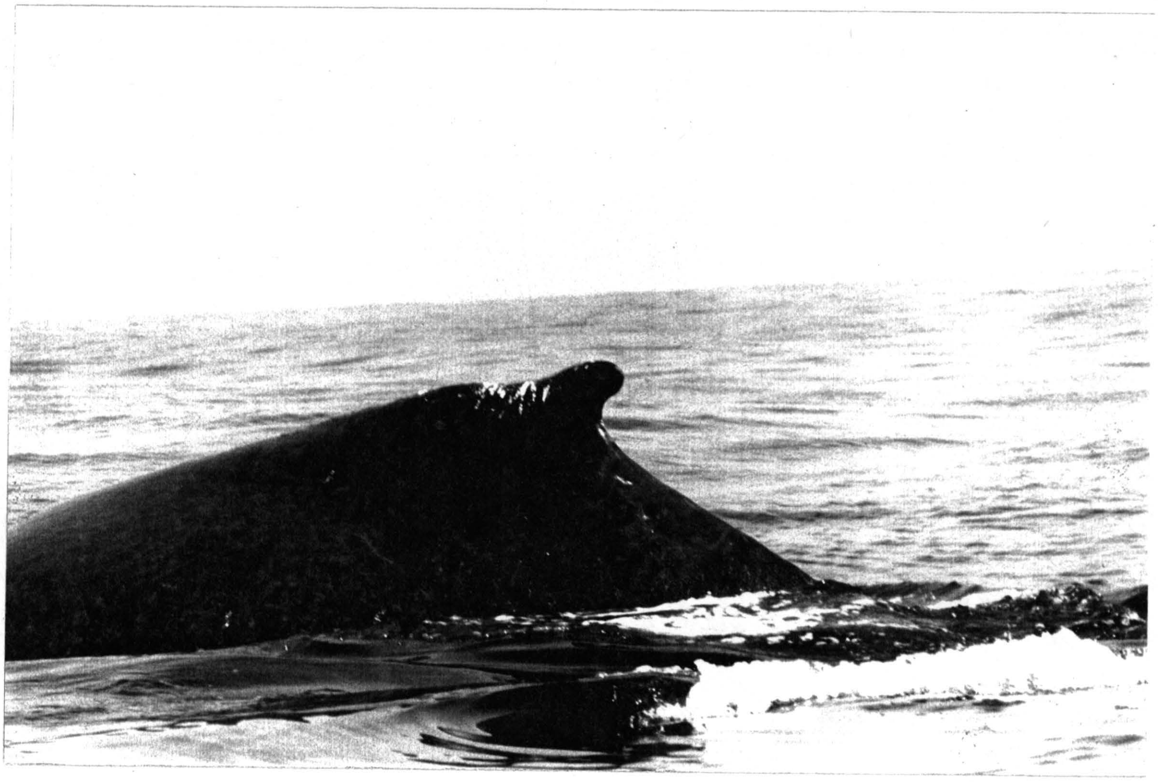


Plate 7.6 An individual humpback whale resighted within Mozambique waters in 1991 from the left dorsal aspect (resighting (d) in Table 6.10).



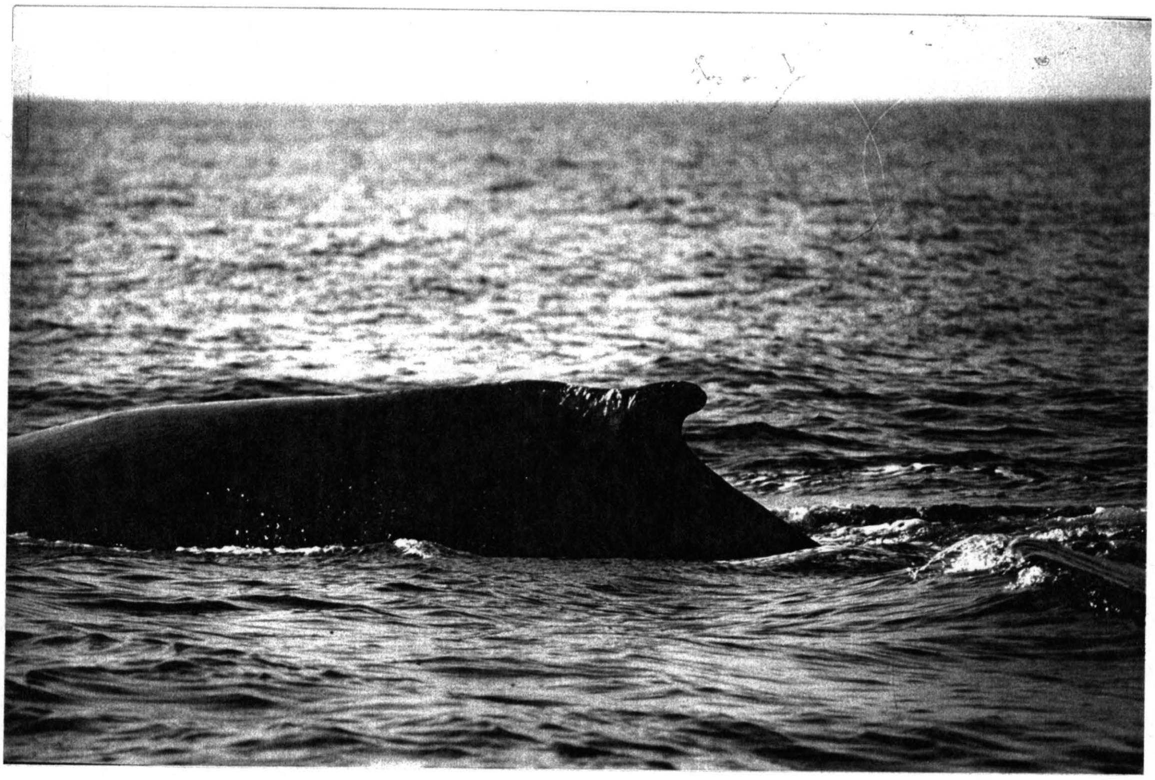


Plate 7.7 An individual humpback whale resighted within Mozambique waters in 1991 from the left dorsal aspect (resighting (e) in Table 6.10).

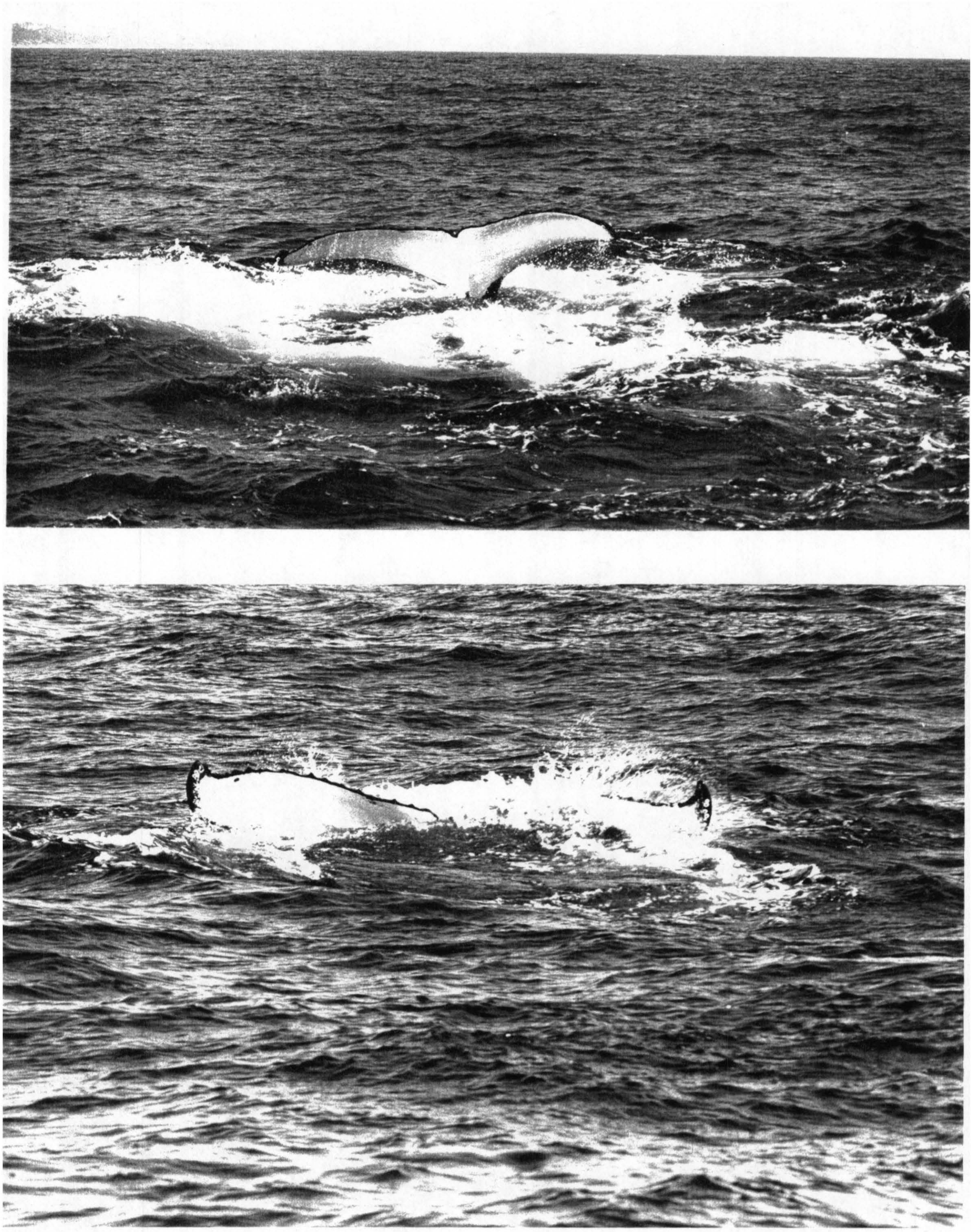


Plate 7.8 An individual humpback whale resighted within Mozambique waters in 1991 from the ventral fluke aspect (resighting (f) in Table 6.10).

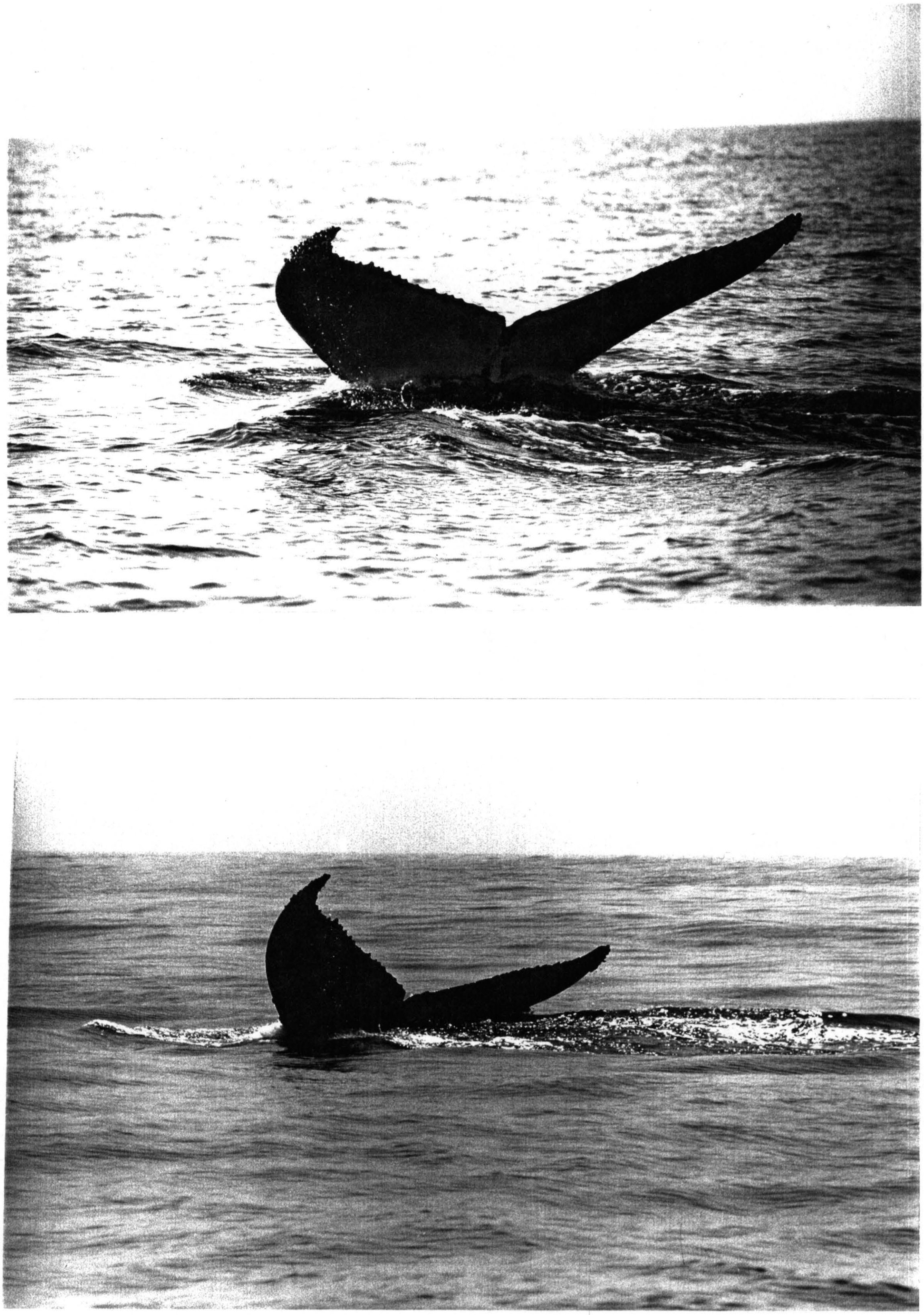


Plate 7.9 An individual humpback whale resighted within Mozambique waters in 1991 from the ventral fluke aspect (resighting (g) in Table 6.10).

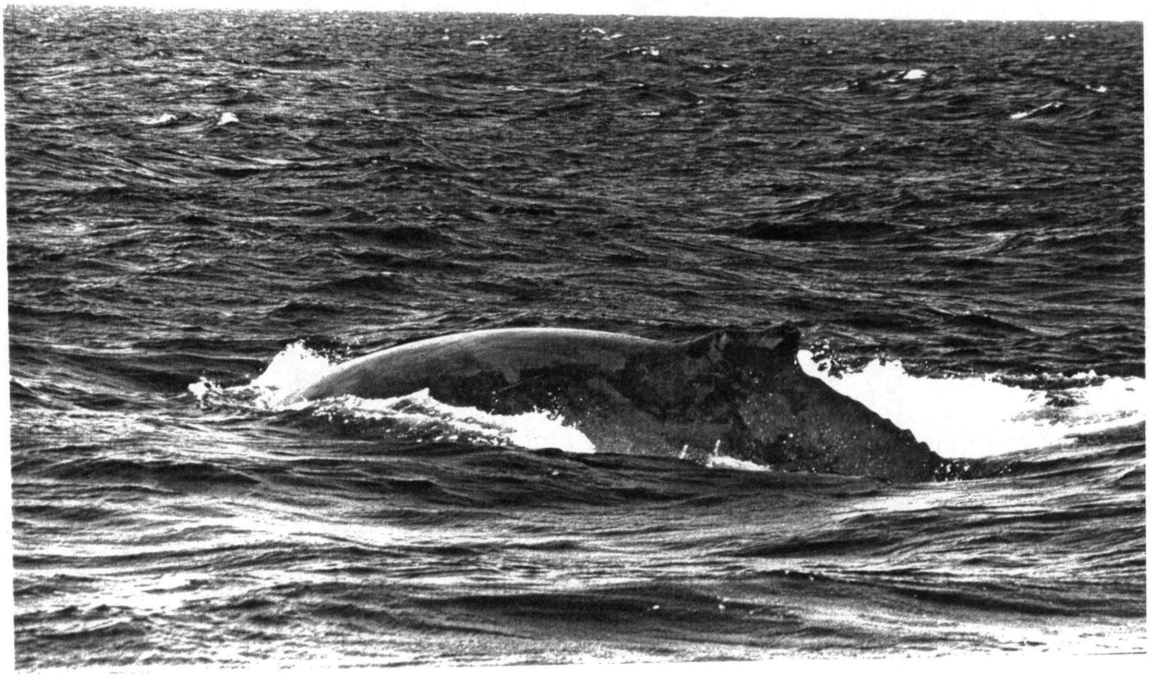


Plate 7.10 A possible resighting in Mozambique in 1991 of an individual originally photographed off Cape Vidal in 1989 (resighting (a) in Table 7.3).

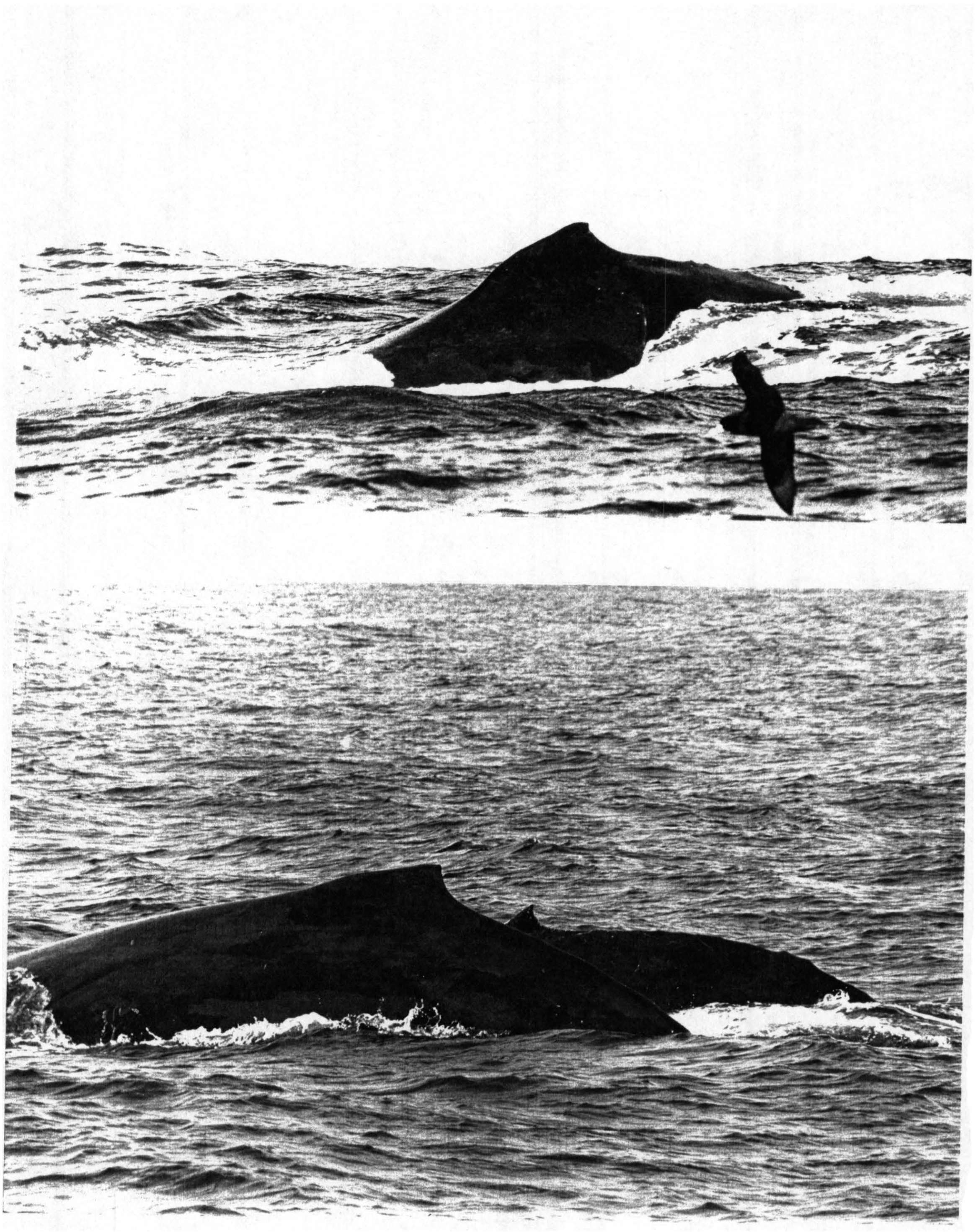
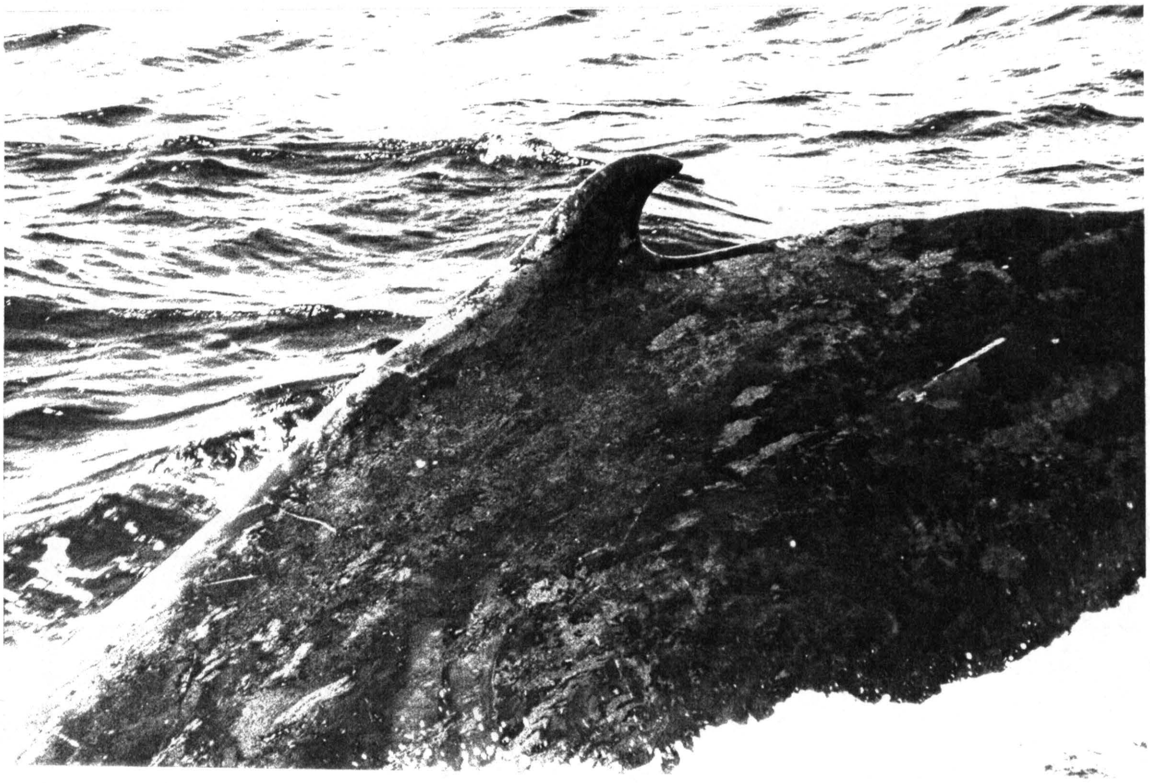


Plate 7.11 A possible resighting off Cape Vidal in 1989 of an individual originally photographed off Cape Vidal in 1988 (resighting (b) in Table 7.3).



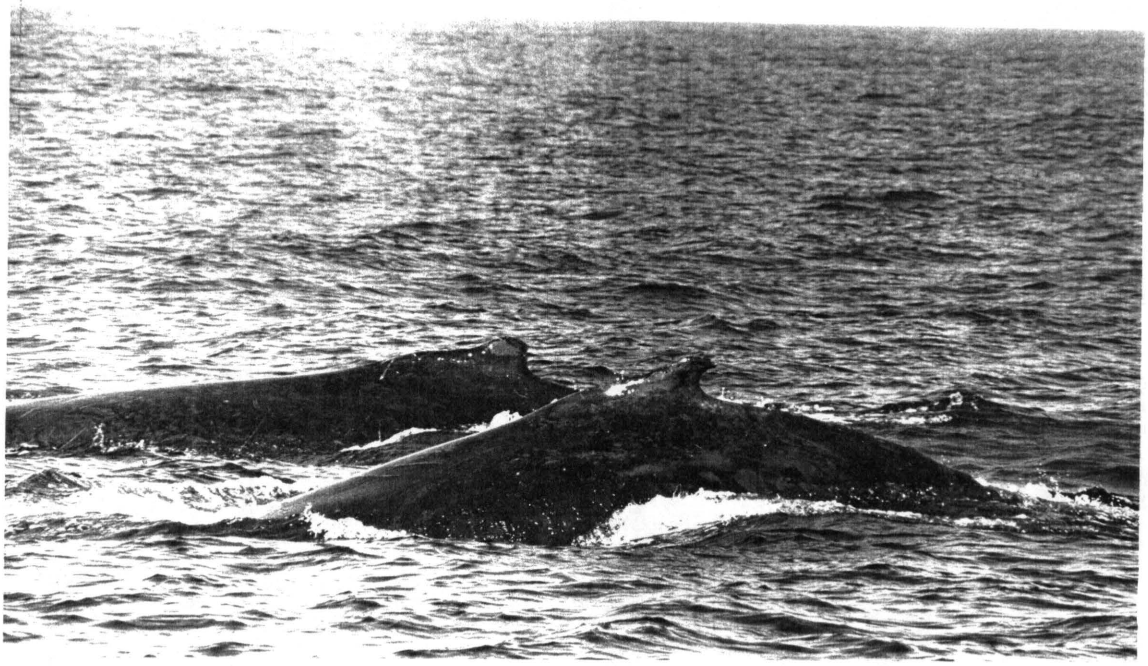


Plate 7.12 A possible resighting off Cape Vidal in 1990 of an individual originally photographed off Cape Vidal in 1989 (resighting (c) in Table 7.3).

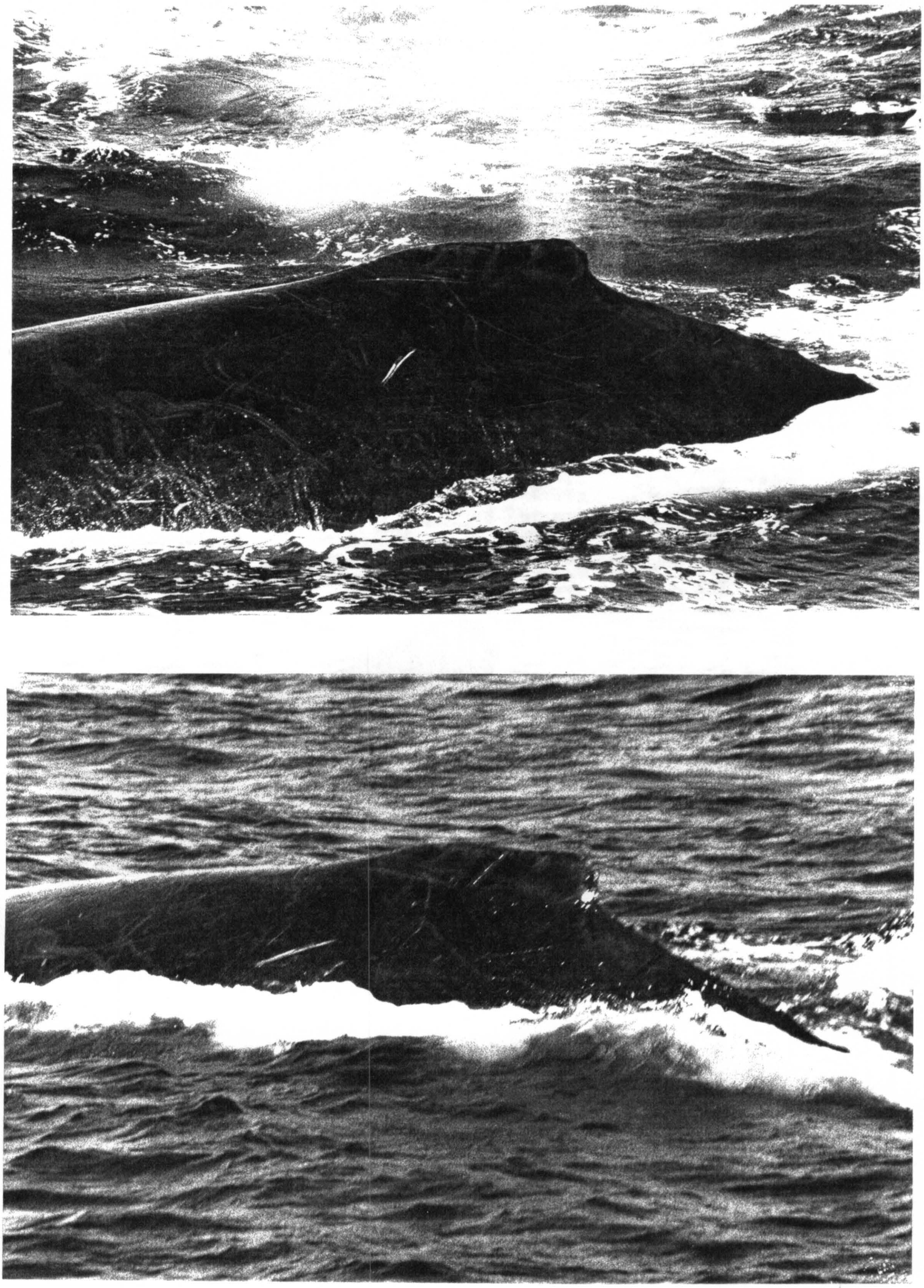


Plate 7.13 Two images of the left dorsal aspect of a humpback whale showing a difference in the orientation of scars at different angles of photography. Both images were taken during the same interception.