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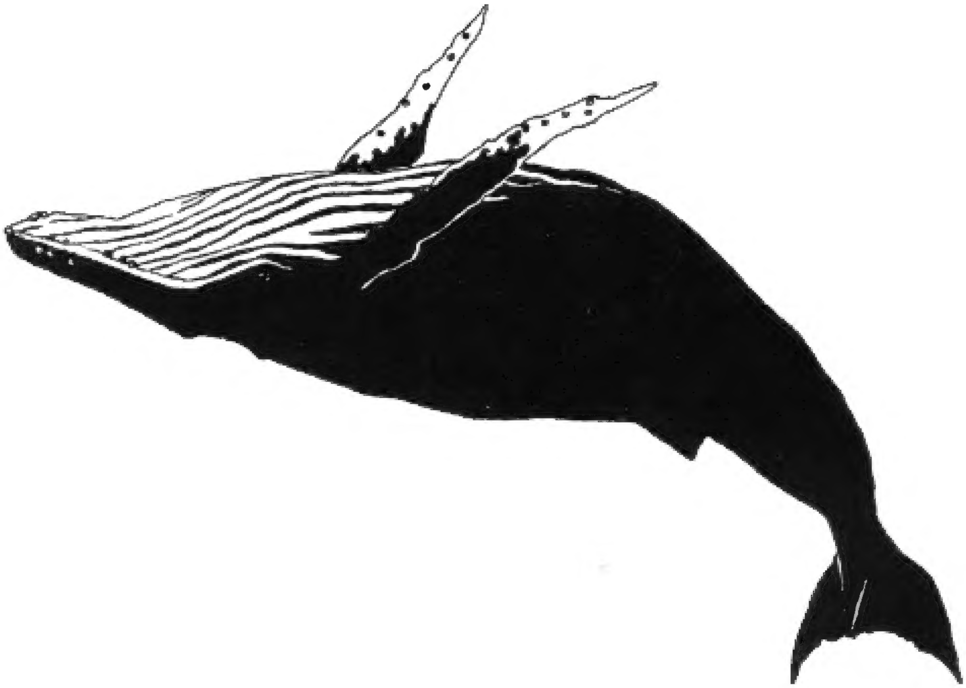

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Preface

Papers contained in this number of the Memoirs of the Queensland Museum were among those presented at the Humpback Whale Conference hosted by the Queensland Museum in September 1990. Delegates from Australia, Colombia, Japan, New Zealand, South Africa and the United States of America honoured Drs R.G. Chittleborough and W.H. Dawbin, the pioneers of Australasian Humpback Whale research during the last, and probably final, period of exploitation of the species in the 1950s and early 1960s. Research initiatives in the post–whaling period have reflected increasing concern not only for Humpback Whales but also for the ecosystem in which they live.

It was particularly appropriate that the official ceremony to acknowledge the display of life size models of Humpback Whales over the front entrance to the Museum was held during the conference and conference delegates were in attendance (see photograph over page).

With the increasing numbers of Humback Whales appearing off the Australian coast, greater understanding ,through the sorts of research reported herein, will be necessary to develop harmony between whales and humans. The growing tourist interest in Humpback Whale activities in Hervey Bay must be accommodated but the interests of the whales must also be considered especially in view of the past decimation of the species wrought by commercial whalers.

The Humpback Whale Conference was most notable for the many different aspects considered by the speakers (photo-id, anatomy, strandings, songs, management, modelling, to name but a few) and this diversity is reflected in the volume that follows despite its containing only a percentage of papers delivered at the conference. The Queensland Museum is proud to have been associated with this meeting of the Humpback fraternity, both as host and as publisher of the proceedings.

Peter A. Jell and Robert A. Paterson
Brisbane
10 May 1991.

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POTENTIAL IMPACTS OF CLIMATIC CHANGE ON THE SOUTHERN OCEAN ECOSYSTEM

R.G. CHITTLEBOROUGH

Chittleborough, R.G. 1991 07 01: Potential impacts of climatic change on the Southern ocean ecosystem. *Memoirs of the Queensland Museum* 30(2):243–247. Brisbane. ISSN 0079-8835.

Global climate change has the potential to disrupt the delicately poised thermal balance in surface waters of the Southern Ocean around Antarctica, threatening this highly productive ecosystem with severe and permanent collapse. Pivotal in this process is a diminution of the important (but little studied) $C0_2$ sink in the Southern Ocean, resulting in a series of feedback loops accelerating global warming and intensifying impacts upon the Southern Ocean ecosystem.

As well as outlining the processes involved and stressing the urgent need for further research, this paper underlines our wider social responsibilities to press for fresh policies essential to arrest the global changes before irreversible harm is done to the Antarctic environment and ecosystems, with their global consequences to our life support system.

R.G. Chittleborough, 24 Watt St., Swanbourne, Western Australia 6010; 4 January 1991.

The Convention for Conservation of Antarctic Marine Living Resources, (CCAMLR), while "RECOGNISING the importance of safeguarding the environment and protecting the integrity of the ecosystem of the seas surrounding Antarctica"; places its main emphasis on the impacts which harvesting may have, not only upon target species but also upon ecological relationships. Article II of the Convention also commits us to the conservation principle of "prevention of changes or minimisation of the risk of changes in the marine ecosystem which are not potentially reversible over two or three decades..."

However, even if there was no exploitation of living (or mineral) resources in the Antarctic, the environment and ecosystems there are now threatened by accelerating climatic changes being triggered globally by mankind.

Not surprisingly, the main focus of attention presently being given to global climatic change is how the changes will impact on ourselves. We have begun to consider how quickly we may have to adapt in terms of water supply, agriculture, forestry, transport, coastal developments, etc. Far less attention is being given to potential impacts upon natural ecosystems, particularly the more remote Antarctic ecosystem.

PROCESSES MAINTAINING THE SOUTHERN OCEAN ECOSYSTEM

The main driving force of this system is the annual pulse of winter sea ice extending northwards from Antarctica to cover some 20 million square kilometres of the Southern Ocean, retreating each summer almost to the mainland coast. This annual pulse drives the vertical circulation of these waters (Fig. 1), cold brine released by the formation of sea ice sinking along the continental shelf, with compensatory upwelling of nutrient rich water farther offshore at the Antarctic Divergence (Sverdrup *et al.*,1942). Microalgae growing from the base of the sea ice, and phytoplankton blooms each spring and summer within the nutrient rich Antarctic Surface Water, are the main basis of the high productivity of the Southern Ocean ecosystem (Chittleborough, 1984). Estimates of gross annual production of phytoplankton are 6.1-38 billion tonnes. This represents an annual uptake of 1.5–10 billion tonnes of CO_2. Part of that CO_2 is released again during metabolic activity of consumers, but a proportion sinks as detrital organic carbon into Antarctic Bottom Water.

Some dissolved CO_2 from the atmosphere is also carried down in both the Antarctic Bottom Water and the Antarctic Intermediate Water sinking at the Antarctic Covergence.

While it is widely accepted that the Southern Ocean is a major sink for CO_2 measurements of the sink are not available. Takahashi (1987) estimated that the Southern Ocean removes 6.67 billion tonnes of CO_2 per year from the atmosphere or 70% of total uptake flux of all oceans.

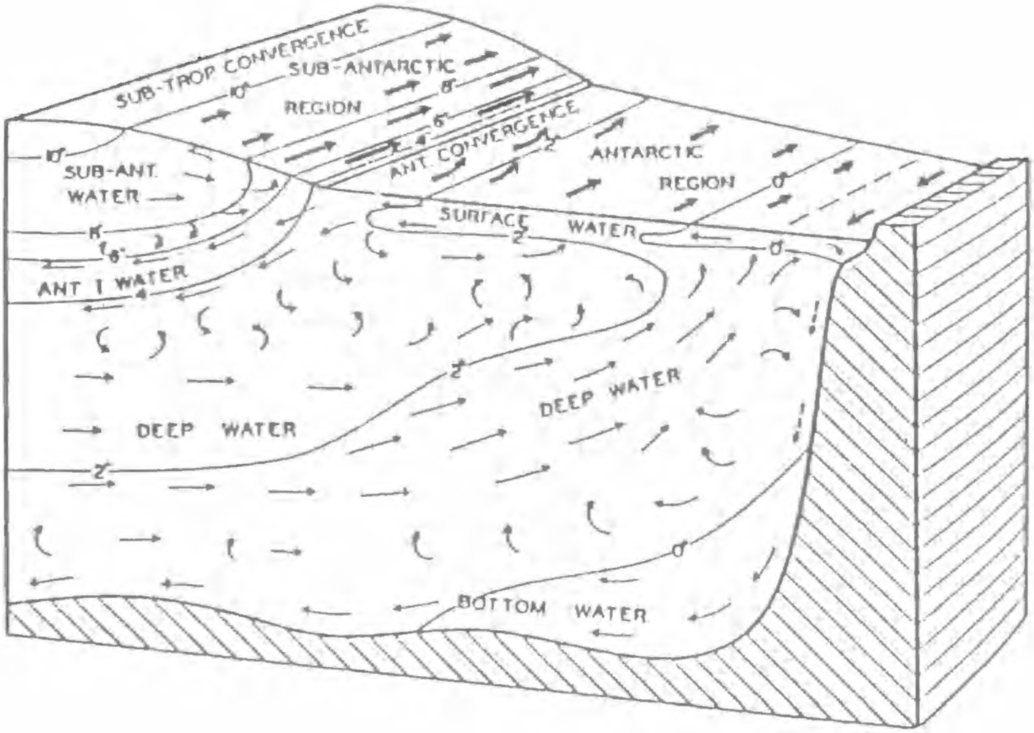

Fig. 1. Representation of currents and water masses of the Antarctic regions (after Sverdrup et al., 1942).

THERMAL STABILITY

The advent of satellite sensing affords a practical means of assessing long term variations in thermal stability of the Southern Ocean. Jacka (1983) stressed the importance of monitoring the extent of winter sea ice, as this parameter is likely to be one of the earliest indicators of any significant climatic change.

As satellite images of the winter sea ice around Antarctica became available, extensive open waters within the ice (polynyas) were discovered. The largest of these, the "Weddell Polynya" (actually situated to the east of the Weddell Sea) measured 1100 x 650 km in September 1975. The Weddell Polynya appeared in three consecutive winters, 1974–1976, then disappeared until 1980 (Comiso and Gordon, 1987). Farther east at c. 45°E, the Cosmonaut Polynya appeared in 1973,1975, 1979,1982 and 1986. While it is not suggested that these polynyas were caused by the greenhouse effect, they do serve to illustrate the delicate balance in the formation and maintenance of sea ice.

Rather more information is available on the extent and distribution of residual sea ice during summer, as this is the time of greatest shipping activity in the Southern Ocean. While much of this information is still to be collated, an analysis by Bentley (1984) indicates that the extent of the Antarctic sea ice in summer decreased by 2.5 million square kilometres between 1973 and 1980, and perhaps by more since the 1930's.

There is evidence of a recent increase in air temperature over the Southern Ocean. Budd (1980) recorded an increase in mean annual air temperature at subantarctic islands of 0.4° C during 1958–1978 and by 0.6° C at stations on the edge of the Antarctic continent. At Kerguelen Island, situated on the northern edge of Antarctic Surface Water, the mean annual air temperature has risen during 1964–1982 by 2.1° C (Jacka, Christou & Cook, 1986), the increase being more marked in summer than in winter. Similar rises in mean annual air temperature are recorded for Amsterdam Island and Marion Island.

On glaciated subantarctic islands such as Heard Island, glacial retreat has accelerated dramatically in recent decades (Allison and Keage, 1986). Heard Island, located towards the outer margin of Antarctic Surface Water, and its glaciers moving rapidly on steep slopes (short residence time of the ice), affords sensitive indicators of changes in climate.

While there is a paucity of hard data on variability within the Southern Ocean region, it is evident from the great changes occurring seasonally and in the longer term, that the thermal balance of this region is delicately poised.

POTENTIAL FOR CHANGE

Global climate models used to predict surface air temperature changes due to increasing atmospheric CO_2, generally indicate greater increases in temperature at higher latitudes. For example, Rind (1984) indicated that a doubling of atmospheric CO_2 would raise mean annual air temperatures over most of Australia by 4+°C, while over the Southern Ocean around Antarctica increases of 6–8°C could be anticipated. Sea surface temperatures in the Southern Ocean can therefore be expected to rise by a greater amount than in lower latitudes.

The most immediate effect of Southern Ocean surface isotherms contracting southwards would be to further restrict the distribution of cold tolerant species living within Antarctic Surface Water. For example, most of the stock of *Euphausia superba* is confined to waters less than 2°C (Marr, 1962), while *E. crystallorophias* is restricted to waters of even lower temperature. The shrinking range of such key food species will compress dependent consumer species into a narrower band around Antarctica, increasing competition between predators. Around some sub-Antarctic islands, vital food resources may then be beyond the foraging range of adult seals and birds during the critical period of rearing the young. Croxal et al. (1987) showed that this already occurs sporadically at South Georgia.

One of the most far reaching effects of rising sea surface temperatures in the Southern Ocean would be a progressive reduction in the extent of sea ice, both in winter and summer. In an initial modelling of the potential impact upon Southern Ocean sea ice, Parkinson and Bindschadler (1984) concluded that a rise of 5°C in air temperature could result in the winter extent and volume of sea ice to be halved. As the increase in air temperature at high latitudes is anticipated to continue to rise well beyond that level, the winter extent of sea ice could be reduced even further.

Direct ecological impacts of a reduction in sea ice include loss of substrate for ice algae (an important component of primary production during winter and early spring), and less ice floes suitable for pupping and mating of ice seals (particularly crabeater and leopard seals) at the critical period during late October and early November each year.

One of the physical effects of a reduction in the extent of sea ice would be a loss of albedo and further absorption of solar energy into the surface of the Southern Ocean, accelerating the change in the energy balance.

An even more important feedback loop from a much reduced extent of winter sea ice would be a severe reduction in the pulse driving the vertical circulation of the waters of the Southern Ocean. With less sea ice formed, there would be less brine released to sink as Antarctic Bottom Water and hence diminution of the passage of dissolved CO_2 to be held in the deep ocean sink. With the weakening of the vertical circulation there would also be a decline in compensatory upwelling of nutrient rich water upon which phytoplankton and all higher consumers are totally dependent. A failure of phytoplankton blooms would represent a massive reduction in the fixation of CO_2 in Antarctic Surface Water, again feeding back to accelerate global warming.

A severe reduction in primary production within Antarctic Surface Water would have a disastrous impact on the Southern Ocean ecosystem as a whole, including the harvested species which CCAMLR is attempting to manage and conserve. Furthermore, a diminution of krill stocks through man-induced climate changes would severely retard (or reverse) the recovery of previously depleted populations of blue, fin and humpback whales, negating much of the hard-won ground by the IWC.

Further potential for impact upon the Southern Ocean ecosystem derives from the ultraviolet wavelengths penetrating the ozone hole now evident in the stratosphere over Antarctica each spring and early summer. Increasing penetration of UV band into the sea surface has potential to depress photosynthesis or even to be lethal to the more sensitive species in the phytoplankton, again depressing the productivity of the ecosystem as well as reducing the uptake of atmospheric CO_2. Precise field measurements are lacking, but Pittock et al. (1981) suggested that phytoplankton in surface waters would suffer appreciable mortality by a reduction of the ozone shield in the range of 16–30%. In October 1985 ozone levels over Antarctica declined by 50% (Ember et al., 1986). Concentrations of

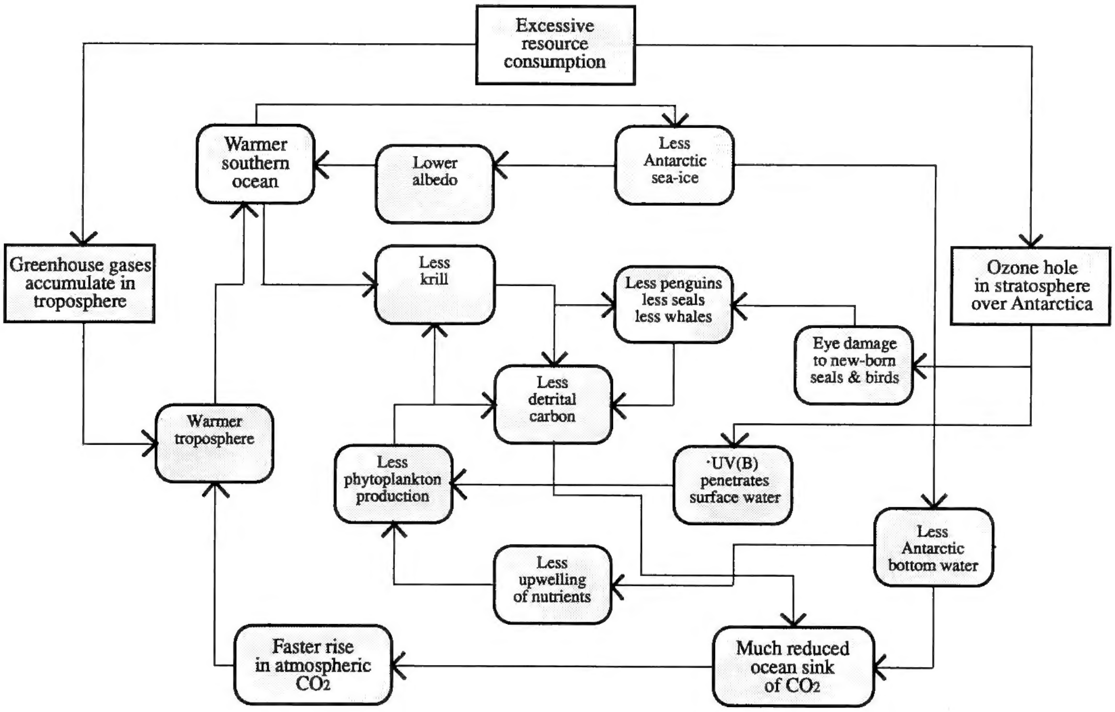

Fig. 2. Potential feedback loops within the Southern Ocean ecosystem resulting from climatic changes.

phytoplankton some tens of metres below the surface may be afforded some protection from UV radiation, but turbulent wind mixing bringing these organisms close to the sea surface may well make them more vulnerable.

Of more immediate impact could be the eye damage that the UV band might bring to newborn seals and birds. Particularly vulnerable here would be the pups of crabeater seals, born on ice floes in high latitudes late in October, close to the peak of the ozone hole. Again, direct measurements of sensitivity are lacking.

There are many potential feedback loops impacting on the Southern Ocean ecosystem from global warming and weakening of the ozone shield (Fig.2). Even if subsequent research finds that one or two of these processes are of relatively minor extent, the overall prognosis for the Southern Ocean ecosystem is extremely poor. Furthermore, the collapse of the important Southern Ocean CO_2 sink has global implications, greatly accelerating the rates of climate change that each of us will have to face.

It should be noted that other feedback systems in the Antarctic, not directly relating to the Southern Ocean ecosystem, but having potential to affect global climate change, are not discussed here. These include acceleration of break-up from the fringes of the Antarctic glacial ice sheet, and a weakening circulation of the Southern Ocean triggering a permanent ENSO phenomenon. As stressed by Thomas (1984) "we cannot rule out the possibility that a climate change of magnitude predicted for CO_2 doubling could radically alter ocean circulation". In particular, he points out that if the relatively warmer Circumpolar Deep Water is able to reach the major ice shelves without considerable cooling, ice shelves could thin enough for massively enhanced calving. "Clearly", he concluded, "we need to learn more about ocean behaviour near Antarctica."

CONCLUSION

There can be little doubt that the Southern Ocean ecosystem is threatened with severe and permanent collapse as a result of impending climatic changes. Such a collapse would halt the present recovery of humpback whale populations.

As scientists, we can design fascinating studies of the physical and biological impacts upon the Antarctic environment as global climatic changes progress. But do we not also have a wider responsibility to press for policy changes aimed at arresting the global processes before irreversible harm is done to the Antarctic environment and ecosystems? Although it is quite evident that we need far more research in this area, we can hardly afford to regard the Southern Ocean as a giant experimental unit if we are likely to lose control of the experiment.

Our role should be far more than the gathering of information. We would be failing in our social responsibilities if we do not make a clear statement on the urgent need for action to circumvent the setting up in the Southern Ocean of irreversible processes having high potential to cause massive environmental and ecological changes around Antarctica, as well as greatly accelerating changes in climate (and sea level) throughout the world.

Unless we act quickly and decisively, the conservation strategies presently being pursued by Australia within the IWC, CCAMLR and the Antarctic Treaty itself, become meaningless gestures. As stated recently by Dr Noel Brown of UNEP, the next decade is our last window of opportunity to make effective changes. Let's use that time to the full.

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HUMPBACK WHALE SONGS ALONG THE COAST OF WESTERN AUSTRALIA AND SOME COMPARISON WITH EAST COAST SONGS

WILLIAM H. DAWBIN AND ELIZABETH J. EYRE

Dawbin, W.H. and Eyre, E.J. 1991 07 01: Humpback Whale songs along the coast of Western Australia and some comparison with east coast songs. *Memoirs of the Queensland Museum* 30(2): 249–254. Brisbane. ISSN 0079-8835.

Humpback Whale songs have been recorded since 1986 off Western Australia. These songs share no themes with those recorded off eastern Australia, supporting other evidence that the two breeding stocks are separate despite some overlap in Antarctic feeding areas.

William H. Dawbin, Australian Museum, 6–8 College Street, Sydney, New South Wales, 2000; Elizabeth J. Eyre, 16/83–85 Alfred Street, Ramsgate Beach, New South Wales 2217; 27 March 1991.

Humpback whales regularly migrate along continental coastlines in the Southern Hemisphere (Dawbin, 1966), and produce complex songs (Payne and McVay, 1971) which change over time (Payne et al., 1983). To date most detailed studies refer to Northern Hemisphere stocks. This report describes the results of studies from the west coast of Australia which began in 1986, together with comparison with data collected from the east coast in 1989

Studies of populations of humpbacks in the Northern Hemisphere have shown that songs are similar within oceans, but differ significantly where oceans are isolated by a land mass (Payne and Guinee, 1983 ; Winn et al., 1981). The Australian populations of Areas IV and V also exhibit major differences from each other in song length and content.

Evolution of songs can be a gradual or rapid process, with songs changing not only from year to year, but also within the year, as the whales migrate to and from the breeding grounds.

This paper will examine some of the song changes that have occurred amongst the Area IV population during 1986–1989, with recent data from 1990 included. Recordings from the east coast will be examined briefly for comparison between populations.

METHODS

Equipment used was a Clevite Ordnance Oyster hydrophone (CH-15) with 30 m of cable, a preamplifier and a Sony WMD6 cassette recorder. Recordings used for analysis were made during the migration period from Dampier (20° 39'S, 116° 45'E) to Rottnest Island (32° 00'S, 115° 30'E). Other recordings have been made along the west coast from its northern most to southern most extremities (Dawbin and Gill, this memoir). Spectrograms of the songs and short hand use of descriptive words for each sound were incorporated for song analysis. The spectrograms were traced for the purposes of this report to eliminate background noise and enable clearer definition of song units.

Themes were numbered by allocating the last theme as that which included sounds which were nearest in character to the "surface ratchet" described by Winn et al. (1971). As songs may differ between singers, comparisons here are made on what are regarded as representative song samples.

Table 1, demonstrating song change, uses methods as described by Helweg et al. (1990). The Western Australian 1986 song is used as a reference, with each theme occurring after the surface ratchet labelled successively from A to E. Themes from following years which correspond to any of those in 1986 fall into A to E, but new themes are given subsequent new letters.

RESULTS

The song changed in the first theme from 1986 to 1988 and 1990 (Fig. 1). Between the 1986 and 1987 songs there was substantial change, with little similarity between themes. In 1988 there was substantial change from the 1987 song repertoire. From 1988 onwards, however, the arrangements of sounds within themes became more similar, with only slight progressive change between units of sound from 1988 to 1990.

The change in song from 1986 to 1987 was not as great as it was from 1987 to 1988 (Table 1). The number of themes remained the same over

FIG. 1. Comparison of the first theme along the west coast of Australia from 1986 to 1988 and 1990, using tracings of spectrograms to illustrate the changes that have occurred.

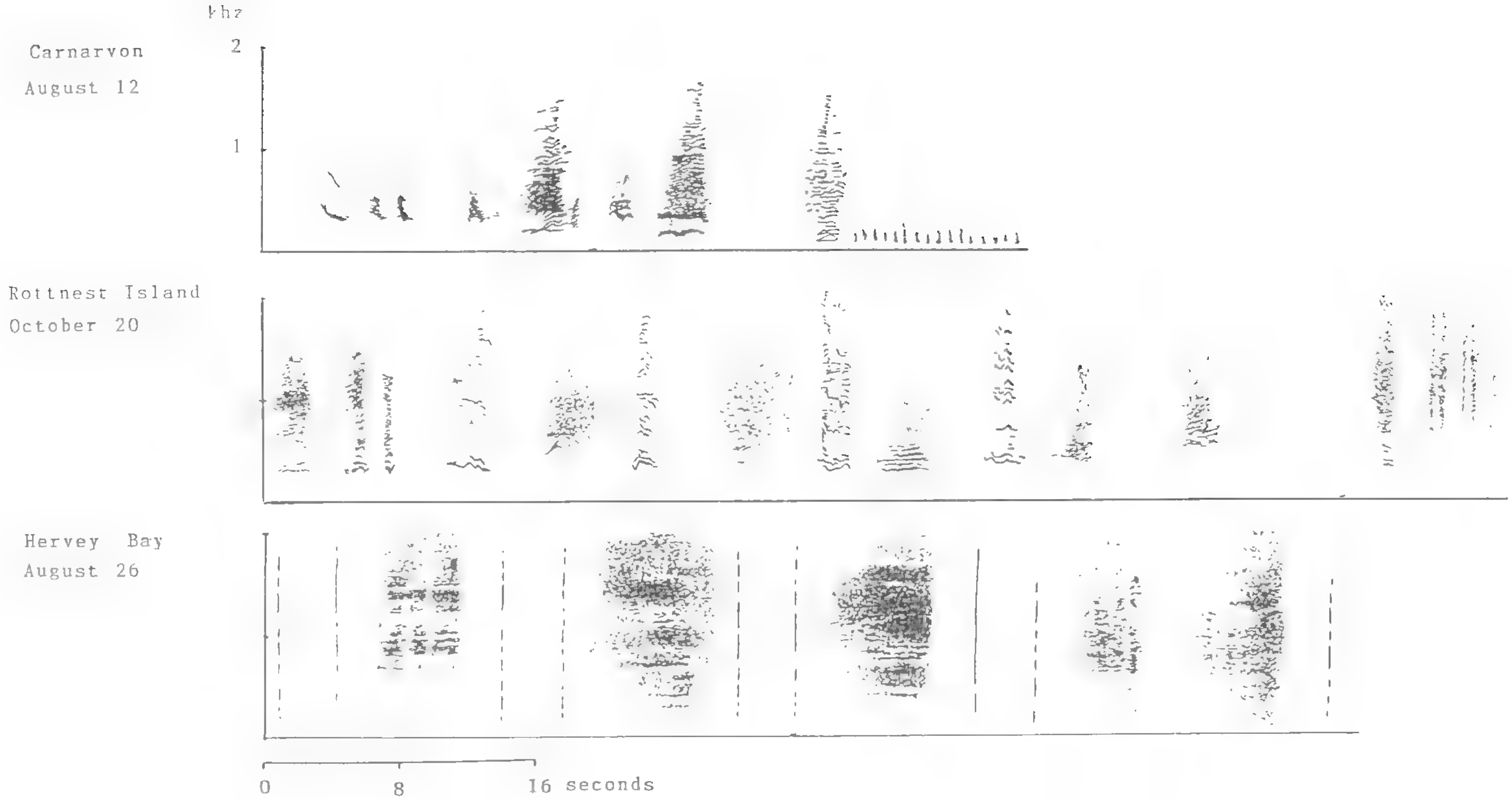

FIG. 2. Spectrogram tracings comparing a representative phrase of the last theme from different recordings during 1989. The first two samples illustrate northern and southern migration song, respectively, along Western Australia. The second sample shows more repetitions of sound units than the first, resulting in a longer phrase. The third tracing is from the east coast and demonstrates a difference in the content of the last theme between each coast. The time scale is approximate.

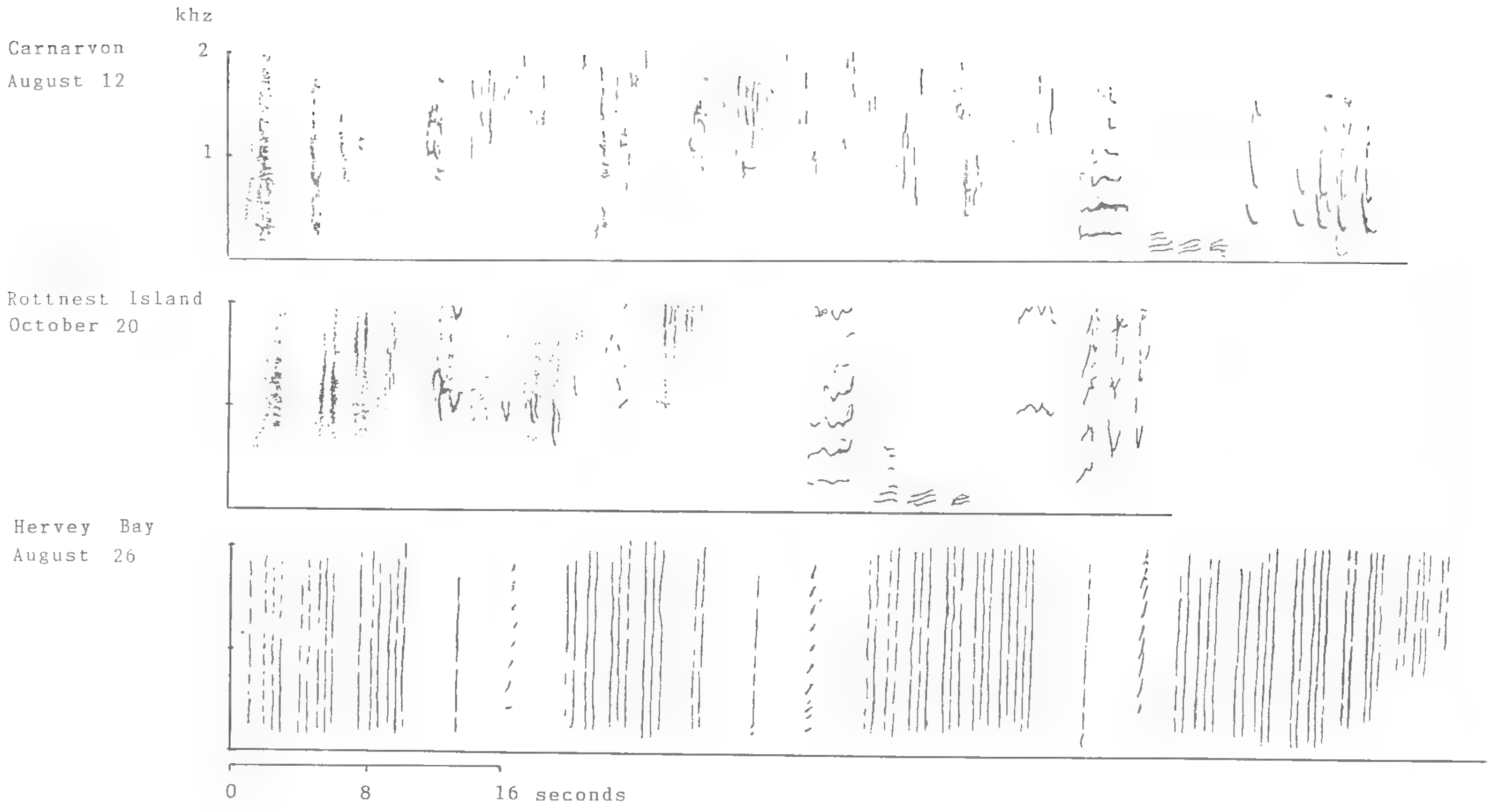

FIG. 3. Spectrogram tracings comparing a representative phrase of the first theme from different recordings during 1989 for the same data as Fig. 2. Again, the West coast samples show different numbers of repetitions of sound units, and thus different phrase durations.

1986 and 1987 and then decreased from 5 to 4 in 1988 (Table 1). The song remained stable during 1988 and 1989, and then in 1990 two themes were incorporated into one, dropping the theme number from 4 to 3.

For further comparison, Fig. 2 shows the last theme from the year 1989, and Fig. 3 the first theme from the same year. Both northern and southern migration songs are represented from Western Australia and these resemble each other. These first and last themes of 1989 resemble the first and last themes of 1988 and 1990 (Fig. 1).

THEME	WA86	WA87	WA88	WA89	WA90	HB89
A	*					
B	*					
C	*					
D	*					
E	*	*				
F		*				
G		*				
H		*				
I		*				
J			*	*	*	
K			*	*	*	
L			*	*	*	
M			*		*	
N						*
O						*
P						*
Q						*

TABLE 1. Repeated and new themes over five years on the west coast and a comparison with one year from the east coast of Australia. The 1990 song consists of three themes, but the first theme is actually an incorporation of the first and second theme from 1988 and 1989.

The east and west coast show no similarity in song content. The 1989 Hervey Bay sample has no shared themes with the west from any years (Table 1). There is no similarity between coasts in song elements in the first and last themes during 1989 (Figs 2,3). This contrasts with the sharing of at least some themes between Hawaii, Mexico and Bonin Islands (Helweg et al., 1990). Evidence from "Discovery" marks indicates that two animals marked off eastern Australia were killed off Western Australia (Chittleborough, 1965) but acoustic data from the present study suggest a high degree of independence between east and west coast breeding stocks.

DISCUSSION

Song change can occur on many levels. Recordings from both coasts of Australia have shown that the content and structure of a song may change between years or within years during the northern and southern migrations. There can also be differences between individual singers and each song rendition of an individual. Change can occur either suddenly or progressively, and even within the songs themselves there can be different rates of evolution.

Recordings from east and west show that little or progressive change tends to occur in the last and first theme, and that the majority of change occurs in the 'body' of the song. Therefore gradual change is more likely to happen at the end or beginning, with more rapid change taking place in the middle. This rapid change was seen in the middle themes from 1986 and 1987, with the first and last themes evolving at a slower rate. In contrast, a slower change from 1988 to 1990 occurred during the whole song, with some themes not changing at all.

Recordings were made during migration as opposed to on the breeding grounds. This is a difficult environment to record in, as the whales are in transit on active migration, and weather conditions are more frequently unfavourable. This enabled only a small sample of song to be collected each year, and the identification and subsequent resighting of individual singers was virtually impossible.

Our studies have shown, however, that Australian Humpback Whale song differs between the west and east coast and that these songs change over time. The variability in song and the different rates it can occur at have been presented here, but what determines the rate of change remains unknown.

ACKNOWLEDGEMENTS

Thanks go to Chris Burton, Robert Mannell, Hec Goodall and the staff at The Pet Porpoise Pool, Ross Isaacs and Peter Gill. This project has received financial support from a Marine Sciences and Technology Research Grant to Dawbin and Cato. Discussions with Dr. Doug Cato have been helpful and much appreciated. The N.S.W. National Parks and Wildlife Service have provided valuable vessel support for sound recording.

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HUMPBACK WHALE SURVEY ALONG THE WEST COAST OF AUSTRALIA: A COMPARISON OF VISUAL AND ACOUSTIC OBSERVATIONS

WILLIAM H. DAWBIN AND PETER C. GILL

Dawbin, W.H. and Gill, P.C. 1991:07:01: Humpback whale survey along the west coast of Australia: a comparison of visual and acoustic observations. *Memoirs of the Queensland Museum* 30(2): 255–257. Brisbane. ISSN 0079 8835.

The results of a survey of humpback whales, using visual and acoustic detection techniques, along the Western Australian coast during the winter and spring of 1989 are reported.

William H. Dawbin, Australian Museum, 6–8 College Street, Sydney, N.S.W. 2000; Peter C. Gill, Oceanic Research Foundation, PO Box 247, Windsor, New South Wales 2756; 10 January, 1991.

The migratory cycle of humpback whales (Dawbin,1966), and the population characteristics of Area IV humpbacks (Chittleborough,1965) and their increase in abundance in Area IV since exploitation ceased in 1962 (Bannister,1990) are well known. Less well studied is distribution of Area IV animals off Western Australia, when they congregate in warm inshore waters to breed. This study was conducted from a 20m schooner, the R/V "Thistlethwayte", while on a circumnavigation of Australia during the austral winter and spring of 1989. The voyage allowed a survey of inshore waters along the Western Australian coast during the humpback breeding season.

Acoustic and visual detection of whales has been used to determine migration routes. Folkow and Blix (1990) detected several species during a sound survey of the mid-Atlantic, while Clapham and Mattila (1990) detected humpback song at sea in the western Atlantic, distant from land. Studies of humpback song on breeding grounds elsewhere are well known and too numerous to list here, but humpback sounds are known to be indicators of stock identity (Payne and Guinee, 1983), and songs from Western Australia have been shown to differ from those on the east coast (Dawbin and Eyre, this memoir). WHD and Chris Burton have recorded humpback sounds in various latitudes off the Western Australian coast, as far south as Cape Leeuwin (34° 20'S). It was therefore decided to use acoustic and visual observations to monitor humpbacks during the southward passage.

The vessel left Darwin in mid July 1989, and sound samples were taken at intervals of no more than four hours, navigation and weather permitting, while at sea. The vessel stayed as close to the coast as was navigationally prudent. On July 24, humpbacks were first encountered visually and acoustically at 15° 17'S, 123° 52'E. This was considerably further north than the generally accepted limits of Area IV breeding grounds (Harrison and Bryden, 1988), though fisherfolk familiar with these waters later reported that humpbacks are commonly seen in the area (P.Canney, pers.comm.). We regarded our timing as favourable, because the majority of whales are still moving north at this time.

Sound was monitored over 33 days at more than 100 stations, with 92 stations between the first and last recordings; stations spanned 15° of latitude and 1600 nautical miles. Generally the weather was calmer north of Broome, with frequent short spells of bad weather to the south.

Sightings and sound recordings were made as far as 30° 24'S, with animals being detected three times as often by sound as by sight. A total of 40 humpbacks were sighted on 21 occasions, and a conservative total of 127 heard on 64 occasions. Conservative, because when more than one animal was singing faintly, it was often difficult to distinguish how many were singing. In these cases, the minimum definite number was recorded. Animals were heard singing at all times of the day and night. Humpback sounds typically consisted of a "chorus" of several animals singing the same song, apparently independently of each other. Occasionally "social" (non-song) sounds were heard, often during observed vigorous displays of social behaviour, as described by Silber (1986). Only at 23 (25%) stations were no whales detected at all. In 13 of these, detection may have been hampered by surface waves (sound), or by darkness or whitecaps (sight).

Dawbin (1956) discussed factors affecting the coastal migration routes of humpbacks. To these

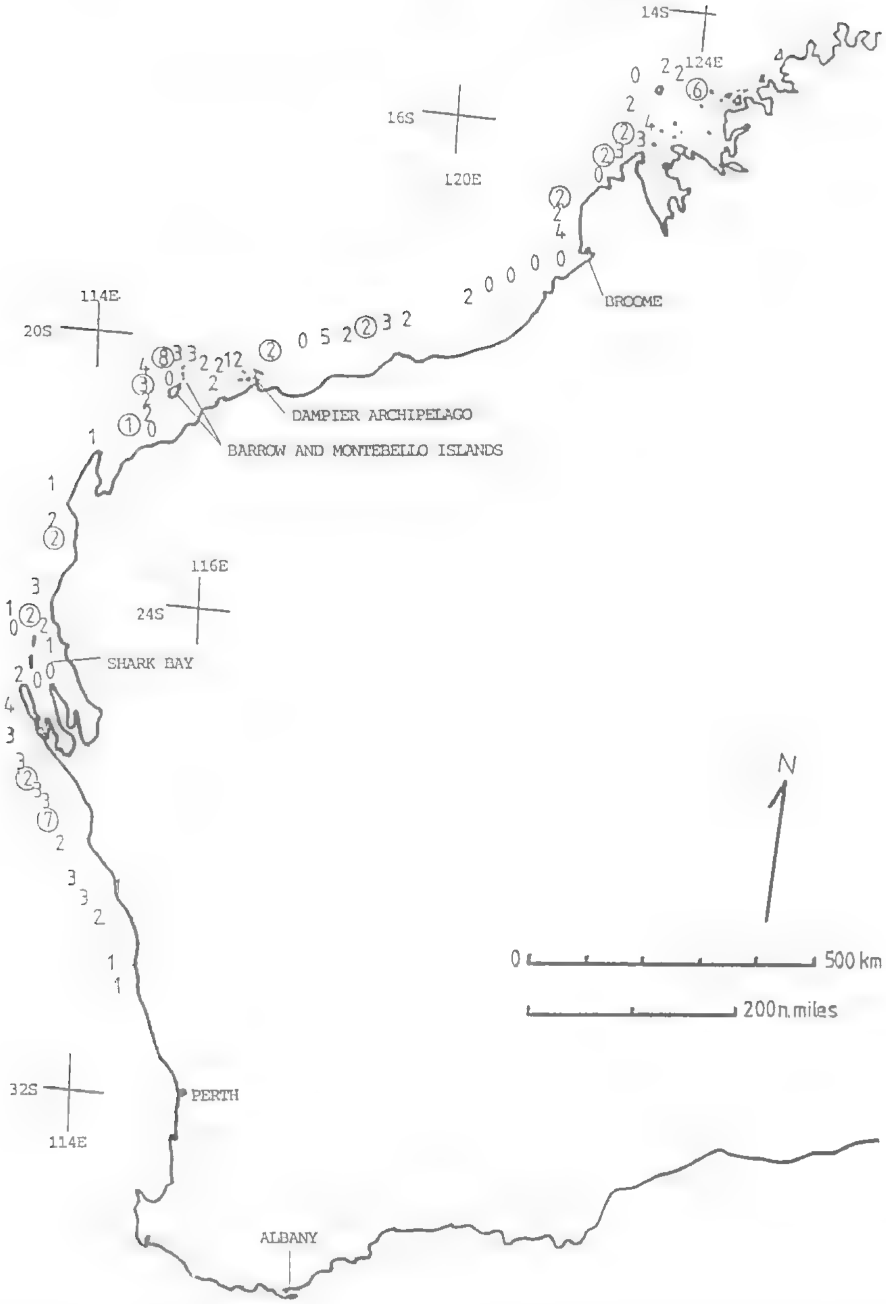

FIG. 1. Map of Western Australia, showing numbers and locations of humpback whales located during the survey. Animals detected by sound alone are denoted by a plain number; those detected visually are denoted by a circled number. This does not mean that the sightings and soundings are mutually exclusive; sound was often detected during sightings. Not all monitoring stations are shown.

we must add consideration of the possible effects of large-scale offshore oil and gas development. Gas rigs in the vicinity of Barrow Island created mechanical underwater noise levels which would certainly hinder cetacean communication, and which may even have resulted in a localised modification of the humpback migration path. Bowhead whales in the Beaufort Sea have shown avoidance behaviours in reponse to oil exploration and drilling (Richardson et al.,1985,1986).

The extent of Area IV humpback breeding grounds is still undetermined. Townsend (1935) showed that humpbacks were taken off the northwest coast, west of Broome. In this study, almost all of the animals observed south of Broome were travelling in a northward direction, while animals to the north of Broome were generally static. Two cows with young calves were seen north of Broome, a town previously regarded as the extreme northern limit of the breeding area: these were the only calves seen during the survey. This indicates a wide latitudinal range in which humpbacks may calve: parturition has been reported as far south as Albany, at 35°S (Chittleborough,1965). Water temperatures and depth profiles north of Broome are comparable to those of humpback breeding areas in the West Indies (Whitehead and Moore,1982). Animals apparently engaged in courtship were also observed north of Broome.

Visual monitoring would have indicated only 1/3 the whales detected by hydrophone. This is despite the fact that Humpback songs are regarded as being almost exclusively produced by males. Past catch records indicate that females occur in almost equal abundance off W.A.

Acoustic monitoring has the advantage of being able to operate in darkness or reduced visibility; even in reasonable conditions whales may evade visual detection where they are not expected. In 1986 WHD recorded humpback sounds off Rottnest Island near Perth, when there had been no visual reports for many years. The combined results of this survey, and earlier surveys by WHD and Chris Burton show that humpbacks vocalise, and can therefore be monitored acoustically, along the Western Australian coast between 15–34°S.

ACKNOWLEDGEMENTS

Special thanks to the crew of the "Thistlethwayte"for their enthusiastic help during the survey. Thanks also to Pam Canney and Ian Lew of F/V "Rachel" in Broome, for their hospitality and valuable information about humpback sightings. Financial assistance was providedby a Marine Sciences and Technology Research Grant, and by a grant from the Australian Whale Conservation Society

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WESTERN AUSTRALIAN HUMPBACKS SINCE 1963

J.L.BANNISTER

Bannister, J.L. 1991 07 01: Western Australian humpbacks since 1963. *Memoirs of the Queensland Museum* **30**(2): 258. Brisbane. ISSN 0079-8835.

Aerial surveys off Shark Bay, Western Australia, since 1976 have demonstrated a significant increase in Southern Hemisphere "Group IV" Humpback Whales since whaling ceased off Western Australia in 1963. "Group IV" animals are humpbacks which summer in Antarctic Area IV (70°E –130°E) and winter north of that area, off Western Australia.

Flights have been timed for comparison with data available from whaling company spotter aircraft operations in 1963. Since 1977 they have been undertaken over a ten day period in mid-July, when most sighted whales are still travelling northwards. Results demonstrate that the number had at least doubled between 1963 and 1982. The best estimate of the increase rate is 8.8% per annum. It is possible that recovery may have been somewhat delayed. To detect any further increase, it is planned to repeat the surveys, using the standardised techniques already adopted, for the same period and at the same time of the year, in 1991 and 1994.

Given an estimate of some 500 animals remaining at the end of 1963, of which at least half would have been immature, and allowing for a possible delay in recovery, the present number off Western Australia in winter/spring seems to be around 2,000–3,000. That result is broadly consistent with the sighting rate of 17 per day, mostly moving north, in the Shark Bay aerial survey in 1988 and an encounter rate of 1.5 per hour, mostly moving south, in field operations for photographic identification off the Dampier Archipelago in 1990.

John L. Bannister, Western Australian Museum, Francis Street, Perth, Western Australia 6000; 8 February, 1991.

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SIGHTING ANALYSIS AND PHOTO-IDENTIFICATION OF HUMPBACK WHALES, OFF WESTERN AUSTRALIA, 1989

CHRISTOPHER L.K. BURTON

Burton, C.L.K. 1991 07 01: Sighting analysis and photo-identification of humpback whales, off Western Australia, 1989. *Memoirs of the Queensland Museum* 30(2): 259–270. Brisbane. ISSN 0079-8835.

During 1989, 492 humpback whales *Megaptera novaeangliae* of the Southern Hemisphere Group IV stock were observed off the Western Australian coast, and 118 of these were photographically identified using tail fluke and lateral body pigmentation patterns. Most observations were made during whale-watching cruises conducted off Perth, with the highest sighting rates (whales/sighting hour) being recorded in September and October. Sightings of mother-calf pairs increased in November. To improve efficiency of identification, animals were classified into 4 Types according to the proportions of white and black pigment on the lateral body and the ventral side of the tail flukes. The degree of coverage of yellow colouration on the tail flukes, presumably caused by the diatom *Cocconeis*, was classified using the same proportional method. ☐Humpback Whale, *Megaptera novaeangliae*, pigmentation, photo-identification, sighting, Western Australia.

Christopher L.K. Burton, c/- W.A. Marine Research Laboratories, P.O. Box 20, North Beach, Western Australia 6020; 20 December 1990

Humpback whales (*Megaptera novaeangliae*) which migrate along the Western Australian coast, comprise the Southern Hemisphere Group IV stock that was severely depleted by commercial whaling from an estimated 12,000–17,000 animals to c. 800 by 1962 (Chittleborough, 1965). Recent aerial surveys show that the stock has been increasing, having at least doubled between 1963 and 1982, and having continued to increase since then (Bannister, this memoir). On that basis the stock may now be more than 2000 animals.

Tail fluke photography is a valid means for humpback whale identification (Katona, 1979; Glockner & Venus, 1983; Baker et al., 1986; Stone, Katona & Tucker, 1987). Photographing the lateral body pigmentation patterns in addition to flukes increases the number of individually identified whales (Kaufman, Smultea & Forestell, 1987).

Photographic identification of individuals will assist in analysis of migration patterns, distribution and stock identity of this population of humpback whales. Whale watching tours provide an opportunity to photograph many individuals and collect abundance and pod composition data over a short time span within a specific area.

Watching humpback whales has become a viable industry on the east coast of Australia, where much research has been conducted into identification and monitoring of the Area V population (Bryden & Slade, 1987; Bryden, Corkeron & Slade, 1988; Kaufman, Smultea & Forestell, 1987; Paterson & Paterson, 1989).

In Hawaii, observations from consecutive years of commercial whale watching have been used to investigate changes in humpback pods and calf encounters (Salden,1988). In Perth, whalewatching tours by Underwater World from Hillary's Boat Harbour provided a valuable platform for research on humpback whales. This paper presents in two parts, results from analysis of photographs obtained during 1989 and from data collected during the whale watching cruises.

PART 1 - PHOTO-IDENTIFICATION

METHODS

During July and August 1989, humpback whales were photographed in Shark Bay from a 5.3m runabout, and off North West Cape from a professional fishing boat. From September to November 1989, photographs were taken during whale watching and from a 5.4m runabout. Locations of all sampling areas are shown in Fig. 1.

A 35mm SLR camera with a 35–200mm zoom lens was used for all photographs. The larger tour operators' vessels operators came no

FIG. 1. Humpback whale observations and photographs, 1989. (observations/photo-ids).

closer to the whales than 50m. Interference to the pods was minimised, and often good photographs were obtained when whales themselves became the curious observers.

Data collected included details of pod structure, behaviour, time and photographs. Adults were presumed to be female only if in close association with a calf. Differentiation between adults and subadults was not made. The number of whales observed daily was recorded, as not all whales could be photographed. Copies of the photographs were sent to the Western Australian Museum and to the Pacific Whale Foundation for use in compiling catalogues.

Classification of the lateral colouration of individuals follows that described by Kaufmann et al. (1987) (Fig. 2) using the proportion of white pigmentation on the lateral body, with Type 1 having the greatest and Type 4 the least (Fig.3). Whales which did not present sufficient lateral body when surfacing to accurately classify were classified as undetermined.

Colouration of the ventral sides of the tail flukes was also assessed, using a similar proportional method to the lateral colouration, with Type 1 mostly white and Type 4 mostly black. The flukes were divided by a straight line from

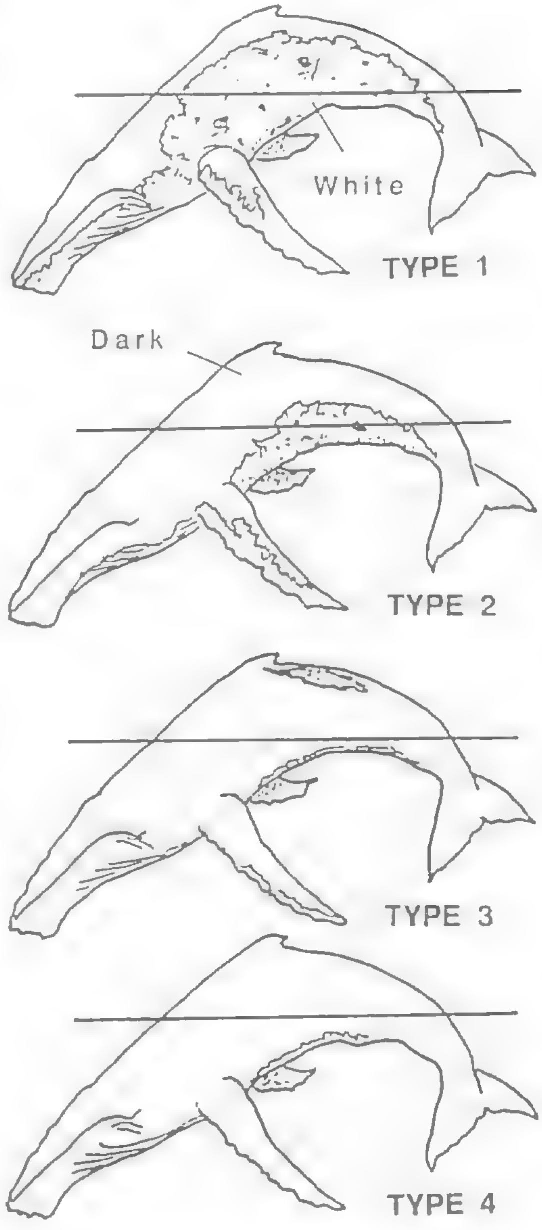

FIG. 2. Lateral body pigmentation types displayed by Australian Humpback Whales. Illustrations by Lili Hagen. courtesy of G. Kaufman, Pacific Whale Foundation. TYPE 1, White coloration reaches above the horizontal mid-line of the body, generally extending anterior to dorsal fin. TYPE 2, White coloration extending to body midline or above, with coloration generally observed near the caudal peduncle.TYPE 3, An obvious but less distinct whitish-grey coloration patch along the dorsal surface of the caudal peduncle posterior to the dorsal fin. TYPE 4, Lack of obvious white pigmentation patterns.

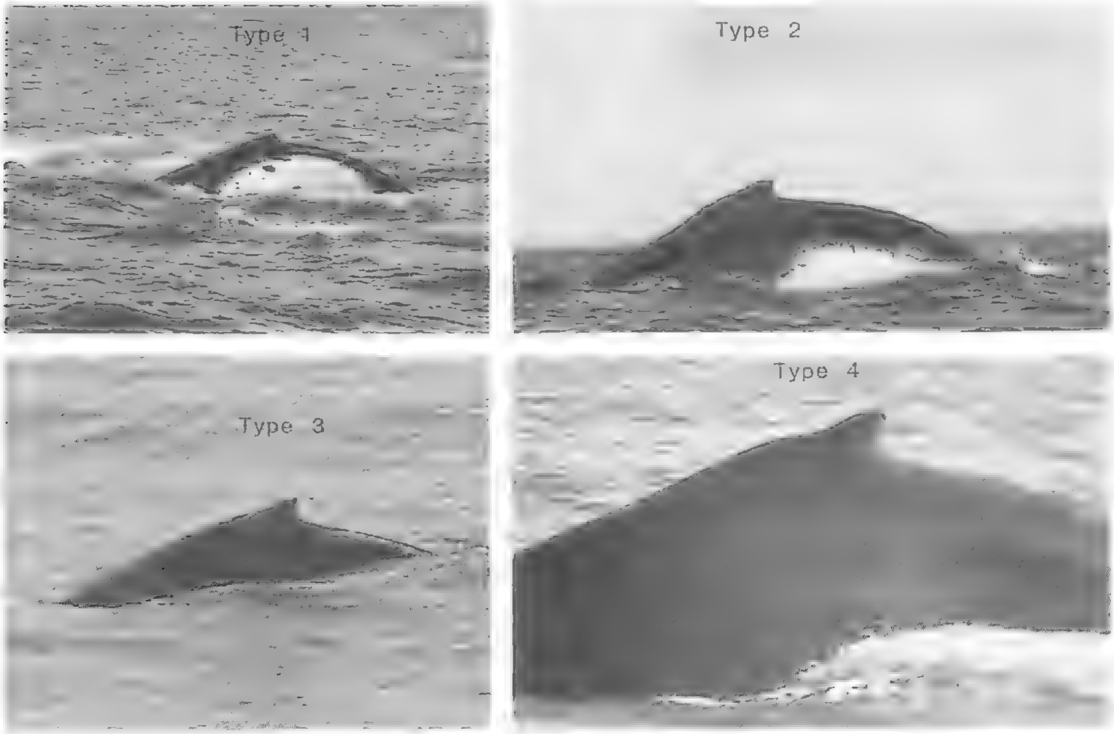

FIG. 3. Identified Humpback Whales from W.A., showing 4 lateral pigmentation types.

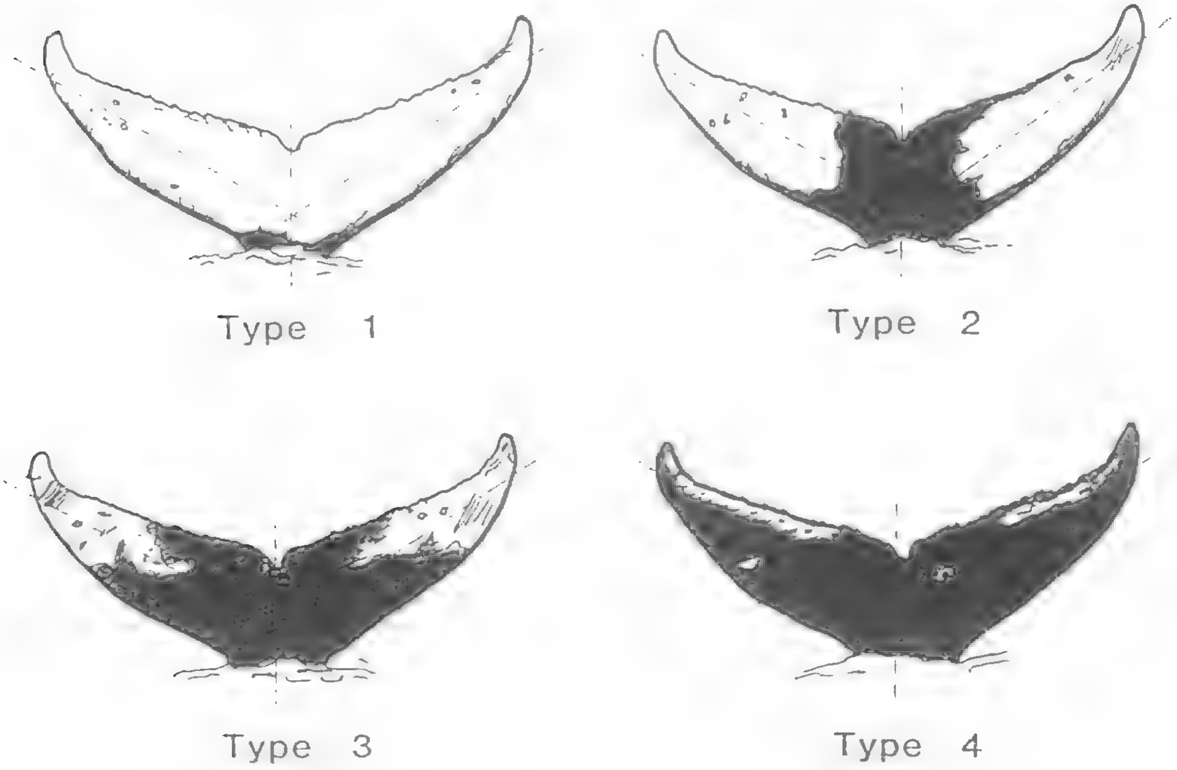

FIG. 4. Tail fluke pigmentation types of humpbacks off WA.

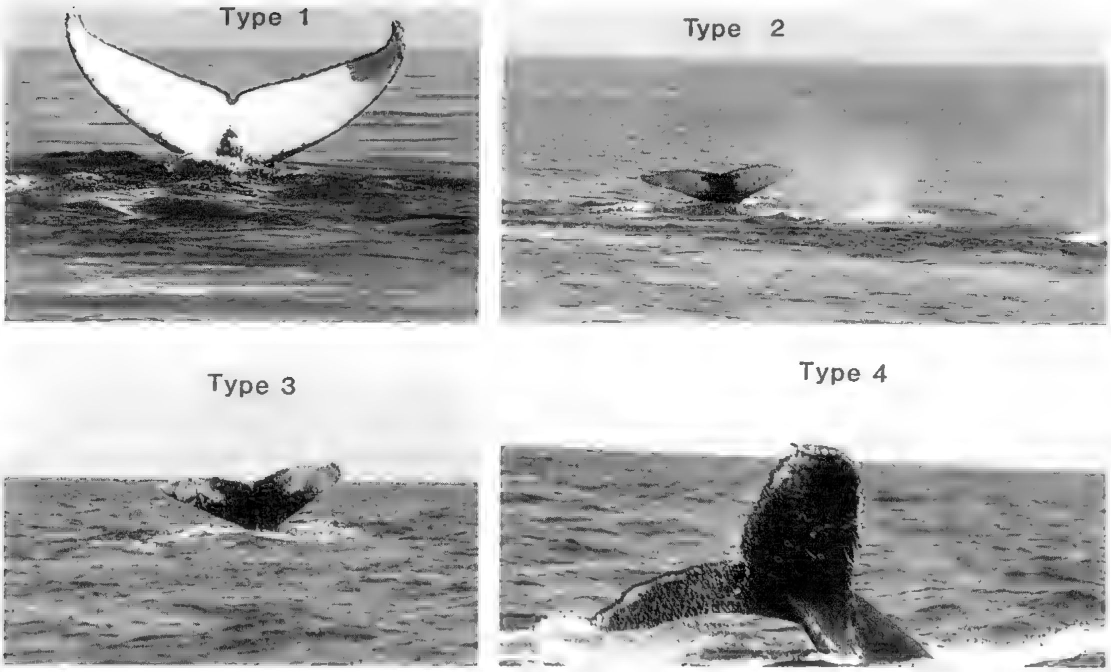

FIG. 5. Identified humpback whales from WA showing 4 tail fluke pigmentation types.

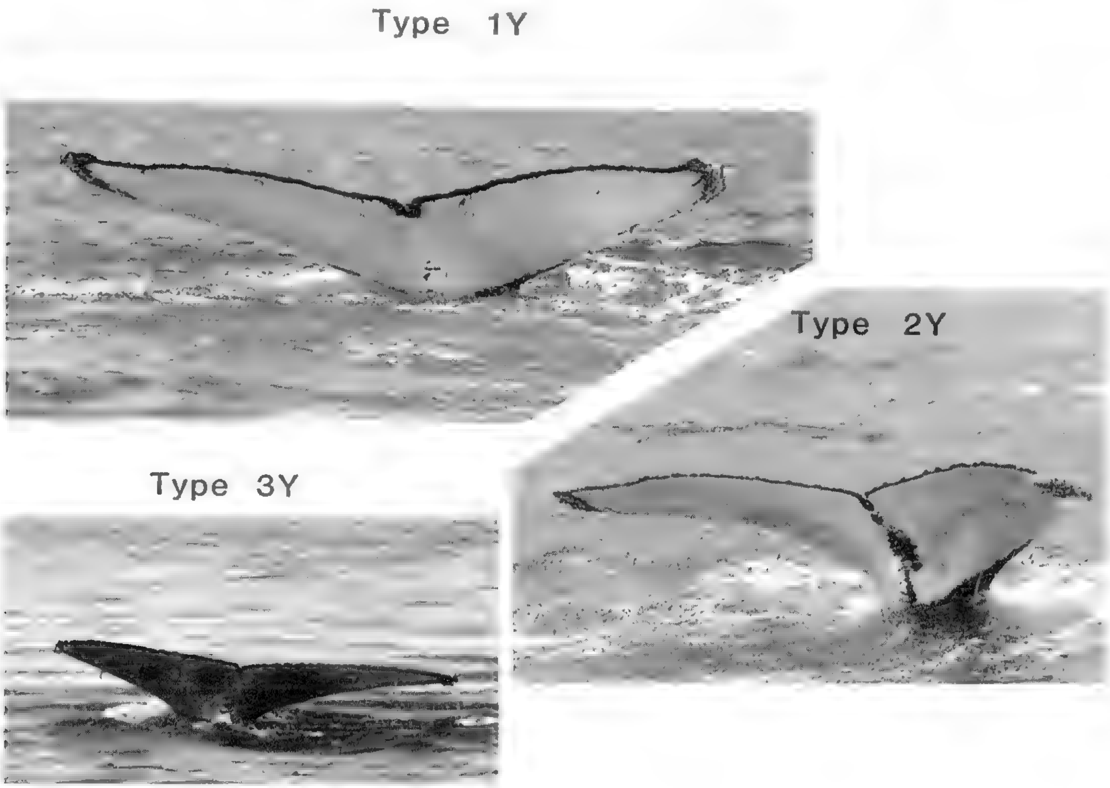

FIG. 6. Photographs of identified whales off WA, showing 3 of the 4 tail fluke diatom colouration categories (yellow).

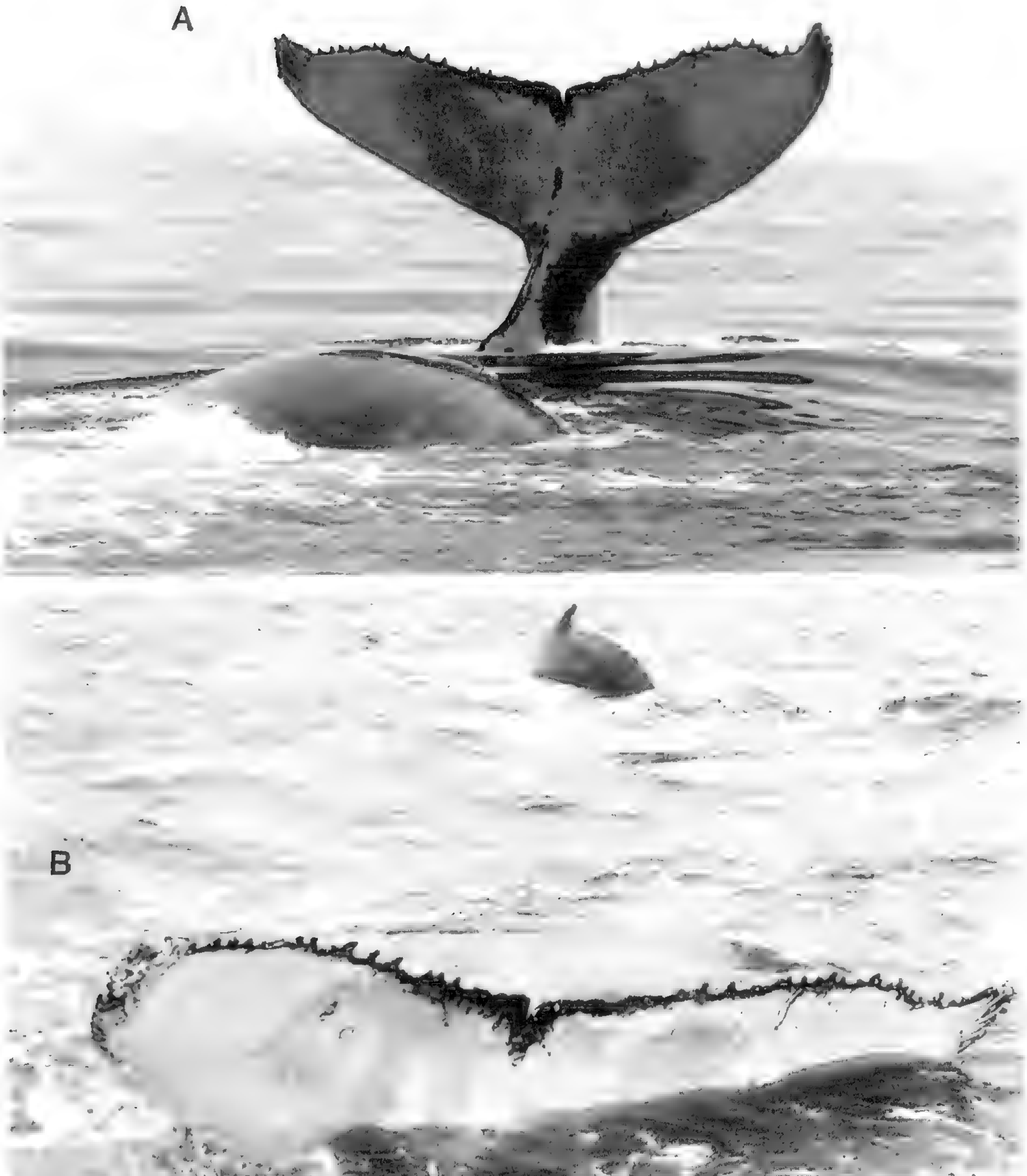

FIG. 7. Tail fluke pigmentation and diatom colouration photographs of a resighted humpback; A, Shark Bay, 12 July, 1989. B, Perth, 27 and 30 September, 1989.

the fluke tip to the centre of the median strip between each fluke to assist in determining Type 2 and Type 3 animals (Fig. 4). A Type 2 fluke is categorised as having <50% black pigmentation and a Type 3 fluke having >50% black (Fig.5).

Many identified animals had some yellow colouration on the underside of the flukes, presumably due to a film of the Antarctic diatom *Cocconeis ceticola*. The typically yellowish colour of this species on the skin of whales in warmer waters of the Southern Hemisphere has been taken to indicate movement of the whale from colder waters (Bannister, 1977).The degree of diatom coverage on the underside of the tail flukes was assessed using the proportional method described above for the white/black pigmentation patterns, with Type 1 having little yellow and Type 4 being mostly yellow. Types 2 and 3 animals have < and >50% yellow colouration, respectively (Fig.6). Tail flukes of animals which were too distant and had uneven lighting, or which were at too low an angle to accurately see the black and white or yellow colouration, were classified as undetermined.

RESULTS

LOCATION	NO. OF WHALES	
	observed	photo-ID
Perth	474	106
Shark Bay	14	9
Northwest Cape	3	2
Dampier Archipelago	1	1
TOTAL	492	118

TABLE 1. Humpback whales off WA during 1989. Observations were made by the author except for the one off the Dampier Archipelago. 417 observations and 69 IDs were made during whale watching tours.

Class	Lateral body or fluke	Lateral body only	Fluke only	Total
Adult	13	40	50	103
Female	5	1	2	8
Calves	0	7	0	7
Total	18 (15.2%)	48 (40.7%)	52 (44.1%)	118

TABLE 2. Humpback whales identifed on lateral or fluke pigmentation patterns. Calves identified by lateral observation as none were observed fluking up.

LATERAL PIGMENTATION		
Category	No. of whales	% of types
Type 1 (mostly white	14	28%
Type 2 (<50% black)	9	18%
Type 3 (>50% black)	7	14%
Type 4 (mostly black)	20	40%
Undetermined	16	
Total	66	

TABLE 3.Classification of whales on degree of lateral pigmentation. Undetermined whales were identified by body marks, scars or dorsal fin characteristics.

FLUKE PIGMENTATION		
Category	No. of whales	% of types
Type 1 (mostly white)	50	75.8%
Type 2 (<50% black)	13	19.7%
Type 3 (>50% black)	3	4.5%
Type 4 (mostly black)	0	
Undetermined	4	
Total	70	

TABLE 4. Classification on degree of white and black pigmentation on the underside of the tail flukes.

DIATOM COLOURATION		
Category	No. of whales	% of types
Type 1 (mostly white)	15	36.6%
Type 2 (<50% yellow)	24	58.5%
Type 3 (>50% yellow)	2	4.9%
Type 4 (mostly yellow)	0	
Undetermined	29	
Total	70	

TABLE 5. Classification on degree of yellow colouration (diatoms) on the underside of tail flukes.

		DIATOM COLOURATION				
FLUKE COLOURATION	TYPES	1	2	3	4	Undet
	1	11	20	2		16
	2	3	4			6
	3	1				2
	4					
	Undet					5
	TOTAL	15	24	2		29

TABLE 6. The degree of diatom coverage according to fluke categorisation type.

One animal, identified in Shark Bay, was categorised as Type 2 yellow, and was still in that category when resight ed off Perth 77 days later with very little change in diatom distribution on its tail flukes (Fig. 7).

INITIAL SIGHTING			RESIGHTING		
Location	Date	ID No.	Location	Date	Elapsed days
Shark B.	12.7.89	4	Perth	27.9.89	77
			Perth	30.9.89	4
Perth	9.11.89	100	Perth	15.11.89	7
Perth	9.11.89	101	Perth	15.11.89	7

TABLE 7. Resightings during 1989.

DISCUSSION

During the present study which focussed predominantly on the southern migration, 41% of animals were identified using only lateral and 44% using only fluke pigmentation patterns, compared to 25% and 17% of the animals of the Area V stock on the east coast (Kaufman *et al.*, 1987). Futhermore, a higher number of identified animals (58%) was obtained using either lateral or fluke patterns on the east coast compared to 15% on the west coast. This large difference may reflect the greater ease of manoeuvrability of smaller craft and the persistence of the researchers in obtaining both lateral and fluke photographs ie. a difference in methods. 1989 was the first year in which a concerted effort was made to identify many animals on the west coast.

LATERAL PIGMENTATION

The 28% Type 1 and 40% Type 4 of my observations compare with 7% Type 1 and 37% Type 4 in eastern Australia (Kaufman *et al.*, 1987). From these initial data, it appears that the Group IV stock has a larger proportion of Type 1 animals.

FLUKE PIGMENTATION

The 70% Type 1 and 95% Types 1+2 of my observations compare with 87% of flukes from 1984,85 animals of the Group V stock being 75% white (Kaufman et al., 1987). In the Northern Hemisphere nearly 62% of animals, including calves, had mostly black flukes (Glockner and Venus, 1983); their Types 4 and 5 equate to my Type 4. Although I identified no mostly black flukes, at least 2 were photographed by other people (G. Pobar, pers comm).

Categorising fluke patterns may help simplify resight analysis, as each ID can be placed in a type category rather than being checked against all other animals.

DIATOM COVERAGE

Assessment of yellow colouration on specific whales which may be resighted after their northern migration may enable quantitative comparison over time of the change in diatom coverage. Colour photographs of flukes are better for assessment of diatom coverage than are black and white photographs. Of 41 individuals categorised, 95% had <50% diatom coverage whereas on the east coast there was little evidence of diatom coverage at all (M.Osmond, pers. comm). Difference in diatom coverage between Groups IV and V stocks may reflect geographical differences in the Southern Ocean feeding areas, but further comparisons are necessary before making any conclusions.

It is unclear how differences in diatom coverage relate to different fluke colourations. The extent to which diatom coverage may have been reduced by time spent in warm waters is unknown.

RESIGHTS

A mother-calf pair was sighted twice in 7 days in the same area off Perth, while another individual was resighted after 4 days. Many more whales are seen off Perth and south coastal areas from September to December than at other times. Certain population classes, for example, mother-calf pairs, may use the large bays and embayments off Western Australia (Shark Bay, Geographe Bay, Perth-Rottnest) for 'resting' areas during their southern migration. Photo-ID in Hawaii indicates residence times of up to 11 weeks (Darling,Gibson & Silber, 1983), and in Hervey Bay, Queensland, times of mainly 1 to 2 days, and up to 19 days (Bryden, Corkeron & Slade, 1988).

With the development of whale-watching as an industry off the coast of Perth, information on the distribution, behaviour, identification and ecology of whales will be essential, to properly understand and manage the interactions between people and whales.

PART 2 - SIGHTING ANALYSIS

METHODS

Whale-watching tours are conducted from September to November during the southern

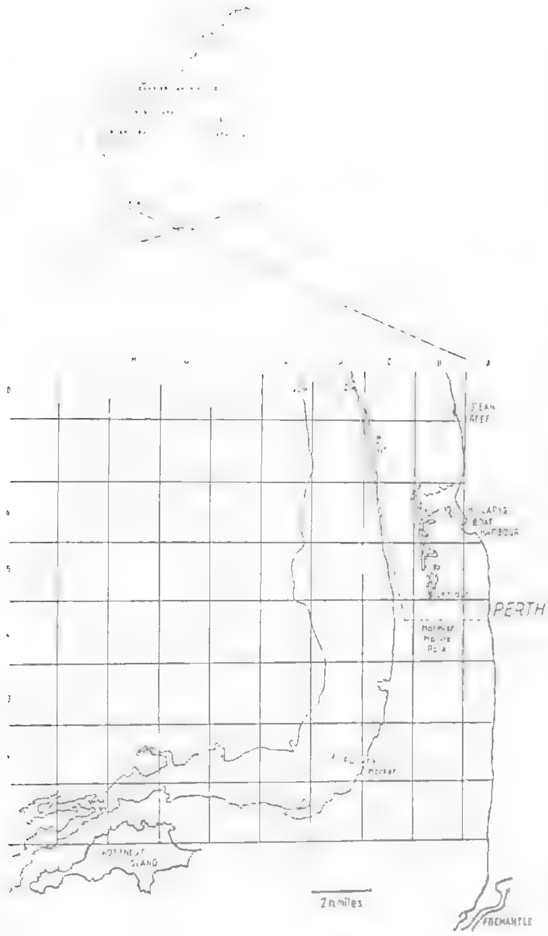

FIG. 8. The area of Indian Ocean between Perth and Rottnest Island where the whale watching tours were conducted during 1989.

migration of humpback whales which occurs between August and December.

AREA

The Indian Ocean, adjacent to Perth and north of Rottnest Island, was divided into grids of approximately 2 x 1.8 nautical miles to define sightings distribution (Fig 8). Tours were conducted west of the shallow limestone reefs which run parallel to the coast, and north of Rottnest Island, generally when wind speeds were below 15–20 knots.

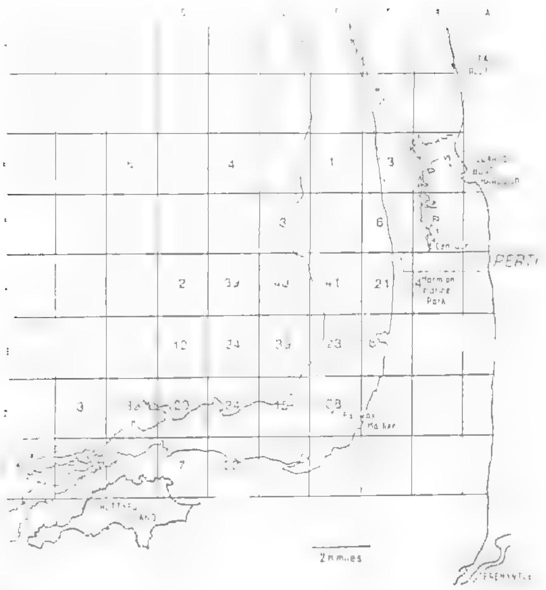

FIG. 9. Numbers of humpback whales (adults + calves)observed in each grid square during the southern migration.

VESSEL

Two vessels were used for the tours; a 15m aluminium monohull fishing vessel and a 10m fibreglass shark cat. The larger vessel had radar, and was used on most occasions. The vessels departed from the boat harbour at Hillary's and headed southwest towards Rottnest Island around the southern most Centaur Reef. At least 2 or 3 observers were continually looking for whales, and on most occasions the blow was the initial sighting cue.

DATA COLLECTION

Cruise description data gave starting and ending times and weather conditions during observation outside the fringing reefs. Locations of pods were specified by radar or compass bearings. A cruise path description was made on a grid as it was not possible to continuously plot each cruise using more accurate equipment. Sighting data consisted of individual whale counts, pod sizes, reproductive status, behaviour and photographs. Searching time included that spent with each pod and assumes that searching continues while with one pod. Searching time with the vessel moving would have been much

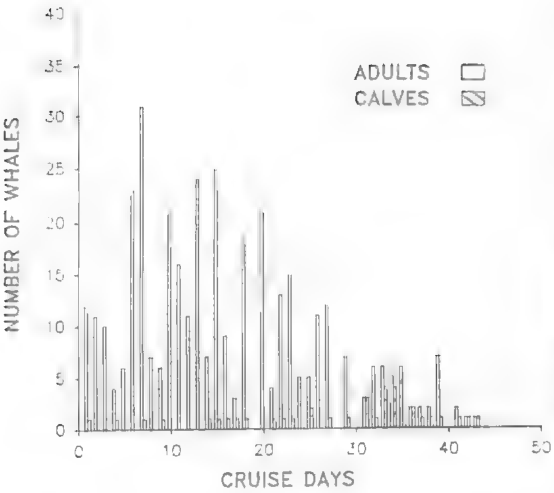

FIG. 10. Adults + calves sighted per day during the cruises, from September to December (southern migration), Perth, 1989.

less if time spent with each pod had not been included.

PHOTOGRAPHIC DOCUMENTATION

Efforts were concentrated in obtaining photos of the ventral side of the tail flukes and lateral views of each whale. Whales were inferred to be female if accompanied by a calf; mother–calf pairs were obvious, even when other adults were nearby.

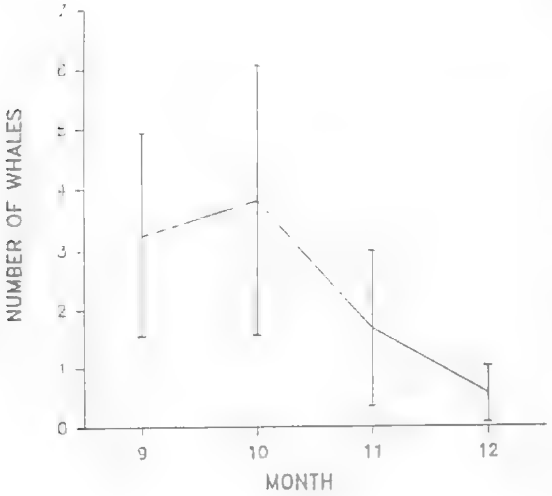

FIG. 11. Humpback whales (adults + calves) per daily sighting hour; southern migration, Perth, September-December, 1989 (mean ± SD).

RESULTS

MONTH	DAYS	CRUISES	PODS	ADULTS	CALVES	0 PODS	REPEAT PODS
Sept	6	7	21	65	2	-	3
Oct	21	34	77	265	13	3	11
Nov	14	19	25	48	20	5	1
Dec	3	3	2	2	2	1	1
Total	44	63	125	380	37	9	16

TABLE 8. Monthly data collected during whale watching cruises.

MONTH	DAYS	CRUISES	WHALES	MEAN HR/CRUISE	WHALES/HR
Sept	6	7	67	3.54	3.24
Oct	21	34	278	3.28	3.82
Nov	14	19	68	3.20	1.67
Dec	3	3	4	2.36	0.55

TABLE 9. Summary of cruise searchtime, number of whales and daily sighting rate.

An ANOVA was performed on the transformed data (log10) to test differences between months for whales/cruise hour. A significant difference was noted (F=5.32, df=43, P=.0035), and tests (Tukey, Scheffe, SNK) between monthly means indicate that December is different from the remaining months. Removing December also resulted in a significant difference for November (P=.0092) from Sept–Oct.

DISCUSSION

No comparative data on humpback whale numbers in the near shore waters off Perth are available; estimated population size is more than 2000. It may be that a significant proportion of the population migrate south close to the coast, using the large bays as resting areas. To what extent and duration these bays are used remains

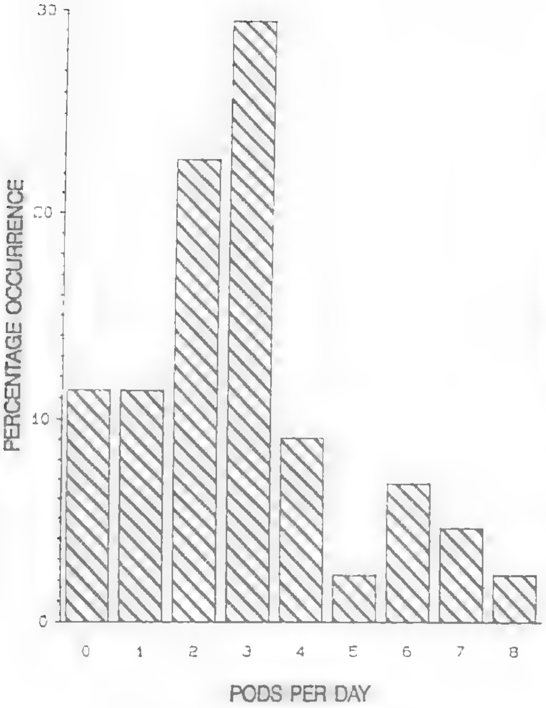

FIG.12. Pods of humpback whales observed per day during the cruises; southern migration, Perth, 1989.

to be determined. The photo-id work in 1989 indicates residence times of 4–7 days off Perth.

The distribution of whales over the gridded area suggests that they limit their approach to the coast to depths greater than 20m. Concentration of sightings in the southern region of the study area reflects cruise paths. A series of aerial survey flights over the area would provide a more accurate estimation of their distribution and give some indication of the proportion of whales which pass at a greater distance from the coast and are not seen by the cruise vessels. The effect of the warm, southward flowing Leeuwin current along the Western Australian coast on the spatial distribution of these animals may have to be considered. The number of adults decrease from October. Since the cruises did not commence until late September the initial rise in numbers was missed, and may follow a normal disribution curve, similar to that observed in Queensland from shore (Bryden et al., 1987).

The number of calves increased in November, as previously noted (Chittleborough, 1965). This earlier work by Chittleborough also indi-

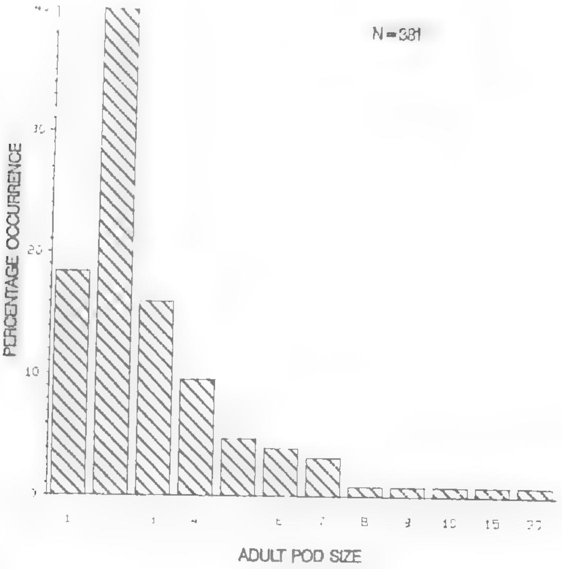

FIG. 13. Frequency of pod sizes observed during the southern migration, Perth, 1989.

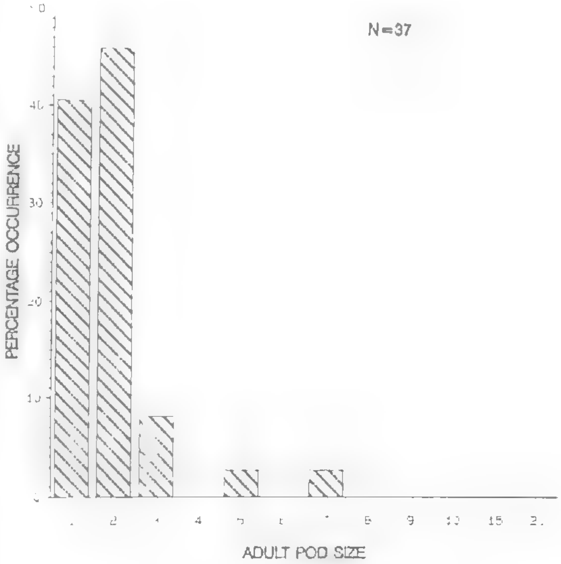

FIG. 14. Frequency of calves with different adult pod sizes observed during the southern migration, Perth, 1989.

cated that the southern migration had passed the Australian mainland by the end of October with a few stragglers remaining in November and December. The numbers of whales seen off Perth in 1989 during November and December were fewer than in October, but still accounted for 17% of observations. Some were also reported in Geographe Bay, south of Perth in November and December; they may be part of the migration which pass close to Perth. Further observations will be necessary to determine if there has been a real change in migratory behaviour compared with that observed by Chittleborough (1965). It is likely that the apparent change in migration over 30 years reflects differences in data collection. On the east Australian coast Paterson and Paterson (1989) recorded a similar migration pattern in 1987 to that recorded by Chittleborough in 1961 but they received reports of some late southward migration during the summer months. However, Stone et al. (1987) have shown differences in the timing of the migration past Bermuda in the North Atlantic Ocean in recent years compared with historical records from the 17–19th centuries.

ACKNOWLEDGEMENTS

I thank Mr Bill Mills and Mr Gavin Barr who skippered both vessels with expertise and regard for the whales during the Underwater World whale-watch cruises. I sincerely thank Mr Henry Hall, who has given considerable time and effort while taking photographs and recording songs off Perth. Special thanks to Mr Trevor Cook of Carnarvon, who has helped me in a similar manner in Shark Bay. Mr Danny Cassidy from Exmouth co-operated in obtaining photographs from North West Cape and Mr Ken Maley of Karratha supplied the ID from Dampier.

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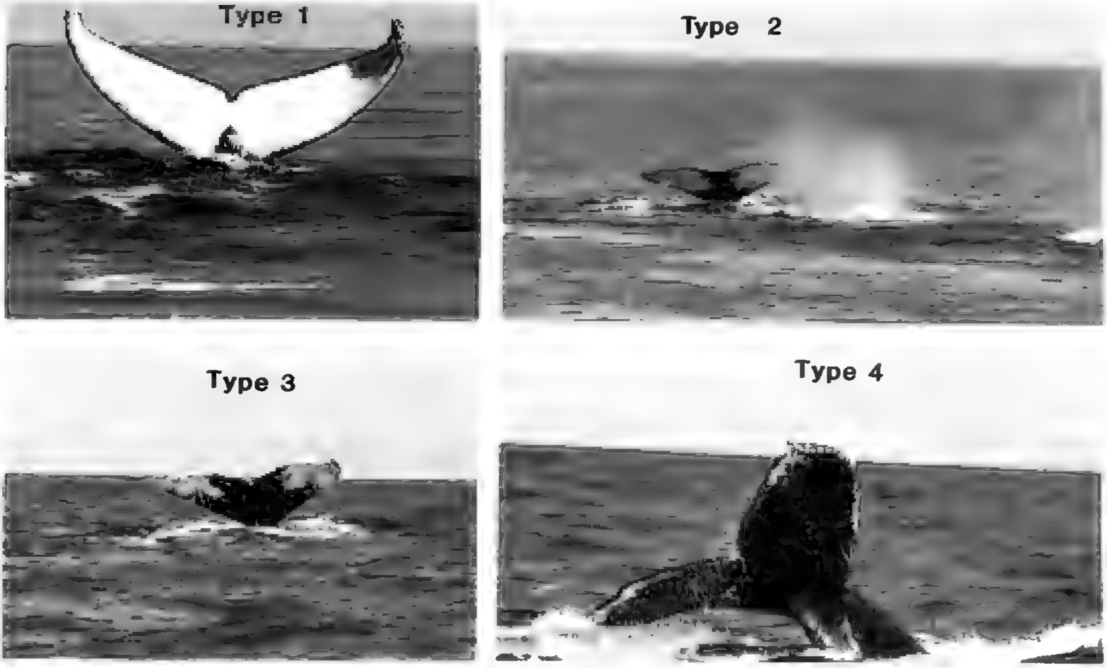

FIG. 5. Identified humpback whales from WA showing 4 tail fluke pigmentation types.

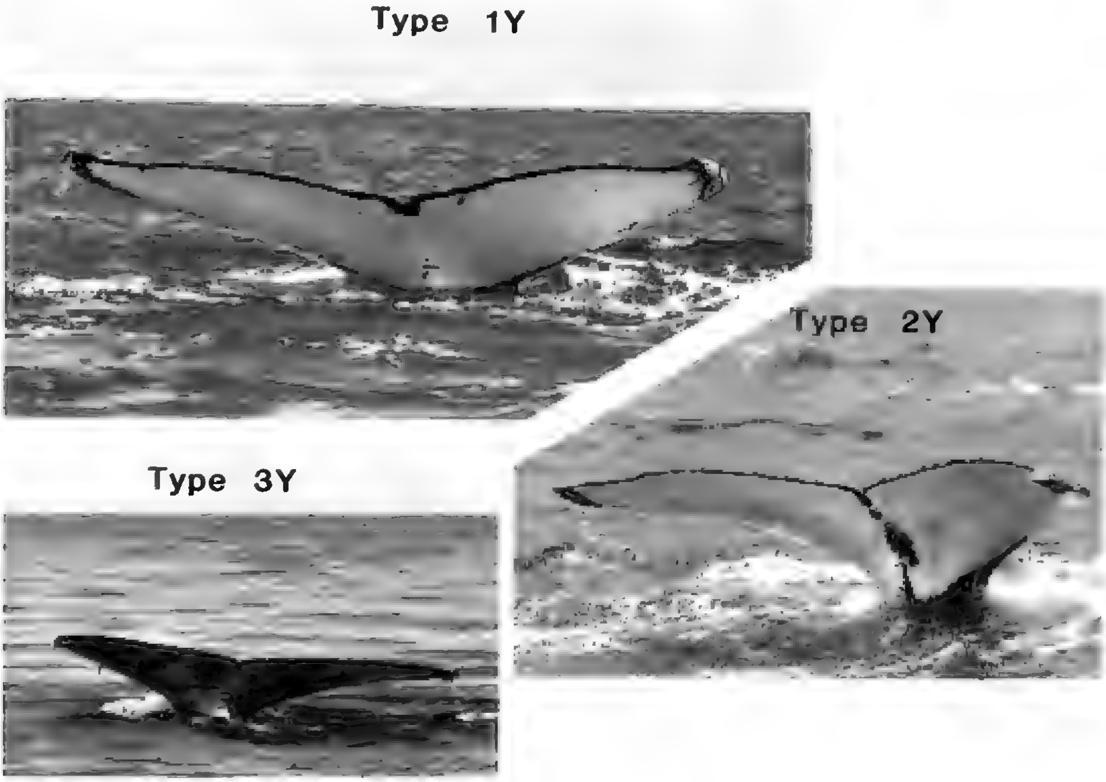

FIG. 6. Photographs of identified whales off WA, showing 3 of the 4 tail fluke diatom colouration categories (yellow).

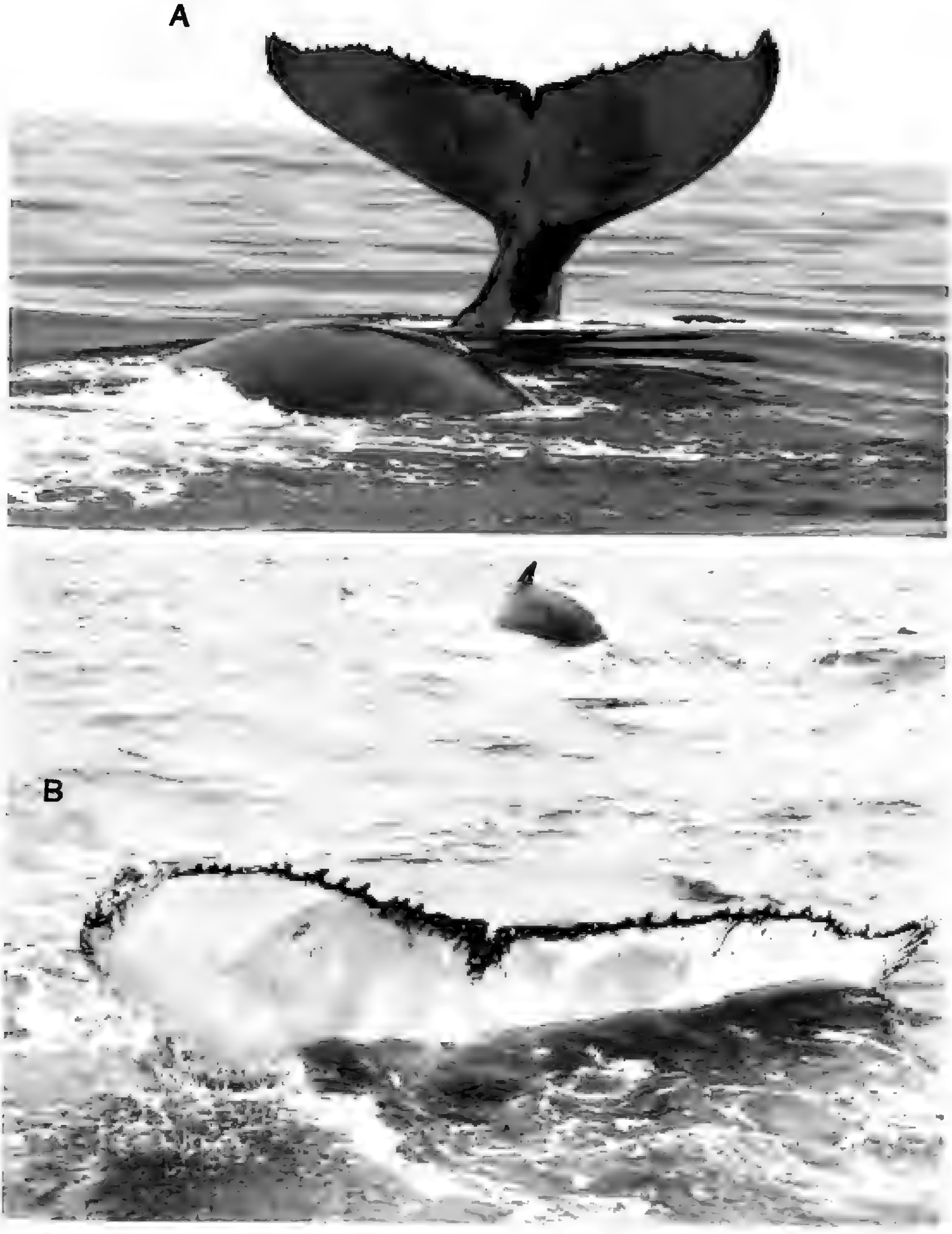

FIG. 7. Tail fluke pigmentation and diatom colouration photographs of a resighted humpback; A, Shark Bay, 12 July, 1989. B, Perth, 27 and 30 September, 1989.

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A HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, SKELETON DISCOVERED AT AN UNUSUAL LOCATION ON MORETON ISLAND, QUEENSLAND

V.C. BUSHING

Bushing, V.C. 1991 07 01: A humpback whale, *Megaptera novaeangliae,* skeleton discovered at an unusual location on Moreton Island, Queensland. *Memoirs of the Queensland Museum* **30**(2): 271–275.Brisbane. ISSN 0079-8835.

Chance discovery of a humpback whale, *Megaptera novaeangliae,* skeleton on Moreton Island is described. Its distance above and behind present high water mark poses conjecture as to the manner and timing of its deposition. Radiocarbon dating indicates that its age is less than 1500 years BP thus excluding the possibility of deposition during the last interglacial high sea level period. It is most likely that the whale was washed ashore during a cyclonic surge or other extreme weather conditions. ☐*Humpback whale, Megaptera novaeangliae, skeleton, Moreton Island, Queensland, radiocarbon dating.*

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During a routine patrol on sand dunes behind Spitfire Creek (27°04'S, 153°27'E) on the eastern or oceanic shore of Moreton Island, on 29 October 1984, large animal bones were seen in a sandblow (Figs 1–4). At first they were considered to be those of a horse but closer inspection and hand-digging revealed large cetacean vertebrae.

The site was re-examined on 4 November 1984 and skeletal elements, including a maxillary tip, cervical, thoracic and caudal vertebrae as well as the sternum and ribs, were recovered. The skeleton was identified as that of a humpback whale when a radius, characteristic of the species, was located (Fig.5). The skeletal elements were deposited and registered (JM 5252) in the Queensland Museum and comparison with other Humpback Whale material in that collection (Paterson,1986) indicated that they were those of an adult.

The skeleton lay in a SE/NW line in the sandblow which sloped to the northeast (Fig.6). The maxillary fragment and caudal vertebrae lay at the extreme northwest and southeast aspects of the site, respectively. The highest point of the sand dune in which the site was incorporated is 12.6 m and the midpoint of the skeletal deposit, from where the thoracic elements were recovered, is 4.8m above and 190m behind present high water mark.

During the last interglacial period, c. 120,000 yr BP (Flint,1971) sea levels were approximately 5m higher than at present. If the whale had stranded at that time it may have been located in this position in normal weather conditions. Radiocarbon dating with correction for isotopic fractionation dates the skeleton at 1410 ± 70 yr BP. However, its age may be substantially less because of depletion of C^{14} in the Antarctic oceanic water mass. This phenomenon is termed the reservoir effect and a correction is applicable to material of Antarctic origin (Omoto,1983). Although Southern Hemisphere humpback whales spend considerable periods in temperate waters (Dawbin,1966) their periods of rapid skeletal growth occur at the Antarctic feeding grounds (Matthews,1937). Accordingly, reservoir effect correction of JM5252 is required. Freshly killed seals and penguins in the Ross Sea had radiocarbon dates ranging between 1750 ± 70 and 1300 ± 50 yr BP (Omoto, 1983). It is clear that JM 5252 does not date from the interglacial period and other reasons for its location must be considered.

Anatomical distribution of skeletal elements in the sandblow excludes the remote possibility that they were relocated by humans from a site nearer to the sea. Forman et al., (1987) observed that whale bones are gradually scattered along the littoral zone by tide and weather action. The relatively undisturbed skeleton of JM 5252 suggests that it had not been subjected to further significant tidal action.

The Spitfire Creek depression is the last substantial breach in the present frontal dune system proximal to the Cape Moreton headland (Fig. 1) and the sea enters its easterly aspect in rough, southeast weather. In the winter of 1957 water

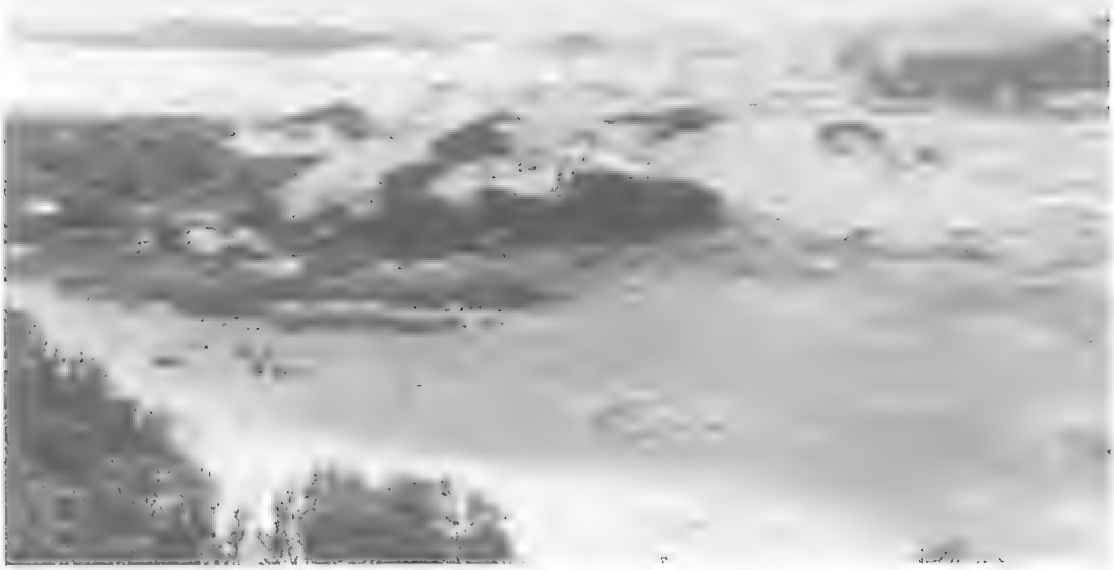

FIG.1. Spitfire Creek, Moreton Island. Cape Moreton is seen in the far right of the photograph. The sand-blow in which JM 5252 was found is in the centre of the photograph.

FIG.2. The sand-blow which contained JM 5252. A view seawards from its northwest aspect. The thoracic elements were recovered from the region of the marking stick.

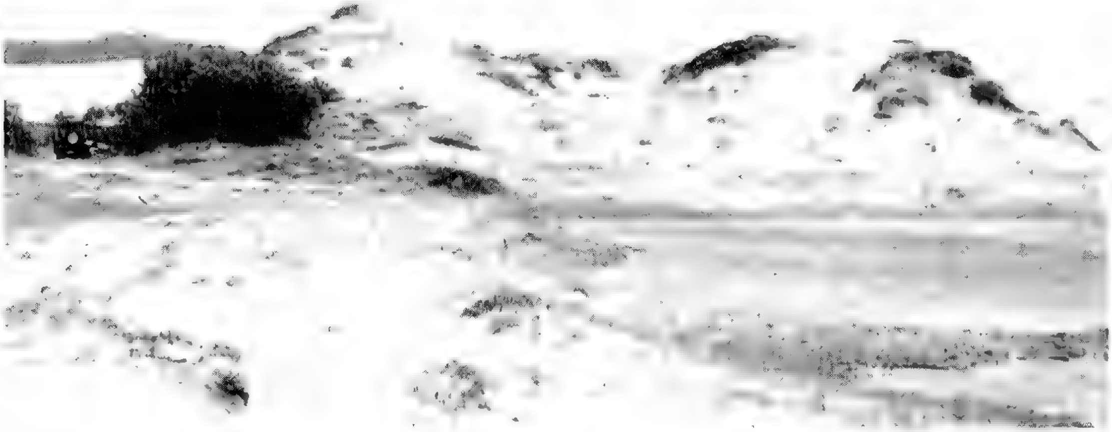

FIG.3. The sand-blow which contained JM 5252. A view from the present low frontal dunes to demonstrate the extent of the Spitfire Creek depression.

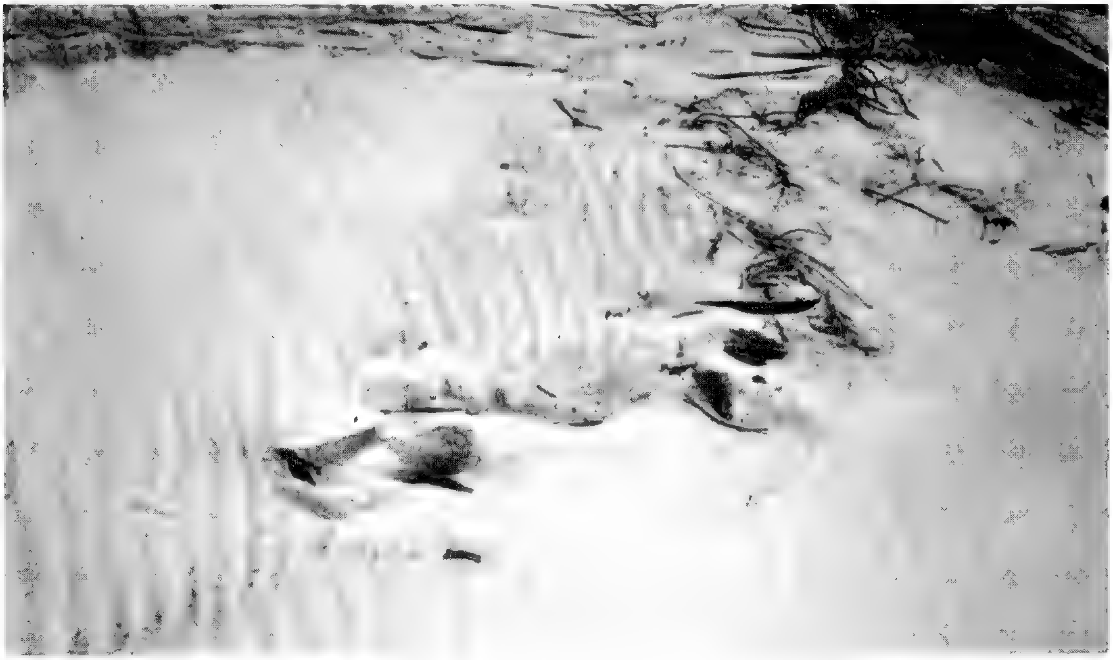

FIG.4. Skeletal elements of JM 5252 at the time of discovery.

was trapped to a depth of approximately 1.5m behind a barrier of logs and dune grass at the entrance to Spitfire Creek (R.A. Paterson, pers. comm.). This debris had accumulated during a prolonged period of rough weather associated with strong southeast winds.

Decomposing whales are extremely buoyant, particularly if their integument is intact (Tønnessen and Johnsen, 1982). It is suggested that the most likely reason for the unusual location of JM 5252 is that its carcass was washed into the Spitfire Creek depression during cyclonic or other extreme weather conditions associated with abnormally high tides.

FIG.5. The radius of JM 5252 during excavation.

FIG.6. The sand-blow which contained JM 5252. Its northern aspect is to the right of the photograph.

ACKNOWLEDGEMENTS

Peter Jell of the Queensland Museum kindly arranged for radiocarbon dating of JM5252 which was performed by Beta Analytic Inc. Ms Gillian Taylor of the N.W.G. MacIntosh Centre for Quaternary Dating kindly provided information concerning the Antarctic reservoir effect. Mr Neville Hawkins transported the skeletal material from Moreton Island and Dr Robert Paterson assisted with the excavation and identified the specimen.

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SONGS OF HUMPBACK WHALES: THE AUSTRALIAN PERSPECTIVE

DOUGLAS H. CATO

Cato, D. 1991 07 01: Songs of Humpback Whales: the Australian perspective. *Memoirs of the Queensland Museum* 30(2): 277–290. Brisbane. ISSN 0079-8835.

Humpback whale songs have been recorded in Australian waters since 1979, mainly off the east coast and generally these have shown the complex and stereotyped structure associated with Humpback Whale songs observed in other parts of the world. Detailed study of the 1982/83 song off the east coast demonstrated a stereotyped, repeating song and established "rules" that governed the song for that period. These rules are broadly similar to those established for the Northern Hemisphere with differences in detail. The sounds that make up the song are also different. The song has changed progressively with time. In some years this has been gradual, but in 1984 the change was so substantial that the 1985 song bore little resemblance to that for 1982–84, and was relatively unstructured. Studies in Australian waters provide a somewhat different perspective to those of the Northern Hemisphere because of differences in the environment and the access to whales. Whereas most Northern Hemisphere recordings have been obtained on the breeding grounds (with the notable exception of the Bermuda area) we have access to the whales along the migration paths which extend for thousands of kilometres along the east and west coastlines. From our observations, the integrity of the song appears to be maintained over large distances (1500 km) of the migration paths, although the sample size is small. However, songs off the east coast are distinctively different to those off the west coast.☐

Humpback Whales, songs, marine acoustics, animal behaviour.

Douglas H. Cato, Materials Research Laboratory (MRL), DSTO PO Box 50, Melbourne, Victoria 3032; 3 January, 1991.

Humpback Whale songs have been studied extensively for stocks in the Northern Hemisphere. Payne and McVay (1971) first demonstrated the existence of a structured, stereotyped and repeating song from recordings of migrating whales off Bermuda, and Winn, Perkins and Poulter (1971) observed similar songs in the West Indies. The song is repeated for long periods and appears to be stereotyped between singers of the same geographical breeding stock, but different oceans have different songs (Payne,1978; Winn and Winn,1978; Winn et al., 1981). In addition, the songs of any stock gradually change with time (Winn and Winn, 1978; Payne and Payne, 1985). Sounds attributed to Southern Hemisphere Humpback Whales were first recorded in the late 1950's (Kibblewhite et al., 1967), but song analysis has been reported for only one recording (Winn et al., 1981), apart for some preliminary work on the east Australian song (Cato,1984).

With the notable exception of the Bermuda recordings, much of the work in the Northern Hemisphere has been in tropical breeding grounds such as Hawaii and the West Indies, and discussion has often focussed on the significance of the song to breeding activities. In the North Pacific and North Atlantic Oceans, Humpback Whales are more readily accessible on breeding grounds than on the migration paths. The situation is reversed in the Australian region, where migration paths follow coastlines for thousands of kilometres, and breeding grounds are diverse (Chittleborough, 1965; Dawbin, 1966). Recent sightings of humpbacks extend along the entire coastline of eastern Australia (Paterson and Paterson, 1984, 1989; Simmons and Marsh, 1986). Known concentrations of whales are along the migration paths rather than on breeding grounds. This paper discusses songs recorded between 17°40'S and 35°20'S on the east coast and between 19°40'S and 32°S on the west coast. While some results are from breeding grounds, most were obtained on migration routes.

There is some interest in the songs of Southern Hemisphere Humpback Whales. It seems that stocks in the two hemispheres are well segregated because most stocks do not usually cross the equator and because migrations are seasonal and thus six months out of phase. Songs in the two hemispheres may have evolved independently over a considerable period of time.

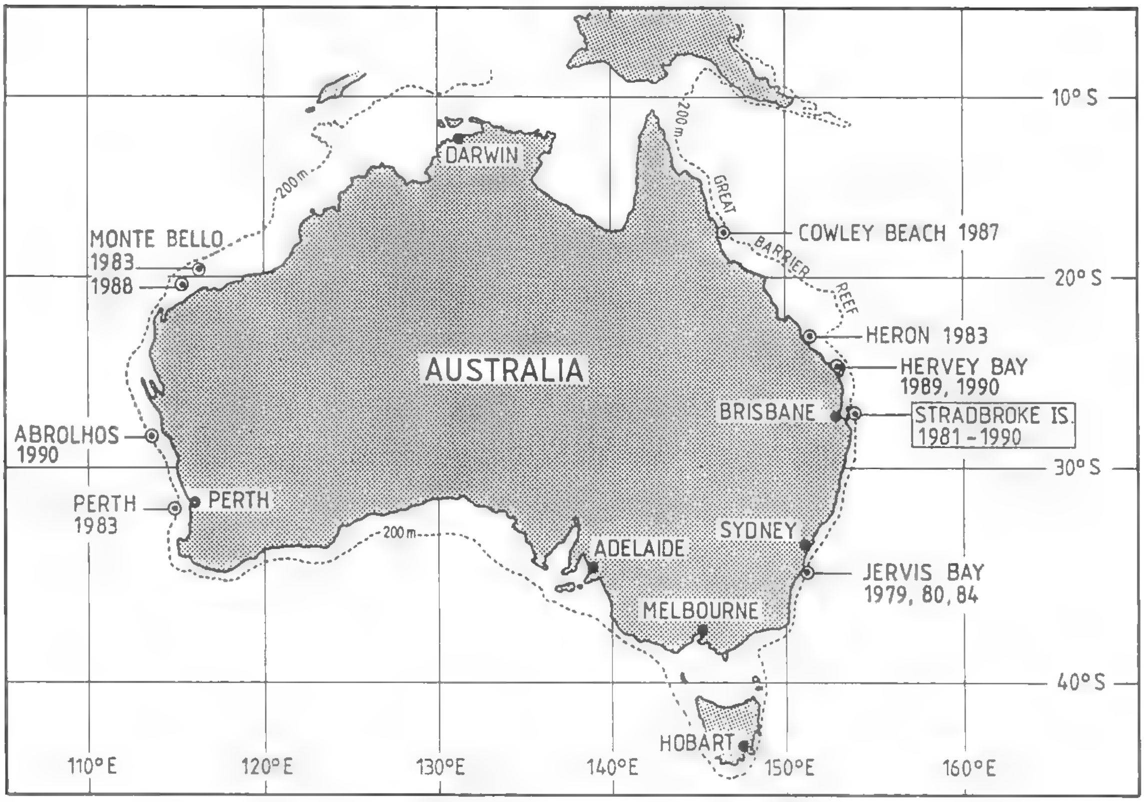

FIG. 1. Map showing the location and year of the song recordings discussed in this paper.

The first Southern Hemisphere recordings of Humpback Whale songs were obtained off New Zealand during 1958–1963 by Kibblewhite, Denham and Barnes (1967). They observed intense activity during April–September, the time of year when most Humpback Whales might be expected in these latitudes (Dawbin, 1966). During 1960–1963 sound activity decreased markedly, coincident with the similarly marked decline in the Humpback Whale population. No analysis of song patterns has been published.

This paper reviews some results of studies of Humpback Whale songs in Australian waters with particular reference to differences in perspective that the Australian region provides, and how these may lead to a better understanding of the song and its purpose.

Samples of songs discussed in this paper are available on compact disc entitled "Songs of the Humpback and Frog Calls of Brisbane and Environs",issued by the Queensland Museum.

METHODS

Data Recording

Sound recordings have been made at a number of locations on migration paths and in breeding grounds along Australian coastlines including those discussed in this paper (Fig. 1). These were single session recordings of a few hours duration, except off Point Lookout, Stradbroke Is. (27°25'S), where data have been recorded on a number of days every year since 1981. Since 1982, recordings have been made off Coffs Harbour (30°18'S) and single session recordings have been made at other locations by an Australian Museum team (W.H. Dawbin, pers. comm.; Dawbin and Eyre, this memoir).

Recordings off Stradbroke Is. were coordinated with the observations of Paterson and Paterson (1984, 1989), and were timed to coincide with the peak of the migration past this point. Recordings have been made during the southern migration in each year (late September, early October) and during the northern migration (late June, early July) in 1984, 1989, and 1990. Stradbroke Is. is at the most easterly part of the east coast, and this is where the migration paths converge. On the basis of experience during whaling activities in the area, most humpbacks could be expected to pass within 15 km of the shore (Chittleborough, 1965). When this study commenced, this was the largest known concentration of Humpback Whales on the east coast. Even so, long periods of monitoring were required to obtain even a small sample of the song because of the small population at the time (<1/2 the present number;see Paterson and Paterson,1989). As a consequence, sample sizes during the early years of recording were small.

Recordings off Stradbroke Is. were made from a small boat which was allowed to drift in the vicinity of the whale paths off Point Lookout. Whales are in transit at this point, and although they show some meandering, there are only occasional departures from general north or south passage through the area (Cato, 1984). This is an exposed oceanic coast and weather conditions have been unsuitable for recording on about half the days allocated to monitoring.

The recording system consisted of a hydrophone connected via a high pass filter to a low noise preamplifier, and from there to a tape recorder. The preamplifier provided a sufficiently high input impedance to give adequate low frequency response. During recordings, it is desirable to minimise any water flow past the hydrophone, because the pressure fluctuations of the flow, although not acoustic, are detected by the pressure sensitive hydrophone and appear as low frequency noise on the recording. Under some conditions they may be of sufficient level to overload the preamplifier and cause distortion. There is little problem if, as in the absence of wind, the boat and hydrophone drift with the water mass. Usually, however, there is sufficient wind drift to cause some motion of the hydrophone relative to the water. In most cases it was necessary to use the high pass filter to attenuate the low frequencies to avoid overloading the amplifier. Since this filter has a gradual roll off with decreasing frequency, it was possible to correct for its effect in the measurements from tape replay. By experimenting with fairings on the cable, it was found that string wound spirally along the cable substantially reduced the noise from waterflow, presumably by disrupting the shedding of vortices. This was effectively from 1987.

During 1981-1983 the system used was a General Instrument Corporation Z3B hydrophone on 30m of cable, RAN Research Laboratory (RANRL) designed low noise preamplifiers and a Kudelski Nagra III tape recorder. System response was ±3dB from 20Hz to 17 kHz, but it was often necessary to use a high pass filter (-6 dB at 55 Hz, –20 dB at 20 Hz) to attenuate low frequency noise from turbulence. From 1984, Clevite CH17 hydrophones and Sony WMD6 or TCD5M cassette recorders were used, giving a system response of 30 Hz–15 kHz, modified by the above filter response when used.

DATA ANALYSIS

Sonagrams (spectrograms) were produced using a Kay Elemetrics Corp. Digital Sonagraph and a Spectral Dynamics SD-311 analyser. Spectral measurements were made using a Hewlett-Packard 3582A analyser and Bruel and Kjaer 2112 analyser and 2305 level recorder.

Payne and McVay (1971) defined a "sound unit" as any sound that is continuous to our ears when heard in "real time" (i.e., when replayed at the same tape speed as recorded). These are the individual sounds, or elements of the song. Winn and Winn (1978) used the term "syllable" for a similar purpose. A Humpback Whale song cycle comprises hundreds of sound units but it can be shown that these can be categorised as belonging to one or other of a small number (typically 12-15) different sound types. The term "sound type" is defined here to mean the particular type of sound that a unit belongs to. One sound type is distinguished from another by having different acoustical characteristics. These characteristics can be measured by various methods of analysis, to demonstrate that the sound types are distinctly different. The characteristics of Humpback Whale sounds are such that they are well suited to human aural perception. Thus, with a little experience we can easily distinguish between different sound types by ear. To simplify discussion, descriptive names are used to identify sound types, e.g. "growl", "moan", "whistle". The choice of a name is, of course, subjective but once chosen becomes the definitive name for that particular sound type . It is convenient, in this definition, to allow sound units of a particular sound type to show some variation in character, so long as this variation is small compared with the variation between different sound types. The characteristics of the sound units of a sound type may change with time. If the change exceeds the acceptable variation in the sound

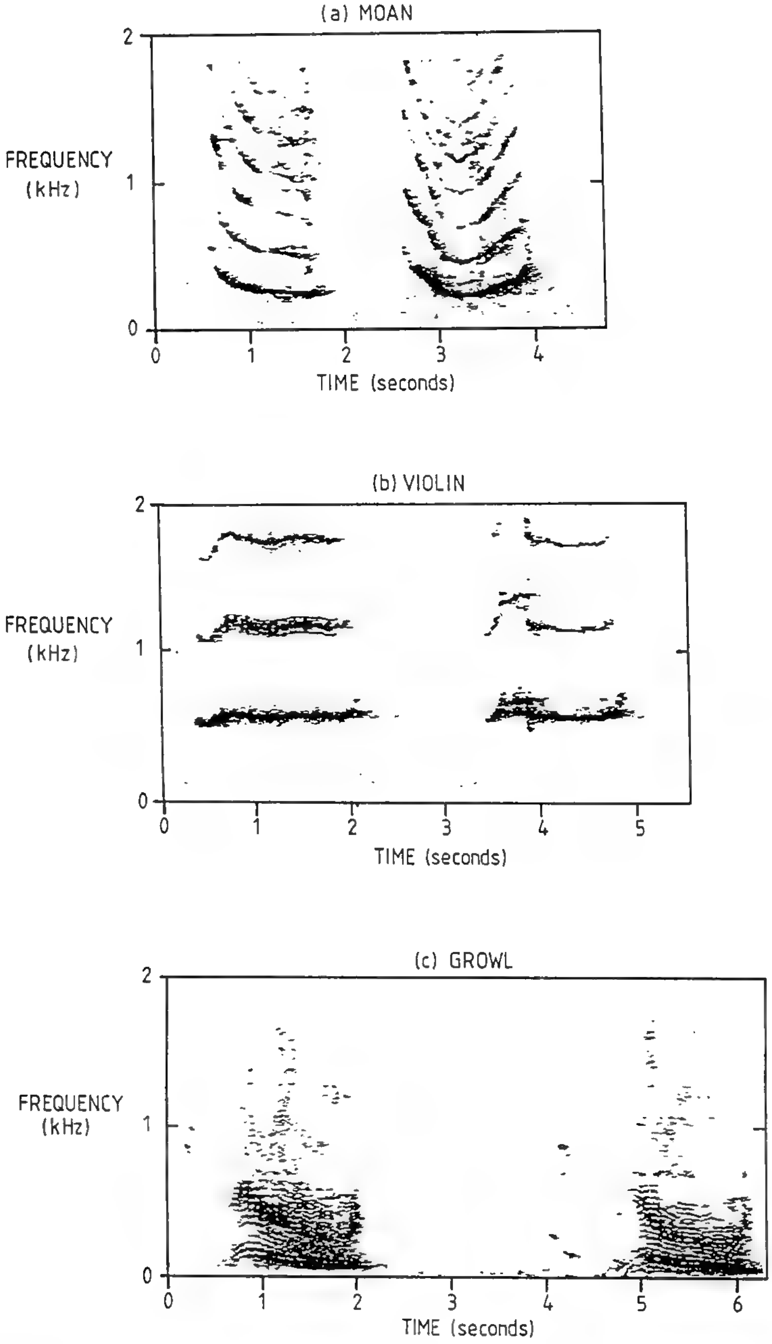

FIG. 2. Sonagrams of two samples of the following sound types: (a) "moan", (b) "violin" and (c) "growl", from theme 5 of the 1983 song off the east coast. The filter bandwidth was 11.3 Hz.

type characteristics, a new sound type must be defined. Sounds type names can be identified with particular years by affixing the year, so that "moan(82)" would apply to 1982 only.

Because sound types are so readily distinguished by the human ear, a major part of the analysis consists of listening to the tapes and noting the sequence of sounds using some shor-

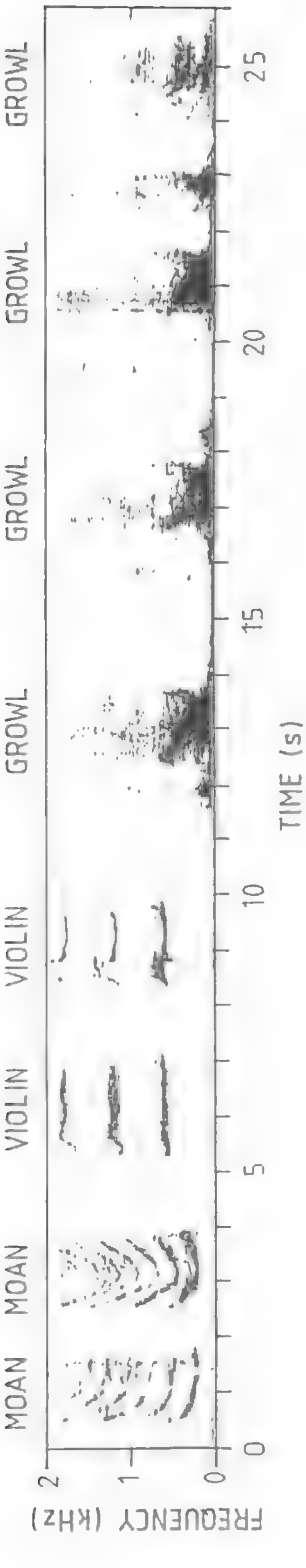

FIG. 3. Sonagram showing how the sound types of Fig. 2 go together to form one complete phrase of theme 5 of the 1983 song off east Australia. The filter bandwidth was 11.3 Hz.

thand notation. From this, the song structure or pattern can be determined. The sounds are also displayed visually as sonagrams which show as a grey scale plot the sound intensity as a function of frequency and time (Figs 2,3). The distinction between sound types and the way they are arranged to form the song pattern can also be determined from sonagrams. The two methods complement each other. Some subtleties detectable by ear are difficult to display or distinguish on spectro-graphic analysis. On the other hand, quantitative comparisons in frequency and time are possible on sonagrams. Sound types can be more readily detectable by aural analysis when the signal to noise ratio is poor (as is the case of distant whale sounds), and a significant proportion of the data can only be analysed effectively by ear. Generally, aural and visual analysis produce consistent results. In the one case we use our aural perception for acoustic analysis and interpretation, in the other we use an instrument to do the analysis and our visual perception for the interpretation. The ear is an effective acoustic analyser, but our aural perception is not equally sensitive to all measurable characteristics of a sound. On the other hand, our instruments have limitations, and their outputs require some assessment, such as the visual interpretation of the sonagram. The sonagram, for example, does not contain all the information in the original sound If we are interested in the importance of the sounds to the whales, we would like to know what characteristics of a sound are detected by the aural perception of a whale. This, of course, is not known. It may be, however, that our aural perception of a sound rather than our visual perception of a sonagram, is closer to the whales' aural perception of the same sound. If we are interested in other aspects of the sounds, such as the mechanism of production, and how they propagate through water, the measurable physical characteristics of the sounds may be more useful than our aural perception.

PROPAGATION OF HUMPBACK WHALE SOUNDS AND THEIR DETECTION AND RECOGNITION

The question of how far Humpback Whale sounds are detectable is of some importance in a study of the song, because it determines the range over which the song can have an effect, whatever its purpose. Unfortunately, because of the nature of sound propagation in water, there is no simple answer to this. Sound is a fairly localised phenomenon in air because the high absorption attenuation causes the level to fall rapidly with distance from the source. Such attenuation is very much lower in water (at least at the frequencies of Humpback Whale sounds) so that sound levels fall far more gradually with distance. A doubling of distance in typical ocean conditions results in a decrease in level of about 6 dB, whether the doubling is from 100-200m, or from 5–10 km. The detectability depends on the signal to noise ratio at the receiver, that is, the ratio of the whale sound level (the signal) to that of the background noise level. A variation in the signal to noise ratio of 10 db would not be unusual, either through variation in propagation conditions or in the level of the background noise. This corresponds to a variation of a factor of three in detection range. Thus on this basis alone, the uncertainty in estimating the distance to which the sounds are detectable is a factor of three.

The other factors required in this calculation are the source level and the minimum signal to noise ratio for which detection is possible (the detection threshold). Winn et al. (1971) measured broad band source levels of different sounds from the song in the West Indies to range 175–188 dB re $1\mu Pa^2$ at 1m. Thompson, Cummings and Ha (1986) measured source levels of non-song sounds of comparable level. Because of the difficulties of identifying singers and measuring their distances during our recordings, we have no estimates of source levels of sounds in Australian waters. We can, however, estimate a lower limit by using the closest possible estimates of the distances of whales during recordings, where this is known. The results support the estimates of Winn et al. Variation in the received level between sound types of the 1982 song recorded from one singer off Stradbroke Is. was about 10 dB. This result and the measurements of Winn et al. indicate that variation in the source level of different sound types from one singer would cause the detection distance to vary by a factor of 3–5. Greater variation would occur if source levels varied between individuals.

Under typical ocean conditions, the distance the sounds would propagate for the levels to fall to that of the average background noise, i.e to give a broadband signal to noise ratio of O dB is about 5.6km for the lowest source levels measured by Winn et al., and 25km for the highest source levels. However, the sounds would actually be detectable at significantly lower signal to noise ratios and thus much greater distances because the acoustical characteristics of the sounds are distinctively different from the background noise. Just how much further the sounds can be detected depends not only on these relative acoustical characteristics, but also on the auditory perception if the receiver is an animal, or on the signal processing gain if the instrumentation is used. A simple experiment in the detection of some Humpback Whale sounds with varying signal to noise ratios by a human subject showed that the threshold of detection occurred at a signal to noise ratio of about -14 dB, corresponding to an increase in detection range of a factor of about five. This was not a rigorous, controlled experiment, and the result should be used only as an indication that detection by a human listener would be at substantially greater distances than the values at which the signal to noise ratio falls to 0 dB. It seems likely that whales are also able to detect the sounds when signal level is less than noise level.

It seems likely, therefore, that Humpback Whales should be able to detect and recognise the song from other individuals for large distances, probably some tens of kilometres, but detection distance will vary significantly under varying conditions, and the actual values cannot be determined without knowledge of the capabilities of the auditory perception of the whales. This may be an important factor in the significance of the song. If the song is detectable for distances of tens of kilometers, behavioural reactions in response to the song may also occur over such distances. The possibility needs to be investigated and the Australian coastlines provide the opportunity for such studies along migration paths.

EARLY RECORDINGS

The first recordings of Humpback Whale sounds in Australian waters were made by Millington and Sneesby off Jervis Bay in October 1979 and in the same area in October 1980. These recordings were obtained incidental to other work and were passed to the author for analysis. In 1979 two whales were observed by aircraft at the time of the recordings (the actual species was not identified). They were estimated to be about 10 km from the hydrophones. There is no direct evidence to indicate that the singer was one of these. However, the recorded sound levels were consistent with a source at that distance, based on the source levels of Winn et al. (1971). Also, given the size of the population in

1979, and the evidence that southward migration paths tend to broaden outwards from the coast well before the latitude of Jervis Bay is reached, it is unlikely (although of course not impossible) that there would have been another whale in audible range. A sample from the 1979 recordings is given on track 1 of the compact disc.

The 1979 recordings are characteristic of an intense, distant source. There is some waxing and waning of the signal consistent with variation in propagation loss and some echoing characteristic of deep water. The background noise was characteristic of the deep ocean, being predominantly from sea surface motion and distant shipping (Cato,1978). As such, it is characteristic of broadband noise – rather featureless, so allowing the distinctive Humpback Whale sounds to be more readily detected than in an environment where a variety of other sounds are present.

The 1979 recordings comprised about four hours of song. Several different sound types were evident and there was evidence of repetition or cycling over periods of minutes, consistent with the Humpback Whale song structure. At the time, identification of the sounds, as due to Humpback Whales, relied on comparison with the extensive knowledge of sounds from other marine animals. The acoustical characteristics of the sounds are such that they are beyond the capability of fish and are indicative of marine mammals. Of the known whale sounds, only those of the right whale have similar acoustical characteristics. However, recordings by the author of sounds of a right whale five weeks earlier (September, 1979) off Wollongong, were different, and showed no evidence of the cyclic and structured characteristics of the sounds recorded off Jervis Bay and typical of the Humpback Whale song. The 1980 recording was about 15 minutes duration, and sound types were generally similar to those of the 1979 recordings. Given the extensive data now available of Humpback Whale sounds off east Australia, there can now be little doubt that the 1979 and 1980 sounds are from humpbacks. Even though the actual sound types are different to any recorded later, their characteristics fall within the same range of variability observed for later recordings.

There are significant and regular gaps in the 1979 and 1980 recordings. This is to be expected for sounds from a distant Humpback Whale. Measurements of source levels of Humpback Whale sounds by Winn et al. (1971) showed a range of 13 dB from the sounds of the highest source levels to those of the lowest source levels. Given a typical propagation loss of 6 dB per distance doubled for deep water, 13 dB propagation loss corresponds to a ratio of propagation distances of four to five. Thus, the higher source level sounds of Winn's data would be detectable at four to five times the distance of the sounds of lower source levels, other things being equal (detectability will also depend on the actual characteristics of the sounds and their relationship to those of the background noise). Although the sounds recorded by Winn et al. (1971) are different to those recorded in Australian waters, it is evident that high source level sound types will be audible at significantly greater distances than those of lower source levels. From song recordings in later years it is apparent that as the signal levels fall relative to the background noise, the lower source level sound types cease to be detected. Gaps in the data appear in a manner similar to those of the 1979 and 1980 recordings.

Since some of the sound types are missing in the 1979 and 1980 data, it has not been possible to make a complete analysis of the song structure. It is clear, however, that the sound types in these songs are unlike those in later recordings off the east coast of Australia, the first of these being off Stradbroke Is. in September, October 1981. This poses the intriguing question: why are the 1981 recordings so different to those of 1979 and 1980? Was there a substantial change in the east Australian song in the 11 months between the 1980 and 1981 recordings, or were the 1979 and 1980 songs alien to this stock?

Since we have never observed alien songs in later recordings, and the 1979 and 1980 songs are very similar, it seems unlikely that they were alien songs, and more likely that the song did undergo a substantial change. We cannot answer this question without further data from that period, but that, of course, is not possible. These songs are now extinct.

The next recordings were obtained off Stradbroke Is. in September, October 1981. Although song data totalled about 65 minutes not all sound types were audible. In July 1982, Dr Dawbin recorded about 20 minutes of song off Cape Byron (pers. comm.).

ESTABLISHMENT OF THE SONG PATTERN AND CHARACTERISTICS

To establish the existence of a repeating stereotyped song, and to determine the rules governing the pattern for comparison with the songs of the Northern Hemisphere, requires the analysis of many song cycles recorded from a number of individuals. Although there have been recordings of Humpback Whale sounds in Australian waters since 1979, the first data that could be considered adequate for this purpose were not obtained until September, October 1982 off Stradbroke Is. during the south bound migration. This comprised 27 song cycles on 26 September, 7 on 28 September, and 1 on 1 October. Earlier recordings were either too short in duration or not all sound types were detectable.

THEME	SEQUENCE OF SOUND UNITS IN PHRASE		TYPE OF PHRASE
1		MOAN	REPEATING
	6–11	WHISTLES	
		SIGH	
2		MOAN	REPEATING
	3-6	VIOLINS	
		SIGH	
3		MOAN	REPEATING
		VIOLIN	
	2	SQUEALS	
		SHORT SQUEAL	
		SQUEAL	
4	1,2	MOANS	REPEATING
	1,2	VIOLINS	
	4-8	GULPS	
5	2	MOANS	REPEATING
	1,2	VIOLINS	
	3–6	GROWLS	
6	2	MOANS	EVOLVING
		SIGH	
	Several	CHUGS,2 SIGHS	
		(repeats)	
		CHAINSAW	
		(repeats)	
	Several	YAPS, CHIRPS	
		(repeats)	

TABLE 1. Basic structure of the Humpback Whale song off east Australia in 1982 and 1983. The sequence proceeds down the table. The phrases of themes 1 to 5 repeat a number of times to form the theme. There is only one phrase of about 20 steps in theme 5.

The song pattern was initially determined from the 4hrs 15mins of data recorded between 0740 and 1240 on 26 September 1982 off Stradbroke Island. Sounds were audible from the time listening commenced until it ceased (because of deteriorating weather conditions) so the period of continuous calling may have extended well beyond 5hrs. In all, 27 song cycles were recognisable, of which 18 were recorded in full. Seven cycles were incomplete because of gaps in recording either due to repositioning the boat or by loss of signal as another boat passed by. The gaps were short enough (equivalent to one to three themes in length) for the continuity of the song to be followed, i.e. the duration of the gap equalled the usual duration of the missing themes. The remaining two cycles were incomplete because of an aberration in the singing. The song jumped from theme 3 of one cycle to theme 2 of the next, with a fragment of theme 6 separating the two, and with no apparent pause in singing. There was an additional gap of 30 min possibly representing 3 cycles of the song, suggesting that there might have been a total of 30 cycles over 5hrs. Song cycle durations (complete) varied from 7 1/2–11 1/2 mins, the average being 9 1/4 mins.

During the period of recording, two groups, each of three whales were observed at distances varying from a few hundred metres to a few kilometres. One group included a calf, however, a comparison of the received signal levels, with the estimates of source level of Winn, Perkins and Poulter (1971), indicated that the other group of three was responsible for the song. For a short period a more distant song was audible.

The general pattern of the song established from these recordings is shown in Table 1. The choice of theme 1 as the start of the song was based on the following criteria, using data from this and later years. On 10 out of the 11 occasions when we heard a whale stop singing at the end of a song session, it has been at theme 6 or the equivalent theme in later years. The eleventh occasion was a rare example in our experience of aberrant singing where themes had been omitted in the two cycles preceding the cycle in which the session stopped (at theme 2). On the one occasion when we observed the start of a song session, it began with theme 1.

Usually the song in 1982 progressed from theme to theme without pause, with the exception of the transition from theme 6 to theme 1 where a pause was sometimes, though not always, observed (data from later years showed a more pronounced pause at this point). Often the sound intensity diminished towards the end of theme 6. On the basis of Northern Hemisphere work, this is indicative of the point in the song where the whale approaches the surface to breath, and is thus a further criterion of the end of the song. A reduction in intensity is to be expected as a singer approaches the surface because of the interference between the sound waves incident on (striking) the surface and those reflected from it, since they are out of phase. Winn et al. (1971) and Winn and Winn (1978) were able to localise on singers in the West Indies using a directional shipboard sonar, and found that singers came to the surface to breathe at a particular part of the song. Tyack (1981) noted the reduction in sound intensity that occurred at this point of the song and used this as a means of identifying the singer.

It may, however, be misleading to talk of the start and end of a song cycle. Theme 6 could alternatively be viewed as a link between cycles and it is interesting to note that a song session usually stops part way through theme 6 rather than at the end. The structure of theme 6 also differs from that of the other themes.

In structure, the 1982 song broadly follows the rules established for the songs of the Northern Hemisphere. The themes are emitted in the order shown (with rare exceptions) and each comprises a variable number of repetitions of a phrase specific to that theme, except that theme 6 has only one phrase. Phrases comprise a number of sound units in a fixed order separated by gaps of silence which vary from <1/2 sec. to 3 secs. The duration of the sound units varies from 0.1secs for the "whistles" to 4.3 secs for the "chainsaw". There is some variation in the number of repetitions of certain sound types in a theme (Table 1).

Theme 6 differs from the others in that it contains only one long phrase of about 2 mins duration with about 20 steps. Early steps comprise several "chuggs" and terminate with one or two "sighs". Following steps consist of one long sound unit – "chain saw" – rather like the merging of several "chuggs" to form one continuous sound. The final steps consist of several discrete units – the "yaps" – and terminate in "chirps". Themes 1 to 5, on the other hand, contain a number of repetitions (up to 12) of short phrases of 15–25 secs duration each comprising a number (5–13) of sound units.

There are more subtle patterns within the basic pattern (Table 1), and some minor variations. These will be discussed in a later paper. This basic song pattern was generally adhered to in the 40 song cycles from five individuals recorded in September and October 1982. The only exception was the omission of themes in two consecutive cycles out of the 27 recorded on 26 September. Themes 4 and 5 were missing from one cycle, theme 1 from the next. Otherwise, theme order and phrase structure was unchanged.

Songs recorded off Stradbroke Is. in September and October 1983, and off Heron Is. in October 1983 were similar to those recorded a year before with only minor changes. There was so little change in the song pattern, that the structure in Table 1 can be considered to apply equally to both the 1982 and 1983 songs. Some of the sound types showed changes in character but were still clearly recognisable as variants on the 1982 versions.

Sonagrams of samples of three of the sound types from the 1983 song (Fig. 2) have two consecutive samples of each sound type, all from a phrase of theme 5. Note that acoustical characteristics of the sound types are different, but each sound type shows some variation between the two samples, though much less than the difference between sound types. Both "moan" and "violin" are harmonic sounds and would be perceived as having characteristics similar to musical sounds. The fundamental frequency is equal to the interval between the harmonics and this is substantially higher in the case of the "violin", so that it is perceived as having a higher pitch. The frequency (and thus the pitch) is relatively steady in the case of the "violin" but varies significantly over the duration of the "moan", initially falling, then rising. The "growl" has different acoustical characteristics consisting of a rapid succession of broad band pulses.

Figure 3 shows the sound types of Fig. 2 as they occur together to form a phrase of theme 5 (1983).

A sample of the 1983 song commencing with theme 2, is given on track 2 of the compact disc. There are two phrase renditions of theme 2, 6 of theme 3, 1 of theme 4, and 3 of theme 5 in this particular sample. Theme 6, as discussed above, has only one long phrase. The song ends at the "chainsaw" of theme 6 where the whale stopped singing. The sonagrams of Figs 2 and 3 were taken from this particular sample. The recording was made off Point Lookout, Stradbroke Is. on 29 September 1983 in the presence of seven whales (Cato, 1984).

CHANGE IN THE SONG WITH TIME

Over the 12 months from September 1982, the east coast song changed in the character of some of the sound types and in the song pattern. Not all sound types are audible in the recordings of September 1981 so the pattern for only about 2/3 of the song can be determined. This part of the song is, however, similar in pattern, to the song of 1982, and the audible sound types are similar in character to their 1982 versions.

The song recorded in June, July 1984 (four singers, on separate days) was generally similar to that of 1982/83 in pattern, and changes in the character of the sound types were small. From July to September 1984, however, the song changed substantially. Recordings in early October and November (two singers, on separate days) showed that themes 3 and 5 were much diminished in duration, and the character of the sound types in themes 1, 2 and 6 had changed significantly. By 1985 the changes were so pronounced that it was difficult to recognise similarities to the 1982/83 song (eight singers, over three days). Themes 3 and 5 were extinct, and many of the sound types of the other themes had changed almost beyond recognition - they had to be considered to be new sound types, even though they may have evolved from the old ones. Themes 1 and 2 became relatively unstructured. Theme 6 now occupied 1/2 the song, partly because of reduction in the earlier themes and expansion of theme 6. The result was a shorter, significantly more poorly structured song than in 1982/83.

Thus, while the song showed a relatively gradual change from late in the singing season of 1981 to early in the season of 1984, the change during the season in 1984 was substantial. By late 1985 song was quite different to that of 1982/83, not only in song pattern and character of the sound types, but also in form of song, being relatively poorly structured. Mednis (this memoir) shows from an analysis of songs recorded off Stradbroke Is. in 1988, that the song later returned to the well structured form of 1982/83.

As discussed above, the sound types observed in the 1979 and 1980 songs off the east coast were different from those of 1981 and later years. The possibility that this was the result of a substantial change in the song in the 12 months from October 1980, thus seems more plausible, in view of the substantial change observed in 1984.

A sample of the 1985 song is given on track 3 of the compact disc. Other singers are audible in the background. This sample is one of the few examples where the last theme (the one that evolved from theme 6 of 1982/83) is repeated, so it is rather longer than most song cycles of 1985.

GEOGRAPHICAL FACTORS IN SONG CHARACTERISTICS AND SINGING BEHAVIOUR

Studies of Humpback Whale songs in the Northern Hemisphere have tended to concentrate on the tropical breeding grounds, with the notable exception of Bermuda (32°20'N). In the north Pacific and North Atlantic, Humpback Whales are most accessible on breeding grounds, because of the congregations in near shore shallow waters such as Hawaii and the islands of the West Indies. Migration paths, on the other hand, tend to be well off shore, and it is only where they approach islands such as Bermuda that there have been significant recordings on the migration paths. Studies to relate song production and behaviour have concentrated on breeding grounds, notably Hawaii (Tyack, 1981, 1983).

The situation is reversed in Australian waters. We have most ready access to the whales along the migration paths which follow the thousands of kilometres of the east and west coastlines. Breeding grounds on the east coast appear to be between the Great Barrier Reef and the coast (Paterson and Paterson, 1984, 1989; Simmons and Marsh,1986). On the west coast they appear to lie in the shelf area off northwest Australia. No concentration of whales on either breeding ground has been discovered. As a consequence, most recordings of the song have been from the migration paths, with very little from what could be considered to be breeding grounds (only the two most northerly points on the east coast (Fig. 1) could be considered to be on the breeding grounds). Stradbroke Is. was chosen as the place to record the song when this study commenced in 1981, because this was where a significant concentration of whales were known. More recently, a concentration of humpbacks in Hervey Bay during the southern migration has been established (Bryden et al., 1988).

Humpback whales have been observed along the entire east coast of Australia (10–38°S). The shortest distance by sea between these points while keeping within, say, 50 km of shore is in excess of 3500 km. Humpback whales have also been observed over a large range of latitudes off the west coast (Bannister, 1985; Dawbin and Gill, this memoir). In this study, songs have been recorded off the east coast at a number of locations between Jervis Bay (35°20'S) and Cowley Beach, near Innisfail (17°40'S). The shortest distance by sea between these two locations is about 2400 km. Off the west coast, recordings have been made between Perth (32°S) and the Monte Bello Islands (19°40'S).

Because the song changes with time, comparisons between recordings from different locations must be confined to recordings that could be considered to be contemporaneous, i.e. separated in time by no more than a few weeks, if any observed differences are to be associated with the differences in position. Recordings off the east coast (Fig.1) were contemporaneous with recordings off Stradbroke Is., with the exception of the 1979 and 1980 recordings off Jervis Bay. In these comparisons, no greater differences could be detected between contemporaneous songs at different locations than between different songs at the same location. The largest separations in these comparisons were Cowley Beach to Stradbroke Is. (1400 km) and Stradbroke Is. to Jervis Bay (970 km).

The first recordings of Humpback Whale songs off the west coast were obtained by a naval vessel in October 1983 off Perth and the Monte Bello Islands, a separation of 1600 km by shortest path. The recordings were separated by only 13 days and comprised one song cycle at the northern location and little more than half the cycle in the southern recording. The part of the song that is common to both recordings is similar. On the other hand these recordings are distinctively different from any recordings off the east coast, including those recorded within a few days off Stradbroke Is. The difference is fundamental: the sound types recorded off the west coast were different in their acoustical characteristics to those off the east coast. Recordings in later years have also shown the difference between the two coasts, for example, the songs recorded near the Monte Bello Islands in 1988 (several song cycles, two singers), and those discussed by Dawbin and Eyre (this memoir).

Although the sample size is small, these results suggest that the Humpback Whale song retains its integrity without geographical variation over a wide range of latitudes along the migration paths of the east coast of Australia.

Humpback whale populations off the east and west coasts of Australia are considered to be separate breeding stocks, with some intermingling in the Antarctic feeding grounds (Chittleborough, 1965; Dawbin, 1966). Evidence from marks recaptured from whales during whaling activities from 1950 to 1962 (Dawbin, 1966) indicates that outside the feeding grounds, the two stocks are well segregated but that a small amount of interchange does sometimes occur. Of whales marked off the east coast, 46 were later captured off the east coast, two off the west coast. Evidence from sightings, catches and catch compositions also indicates that stocks were well segregated, but Chittleborough takes the absence of any statistical differences in morphology as an indication of a small interchange between stocks.

Humpback whale songs in the North Atlantic Ocean differ substantially from those of the North Pacific Ocean (Payne, 1978; Winn and Winn, 1978; Winn et al., 1981). Geographical barriers do not allow the opportunity for interchange between stocks in these oceans as there is south of Australia. On the other hand, similar songs have been observed between breeding grounds which are widely separated by open water at similar latitudes in the same ocean, even though the separation is greater than between the east and west coasts of Australia. The similarities of songs between Hawaii and the Revillagigedo Is., (west of Mexico) in the North Pacific Ocean and between the West Indies and Cape Verde in the North Atlantic Ocean have been reported by Payne and Guinee (1983) and Winn et al. (1981), the separation distances being 5000 km and 4300 km respectively. Using tail fluke photographs to identify individuals, Darling and Jurasz (1983) found one example of interchange between Hawaii and Revillagigedo Is. These results suggest, therefore, that a geographical barrier between breeding grounds or between breeding grounds and a substantial part of the migration route is more important than the separation distance in determining different songs. It might be expected that the geographical separation would need to extend sufficiently far to separate that part of the migration paths over which significant singing occurs. However, a more definite conclusion requires comparisons from other areas, e.g. between east Australia and New Zealand.

TENTATIVE SONG RULES 1982-1985

To facilitate comparisons between hemispheres it is useful to formulate some tentative "rules" which govern the song pattern and sound character off Australia. These "rules" are designed to match as closely as possible the "rules" of song structure already determined for the Northern Hemisphere and given in the papers cited above. They are thus not necessarily new findings but rather an expression in a way designed to simplify comparison. "Song pattern" is defined as the order in which sound units of the different sound types occur. "Sound character" is defined as the spectral and temporal characteristics of a particular sound type. The definition of "sound type" is given in the section on "Methods" From the analysis the following features of the song have been established :-

(a) The song consists of several themes (six in 1982/83) in a fixed order, each comprising a variable number of renditions of a phrase which is specific to that theme

(b) Each phrase consists of several discrete sounds (syllables or units) in a fixed order separated by short periods of silence (typically 0.5-4secs).

(c) Each sound unit is a sample of one or other of a small number of basic sound types (12 in 1982/83) appropriate to that particular song. These are distinguished by their temporal and spectral characteristics (referred to as 'character' in this paper).

(d) The song pattern and the sound character at any time appear to be maintained by individuals of a stock for great distances along the migration paths and breeding grounds, although the sample size is small.

(e) The songs are distinctively different between stocks on the east and west coasts.

(f) Both song pattern and character of the sound types change progressively with time.

(h) Songs heard simultaneously appear to be independent and unsynchronised.

DISCUSSION AND CONCLUSIONS

Humpback whale songs recorded in Australian waters show a structure that is basically similar to that of the Northern Hemisphere songs. Although a song may contain some hundreds of sound units, all belong to one or other of a small number of sound types (12 in the 1982/83 song off east Australia). The song changes with time at a non uniform rate. Off east Australia the rate of change was gradual in 1982 and 1983, but a substantial change during the singing season in 1984 led to a substantially different song in 1985. This song was unusual in being poorly structured compared to the earlier songs.

There are more subtle patterns in the song than have been addressed in this paper. There are also small variations in pattern and in the characteristics of the sound types that warrant more detailed analysis. Information theory indicates that a signal can carry information only to the extent that it is unpredictable. Thus in a generally stereotyped song, it is the variation from the stereotype that has the potential to carry information.

Songs are distinctively different between the east and west coasts of Australia. It seems that a geographical barrier between stocks where most of the singing occurs, i.e. on the migration paths and breeding grounds may be enough to ensure that songs are unrelated, even though the stocks may intermingle in the feeding grounds.

In the samples available, the song appears to maintain its integrity over the very wide range of latitudes over which singing occurs off the east coast. This leads to a number of interesting questions. How are changes in the song communicated along the coast, and at what rate? Do the changes originate at any point where singing occurs or are there preferential source regions? At what distance from a singer does the song affect the behaviour of other whales?

The Australian coastlines provide access to Humpback Whales for thousands of kilometres along the migration paths and into the breeding grounds. The breeding grounds appear to be diverse and there may be no clear demarcation between these and the migration paths. Although whales appear in Hervey Bay as they migrate south, their behaviour shows a greater proportion of activity of the type associated with the breeding grounds than is observed further south off Stradbroke Is. These conditions provide the opportunity to study the relative significance of the song in breeding and migration. Does the proportion of whales singing and related behavioural reactions vary along the coastline? The population of Humpback Whales off the east coast has more than doubled since the early recordings were made (Paterson and Paterson,1989) and there are now more people making recordings, so that we now have prospects for obtaining much larger data samples than were available for the analysis on which this paper was based. There are good prospects for progress in understanding the significance of the song in migration and breeding.

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HUMPBACK WHALES *MEGAPTERA NOVAEANGLIAE* IN THE GORGONA ISLAND, COLOMBIAN PACIFIC BREEDING WATERS: POPULATION AND POD CHARACTERISTICS

L. FLÓREZ-GONZÁLEZ

Flórez-González, L. 1991 07 01: Humpback Whales *Megaptera novaeangliae* in the Gorgona Island, Colombian Pacific breeding waters: population and pod characteristics. *Memoirs of the Queensland Museum* 30(2):291–295. Brisbane. ISSN 0079-8835.

Photo-identification was used to study the Humpback Whale population which arrived at the Parque Nacional Natural Isla Gorgona between 1986 and 1988. Fifty animals were identified in 1986, 40 in 1987 and 35 in 1988 for a total of 108. Eleven individuals were common to 1986/1987 and 6 to 1987/1988. Three individuals were common for the three years. Using Petersen's formula, the estimates of the population for the 3 years ranged from 170 to 450. Gorgona has suitable environmental conditions required for humpback reproduction. The importance of Gorgona as a calving area is shown by the fact that 26.5% of animals seen were calves. The groups that stayed the longest time in the area were females accompanied by their calves but in general the frequencies were low. Humpbacks visit the region from June to November, the breeding season for Southern Hemisphere populations. During the years of study, behaviour of individuals and groups was analysed.

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This is the first biological contribution on humpbacks in Colombia. Due to its geographic position, Colombia may potentially be a meeting place for Northern and Southern Hemisphere populations; therefore, this study may help to identify part of the migratory routes of both populations and may contribute to the protection and management of the species.

Photo-identification (Katona et al.,1979) permits identification of individuals based on pigmentation patterns, natural markings and scars; it has been used by various authors in different areas, and represents a useful tool for the estimation of populations, distribution, migration patterns and social dynamics (Herman et al., 1979; Whitehead, 1981; Whitehead, 1983; Balcomb and Nichols, 1982; Darling and MacSweeney, 1985; Mayo et al., 1985; Baker et al., 1987; Clapham and Mayo, 1987; Kaufman et al., 1987; Chu and Nieukirk, 1988).

Humpback whale research in the Southern Hemisphere in America is limited. There are some studies that discuss the presence of this species (Alberica, 1986)as well as the lack of conservation and management policies (Aguayo-Lobo and Torres,1967; Paiva and Grangeiro, 1970; Pinedo and Castelo, 1980; Càrdenas et al., 1986; Guerra-Correa et al., 1987).Only one study similar to that reported herein has previously been carried out in South America; that study, in 1988, at Abrolhos Bank, an important breeding site off northeastern Brazil employed photo-identification and identified 64 individuals (Siciliano et al., 1990).

In Area 1 (feeding site) of the Antarctic, Stone and Hamner (1988) identified 32 individuals in 1985–1986. With the aid of a photographic catalogue, a Humpback Whale has been identified at both the Antarctic Peninsula and Gorgona Island areas. This is the first time that a Humpback Whale has been shown to cross the equator, and the first time an Antarctic Humpback Whale has been documented in South American waters (Stone, Flórez-González and Katona, 1990).

STUDY AREA

The research was carried out in the Parque Nacional Natural Isla Gorgona, an area of approximately 49200 hectares, including Gorgona and Gorgonilla Islands (Fig.1) and established in June 1985. It is on the Pacific continental shelf of Colombia (2°47'–3°06'N and 78°06'–78°18'W), 56 km from Guapi the nearest mainland town. Gorgona is approximately 10x3 km; its maximum height is 330m. The study area is located within the Intertropical Convergence Zone and thus endures variable winds and high pluviosity (7000–8000 mm annually). Salinity

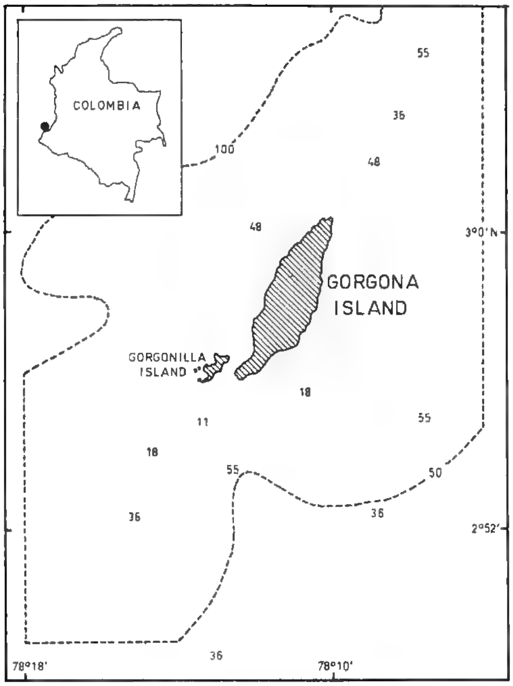

FIG. 1. Location map of study area. The broken line designates the Parque Nacional Natural Isla Gorgona limits. The dotted lines indicate isobaths in metres. The dot on the inset map indicates Gorgona Island in the Colombian Pacific.

around Gorgona is 31–33 parts per thousand. Water temperature is 26–28°C (INDERENA, 1986; Llinás et al.,1990).

METHODS

Monitoring was carried out daily between 10 am and 6 pm. The surveys were conducted from a fibreglass taxi boat with a 25 horsepower outboard motor. On some occasions, the animals were followed 15–20 km from the island, but normally no more than 5 km. When conditions prevented use of a boat observations were made from the high bay coast guard tower.

Song recordings were made with a Sony, TC-D5M, Tape recorder and a hydrophone with a frequency response 50–10000 Hz. Analysis of the song recordings have not been included in the present paper, however this field information permitted location and identification of individual singers.

RESULTS AND DISCUSSION

Three years of observations in the area permitted the photo-identification of 108 individuals. Fifty animals were identified in 1986, 40 in 1987 and 35 in 1988; 17 individuals were sighted in more than one year: 11 were common to 1986-1987 and 6 were common to 1987-1988, 3 individuals were common for the three years . The 17 common individuals were: 3 females, 2 males, 1 calf, 4 adults, 1 immature and 6 non discriminated. Using Petersen's formula (Begon, 1979), the population for the three years was estimated at 170–450.

Of the 108 individuals, 42 (39%) were identified by their back and the ventral surface of the flukes, 44 (41%) were identified exclusively by the ventral surface of the flukes and 22 (20%) using only the back. In 30 individuals, other characters (pectorals, dorsal region of the flukes, ventral region of the body and the head) were employed in identification.

Five (5) fluke and six (6) back photographs show a thin layer of diatom growth. Five (5) underside tail region photographs show killer whale teeth scars.

As previously established, Humpback Whales, during breeding activities, prefer meeting in groups near continents and around islands, in shallow waters, with protected beaches and temperatures 24–28°C. The eastern and extreme southern regions of Gorgona present these factors and this makes the island an ideal breeding site. Here 26.5% of observed animals were calves.

Individual Activities

Apparently, irrespective of age or sex, whales were observed in the following activities: spinning breach, full breach, chin breach, tail breach, lobtail, flippering, rolling, spyhop, and drifting. These activities have been described in humpback populations in different regions (Whitehead, 1981,1985a,b; Mayo et al., 1985; Pittman and Danton, 1985; Kaufman and Forestell, 1986; Silber,1986).

Group Characterisation

The Humpback Whale population in Gorgona Island was observed in 5 classes of groupings: 1, solitary animal; 2, female and her calf; 3, two animals without calf; 4, three individuals usually a female with her calf and an escort; 5, group of more than three individuals.

Of 35 solitary animals the 14 found in 1986 included 7 male singers; the 17 seen in 1987 included 13 male singers, in 1988 4 were seen but it was impossible to determine if they were male singers. Of the 35 solitary individuals, 7 were heard from the boat without any electronic aid. The solitary animals generally presented an elusive behaviour making immersions of 15–20 minutes, and showing little activity on the surface.

Groups including a female and calf were frequently found near the island, especially on the east, or protected side. For all observed females, epimeletic behaviour was evident. Three females and their calves were found on two occasions in a period of 8 days. One female and her calf were observed in two consecutive years (1987–1988). In the three years, 13 groups of two individuals, none calves, were observed. Most were adults but it was not possible to determine the sex; they showed little activity on the surface. Mobley and Herman (1985) found that the most stable social unit for groups without a calf was that of adult pairs. However, as in this study, it was not possible to determine the sex of the pairs. Tyack and Whitehead (1983), suggested that the pairs are formed by an adult female and an adult male. Six trios had a female, her calf and an escort. Only two escorts were certainly males; for the remaining it was impossible to determine sex. Two triples were observed twice in the same year in the space of 2 and 8 days, respectively. Similar results have been described by Baker and Herman (1984a) who cited observation of a trio on two consecutive days. However, this does not necessarily imply that the trio stayed together during these days. All groups with escorts were travelling, and courtship behaviour was never seen. On all ocassions the small animal was swimming on top or beneath the female and the escort was generally protecting the group, locating itself between the ship and the couple, and sometimes using distractive tactics.

Herman and Antinoja (1977) suggested that the escort whale could have a protective function. However, Tyack and Whitehead (1983), proposed that the escorts are probably males waiting for the opportunity to mate if the female is receptive. This hypothesis is now accepted and it has been supported by other researchers (Baker and Herman, 1984a; Mobley and Herman, 1985). On the other hand, Clapham and Mayo (1987) determined the sex of 91 escorts out of 138 observed, and found that 55 (60.5%) were females and 36 (39.5%) males. This grouping pattern needs further interpretation and to that end determination of the sex of the individuals will probably be useful.

On September 6, 1986 a trio of a female and two males were observed in aggressive behaviour for nearly 15 minutes; one individual left and the other two showed excitement on the surface for more than 10 minutes; they even jumped with their bodies ventrally joined for several seconds. Because it was mostly underwater, the specific function of this activity was not clear.

Sixteen groups of more than 3 individuals were seen in the three years. The maximum number was nine. Most, showed agonistic behaviour (collisions, persecutions, excitement, loud noises, bubble expulsion and other aggressive activities) and constant coming together and splitting off of individuals.

Agonistic and union-disunion behaviour, like those described here, have been reported by investigators in other breeding sites (Herman and Antinoja, 1977; Tyack and Whitehead, 1983; Baker and Herman, 1984a, b; Mobley and Herman, 1985; Silber, 1986).

It seems that a familiar bond may exist among some individuals because they were seen together on more than one occasion in the same year and even in two different years. Unfortunately, it was not possible to determine sex and age.

Traditionally, it has been assumed that Humpback Whales formed stable associations: family groups or reproductive couples (Whitehead, 1983). However, recent investigations show that this is not completely true. In the Antilles and in Hawaii, where humpbacks reproduce in the winter, groups stay together for a short period of time, excluding those formed by a calf (up to 1 year old) and her mother (Whitehead, 1981; Tyack and Whitehead, 1983; Baker and Herman, 1984a; Mobley and Herman, 1985). Further observations are needed to confirm whether the species forms stable family groups and whether it is monogamous or polygamous.

RECOMMENDATIONS

A major obstacle to understanding the social behaviour of humpbacks has been the difficulty of determining the age and sex of the individuals. With long term studies, based on photo-identification and underwater observations to determine sex, the knowledge of this species can be expanded making management and protection policies optimal. Therefore, investigations in the area of the park must be continued.

With the objective of elucidating the migratory routes of the species in the Colombian Pacific, investigations in other areas north of Gorgona must be carried out (Negritos Island, Palma Island, Malaga Bay, Utria Inlet, Cupica Gulf).

It has been recommended to the governmental management institute (INDERENA), to strictly control access of ships, boats and tourism to the Island, to avoid a threat to the Humpback Whale population.

Some sites in the Colombian Pacific where Humpback Whales have been reported are proposed to be managed as whale sanctuaries to ensure preservation through better management of this species which is seriously threatened.

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LARGE-SCALE PLANNING FOR ASSESSMENT AND RECOVERY OF HUMPBACK WHALE POPULATIONS

STEVEN K. KATONA

Katona, S.K. 1991 07 01: Large-scale planning for assessment and recovery of humpback whale populations. *Memoirs of the Queensland Museum* 30(2):297–305. Brisbane. ISSN 0079-8835.

Planning to help humpback whale populations recover from past commercial hunting must acknowledge their seasonal diversity of habitats, frequently governed by different nations, where they are affected by human activities such as shipping, fishing, dredging, waste disposal, and others. Human-induced changes in ocean ecology or resource abundance make it unlikely that populations could regain aboriginal sizes. Comprehensive research programs to assess present distribution and population sizes will usually require coordinated efforts by scientists from many nations. Estimation of present population size is facilitated by seasonal aggregation of whales at feeding or breeding locations, but poor estimation of prehunting abundance make it hard to choose a desired population size or to evaluate present vs past populations. Some populations may require many decades to reach desired population size, owing to the whales' tendency to return to traditional locations and their slow rate of reproduction. Monitoring programs must be long term. The U.S. Humpback Whale Recovery Plan is discussed as an example of a large scale plan covering 3 stocks of humpback whales in two oceans. A research proposal, entitled Years of the North Atlantic Humpback (YONAH), to assess population sizes and movements by an intensive international synoptic study throughout the summer and winter range of the species is summarized.

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The humpback whale, *Megaptera novaeangliae*, was the second species to be protected by the International Whaling Commission, beginning in 1955 with prohibition of commercial (non-subsistence) hunting in the North Atlantic Ocean. Protection was extended to the North Pacific and Southern Hemisphere populations after the 1963 hunting season. The species has not been hunted subsequently except for small subsistence hunts in Greenland (up to 10 per year until 1980 [Kapel, 1979], last whale taken in 1987); Bequia Island, Lesser Antilles (several per year, none caught since 1987 [Ward, 1987; Price, 1985; Adams, 1971, 1975]); and Tonga (up to 10 per year until hunting was stopped in 1978 [Winn and Reichley, 1985]. Winn and Reichley (1985) also noted that at least one humpback was taken by pirate whalers. Forty-one (41) humpbacks were taken in eastern Canada from 1969-1971 by scientific permit (Mitchell, 1973).

Hunting depleted population sizes so greatly throughout their range that Humpback Whales was listed as "Endangered" in waters of the U.S. (Braham, 1984) and "threatened" in Canada (Whitehead, 1987) and are included in Appendix I of the 1973 Convention on International Trade in Endangered Species (CITES).

Classification of an animal as "endangered" entails substantial governmental and scientific responsibilities. In most such cases, active management is required by law, when possible, to facilitate recovery of the depleted population(s). Scientific studies may be required to define more exactly the species' status, potential for recovery, and any actions to be taken. Substantial costs in personnel time and money may be required.

Since the main historical threat to humpback whales, hunting, effectively ended 25 years ago, it might be sufficient to do nothing and simply wait for the protected populations to increase of their own accord. This would be a tempting alternative for governments beset with other acute problems. In the end, time alone might be the most important factor necessary for recovery.

However, a suite of problems that did not exist in the days of hunting now affects some populations of humpbacks and other whales. Many of these threats are much harder to manage than was hunting, and their combined effects could be equally detrimental. These threats are not intentionally directed at humpback whales or other species. Some are unintentional side effects either of longstanding human uses of the sea, such as fishing or shipping, or sloppiness (e.g., pollution by sanitary, chemical or solid wastes). Others involve potential competition between humans and whales for food resources, such as capelin, herring and lately krill, or space, for example where coastal, recreational or industrial development may impact locations used for feeding or breeding (e.g. Nitta and Naughton, 1989).

Some of these threats are subtle and difficult to quantify. Even where effects are dramatic, such as for entrapment or entanglement of whales in fishery gear (Lien *et al.*, 1990) mitigation may be very difficult if no satisfactory alternative methods are available for humans. For example, prohibiting the use of shore-fast nets along the coast of Newfoundland would save the lives of several dozen humpback whales every year, but it would also eliminate the only source of income available to most coastal residents. The cumulative or synergistic effects of different threats, such as food limitation or contamination and challenge by pathogens (Geraci, 1989), are difficult to analyze.

Successful management of the humpback is complicated by their seasonal migrations. During their annual cycle, the whales range through a large geographic area, frequently including waters under the jurisdiction of several nations. Studies sufficiently broad ranging to describe topics such as migration, population structure, or abundance and trends benefit from or require the collaboration by many scientists, often in different countries. Since the whales have relatively long lifetimes, some studies (e.g. investigations on age-specific natality, comparative reproductive fitness, or heritability of behavioral or morphological features) may require decades, sometimes longer than the span of an individual scientific career. Successful incorporation of research results into plans for effective management of the species also faces geographic, temporal and political obstacles. For example, effective management of summer habitats to allow adequate opportunities for feeding is not sufficient to preserve the species if winter habitats for reproduction are not also maintained. Coordination between governments is necessary for management of most humpback whale stocks.

Confounding the issue still further, the terms "management", "conservation" or "preservation" are temporally unbounded. They imply periodic assessment, evaluation and actions to keep a species within certain numeric limits forever. Since natality and mortality vary over time in relation to prevailing ecological forces, management-related research must be carried out at appropriate intervals to determine population sizes and trends. This may become tricky if human-induced mortality causes total mortality to approach natality. In such a situation, and especially in the presence of stochastic factors, it may not be possible at any one time to evaluate whether a population is headed for survival or extinction. Gaskill and Lien (in prep.) emphasized that very long periods may be required to assess the true "health" of a population of whales. Their computer models produced instances in which apparently "healthy" populations went extinct over periods of hundreds of years, even while showing several 50-year periods of steady increase during which scientists or managers would have concluded that the species was progressing wonderfully.

Cautioned by such awareness, management of the humpback whale or of any endangered species cannot be regarded as a task to complete. While there may be some actions that need to be accomplished only once, for example designating certain locations as sanctuaries for the species, other actions may need to be overseen or repeated forever, or until a decision is taken that the species should not be protected.

The following accounts present highlights of two recent approaches to long term, broad scale management or study of humpback whales, namely the U.S. Humpback Whale Recovery Plan and a new research proposal entitled YONAH (Years of the North Atlantic Humpback Whale). Communication of some of the goals, problems and progress of these projects may help them to succeed and may help others to replicate and improve them.

U.S. HUMPBACK WHALE RECOVERY PLAN

The U.S Endangered Species Act (ESA) of 1973, (16 USC 1531 *et seq.*, amended 1978, 1982, 1986) requires Federal agencies to use all reasonable methods available to conserve species of plants and animals that are endangered or threatened with extinction. The U.S. Marine Mammal Protection Act (MMPA) of 1972 (16 usc 1361 et seq., amended 1990) assigned to the National Marine Fisheries Service (NMFS) responsibility for managing most marine mammal populations, including endangered species.

Section 4 (g) of the ESA requires the Administrator of an agency with oversight responsibility for an endangered species to determine whether populations of that species would benefit from a Recovery Plan, and if so, to construct and implement one. A Recovery Plan is "a guide that delineates, justifies and schedules those actions required for restoring and securing an endangered/threatened species as a viable, self-sustaining member of its ecosystem." Guidelines for constructing Recovery Plans specify that a numerical goal is usually required, along with means for evaluating progress toward achievement of that goal.

In 1987 the Administrator of NMFS concluded that humpback whales would benefit from a Recovery Plan and assigned the NMFS Office of Protected Resources to construct it. An advisory group, the Humpback Whale Recovery Team, was selected by NMFS to assist with the Plan (NMFS, 1990). The 10-person Team included experts on marine mammals from the private sector, academia, and government. Construction of the Plan, now in final stages of approval to become policy for NMFS, required nearly 2 years, 2 team meetings, 7 drafts, and 2 periods for public review and comment.

The Plan concentrates primarily on populations of humpback whales occurring seasonally or permanently in waters of the North Atlantic and North Pacific Oceans under U.S. jurisdiction, but it also includes recommendations for populations using waters around U.S. Trust Territories in the South Pacific. The Plan reviews the natural history of humpback whales; summarizes current knowledge about populations in the North Atlantic Ocean and the North Pacific Ocean; discusses known and potential threats to the species; then details a series of actions recommended to achieve recovery goals and a prioritized schedule estimating the time and money required for those actions.

Defining an overall goal for the Plan was not simple. The objective contained in the recovery planning guidelines, namely restoring the species to be a functional member of its ecosystem could not easily be defined or evaluated, so it would not suffice. The goal of encouraging populations to increase to the abundance prevailing before commercial hunting sounded appealing, but reviewers correctly noted that it might not be possible or desirable, since many other conditions had also changed since hunting began. Some new equilibrium would have to be sought that reflected expanded human use and abuse of the sea, since today's oceans could not support aboriginal numbers of whales as well as increased human populations.

The Team then tried to define a suitable percentage of aboriginal numbers for which to strive, but this also proved to be premature. How could one choose such a percentage, or evaluate progress toward that goal, without confident knowledge of prehunting abundance. Despite meticulous historical research (e.g. Mitchell and Reeves, 1983) the few existing estimates of early abundance for the population in the western North Atlantic Ocean were not precise enough to rely upon, and even less information was available for other oceans.

Consequently, the Plan now identifies several longterm goals: (1) the "BIOLOGICAL GOAL" of building and maintaining populations large enough to be resilient to chance events such as epizootics, episodic oceanographic changes, inbreeding or anthropogenic environmental catastrophes; (2) the "NUMERICAL GOAL" of achieving population sizes equal to at least 60% of the historical carrying capacity for populations in the North Atlantic and North Pacific Oceans, since large mammal populations are thought to achieve maximal productivity beginning at approximately that abundance (Fowler and Smith, 1981); and (3) the "POLITICAL GOAL" of being able to reclassify populations of this species from "endangered" to "threatened" or even "unprotected". While tasks identified in the Plan define those longterm goals more precisely, the Plan suggests adoption of an INTERIM GOAL to double the abundance of populations during the next 20 years. Periodic assessments of population abundance are called for in the Plan. Data showing statistically significant trends of population increase overall and reoccupation of portions of the range known to have been occupied during historical times are specified as acceptable evidence of progress toward recovery goals.

Recovery Planning Guidelines require that each action recommended be assigned a priority. Priority 1 denotes an action that must be taken to prevent extinction or to prevent the species from declining irreversibly in the foreseeable future. Priority 2 is an action that must be taken to prevent a significant decline in the species population or habitat quality, or some other significant negative impact short of extinction. Priority 3 is all other actions necessary to provide for full recovery of the species. According to these guidelines, there is nothing that should (or could) now be done for humpback whales that could be classified as Priority 1. However, many things should be classified as Priority 2.

Actions (tasks) were recommended in four general categories: 1) Maintain and enhance habitats used by humpback whales currently or historically; 2) Identify and reduce direct, human-related mortality, injury and disturbance; 3) Measure and monitor key population parameters; and 4) Improve administration and coordination of recovery efforts.

Foremost among the recommendations for habitat maintainance is identifying and designating critical habitat, particularly in the Hawaiian Islands winter range, but also if needed in other locations. Official designation as critical habitat adds a layer of Federal protection to any area within the jurisdiction of the U.S. This task will require better definition of the habitats and habitat features utilized by humpback whales. Other nations are encouraged to take similar actions to protect humpback whale habitats of special importance, as the Dominican Republic had already done by proclaiming Silver Bank a sanctuary for that species. Studies are recommended to ascertain historical abundance or the potential for reoccupation of habitats that may have been more important to the species in the past and that could be used if populations increase. The development of protocol for monitoring physical and chemical factors that could decrease habitat quality, as well as parasite load, biotoxins, and anthropogenic contaminant levels in tissues of whales and their prey is called for. The Plan recommends reducing disturbance from human- produced underwater noise in Hawaiian waters and in other important habitats whenever humpback whales are present. Finally, recognizing the necessity for providing adequate nutrition for whale populations, the Plan recommends monitoring levels of prey abundance, identifying and evaluating the type and amount of fisheries competition, and preventing the initiation of new large scale fisheries for primary prey of humpback whales.

Foremost among the recommendations designed to identify and reduce direct human-related injury and mortality and perhaps easiest to achieve is continuing the ban on commercial hunting of humpback whales. With luck, this alone might allow recovery of the species throughout its range. However luck cannot be trusted in the face of the various known and potential impacts that have been identified, which include subsistence hunting, entrapment and entanglement in fishing gear, collisions with ships; disturbance from vessels and aircraft; underwater noise from ships, boats and aircraft, commercial whale-watching boats (Atkins and Swartz, 1988; Beach and Weinrich, 1989) and research boats; noise from industrial activities; habitat degradation from chemical pollution, including petroleum; activities associated with increased coastal development; and competition for resources with humans. While some of those impacts might become more severe in the future, the most currently pressing task appears to be working with commercial fishermen and regional fisheries management councils to modify fishing gear and/or fishing regulations, where possible, to prevent entrapment or entanglement of humpback whales. Further evaluation of the effect of collisions with ships on humpback populations is also called for. Improved protocol for reporting and investigating carcasses, stranded specimens, and for photographing living whales will all help to provide information needed for these and other tasks.

Important recommendations for measuring and monitoring key population parameters include re-analyzing existing data with improved techniques; systematizing sampling methods for estimating population size; and developing better facilities for obtaining, archiving and analyzing data on humpback whales. Research vessels need to be dedicated to studying humpback whales and other endangered species, by building a new vessel for use in the North Pacific and another for the North Atlantic Ocean, and/or by chartering existing vessels. New field studies on population dynamics are recommended to examine age-specific rates of birth, survivorship and mortality. Better definition of geographic subdivisions of populations are called for, both by analyzing and evaluating existing information and by implementing immediately initial surveys of selected regions. Migration routes and transit times need to be defined more precisely by using long-term radio tags, underwater listening stations and genetic techniques. Finally, better assessments of abundance, status and trends of humpback whale populations are called for through new census surveys, participation in international sightings surveys and implementation of improved sampling programs for capture-recapture studies using individual identification photographs.

Of foremost importance to the objective of improving administration and coordination of the humpback whale recovery program will be selecting a Director for the overall recovery effort. Expansion or reconstitution of a Recovery Implementation Team to include wider representation of agencies such as the Mineral Management Service and National Park Service, and preparation of detailed regional work plans will improve the Plan's chance of success.

An important recommendation is to encourage multinational cooperation to protect humpback whale habitats. Discussing the Plan at international meetings; distributing it to other countries and providing appropriate follow-up communication; integrating recommendations with goals of the International Whaling Commission; and encouraging other nations to develop recovery plans for conservation and management of humpback whales are important long term goals that will benefit the species.

This sounds like a tall order, especially since NMFS, like most government agencies, is already overburdened and underfunded. Some of the recommendations in this Plan might conflict with those in other plans. For example, maintaining large populations of sand lance, herring and capelin for humpback whales could conflict with goals of the Right Whale Recovery Plan if the fish competed with right whales by consuming too many copepods. NMFS is also preparing a plan for managing shark populations, some of which are under heavy fishing pressure. Some of the sharks thus saved will probably eat young humpback or right whales. How all of this will work out remains to be seen.

YONAH (YEARS OF THE NORTH ATLANTIC HUMPBACK)

As demonstrated above, two simple questions need to be answered as a prelude to successful management of a species. Where are they? and How many are there? Answers remain elusive for most species of cetaceans. Fortunately those questions are somewhat easier to answer for humpback whales than for other balaenopterids, because the whales are easier to see and because they gather at traditional locations during winter. Nevertheless, it has not yet been possible to estimate population abundances sufficiently precisely to allow trends to be detected with statistical confidence.

YONAH (Years of the North Atlantic Humpback Whale) is a research project designed to answer those questions by sampling all populations in the North Atlantic Ocean with standardized methods during a two-year period using two techniques relatively new to whale science, photographic identification (Hammond et al., 1990) and DNA-biopsy sampling (Baker et al., 1990) of individual whales. Other unique features of YONAH include simultaneous sampling of all known habitats used during summer by humpback whales in the entire North Atlantic Ocean for two consecutive summers; and intensive sampling on the winter range during the preceding and following winter seasons. Large sample sizes will provide substantially improved description of population abundance, distribution and interchange, for an accurate snapshot of the species ocean wide status.

YONAH requires international cooperation, because most humpback whales in the North Atlantic Ocean feed, migrate, overwinter and/or breed in waters under the jurisdiction of two or more countries. Furthermore, it would be difficult for one government to provide all the funding necessary for such a comprehensive project, and it would be nearly impossible for one research team to accomplish the synoptic sampling program within the time period necessary to achieve the program's scientific goals.

YONAH will benefit from large scale models of collaboration that have already been established. For example, in 1987, Denmark, the Faroes, Iceland, Norway and Spain collaborated in an extensive shipboard and aerial census of whales in the eastern North Atlantic that used scientists from 8 nations (Oritsland *et al.*, 1989).

A significant problem confronts workers using photo-identification or DNA-biopsy techniques to study long range migrations, population subdivision and oceanic abundance. Hammond (1986,1990) described how opportunistic methods used in many such studies may not sample all portions of a population equally owing to geographic, temporal and biological biases. A brief examination of shortcomings in samples currently available for regions of the North Atlantic Ocean is instructive.

Geographic biases include the following examples. Newfoundland's long coastline is seasonally home to most of the whales in the western North Atlantic, but no comprehensive photographic sampling has been carried out since Whitehead's pioneering studies (e.g. Whitehead et al., 1982; Whitehead and Glass,1985). Even those studies visited only a small portion of the coast and spread the work over several years. The situation in Iceland is even more difficult. The conclusions that whales from Iceland's Denmark Strait form a separate feeding aggregation and visit the West Indies to breed (Katona and Beard, 1990) were drawn from a sample of only 20 whales. Luckily, 4 of them were subsequently sighted on the winter range and one returned to Iceland during a subsequent summer. At the other extreme, the Gulf of Maine, a relatively small region seasonally inhabited by somewhat fewer than 500 whales, each year produces thousands of photographs. However, most of those photographs are taken by naturalists or scientists working mutualistically with commercial whale-watch boats, whose working range is usually constrained by the 4 to 5 hour length of scheduled trips. Consequently, relatively accessible locations are sampled disproportionately. Mitchell and Reeves' (1983) early concern that photo-identification studies have not fully determined the boundaries of the populations sampled is still true.

Temporal biases also exist. For example, most photographs in the Gulf of Maine are obtained from April 15 to October 15, the season when commercial whale-watch boats operate. Whales that appear early, perhaps on the way to other feeding aggregations, or whales that stay late, perhaps remaining throughout winter, do not have an equal opportunity to be photographed, particularly if they occur offshore. Disproportionate sampling during summer months is a common feature of studies throughout the North Atlantic. Larger scale temporal inequalities in sampling intensity also occur. For example, entire regions may be sampled during some years, but not others.

A suite of interesting biological biases also exist, such that different age classes, reproductive classes or genders may be over- or under-represented in samples. Resulting problems can be particularly vexing if sampling methods used in different regions cause different types of biases. For example, sampling on the winter range has focused on surface active courtship groups, which present more opportunities for photographing flukes than do mothers with calves or single whales. Since such groups are predominantly male, photographs of that gender may be over-represented. On the other hand, singing whales, thought to be only males, remain submerged for up to 30 minutes, and are likely to be sampled less than other classes. Similarly, a female accompanied by a calf flukes up less often than do other animals, particularly on the winter range. Calves photographed on the winter range are normally excluded from calculations of abundance, because they rarely fluke up and their fluke pigmentation patterns are not yet clearly formed.

Awareness of these biases and recognition that international cooperation would be needed to eliminate them led to the idea for a carefully designed, intensive synoptic investigation of all humpback whale habitats in the North Atlantic Ocean. A research proposal was prepared by scientists from 6 nations (see Acknowledgements) and submitted to the International Whaling Commission (Document SC/40/025) and the Marine Mammal Committee of the International Council for Exploration of the Sea (ICES) (C.M 1990/N:18).

Major goals of YONAH are:-

1. Photographs for individual identification will be obtained from approximately 1500 whales on the summer range during each of two successive summer seasons and 2000 whales on the winter range during the previous and intervening winters. Biopsy samples are anticipated from about half of those animals. Standardized protocols will be used to select areas in the summer range for searching, locate whales or groups of whales, select individual whales from groups for photographic or DNA sampling, and to terminate activity with a whale if samples have not been obtained within a reasonable amount of time. The overall sampling objectives will be to equalize the opportunity for every individual whale to be sampled, compensate for any inequalities in resulting analyses, and achieve precise confidence intervals by obtaining sufficiently large sample sizes.
2. Individual-identification photographs will be centrally archived and analyzed as described by Katona and Beard (1990), in order to be comparable with previous results. Procedures will be developed for providing appropriate access to photographic samples for YONAH collaborators or other interested scientists.
3. Protocol for processing and archiving biopsy samples will insure that at least half of each biopsy sample collected will be transferred to YONAH and used to determine gender of individuals; the number of matrilineal lines (haplotypes) present in mitochondrial DNA in the North Atlantic Ocean and their distribution in different subregions; and to identify nuclear gene sequences that would permit Mendelian analyses for delineating panmictic population

units. Additional studies for genetic fingerprinting and identification of paternal markers may be attempted after primary analyses are completed. Tissue remaining after primary analyses, along with appropriate descriptive data, will be preserved in a central archive at -80° C to insure its long term viability and availability. The YONAH organizing committee will welcome proposals for further analyses of tissue samples and grant permission for their use as appropriate, in consultation with the Project Coordinators for YONAH subregions involved.

4. A comprehensive centralized database will be constructed containing all information on individual photo-identifications, individual genetic data, sightings from which photographic and/or biopsy samples were attempted, and searching effort when locating groups of whales to sample. Data auditing checks will track and coordinate linkage of field and laboratory results so that no data are lost. YONAH collaborators will receive updated copies of the entire database periodically.

5. The YONAH database for the entire North Atlantic Ocean will be analyzed to estimate total population size and rates of exchange of whales between sub regions of the summer range. The representativeness of data collected at the regional level will be investigated and results used to modify methods for estimating population abundance. Likelihood models will be developed for estimating abundance and also for defining DNA haplotypes. Sensitivity analyses will also be conducted to determine the sensitivity of estimates of abundance and interchange to various assumptions.

6. Population abundance will be estimated by applying the Petersen capture-recapture method to individual-identification photographs. The planned sampling design, two successive seasons on the summer range (S_1 and S_2) along with the previous and intervening seasons on the winter range (W_1 and W_2) will permit several independent population estimates using either W_1/S_1; S_1/W_2; W_2/S_2, W_1/W_2 or S_1/S_2 as the capture-recapture samples. Estimates will be prepared for population subregions, including the Gulf of Maine, Gulf of St. Lawrence, Newfoundland, southwestern Greenland, Iceland, and Norway; and also for the whole North Atlantic Ocean .

This is an ambitious project. However, scientific interest is high and it dovetails nicely with some national and international goals of several countries. NMFS appears to be willing to support further planning for organization and development of scientific protocols. Proposals for additional funding are in preparation. Current hopes are that work at sea might begin by January, 1992.

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The discussion of the U.S. Humpback Recovery Plan summarizes my own experience. My comments do not necessarily represent views of the Recovery Team, NMFS or any agency or party other than myself. The Plan is still being discussed and evaluated by NMFS and some of the recommendations mentioned could be modified or eliminated before the Plan becomes NMFS policy. Copies of the Humpback Whale Recovery Plan and the Recovery Plan for Northern Right Whales can be obtained by writing to NMFS, Office of Protected Resources, 1335 East West Highway, Silver Spring, Maryland, USA 20910.

The idea that grew into YONAH was

generated by David K. Mattila, Philip J. Clapham and Charles "Stormy" Mayo, Jr. of the Center for Coastal Studies, Provincetown, Massachusetts. Thanks are due to Tim Smith (Northeast Fisheries Laboratory, NMFS, Woods Hole, Massachusetts) for taking on the task of coordinating the YONAH planning effort and helping to bring that important research project from idea to reality. Subsequent planning and preparation of research proposals involved Nils Oien, (Norwegian Institute for Marine Research), Johann Sigurjonsson, (Iceland Fisheries Research Institute), Finn Larsen (Greenland Fisheries Research Institute), Per Polsboll (University of Copenhagen), Philip Hammond (Sea Mammals Research Unit, Cambridge University), Jon Lien (Memorial University of Newfoundland), David Mattila, Philip Clapham, Stormy Mayo (Provincetown Center for Coastal Studies), Tim Smith and Tom Polacheck (Northeast Fisheries Laboratory, NMFS), and Steven K. Katona and Judith A. Beard (College of the Atlantic).

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HUMPBACK WHALES *(MEGAPTERA NOVAEANGLIAE)* IN THE WESTERN NORTH ATLANTIC OCEAN

STEVEN K. KATONA AND JUDITH A. BEARD

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Individual humpback whales can be recognized by natural markings on their bodies. The North Atlantic Humpback Whale Catalogue contains photographs of the ventral flukes of over 4000 humpback whales. More than a thousand resightings over the past 15 years have yielded information on seasonal distribution, population substructure and abundance. This paper reviews the biology of humpback whales in the North Atlantic Ocean, highlighting contributions made by photo-identification studies, and indicates avenues for future research.

During boreal summer, North Atlantic humpbacks form at least 5 geographically distinct feeding aggregations at latitudes from about 42°–78° N. Known feeding aggregations occur in the Gulf of Maine (c. 400 individuals), Gulf of St. Lawrence (c.200); Newfoundland and Labrador (c.2500); western Greenland (c.350); Iceland-Denmark Strait (up to 2,000); and Norwegian Sea (1000). Photo-identified whales from all feeding aggregations including and to the west of Iceland spend boreal winter near the Virgin Islands, Puerto Rico and the Dominican Republic (c.17°–22°N), where courtship, interbreeding and calving occur. Some of these whales pass close to Bermuda during the northward migration. The winter ground(s) for European humpbacks is not yet known. A variance-weighted estimate for the total population of humpback whales in the North Atlantic Ocean west of Iceland during 1978–1988 is 5066±3266) (95% CI).

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Humpback whales *(Megaptera novaeangliae)* play important roles in the ecology and economy of the North Atlantic Ocean. Here, as in other oceans, they were economically significant to aboriginal people and commercial hunters as a source of meat and oil. Now, the accessibility of their coastal habitats, their willingness to approach boats, and the frequent opportunities they provide for people to watch feeding, breaching or other interesting behaviors have made them the mainstay of whale watching industries along the New England coast and in eastern Canada. Commercial whale watching tours in New England, for example, now take out nearly 1,500,000 people each year, representing over $23,000,000 in ticket sales alone. On the other hand, fishermen along the coast of Newfoundland regard humpbacks as pests, because their frequent entrapment or entanglement in shorefast nets set for salmon, cod or capelin, cause gear damage, loss of fishing time and economic hardship (Lien et al., 1990).

Although the difficulty of estimating prehunting humpback abundance (NMFS, 1990) confounds attempts to evaluate its ecological role in the past, it is certainly important at some locations today. During summer, the species is the major cetacean predator in the southwestern Gulf of Maine and at some locations in the Canadian Maritimes. During winter, humpbacks migrate to warm, low latitude waters where they feed only rarely (Baraff et al., 1991), but where they may be the dominant cetacean in biomass, and their sounds, excretions, or other factors may be of ecological significance (Katona and Whitehead, 1988).

Early descriptions of humpbacks in the North Atlantic came from opportunistic observations at sea or dead animals killed during hunting or found dead along the shore (e.g., True, 1904; Allen, 1916; Ingebritsen, 1929). The comprehensive studies of large samples in the Southern Hemisphere (e.g. Matthews, 1937; Chittleborough, 1958,1965) or the North Pacific (e.g. Nishiwaki, 1959) were not carried out in the North Atlantic, because humpbacks were al-

FIG. 1. Map of North Atlantic Ocean. Modified from Jonsgard (1966).

ready scarce before such studies became routine.

Schevill and Backus's (1960) observation over a 10 day period of a humpback whale swimming near Portland, Maine, was one of the first attempts to study a free-living humpback for purely scientific purposes. Their use of distinctive dorsal fin shape and fluke pigmentation to conclude that the same individual was present on different days may have been the first modern use of the technique that has become a cornerstone of humpback whale research. Examples of the development and use of fluke photographs to identify humpback whales in the North Atlantic and other oceans are contained in Hammond et al. (1990).

METHODS FOR PHOTO IDENTIFICATION OF HUMPBACK WHALES

Pigmentation patterns on the ventral surface of the flukes of humpback whales were photographed, printed in standard format and analyzed as discussed in Katona and Whitehead (1981), Katona and Beard (1990)and Lien and Katona (1990). Approximately 10,000 photographs of the flukes of humpback whales collected by research workers and amateurs throughout the Atlantic region from 1967 to the present are maintained at College of the Atlantic (COA) in Bar Harbor, Maine, as the North Atlantic Humpback Whale Catalogue. Contributors are asked to submit at least one fluke photograph of every individual photographed each season. Each photograph obtained is compared to the entire collection to determine whether it represents a previously known whale or a new whale. Photographs of the same individuals taken at different times and places are used to study long distance migrations, population subdivisions, and to estimate population abundance using capture-recapture techniques (Hammond, 1986). Updated sightings data from the COA catalogue are provided periodically to contributors of photographs, some of whom maintain regional photographic collections containing detailed sighting records for individual whales in localized study areas that are used, for example, to chart reproductive histories of individual females (Clapham and Mayo, 1987a,b; 1990), or investigate social behavior (Weinrich and Kuhlberg, in press).

HUMPBACK WHALES IN THE NORTH ATLANTIC OCEAN

A. Distribution and Feeding on the Summer Range

During summer, humpback whales feed over the continental shelf and along coastlines from the British Isles north to Bear Island (75°N) and Spitsbergen (78°N), and around Iceland, southwestern Greenland, Newfoundland and Labrador, the Gulf of St. Lawrence, and the Gulf of Maine (Tomilin, 1967; Leatherwood et al., 1976; Whitehead et al., 1982; Mitchell and Reeves, 1983; Katona et al., 1983; Perkins et al., 1984, 1985; Payne et al., 1986; Whitehead, 1987).

This distribution was documented relatively early from locations of whaling catches, but previous investigators (e.g. Kellogg, 1929; Mitchell, 1974) had little or no information about movements between those regions and no effective method for obtaining more. About 15 years ago, the questions raised by those authors began to be answered by charting the movements of photographically-identified humpbacks.

Our conclusions regarding migrations, population subdivisions and abundance of humpback whales in the North Atlantic Ocean are drawn from the study of 10,566 photographs, represesenting 4,021 individual whales. By December, 1988, 1,428 individual whales had been seen on more than one day (a total of 4,012 sightings) and 1,083 individuals had been seen in more than one season or in different geographic regions (a total of 3,173 sightings). Photographs from field seasons subsequent to 1988 are still being analyzed.

Geographic patterns of resightings on the summer range (Fig. 2) suggest that during summer the population of humpback whales from Iceland westward is divided into several relatively distinct units. Individually-identified whales from Iceland, southwestern Greenland, Newfoundland and Labrador, the Gulf of St. Lawrence, or the Gulf of Maine returned repeatedly to those same waters. We use the term "feeding aggregations" to describe the groups of whales using those separate parts of the feeding

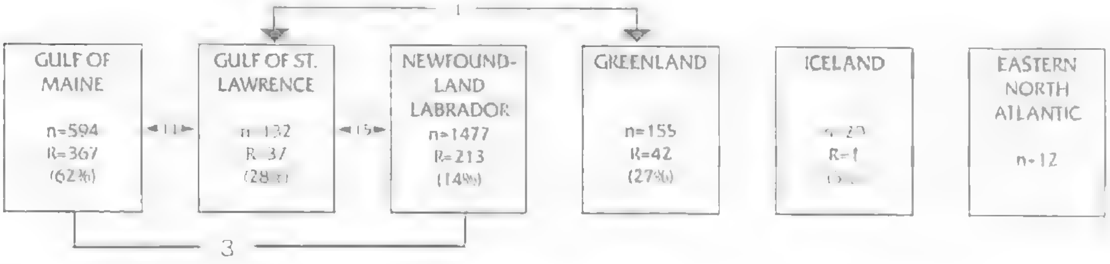

FIG. 2. Movements of photographically identified Humpback Whales on the North Atlantic summer range. Boxes represent regional feeding aggregations. Number of individuals photographed (n); number resighted in a region in different years (R); and percentage resighted in the region in different years are shown. Numbers of individuals photographed in more than one region are shown between boxes.

LOCATION	PREY SPECIES	SOURCES
Iceland	capelin (*Mallotus villosus*) herring (*Clupea harengus*)	
Greenland	small fish, krill, sand lance (*Ammodytes* sp.)	Kapel,1979; Perkins et al.,1982
Newfoundland	capelin (*Mallotus villosus*), euphausiids, haddock, (*Melanogrammus aeglefinus*), mackerel (*Scomber scombrus*), sand lance (*Ammodytes* spp.), squid (*Illex illecebrosus*)	Mitchell,1974; Bredin,1983; Whitehead and Glass, 1985; Whitehead and Carscadden,1985
Gulf of St. Lawrence	herring (*Clupea harengus*), capelin (*Mallotus villosus*), sand lance (*Ammodytes* sp.), euphausiids	R. Sears pers. comm.
Nova Scotia	herring (*Clupea harengus*), krill (*Meganyctiphanes norvegica*)	Brodie et al.,1978; C. Haycock pers. comm., S. Katona unpubl. data
east coast USA	sand lance (*Ammodytes* sp.), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), krill (*Meganyctiphanes norvegica*)	Meyer et al.,1979; Overholts and Nicolas, 1979; Watkins and Schevill,1979; Hain et al.,1982; Katona et al.,1983; Kenney,1984; Hays et al.,1985; Kenney et al.,1985, Kenney and Winn,1987; Winn et al.,1987; Mayo et al.,1988; Geraci et al., 1989

TABLE 1. Prey species utilized by humpback whales in the North Atlantic Ocean

range. Little interchange was seen between feeding aggregations (Fig. 2). In some cases, interchange shown between regions may be animals that happened to be seen while enroute to their feeding destination. For example, the three individuals photographed in both the Gulf of Maine and Newfoundland may have used the Gulf of Maine only for migration, since they were observed there at the very beginning and very end of the feeding season. Interchange between the feeding aggregation in the Gulf of St. Lawrence and those in Newfoundland (including Labrador) or the Gulf of Maine is relatively large because of their proximity. Individuals bound for the Gulf of St. Lawrence probably swim through waters used by other feeding aggregations.

Photo-identification studies from the eastern North Atlantic Ocean are planned or in progress, but not enough data are yet available for comparable analysis. No resightings were found of 12 individuals from the eastern Atlantic represented in the COA collection.

Distribution on the summer range is directly dependent on the distribution and abundance of prey. However, since humpbacks in the North Atlantic utilize several types of prey (Table 1), the pattern is somewhat more complex than in the Antarctic, where krill, primarily *Euphausia superba*, dominates the diet (Matthews, 1937; Laws, 1985). In the western North Atlantic, humpbacks arrive by mid-April at the Massachussetts coast, the portion of the feeding range closest to the winter range. In more northerly areas they usually appear by May or early June, with peak numbers in July or August. Typical annual movements within a feeding region are keyed to annual cycles of prey abundance. For example, the intensive whalewatching industry operating from mid-April to mid-October along the Massachusetts coast exists because many whales remain in that region throughout summer, feeding mainly on a population of sand lance resident at Stellwagen Bank (Mayo et al., 1988). In contrast, humpbacks migrate steadily along the coast of Newfoundland following the northward progression of capelin spawning from June through October (Whitehead et al., 1982).

Feeding areas have changed substantially between weeks or years depending on local abundance and distribution of prey (see Table 1).

No strong evidence of age or sex class segregation has been found on the summer range. For example, in continental shelf waters of the U.S., the geographic distribution of mothers with calves and of juveniles is similar to that of other humpbacks (Goodale, 1982).

By late autumn, most humpbacks begin migrating to lower latitudes. However, winter records from Newfoundland (Williamson, 1961; Jon Lien, pers. comm.), the Gulf of Maine (CETAP, 1982; Mayo et al., 1988; C. Haycock, pers. comm.) and northern Norway (Rister, 1912, cited in Kellogg, 1929) indicate that some whales may stay at high latitudes all winter.

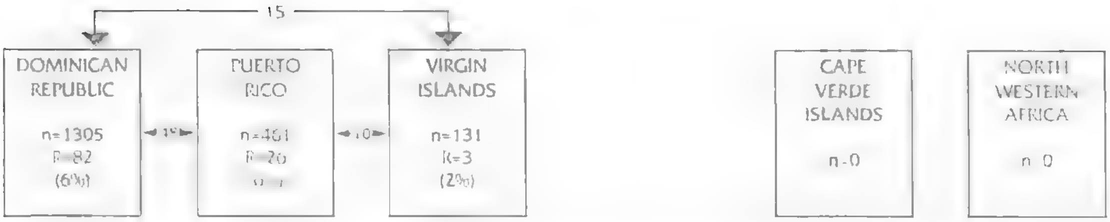

FIG. 3. Movements of photographically identified humpback whales on the West Indies winter range. Number of whales photographed (n) is shown for each breeding location, along with number (R) and percentage of whales photographed at that location during different winters. The number of whales photographed in more than one location is also shown.

Events observed during late November in the southwestern Gulf of Maine, preceeding migration to the West Indies winter range, include increased numbers of whales, energetic swimming behavior and song production (Mattila et al., 1987).

Migration routes of different feeding aggregations between the summer range and the winter range are not known. Humpback whales probably migrate well offshore to their principal winter range around the Greater and Lesser Antilles, since no winter sightings have been recorded along the U.S. coast or at Bermuda. Songs of humpback whales enroute to the winter range were heard on underwater sound recordings made east and south of Bermuda and also southwest of there (Clapham and Mattila, 1990).

B. Distribution on the Winter Range

From late December through early April, most of the western North Atlantic humpback population is found at Silver Bank and Navidad Bank, reefs approximately 607 nm^2 and 157 nm^2, respectively, located about 120 km north and northwest of Puerto Plata, Dominican Republic. At least 2000 humpbacks occur there from December to early March (Balcomb and Nichols, 1978,1982; Whitehead and Moore, 1982). Winn et al. (1975) estimated that 85% of the entire western North Atlantic breeding population used Silver and Navidad Banks. Significant numbers of humpback whales also winter along the Dominican coast (Mattila et al., 1988), the northwest coast of Puerto Rico (Winn et al., 1975; Mattila, 1983) and on the Virgin Bank (Winn and Winn, 1978; Mattila and Clapham, 1989). Movement of whales between those portions of the winter range occurs within a season and between years (Fig. 3). The remainder of the population may be scattered throughout the Lesser Antilles as far as Venezuela (Winn and Winn, 1978).

The wintering grounds of eastern Atlantic humpbacks have not yet been documented by either recovery of artificial tags or photo-identification studies. Humpbacks were killed by hunters during winter around the Cape Verde Islands (Kellogg, 1928; Townsend, 1935; Mitchell and Reeves, 1983) and along the coast of northwestern Africa (Kellogg, 1928). Kellogg's (1928) map of humpback migrations showed all eastern North Atlantic humpbacks using those winter grounds, but the possibility that some eastern Atlantic humpbacks winter around the Antilles can not be ruled out. The Cape Verdes are now being surveyed using photo-identification techniques (F. Wenzel, pers. comm.).

Courtship (Tyack and Whitehead, 1983), singing (Winn et al., 1981; Payne and Guinee, 1983; Payne and Payne, 1985), newborn calves and nursing (Mattila and Clapham, 1989) have all been observed on the winter range. Copulation, which has never been documented in this species, is also presumed to take place there. Differential habitat use by reproductive class occurs on the West Indies winter range. Calm waters around coral heads and reefs providing lee from the trade winds are used preferentially by females with calves (Whitehead and Moore, 1982; Goodale, 1982). Singing males may prefer locations with flat bottoms (Whitehead and Moore, 1982).

Migrations to or from the West Indies winter range have been documented for 339 photographically-identified humpbacks from all feeding aggregations from Iceland west (Fig. 4). Photo-identification has also shown that surface-active courtship groups contain whales from different feeding aggregations (Mattila et al.,

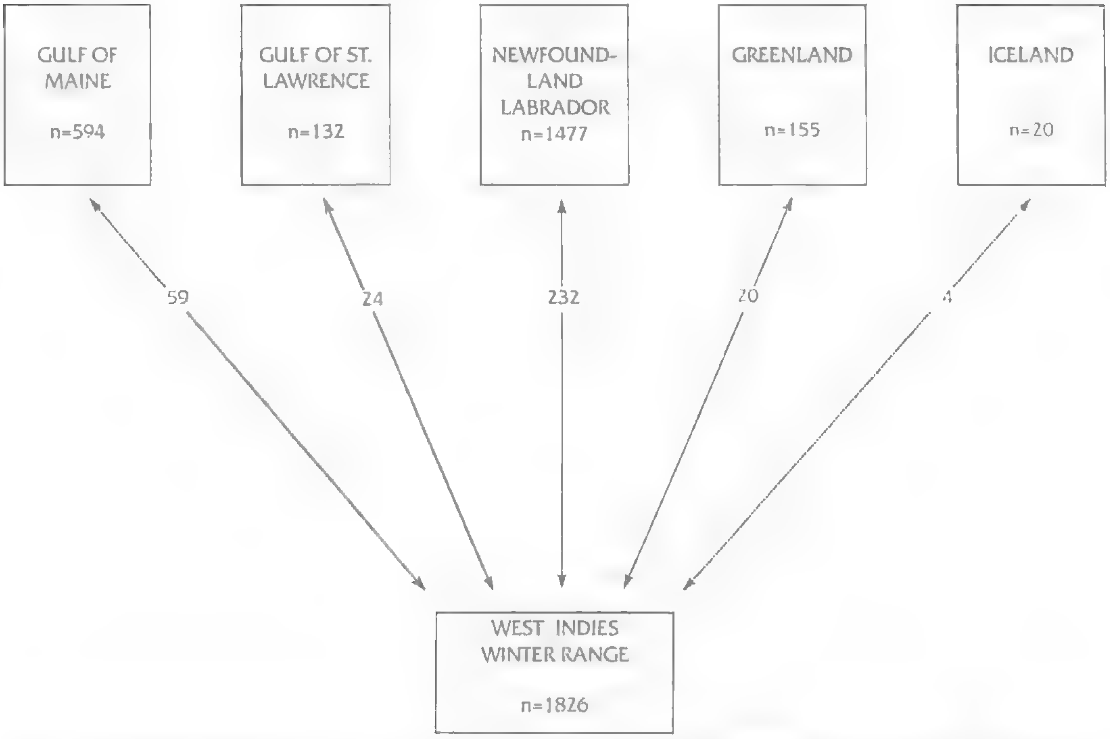

FIG. 4. Migrations between eastern North Atlantic summer range feeding aggregations and West Indies winter range. Number of individuals (n) photographed at different locations is shown along with the number photographed in different locations (on interconnecting lines).

1989), indicating that all humpbacks from the western North Atlantic, at least, probably interbreed.

Some humpbacks remain in the West Indies through March, but most depart earlier. Peak numbers at Silver Bank occured in February (Balcomb and Nichols, 1982). Photo-identified individuals (n=26) from all five western Atlantic feeding aggregations have been observed during northward migration near Bermuda in April and early May (Stone et al., 1987) (Fig. 5), but some whales probably take a a mid-ocean route to the summer range. Minimum mean swimming speeds of 3.29 km/hr (2,684 km in 34 days) and 2.28 km/hr (2,351 km in 43 days) were computed for two photographically-identified whales migrating from the West Indies to the Gulf of Maine feeding aggregation (Clapham and Mattila, 1988). The slower rate was close to mean speeds calculated by Dawbin (1966).

If all western North Atlantic humpbacks interbreed, as suggested by Mattila et al. (1989), and since a calf must nurse during its first migration to the summer range, persistent subdivision of the population on the summer range must be maternally directed. Such divisions probably are caused by the tendency of a calf to return to the portion of the summer range used by its mother and learned during its first summer (Martin et al., 1984; Baker et al., 1990), rather than by a genetically fixed behavior pattern.

Several studies indicate that maternally directed behavioral fidelity to feeding grounds has been maintained for many generations. In the North Atlantic, analysis of the amount of pigmentation on the ventral surface of flukes revealed significant differences between most feeding aggregations (Beard et al., in prep.). In the North Pacific, Baker et al. (1990) found significant differences in mitochondrial DNA haplotypes between humpback whales sampled in southeastern Alaskan waters and those sampled offshore from central California.

C. REPRODUCTION

Reproductive parameters for humpbacks from the New England coast obtained from photo-identified individuals in the Gulf of Maine gave a crude birth rate ranging from 0.45 in 1981 to 0.103 in 1983; the same data yielded reproduc-

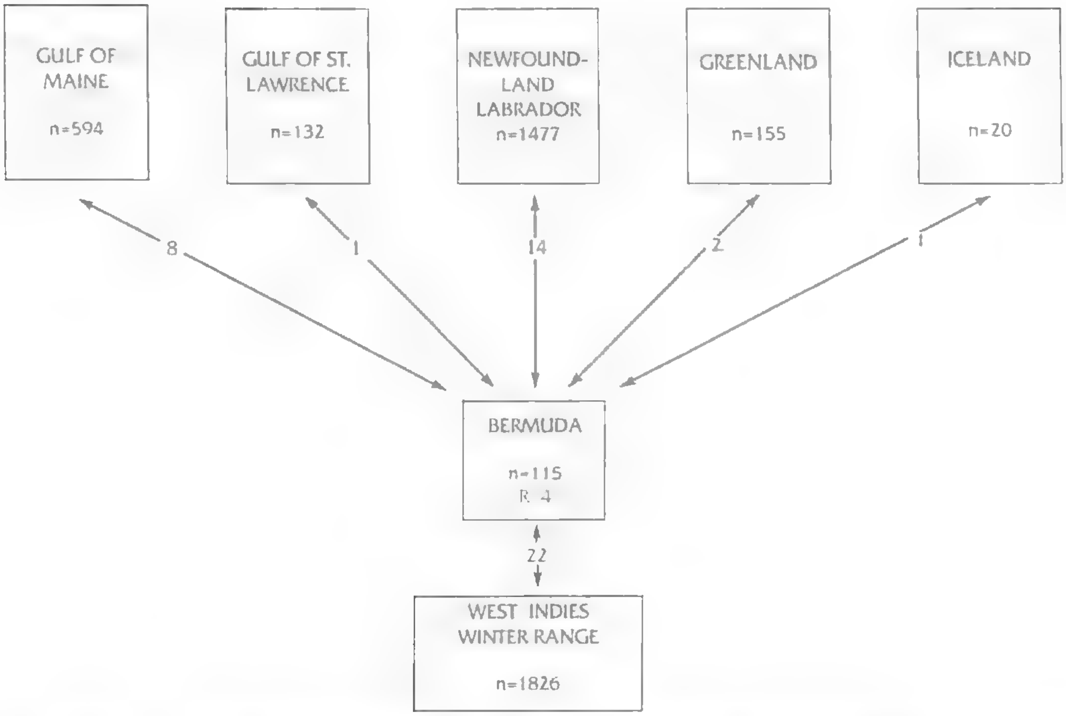

FIG. 5. Distribution of resightings of individually identified humpback whales photographed

tive rates of 0.30-0.43 calves per mature female per year (Clapham and Mayo, 1987a). Those authors and their colleagues at the Center for Coastal Studies (CCS), Provincetown, Massachusetts, now have a sample population of 97 mothers and 207 calves. The numbers of calves produced by individually identified mothers as of September, 1990, are 7 (n=1), 6 (n=3), 5 (n=5), 4 (n=6), 3 (n=14), 2 (n=22) and 1 (n=46). Nine (9) females are now grandmothers, two of them for the second time (L. Baraff, pers. comm.). As detailed by Clapham and Mayo (1987b), calves were usually born at intervals of 2 or 3 years. Two whales known from their birth year and seen annually bore calves of their own, at ages of no more than 4 years and 6 years, respectively; others with incomplete sighting histories calved at minimum ages of 5 (n=2), 6 (n=3), 7 (n=2) and 9 (n=1) years.

D. HISTORICAL ABUNDANCE

Mitchell and Reeves (1983) summarized the history of humpback whale hunting in the western North Atlantic Ocean, starting at Bermuda in 1611, Maine in 1675, Georges Bank in 1725, the Gulf of St. Lawrence in 1819, the West Indies wintering grounds in 1822, and the Canadian maritimes in the late 1800's. They accounted for at least 9,125 humpbacks killed during 1850-1971, and used their assembled catch estimates to calculate that the population size in 1865 was greater than 4,700. Breiwick et al. (1983) used the same data, but incorporated estimates for annual natural mortality (4%) and net recruitment (3%), and revised that estimate to 6,300 whales. However, many more humpback whales may have been present originally, because humpbacks had been hunted for several centuries before 1865, although catches were poorly documented (Reeves and Mitchell, 1982). Winn and Reichley (1985) listed 10,000+ as their estimate for the original population in the western North Atlantic.

Commercial hunting could have reduced the North Atlantic humpback population to as few as 700 animals by 1932 (Breiwick et al.,1983). Hunting of females with calves at locations where humpbacks returned annually for breeding probably contributed to their rapid depletion on some winter grounds Winn and Scott (1981).

No estimate of historical abundance is available for humpbacks in eastern North Atlantic waters. As reported in Reeves and Mitchell (1983), Ingebritsen (1929) calculated that 3,300 whales were killed there during 1885–1927, including 1,500 off Finnmark (central Norway) and 1,500 off Iceland. Since we now know that humpbacks from at least as far east as Iceland migrate to the West Indies and probably interbreed with the western North Atlantic stock (Mattila et al., 1989), it is unclear how Ingebritsen's data could be used to evaluate historical abundance for eastern Atlantic humpbacks.

E. Estimate of Current Abundance

Population estimates for the western North Atlantic have shown an upward trend since the 1960's, however the increase is believed to be principally due to improvements in sampling effort and methodology (Whitehead, 1987). We report here (Fig. 6) a new estimate of 5066 whales (95% confidence interval, 1800-8200), based on whales photo- identified during 1978-1988 and computed by methods detailed in Katona and Beard (1990). This represents about 80% of Breiwick et al.'s (1983) estimate for the population in 1865.

No estimate is available for current abundance of humpbacks in European waters from Iceland eastward. Luckily, Ingebritsen's (1929) statement that hunting appeared "to have entirely exterminated" the species in those waters was not correct, and studies using photo-identification and census surveys are in progress. Gunnlaugsson and Sigurjonnson (1990) used sightings from ships to estimate a population of less than 2000 humpbacks around Iceland. This was considered a great increase since protection began in 1955 and a considerable increase since the 1960's (Sigurjonsson and Gunnlaugsson, 1990). However, as shown in Sigurjonsson and Gunnlaugsson (1990), that estimate includes many sightings of humpbacks in the Denmark Strait that are probably affiliated with the western North Atlantic population, plus others sighted east of Iceland that could be from the eastern Atlantic feeding aggregation(s). Visual surveys from ships, by the Norwegian Institute for Marine Research indicated about 1,000 humpbacks in the Norwegian Sea and along the Norwegian coast in summer(Oien, 1990).

PHOTO-IDENTIFICATION AND FUTURE DIRECTIONS FOR INVESTIGATIONS ON HUMPBACK WHALES IN THE NORTH ATLANTIC OCEAN

For studying migration and population subdivisions, identification of individuals using natural markings provides the same kind of information that was previously obtained by applying artifical tags. For a species like the humpback, which possesses great individual variation in natural markings and an equally salient variety of acquired scars, each individual is marked so distinctively that artifical tags are not needed. Changes in pigmentation that occur in some individuals during early years do not compromise the accuracy of results if photo-comparisons are done carefully (Carlson et al., 1990).

Photo-identification studies do not harm target animals, are relatively inexpensive, and produce many more recaptures than did artificial tagging. For example, out of approximately 3000 humpback whales tagged with "Discovery" tags during commercial whaling or scientific studies in the Antarctic areas IV and V, 123 tags (4%) were recovered (Dawbin, 1966). The recovery rate is even lower in the western North Atlantic, where, according to Mitchell and Reeves (1983), over 160 successful implantations of Discovery tags in humpback whales produced only one significant recapture, an animal that returned to western Greenland waters in successive years (Mitchell, 1974, 1977). By comparison, the percentage of whales resighted in the same feeding aggregation during different years ranged from 5% for Iceland, which has the smallest sample size (n=20), to 62% for the Gulf of Maine, the most heavily sampled region (n=594).

The number of identified humpbacks in research collections is probably now nearly 8,000, including collections from Antarctica (50, College of the Atlantic, Stone et al., 1990, and unpublished data); Australia (600, Kaufman, 1990); Brazil (60, S. Siciliano, pers. comm.), Colombia (80, L. Flórez-González, pers. comm.), and the North Pacific Ocean (perhaps 2,500, Sally Mizroch, National Marine Mammal Laboratory, NMFS, pers. comm., including collections from Mexico, Hawaii, Japan, California, and Alaska). The amount of information on whale movements and life history will increase steadily as the number of photographs increases in future field seasons and as comparisons between regional catalogues are done.

Sophisticated cameras and film necessary for high speed, high resolution distance photography of whales did not exist during most of the period of artificial tagging, nor did the high speed boats that now bring photographers close to whales. Consequently, photo-identification studies now carried out on many cetacean species (Hammond et al., 1990) probably would not have supplanted artificial tagging much earlier than they did.

Despite its current utility, studies of humpback migration using natural markings and those using artificial marking share the weakness that only the beginning and end points of the movement are documented. Tracing migration routes will require improvements in tracking with radio tags using satellite technology (Mate, 1989).

Estimating population abundance using photo-identification is a useful, and sometimes preferable (Hammond, 1986) alternative to visual census surveys from ships or airplanes (e.g. Scott and Winn, 1980; CETAP 1982) and acoustic census surveys (e.g. Winn et al., 1975; Levenson and Leapley, 1978). Abundance estimates presented here for humpback populations of the North Atlantic and similar estimates for the North Pacific Ocean (Perry et al., 1990) are probably the most accurate available for any cetacean population over a whole ocean basin.

Nevertheless, this method can still be improved. Temporal and regional biases in sampling effort exist, and the opportunistic sampling methods usually used may bias for or against certain portions of the population (Hammond, 1986,1990). Use of a standardized sampling protocol to equalize the opportunities for all whales within a population's range to be photographed would improve the accuracy and precision of population estimates.

Data from photo-identification studies provide interesting contrasts to information from hunted specimens. Inspection of tens of thousands of carcasses allowed scientists such as Chittleborough (1958,1965) to compute mean values for life history parameters such as age, age of sexual maturity, fecundity, or growth rate. Precise as they are, such results contain two grades of uncertainty. First, they are necessarily indirect. For example, corpora albicantia, embryos or fetuses show that ovulation or pregnancy occured, but do not indicate whether a calf was born, whether it survived, or exactly how frequently reproduction occurred. Second, mean results do not describe what any real live, individual whale ever did.

Data from long term photo-identification of individuals creates the opposite problem. It can yield precise information on the reproductive rate of individuals (Glockner-Ferrari and Ferrari, 1984; Baker et al., 1986; Clapham and Mayo, 1987b, 1990) and, potentially, the survival and reproduction of their calves. However, since the large sample sizes provided by commercial whale hunting can not be obtained in a short time, statistically precise means for the population are more difficult to achieve. Nevertheless, the ability to describe the activity of a small number of real individuals offers a new perspective on the biology of the species.

A technical problem confronting large scale photo-identification studies is the increased time required for sorting large collections of photographs. It takes only a moment to read the numbers on a "Discovery" tag, and anybody can do it. Comparing photographs requires special skills: patience, attentiveness, facility at pattern-recognition and good visual memory. Only people possessing those skills should match photographs for scientific purposes. Computers get high marks for patience, attentiveness and information retention, but instructing them to find and remember a pattern is laborious. A program developed by Mizroch et al. (1990) uses videodisc storage of photographs and combines the strengths of people and computers to speed photo-comparisons. It is now used routinely in our laboratory and several others.

Use of computers will increase the rate at which photographs can be matched, reducing the number of photographs that must be checked visually, and minimizing tedium. Because it allows photographic collections to be sorted in many ways, Mizroch et al.'s (1990) system has also helped researchers to find duplicates in photographic collections. In collaboration with Sally Mizroch and the National Marine Mammal Laboratory (NMFS), we are incorporating digital analysis of images for comparison of photographs, to enhance speed and accuracy. One side benefit will be to enable researchers to compare large collections of photographs from different oceans, a project too expensive and time-consuming to be undertaken manually.

While contemplating such technological improvements, it is worth emphasizing that our eyes and brains have undergone millions of years of evolution for improved pattern recognition. These organs routinely perform complex visual operations such as translation, rotation, compensation, and decision-making that are cumbersome for even the best of today's computers. Machines will never entirely replace skilled people in analyzing individual identification photographs.

Continuing to look toward the future, challenging scientific puzzles remain to be solved for this species in the North Atlantic and other oceans. (1) During this decade, studies of migrations in the eastern North Atlantic using photo-identification will probably define the location of winter ranges and reveal the degree of separation between those animals and the western Atlantic population. (2) Precise description of migration routes for individual humpbacks is needed to provide clues about navigational mechanisms, evaluate potential energetic benefits from using wave energy to assist locomotion (Bose and Lien, 1990), facilitate detailed studies of migration and ascertain potential environmental risks to whales as they migrate through different regions. (3) Description of where, when and how copulation occurs is needed for comparison with other mating systems (Brownell and Ralls, 1986; Clutton-Brock, 1989). (4) Continued intensive regional sampling of individuals, particularly with improved sampling procedures, is needed to provide improved estimates of natality and mortality, allow construction of a life table, and reveal long term patterns of social behavior. Enough mothers need to be photographed on the winter ground with calves and then later on the summer ground to provide an estimate of calf mortality during the first six months of life. A particularly difficult, but important goal is to learn more about causes of natural mortality. The only causes specifically identified to date are killer whales (*Orcinus orca*) (Dolphin, 1987; Katona et al., 1988), sharks (Winn and Reichley, 1985; Paterson and Van Dyck, this memoir) and dinoflagellate toxins (Geraci et al., 1989). (5) Expanded use of DNA-sampling is needed to facilitate gender identification (Lambertsen et al., 1988; Baker et al., unpublished manuscript), elucidate gene flow produced by migrations (Baker et al., 1990), and contribute to interpretation of longterm matrilineal, patrilineal and social relationships.

Some of the solutions to those puzzles will not only sate our curiosity, but will allow us to respond more effectively to the overall challenge of managing humpback whales and their habitats successfully enough so that the populations recover from depletion by commercial whaling and swim the wide oceans for countless generations to come. Until Star Trek IV comes true, there is probably nothing more beneficial that we can do for this species than gather information like this and use it wisely.

It is humbling to reflect on how much of the data and how many of the future objectives presented here are merely fleshing out of the skeleton erected by previous workers, including particularly Drs. R.G. Chittleborough and W.H. Dawbin, in whose honor this conference has been organized. Everyone working on population biology, migration and reproduction is indebted to their pathbreaking research, as every list of references testifies.

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AN ACOUSTIC ANALYSIS OF THE 1988 SONG OF THE HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, OFF EASTERN AUSTRALIA

ASTRIDA MEDNIS

Mednis, A. 1991 07 01: An acoustic analysis of the 1988 song of the Humpback Whale, *Megaptera novaeangliae*, off east coast Australia. *Memoirs of the Queensland Museum* **30**(2): 323–332. Brisbane. ISSN 0079-8835.

This paper presents an acoustical analysis of the 1988 Humpback Whale song off east coast Australia, particularly of the sound types which comprise the song. The analysis shows that the song represented generally a well structured form, broadly similar to that of 1982/83, even though there was a change to a less structured song in 1984 (Cato, this memoir). A relatively detailed analysis of the structural components of the song, specifically the sound types, has been undertaken. Although the song is relatively stereotyped, variation in the acoustical characteristics of the sound types is observed which may be significant in terms of structural components of the song. The full range structural complexity in the Humpback Whale song may not be fully known. ☐ *Humpback Whale, song, marine acoustics, animal behaviour, marine mammals.*

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Payne and McVay (1971) recognised that Humpback Whale sounds recorded off Bermuda occurred in fixed patterns to form songs. They found that individual sound units were grouped to form phrases which were repeated to form themes. This ordered sequence comprised the song.

Based on studies of Humpback Whale songs in eastern Australian waters since 1979, Cato (1984, this memoir) established the existence of song structures that were broadly similar to those of the Northern Hemisphere. The song of 1982/83 was well structured with six themes, but a rapid change in 1984 lead to a relatively poorly structured song. Cato introduced the concept of "sound type" as a means of categorising the sound units according to acoustical characteristics. He found that sound units of the 1982/83 song could be classified into 12 types.

I present here an analysis of the 1988 song off eastern Australia with particular emphasis on the characteristics of sound types. These are given descriptive names which are definitive to this paper. Sound types are classified according to acoustical characteristics and some of the subtleties in variation of characteristics are addressed.This may allow interpretation in greater detail and contribute to functional understanding of structural components of the song. Cato (1984) noted that, because the song is stereotyped, its potential to carry information is limited. Information transmission depends on variations in the song.

METHODS

Song recording

Song data for 1988 were collected by Dr D. Cato, during the southward migration, 2–4 October, 1988, off Stradbroke Island latitude 27°S. This was close to the peak time of the southward migration as identified by Chittleborough (1965) and confirmed by Paterson and Paterson (1989). Recordings were made from a 3m motor boat, using a hydrophone at about 20m depth, a pre-amplifier, a Sony Walkman Professional WMD6 tape recorder. The frequency responses are uniform within ±3dB over the frequency range 50 Hz–15 kHz.

Song analysis

Song analysis involved aural and spectrographic analysis. Most of the energy of Humpback Whale sounds lies in the range 100–4000 Hz and the sounds are distinctive to our ears (human hearing is within the range of c. 20Hz–20kHz). A considerable amount of analysis of the song structure was therefore done aurally by noting down sound units sequentially using graphic symbols, where each symbol represents a sound type, thus identifying the order and timing of sound units, phrases, themes and song

TABLE 1. Phrase structures of the 1988 song.

THEME	SOUND UNITS IN ORDER OF OCCURRENCE	OCCUR-RENCES
1	n-chug	19-28
	zp	1
	oink	1
2	n-chug evolve into whistles	11–12
	cry	2
	n–whistles	17–20
	cry	5–8
	n–whistles	3–4
	cry	3–12
3	up moan	3
	n–violin	1
	coarse roar	2
	down moan	1
4	up moan	1
	down moan	1
	up moan	1
	down moan	1
	up moan	1
	flat roar	1
	moan staccato	3–4
	screal	1
5	up moan	1
	down moan	1
	up moan	1
	down moan	1
	up moan	1
	flat roar	1
	hmm	5–7
	screal	1
6	up moan	1
	down moan	1
	up moan	1
	down moan	1
	up moan	1
	flat roar	1
	whoomp	5–8
	screal	1
7	whoomp	2
	chain-saw growl	1

cycles. The aural analysis was repeated until the song structure was fully established. This involved a detailed analysis of the data, looking for patterns in the occurrence of the sound units. Sound units were grouped to form phrases and similar phrases were then grouped into themes. As patterns were established, they were checked for consistency between the different song cycles of an individual singer and between the songs of presumably different singers. Acoustical characteristics for each sound type and phrase structure were determined from sonagrams produced on a Kay Elemetrics sonagraph.

Seventeen hours of recorded data were analysed, which included 64 song cycles able to be analysed. Intensity levels for different sound units were determined with a Bruel and Kjaer level recorder type 2305, played through a Rockland low pass filter, to remove unwanted low frequency noise.

RESULTS

SONG STRUCTURE

The 1988 song structure (Table 1) comprises 7 themes in a fixed order, where each theme comprises a particular phrase with a variable number of renditions. This is a well structured song, similar to that of 1982/83 (Cato,1984,this memoir). It has 7 themes and 15 sound types compared with 6 themes and 12 sound types in 1982/83. This shows that the song off east Australia has returned to a well structured form after the change to a relatively poorly structured song in 1985. On average, the song consists of about 160 sound units, depending on the number of phrase and sound unit renditions in different themes.

The Humpback Whale song is complex and relatively stereotyped; considerable analysis may be done in the description and interpretation of the song characteristics. Even though the song is relatively stereotyped, there are certain subtleties in the complex song which are not stereotyped.

DESCRIPTION OF THE SOUND TYPES.

The frequencies of all sound types is in the range 50–8000Hz (more than 7 octaves), the lowest in frequency being the “whoomps” and “down moan” and the highest in frequency being the “n-whistles” and “screal” (Table 2). In the 1988 song the range in the fundamental frequency was 50–4000Hz while Payne and Payne (1985) observed a range of 30–4000Hz in songs in Bermudan waters over 19 years.

The sound types vary from acoustically simple to complex and are classified into four categories (Table 2). These categories are determined from sonagrams and are audibly quite distinctive. Each category can be subdivided according to the frequency range, fundamental frequency and

TABLE 2. General sound type spectral and temporal characteristics.

SOUND TYPE	FREQUENCY RANGE (Hz)	FREQUENCY OF FUNDAMENTAL OR LOWEST S.L.* (Hz)	NO. OF HARMONICS /S.L.*	TIME (s)
HARMONIC				
– rising frequency				
n-whistles	600-8000	600–3000	2–5	0.1–0.3
cry	500–7500	500–700	10–11	0.3–1.35
up moan	200–4000	200–350	2–<16	0.8–1.7
n-violin	100–6000	100	2	0.6
oink	150–2500	150	7	0.4
– falling frequency				
down moan	50–5500	50–200	2–19	0.8–2.2
– steady frequency				
hmm	120-4000	120–250	5–16	0.45–0.7
– collective				0.9–1.7
BROAD BAND WITH SPECTRAL LINES				
coarse roar	400–3750	400–600	2–8	1.2–4.45
flat roar	250–4500	250–350	4–20	0.8–2.4
chain saw growl	100–4000	100–1000	6	3.0–5.7
screal	900–8000	900–1450	3–8	2.0–3.5
BROAD BAND IMPULSIVE				
zp	2000	80	7	0.5
n-chugs	80–6000	impulsive	–	0.2–0.35
COMPLEX				
– moan staccato				1.1–3.0
moan	100–5000	100–340	3–15	0.8–1.8
staccato	300–6800	300–450	3–12	0.3
– whoomp				
harmonic	50–1300	50–100	5–11	0.3–0.5
impulsive	600–4000	50–4000	impulsive	0.1–0.5
– pulse	600–4000	600–1100	pulsation	0.1–0.2

*S.L. = spectral lines

duration. The harmonic sound types "cry" and "up moan", and the complex sound type "moan staccato" (Table 2) (which is actually a combination of two harmonic sounds) have similarities; however, differences in fundamental frequencies, frequency contour on the sonagram and duration separate them (Figs 1–3). The "coarse roar" and "flat roar" (Table 2) are similar; however, the former has a higher fundamental frequency range. The "down moan" is distinctive relative to all other sound types (Fig. 4).

Harmonic sound types with a rising frequency

The "cry" sound type is representative of this subcategory (Fig. 1). It lasts 0.3–1.35 secs depending on its position in the phrase in theme 2, the only theme in which it occurs. Silences between cries range from 1.1–2.8 secs.

The "up moan" occurs in 4 different themes with some variation in the sound character between different themes and within the same phrase of a theme depending on the position of the sound unit in the phrase, i.e. inter theme and intra phrase variation (Figs 2,4). This variation

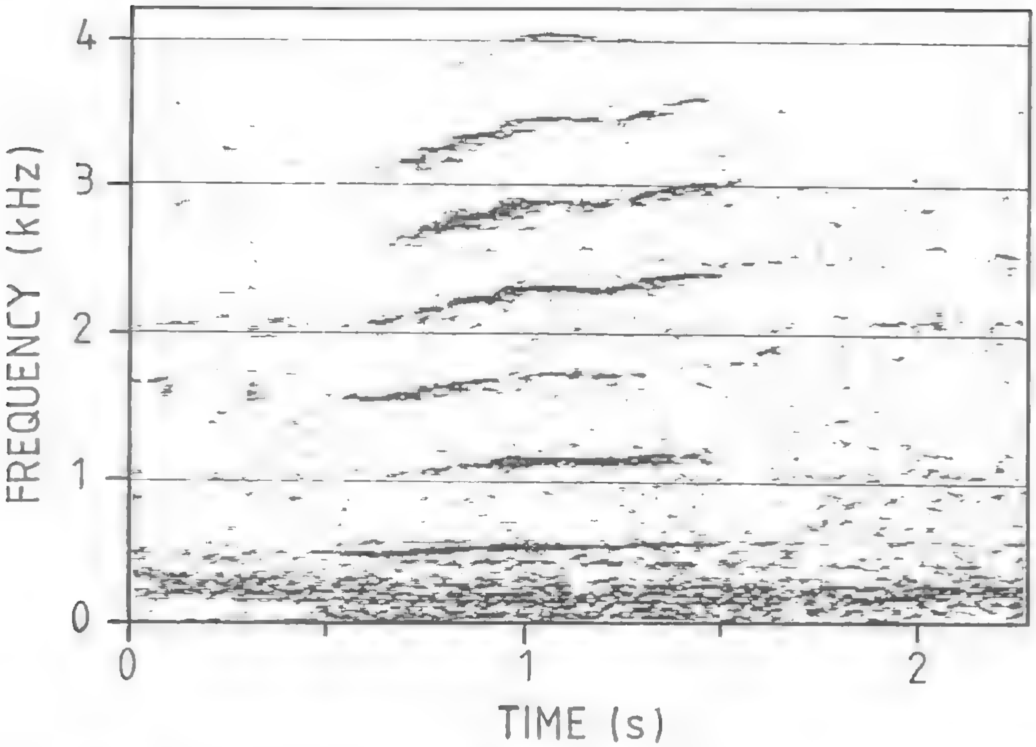

FIG. 1. Sonagram of an harmonic with a rising frequency sound type "cry".

is in the fundamental frequency and duration. The duration of the sound type ranges from 0.6–2.1 secs. Silences of following units in themes 4 and 5 are 1.5–1.9 secs.

Harmonic sound types with a falling frequency

The "down moan" (Table 2) occurs in four different themes with some variation in fundamental frequency and duration between themes (Fig. 4).

Broad band with spectral lines not harmonically related

These sound types are not harmonic but have energy spread over some bandwidth, and spectral peaks evident as spectral lines. The frequencies of these lines are not harmonically related. The "screal" (Table 2) has 3–10 spectral lines (Fig. 5) and occurs once in 3 different themes, consistently as the last sound unit in a phrase. Sound character variation in the different themes is shown in Table 3.

The "chain saw growl" (Table 2) generally occurs at a number of frequencies between 100 and 1600 Hz (Fig. 6). It generally increases in duration with each phrase rendition in the theme. The sound type occurs singularly in the phrase of theme 7.

Harmonic sound types with a steady frequency

The "hmm" (Table 2) occurs in a group of units, like the "n-chugs", where 2–4 sound units

TABLE 3. Variation of "screal" between themes.

THEME	FREQUENCY RANGE (Hz)	FUNDAMENTAL FREQUENCY (Hz)	NO. OF SPECTRAL LINES	TIME (s)
4	900–8000	900–1400	3-10	2.5–3.5
5	900–5500	900–1400	3-6	3.0–3.3
6	1000–6800	1000–1450	5–8	2.0–3.0

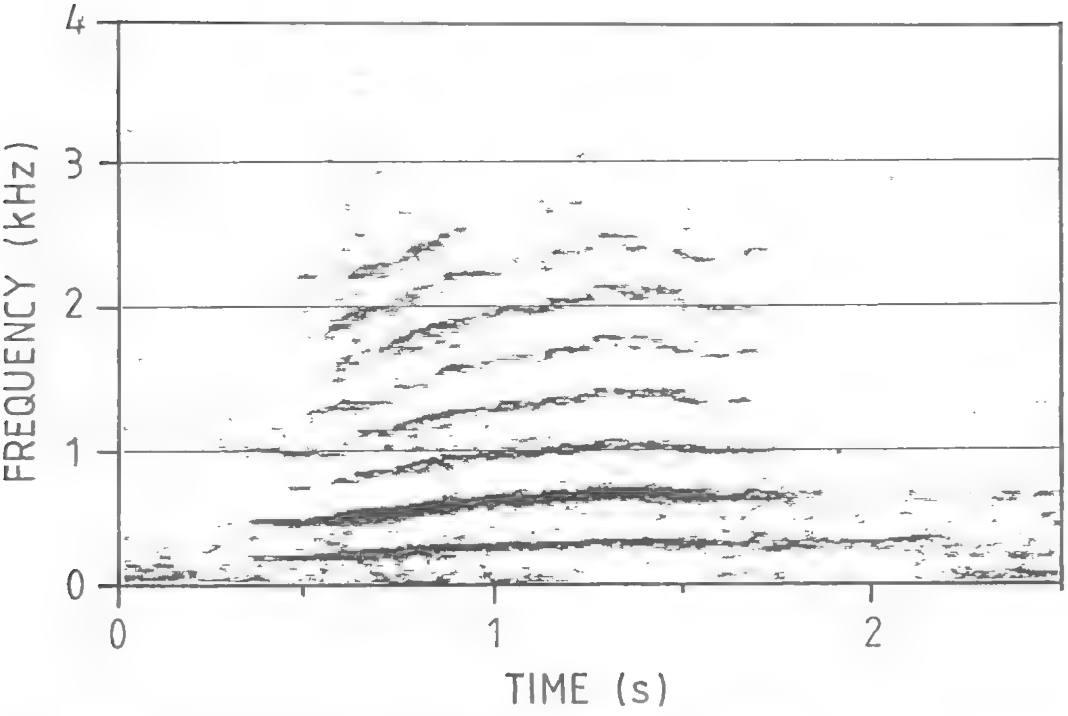

FIG. 2. Sonagram of an harmonic with a rising frequency sound type "up moan".

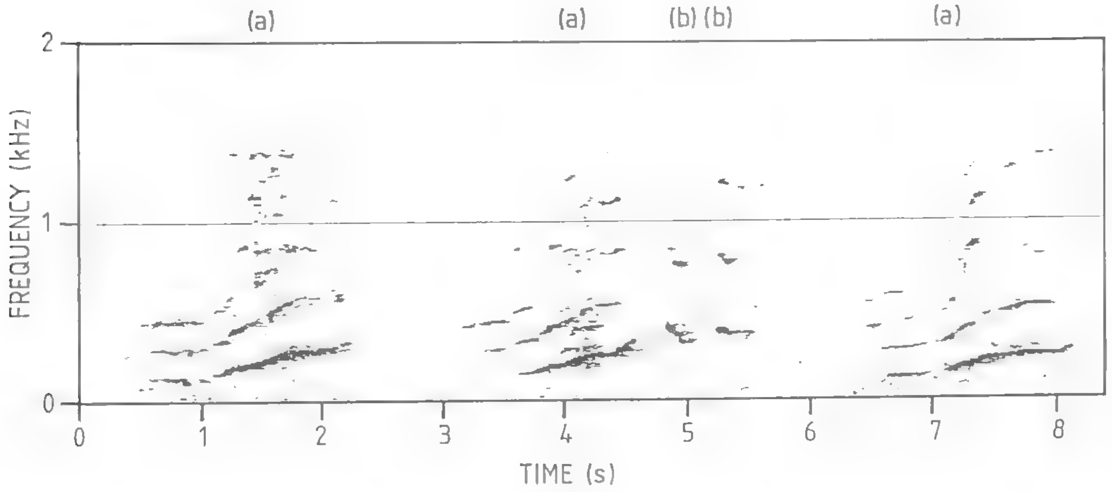

FIG. 3. Sonagram of a complex sound type "moan staccato" including a, moan and b, staccato endings.

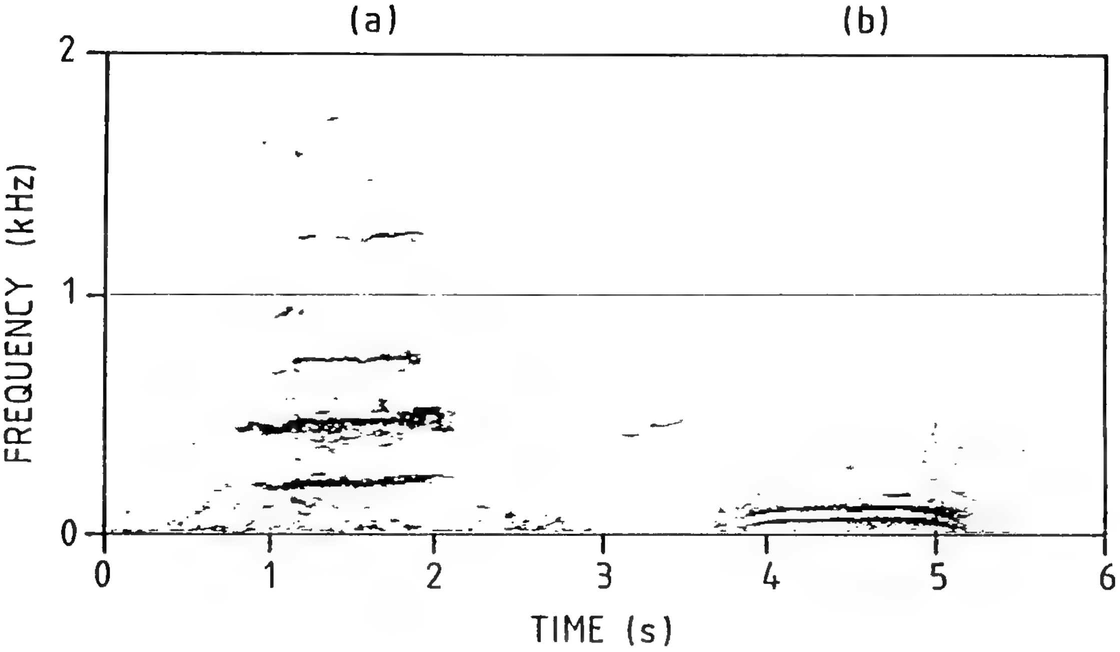

FIG. 4. Sonagram of an harmonic with a falling frequency sound type a, "up moan" and b, "down moan".

may occur in one group. For example, (hmm hmm hmm) (hmm hmm hmm hmm) (hmm hmm hmm), where each hmm represents one rendition of the sound unit. Each sound unit is 0.45–0.7 secs in duration while a collective group may extend 0.9–1.7 secs. The period of silence between units of the same group is c. 0.05–0.1 secs and between groups there are longer silences of 0.4–0.9 secs. It occurs in theme 5 only.

Broad band impulsive sound types

The impulsive sound types are the "n-chugs", occurring in themes 1 and 2 and "zp" occurring in theme 1. The "zp" occurs only once in the phrase of theme 1.

The "n-chug" sound type occurs as a collective unit. For example a collection of "n-chugs" may comprise 28 sound unit repetitions in a particular pattern i.e. (111) (1111) (1111) (11111)

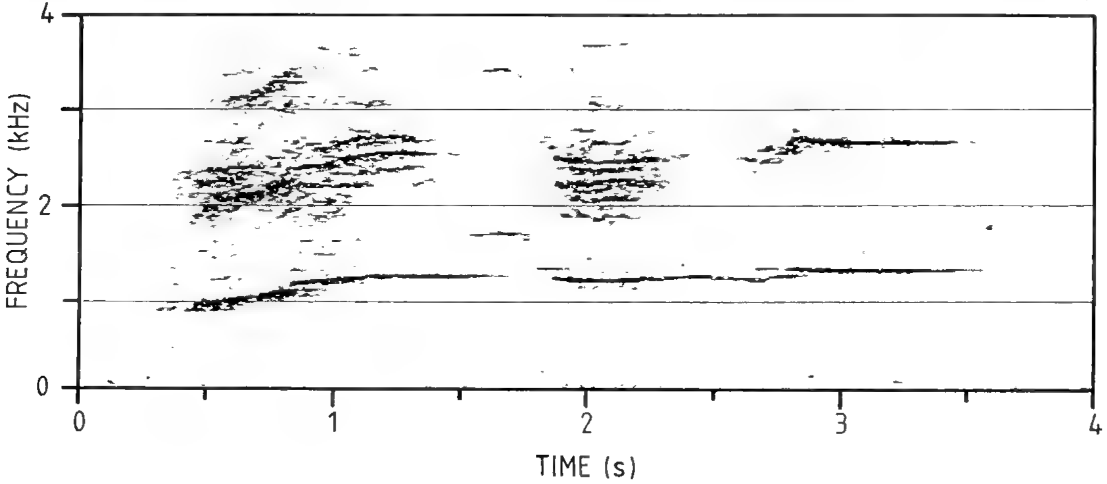

FIG. 5. Sonagram of a broad band with spectral lines sound type "screal".

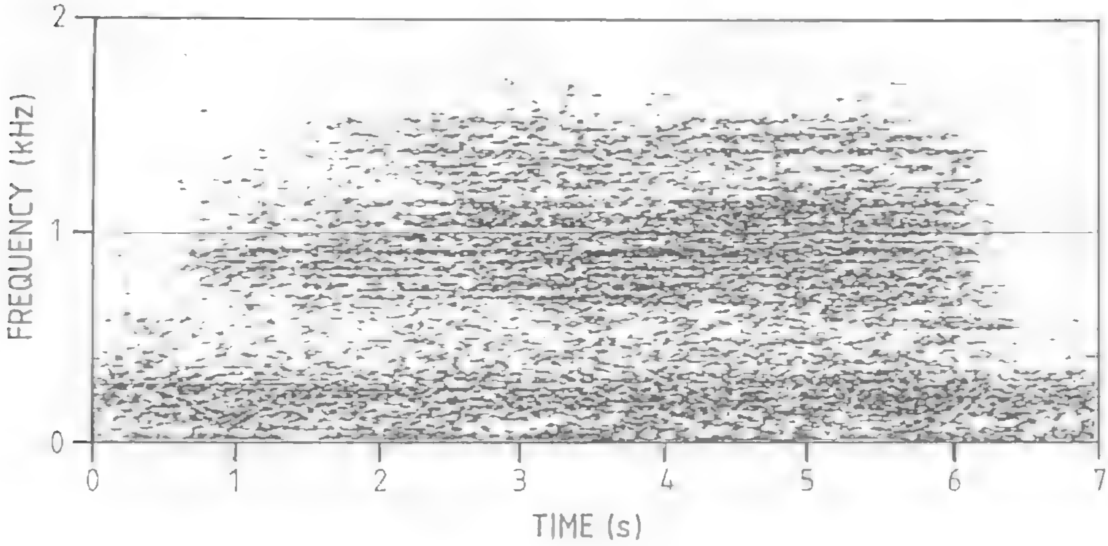

FIG. 6. Sonagram of a broad band with spectral lines sound type "chain-saw growl".

(111111) where 1=1 chug. So that the whole collective consists of subgroups each with a variable number of chug repetitions (Fig. 7). These units are impulsive in structure with most energy between 80–2000Hz and extending to 6000Hz. Silences of 0.20–0.55 secs between subgroups and 0.15 secs between renditions of units within one group were observed.

Complex sound types

Complex sound types are combinations of components which may be harmonic or impulsive. The "whoomp" sound type starts as a harmonic and evolves to an impulse with a pulsating, "possum" ending (Fig. 8). This sound type occurs in themes 6 and 7 with sound character variation between these themes being of a lower frequency, less harmonic in structure and without the terminal impulse in theme 7. While in theme 6 the impulse ending may or may not occur.

It is evident from the above discussion that

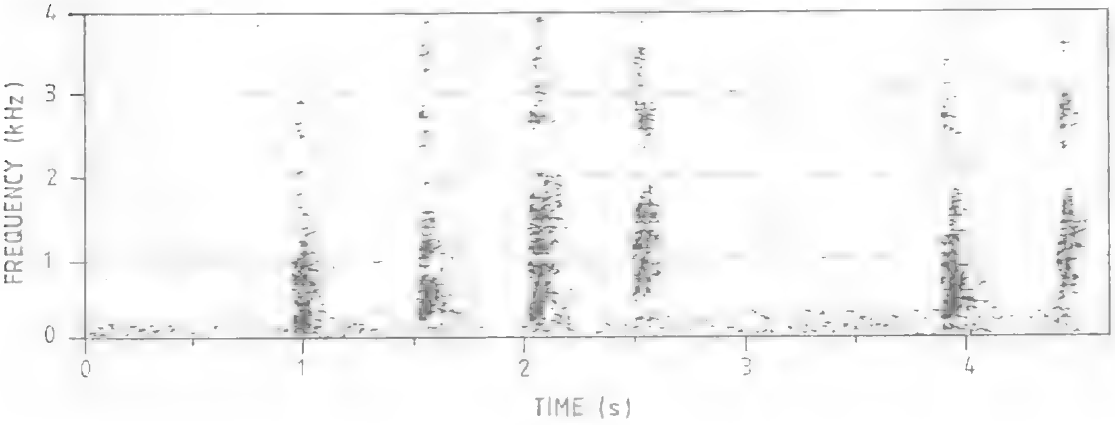

FIG. 7. Sonagram of a broad band impulsive sound type "n-chugs".

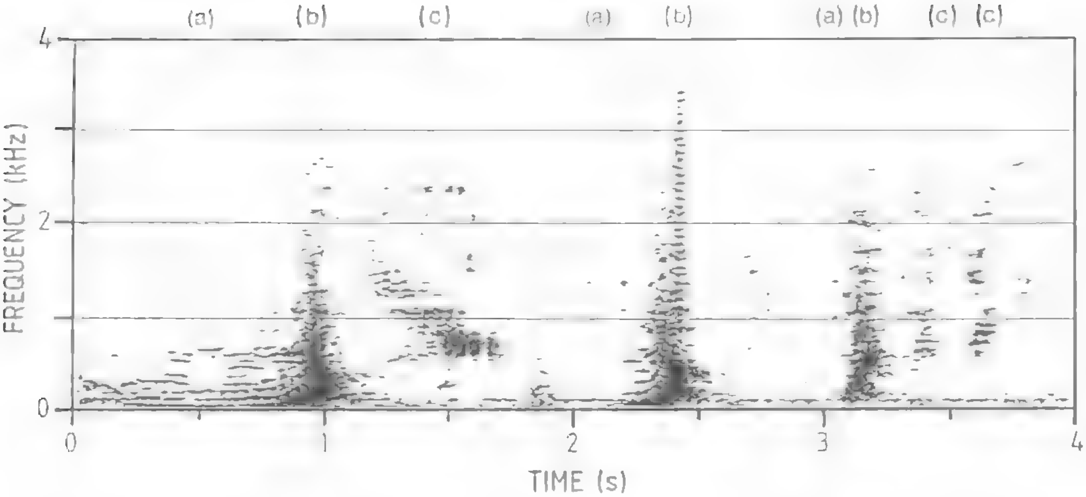

FIG. 8. Sonagram of a complex sound type - "whoomp", including (a) harmonic, (b) impulse, and (c) pulsating ending.

there are variations in the characteristics of the sound types in the song.

Duration of the Sound Types

Sound types vary in duration from 0.1–5.7 secs, the shortest being the "n-whistles" (theme 2) and the longest being the "chain saw growl" (theme 7). Cato observed sound type durations of 0.1–4.3 secs in the 1982 song, where the "whistles" were the shortest and the "chain saw" the longest. However, the "chain saws" of the 1982 song are not the same sound type as the "chain saw growls" in the 1988 song. In Bermudan waters the longest sound type was 8 secs and the shortest <2% of the longest (Payne and Payne 1985).

Variation in Sound Type Abundance and Distribution throughout the Song

The sound types are variable in terms of distribution through the different phrases of the song (Table 1). Some sound types are particular to certain themes i.e. "zp" and "oink" to theme 1 and "n-whistle" to theme 2, whilst other sound types are relatively ubiquitous, i.e. "up moan", "down moan", "screal" and "flat roar", occurring in three different themes and the "whoomp" occurring in two different themes.

Nine of the sound types occur more than once in a phrase. The remaining occur only once in a phrase, for example "n-violin" in theme 3 and, "screal" and "flat roar" in themes 4, 5 and 6.

Variation in Sound Type Character - Inter-Theme and Intraphrase Variation

As sound types are repeated throughout a phrase or as they occur in different themes, the sound character (e.g. a slight change in fundamental frequency, frequency range or duration) may vary depending on the sound type's position in the song. For example, in theme 4 the "up moan" is emitted 3 times, each rendition becoming shorter. However, the same sound type in theme 5 is generally shorter in duration. Additionally, the "moan staccato" may vary in sound character with repetition in a phrase of theme 4, and the number of staccato units may vary with each repetition. The staccato endings are mostly present but sometimes absent. Similarly, the "whoomp" in theme 6, is represented with "possum-like" endings in some phrases but not in others.

The character of a sound type may therefore change with respect to its position in the phrase or in the song. Although there are subtle variations in the character of a particular sound type, the sound types are generally similar from one rendition of the song to the next. Even though there is some variation in the acoustical character of a sound type, this variation is small compared to the differences in acoustical characteristics between different sound types.

Perhaps these observed variations can be related to accentuation of meaning i.e. possibly these variations have specific functions in terms of communication and general behaviour of the singer. A slight modification in the sound type may change the signification of the signifier i.e. the meaning of the sound type.

SOUND INTENSITY

From a limited sample of 6 song cycles over 2 days, intensity varied between different sound types. The "moan staccato" has the highest level of all sound types while the "flat roar", "hmm" and "screal" are the next highest. These are mean values and not always consistent with each phrase rendition. It is important to consider this feature relative to overall rhythm (Guinee and Payne, 1988) and possible "accentuation" of certain sound units. Additionally, sound level diminishes at theme 7, which may be due to attenuation of sound when the whale approaches the surface to breath (Tyack,1981).

SILENCES BETWEEN SOUND UNITS

In the 1988 song, silences between sound units of up to 3.2 secs were observed where the longest silences generally occurred between sound units of themes 1 and 7. Shortest silences were c. 0.15 secs between "n-whistles" in theme 2 and 0.2 secs between "n-chugs" in theme 1. Payne and Payne (1985) observed silences as very short or lasting up to 6 secs. The range in duration of silences between sound units may be important structural features of the song.

CONCLUSIONS

The 1988 song of east Australia shows a well-developed structure similar to that in the 1982-early 1984, compared to the "unstructured" song of 1985.

The 1988 song consisted of 15 sound types. Sound types representative of particular acoustical groups are described with regard to spectral and temporal characteristics, showing the differences between sound types and between renditions of the same sound type. The analysis indicates that while the sound types do not vary to a great extent with different song renditions, there are subtle variations with renditions of the same sound type which may contribute to the overall function of the song, for example the information content. It is possible that these subtleties function as components of the song structure. A more detailed analysis of the song structure and the sound units may reveal the function of these structures and thereby contribute to the understanding of the song.

This paper presents an analysis of the song at a certain level of magnification, however, it is not fully understood whether this level of detail is at a scale appropriate to the Humpback Whale physiological sensory apparatus. It is yet to be determined how representative these identified song components are for communication. Analysis of these structural details may lead to a greater understanding of Humpback Whale song evolution, learning capacity and behaviour, and the role of song in the reproductive success and possible social structure of the species.

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THE MIGRATION OF HUMPBACK WHALES *MEGAPTERA NOVAEANGLIAE* IN EAST AUSTRALIAN WATERS

R. A. PATERSON

Paterson, R.A. 1991 07 01: The migration of Humpback Whales, *Megaptera novaeangliae*, in east Australian waters. *Memoirs of the Queensland Museum* 30(2): 333–341. Brisbane. ISSN 0079-8835.

The east Australian Humpback Whale, *Megaptera novaeangliae*, stock, severely depleted by 1962, is now recovering at approximately 9.7% per annum. Available evidence indicates that shorebased whaling did not affect migration patterns in east Australia. The stock disperses in the sheltered waters of the Great Barrier Reef to breed although some calving occurs at higher latitudes. Future studies may determine if the breeding area for this stock includes the Coral Sea east of the Great Barrier Reef. ☐*Humpback Whale, Megaptera novaeangliae, migration, east Australia.*

Robert A. Paterson, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101; 8 February, 1991.

Humpback whales were exploited from five locations in east Australia during this century (Table 1). After the Second World War, when the re-establishment of Australian shore stations was under consideration, fishermen and other interested persons were requested to report whale sightings (Anon., 1948). Reports from east Australia indicated large numbers of Humpback Whales at 23–27°S during July, August and September. Specific site reports included Cape Capricorn, Lady Elliott Island, Double Island Point and Stradbroke Island (Colwell, 1969).

During the final phase (1952–62) of Humpback Whale exploitation in east Australia, extensive biological data, including timing of northern and southern migrations in the vicinity of 27–28°S, were obtained (Chittleborough, 1965). However, the routes and timings of migrations at lower latitudes were not determined.

Recoveries of "Discovery" tags indicated that Humpback Whales marked in east Australia tended to return after feeding in Antarctic waters although small rates of interchange within Area V (130°E–170°W) occurred between east Australia and New Zealand (Dawbin, 1964) in addition to an isolated exchange from Fijian waters (17°40'S, 178°55'E). Information concerning movement during the northern migration in a single season was also obtained. A Humpback Whale marked at St George Head, N.S.W. (35°11'S, 150°45'E) was captured at Tangalooma (27°11'S, 153°23'E) six days later (Robins, 1955) and another marked in the Cook Strait, New Zealand (41°21'S, 174°25'E) was captured at Tangalooma twenty days later (Dawbin, 1964). In addition to movements within Area V a small number of interchanges with Area IV (70°E–130°E) were demonstrated (Chittleborough, 1965).

When the Southern Hemisphere humpback whaling industry collapsed in 1962–63 the Area V population was estimated to be <5% of the original population of 10,000 (Chittleborough,1965; Chapman,1974). During a whale sighting cruise through the known (Omura, 1953) Area V feeding grounds between January and March 1973 concern was expressed because only seven Humpback Whales were sighted (Machida,1974). It was not until the early 1980s that the first tentative accounts of recovery in the east Australian Humpback Whale population were reported (Paterson,1980,1981).

In the post-whaling era Humpback Whale migrations in east Australia have been assessed by direct observation (Bryden,1985; Paterson and Paterson,1984,1989; Simmons and Marsh,1986) and photo-identification of individuals (Kaufman, Smultea and Forestell,1987). The results of shore-based surveys at Point Lookout (27°26'S, 153°33'E) are discussed in this paper together with reports from other locations in east Australia.

POINT LOOKOUT SURVEY

Point Lookout is the northeastern headland of North Stradbroke Island and was within the operational range of Tangalooma whalechasers

TABLE 1. East Australian Humpback Whale exploitation since 1900.

LOCALITY	PERIOD	CATCHES	REFERENCE
Twofold Bay 37°05'S; 149°54'E	until 1929	Numbers not recorded (small relic industry)	Davidson, 1988
Jervis Bay 35°03'S; 150°45'E	1912-1913	?400-600 (12,500 barrels of oil)	Dakin, 1934
Norfolk Island 29°01'S; 167°58'E	until 1927 1956-1962	Numbers not recorded 884	Dakin, 1934 Chittleborough, 1965
Byron Bay 28°37'S; 153°38'E	1954-1962	1,146	Chittleborough, 1965
Tangalooma 27°11'S, 153°23'E	1952-1962	6,277	Chittleborough, 1965

(Fig.1). Sightings of Humpback Whales made on a weekly basis from a 67m high position during 1987–90 are shown in Figs 2,3 and 4. Observation methods were as described by Paterson and Paterson (1984, 1989). The peak of the northern migration occurred between late June and late July respectively in those years. In the same vicinity in 1961 the peak occurred between the last two weeks of June and the first week of July (Chittleborough, 1965). Dawbin (1956) suggested that undetermined Southern Ocean climatic factors may affect the onset of the northern migration with resultant variations in the timing of the annual peaks. The sighting rates of northbound Humpback Whales passing the east Australian shore-stations between June

TABLE 2: Northbound Humpback Whales seen per 100 hours at 27°S, on the east Australian coast in 1961-1962 and 1987-1990.

PERIOD	RELATION TO WHALING OPERATIONS	SIGHTINGS /100 HRS
12/6/1961-6/8/1961	penultimate whaling year	88.2
18/6/1962-5/8/1962	final whaling year	38.6
15/6/1987-5/8/1987	25 years post-whaling	65.3
11/6/1988-3/8/1988	26 years post-whaling	70.7
11/6/1989-3/8/1989	27 years post-whaling	78.0
11/6/90-5/8/90	28 years post-whaling	78.8

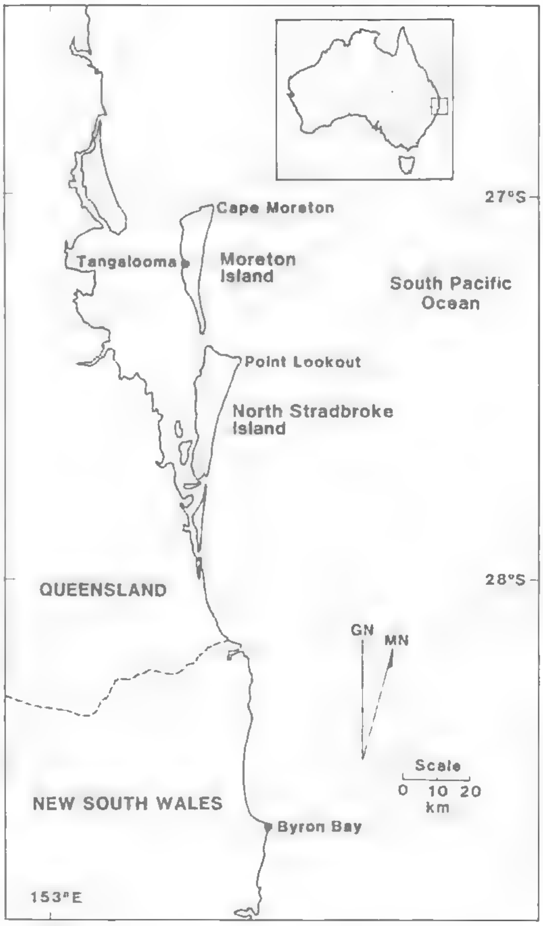

FIG. 1. Location map of former east Australian whaling stations (Table 1) nearest to Point Lookout.

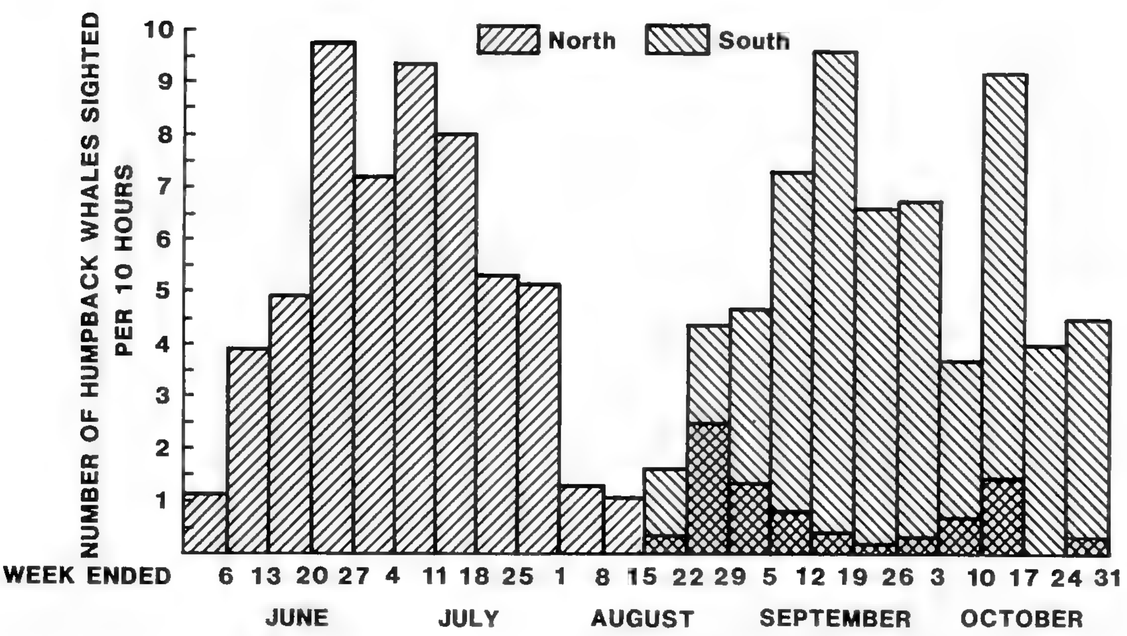

FIG. 2. Humpback Whale sightings from Point Lookout, per 10 hrs of observation, during 1987.

and early August in 1961–62 were used as an index of population decline (Chittleborough, 1965) and now may be used as an index of recovery (Table 2). The sighting rates for 1987-88 and 1988–89 increased by 8.2% and 10.3% respectively, whereas the rate for 1989–90 increased by only 1.0%. That low rate is considered to result from the "lateness" of the northern migration in 1990 (Fig.4). Although substantial numbers of northbound Humpback Whales may have passed Point Lookout after the first week of August in 1990, observations were

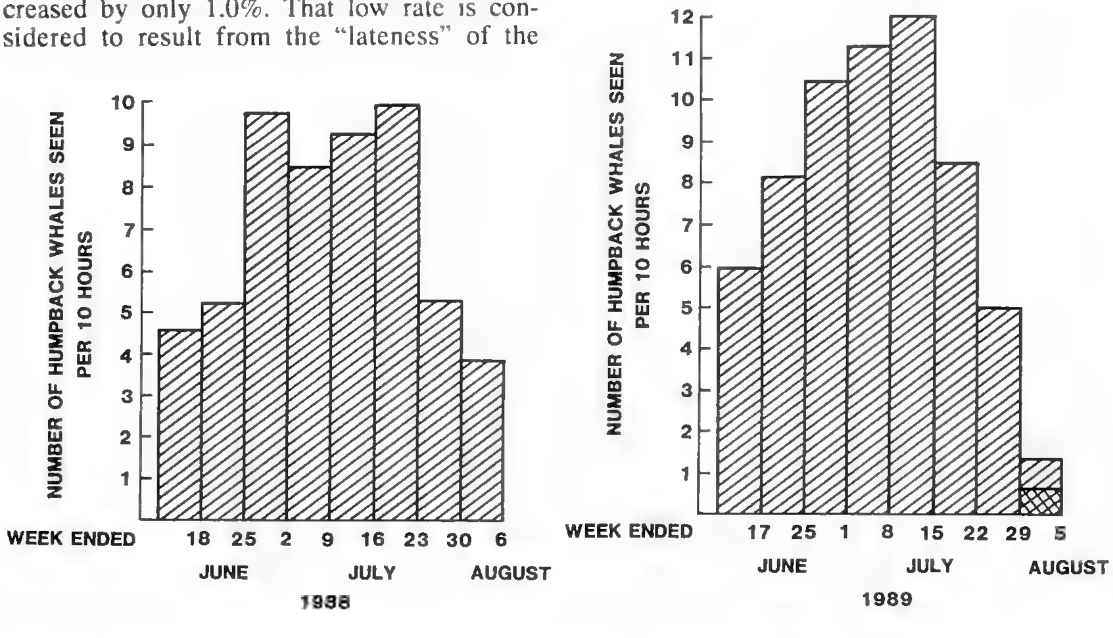

FIG. 3. Humpback Whale sightings from Point Lookout, per 10 hrs of observation, during 1988 and 1989

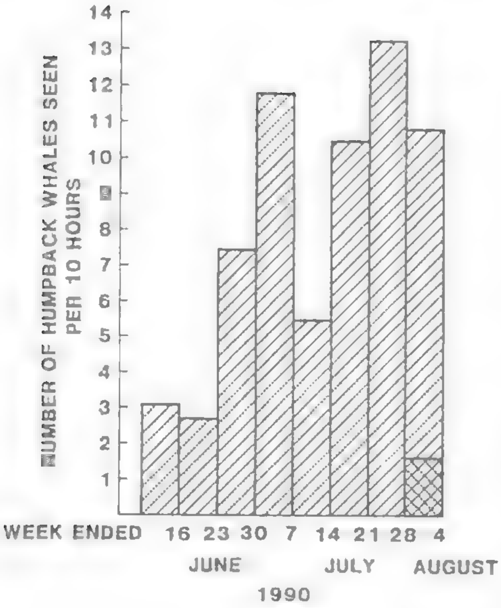

FIG. 4. Humpback Whale sightings from Point Lookout, per 10 hrs of observations, during 1990.

terminated then to conform with the data collections in 1988-89 (Fig.3).

The extended observations in 1987 confirm the findings of Chittleborough (1965) that the northern migration continues at least until late October, albeit at a reduced rate. In 1987, 15.5% of northbound Humpback Whales passed Point Lookout between late August and October. The Antarctic pack ice does not reach its northern limit until November (Slijper, 1962) and presumably "late" northbound Humpback Whales obtain adequate nutrition because those observed at close quarters off Point Lookout in October 1982 were in prime condition (Paterson, 1983).

The lack of a distinct peak during the southern migration in late August, September and October was evident in 1987 and is consistent with the findings of Chittleborough (1965) and Paterson (1984). Small numbers of southbound Humpback Whales are sighted from Point Lookout during mid-summer including two seen on 27 January 1985.

During annual surveys at Point Lookout during 1978-89 almost 1,500 Humpback Whale groups were observed. Whenever possible, their route in relation to Boat and Flat Rocks was noted (Fig.5). During the northern migration 87.5% passed east of both rocks while 3.5% passed east of Boat Rock and west of Flat Rock. During the

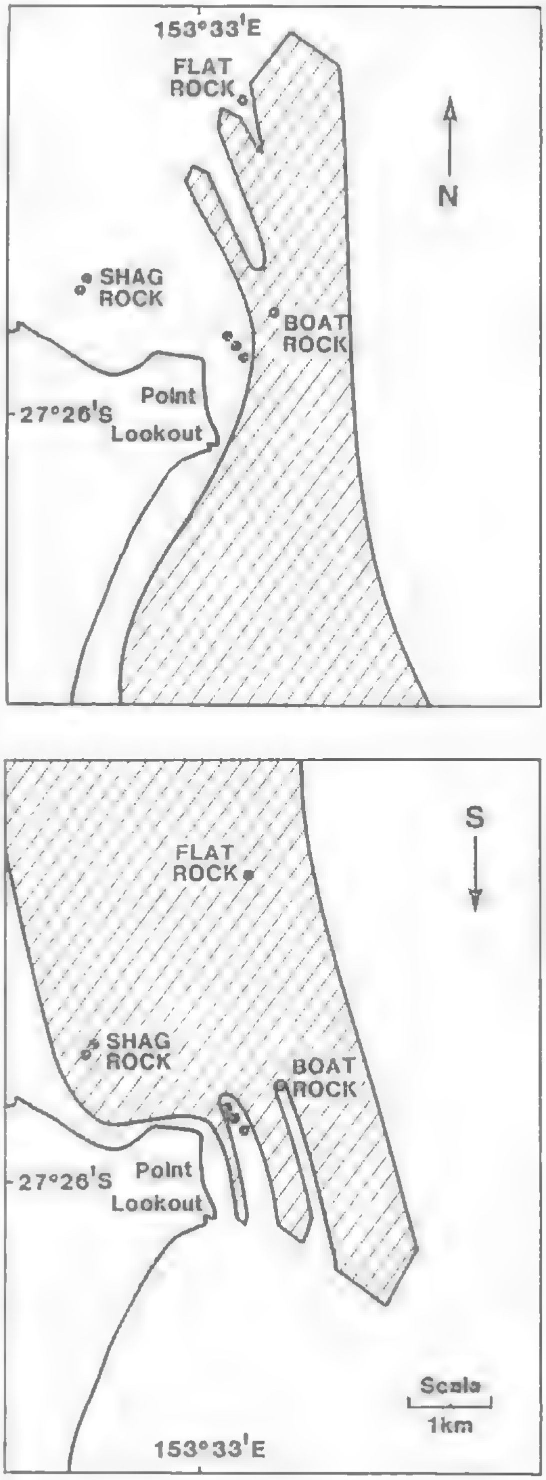

FIG. 5. Maps of the courses taken by Humpback Whales when migrating northwards (upper) and southwards (lower) past Point Lookout (1978-1989).

southern migration 25% passed east of both rocks while 47.5% passed east of Boat Rock and west of Flat Rock. No appreciable alteration in those patterns was noted in any year during 1978-89. The different routes may result from the geographic relationship of North Stradbroke and Moreton Islands (Fig.1). Northbound Humpback Whales generally pass Point Lookout on a northnortheast course until they reach Flat Rock when they move northwest towards Moreton Island. Southbound whales which pass close to Moreton Island may approach Point Lookout from the westnorthwest. They are frequently seen near Shag Rock (Fig.5) as they move east towards Boat Rock before resuming a southbound course.

REPORTS FROM OTHER EAST COAST LOCATIONS

During 1979-86, annual requests for information concerning Humpback Whale migrations were published in *Australian Fisheries* a journal circulated *inter alia* to holders of Australian commercial fishing licences. The response was generous and included reports from amateur and commercial fishermen, lighthouse keepers, surveillance and tuna-spotting pilots and the general public. A comprehensive sighting network developed and many data resulted (Figs 6,7). A survey of this type, which relies on public cooperation, may reflect bias towards areas of high human density (Simmons and Marsh, 1986) and will not result in reports of all sightings (Paterson and Paterson, 1984). Nevertheless, it established the broad pattern of Humpback Whale migration in east Australia.

The peak of the northern migration from the Antarctic feeding grounds occurs during June/July and includes small numbers which pass eastwards through Bass Strait. Although northbound Humpback Whales generally adopt a direct course there are records of some entering bays and estuaries between 27°S and 42°S during June/July, including the Derwent Estuary, Tasmania; Corio Bay, Victoria; Broken Bay, N.S.W. and Moreton Bay, Queensland.

Dawbin (1966) noted when Humpback Whales reach a coastal shore they tend to remain close to it and those findings were confirmed by Bryden (1985) during aerial surveys off the southern Queensland and northern N.S.W. coasts. However, after the migration stream passes Breaksea Spit (24°36'S, 153°20'E) at the northern end of Fraser Island it enters the sheltered waters of the Great Barrier Reef and disperses widely between the outer Barrier and the coast, which inclines to the northwest. Northward movement slows and sightings peak in August with only small numbers reaching latitudes lower than 15°S. The latitudinal and monthly concentrations are similar to those recorded in other Southern Hemisphere breeding locations (Townsend, 1935). Calving has been witnessed at 18–19°S inside the Great Barrier Reef but also occurs at higher latitudes as Humpback Whales accompanied by new born calves have been seen migrating northwards along the southern Queensland coast (Paterson and Paterson, 1989). A dedicated survey, using photo-identification (Kaufman et al.,1987), may demonstrate the movements of individual Humpback Whales in the Great Barrier Reef region.

Small numbers of Humpback Whales commence their southern migration in late July (Figs 3,4) but the majority leave the Great Barrier Reef region between mid-August and mid-October. The migration pattern in the Fraser Island region differs from the northern migration in that large numbers of Humpback Whales pass west of Breaksea Spit and enter Hervey Bay. This phenomenon has resulted in the development of a large whale-watching industry in recent years as the public has the opportunity to observe Humpback Whales at close quarters in sheltered waters at a predictable time of the year. The geographic relationship of Breaksea Spit and Fraser Island to the mainland may explain in part why Humpback Whales enter Hervey Bay. A similar, although less dramatic, course variation during the southern migration compared with the northern migration in the Point Lookout region (Fig. 5) has already been discussed.

By November/December most Humpback Whales have left the east Australian coast for the Antarctic feeding grounds although small numbers have been reported at relatively low latitudes in January/February (Paterson, 1987). Dawbin (1966) noted that southbound Humpback Whales captured at Great Barrier Island, New Zealand (36°S) invariably showed evidence of recent feeding and there is evidence to suggest occasional Humpback Whale feeding activity at similar latitudes on the east Australian coast (Paterson,1987; Ellis,1989).

DISCUSSION

The combination of legal and illegal catches of

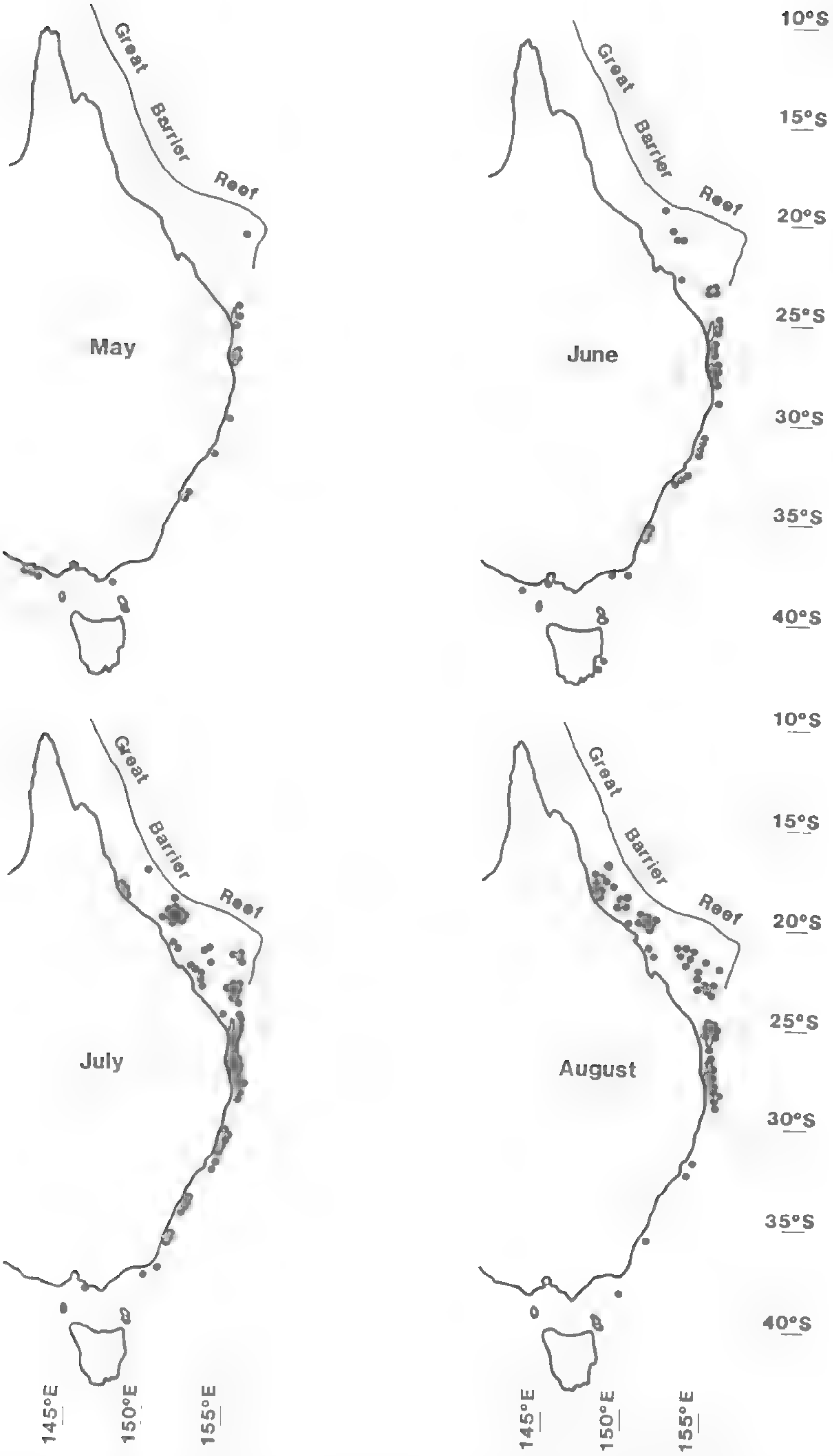

FIG. 6. Spatial distribution of Humpback Whales in east Australian waters, May-August, 1978–1989. Each marking represents one or more Humpback Whale Groups seen during a particular month in one or more years.

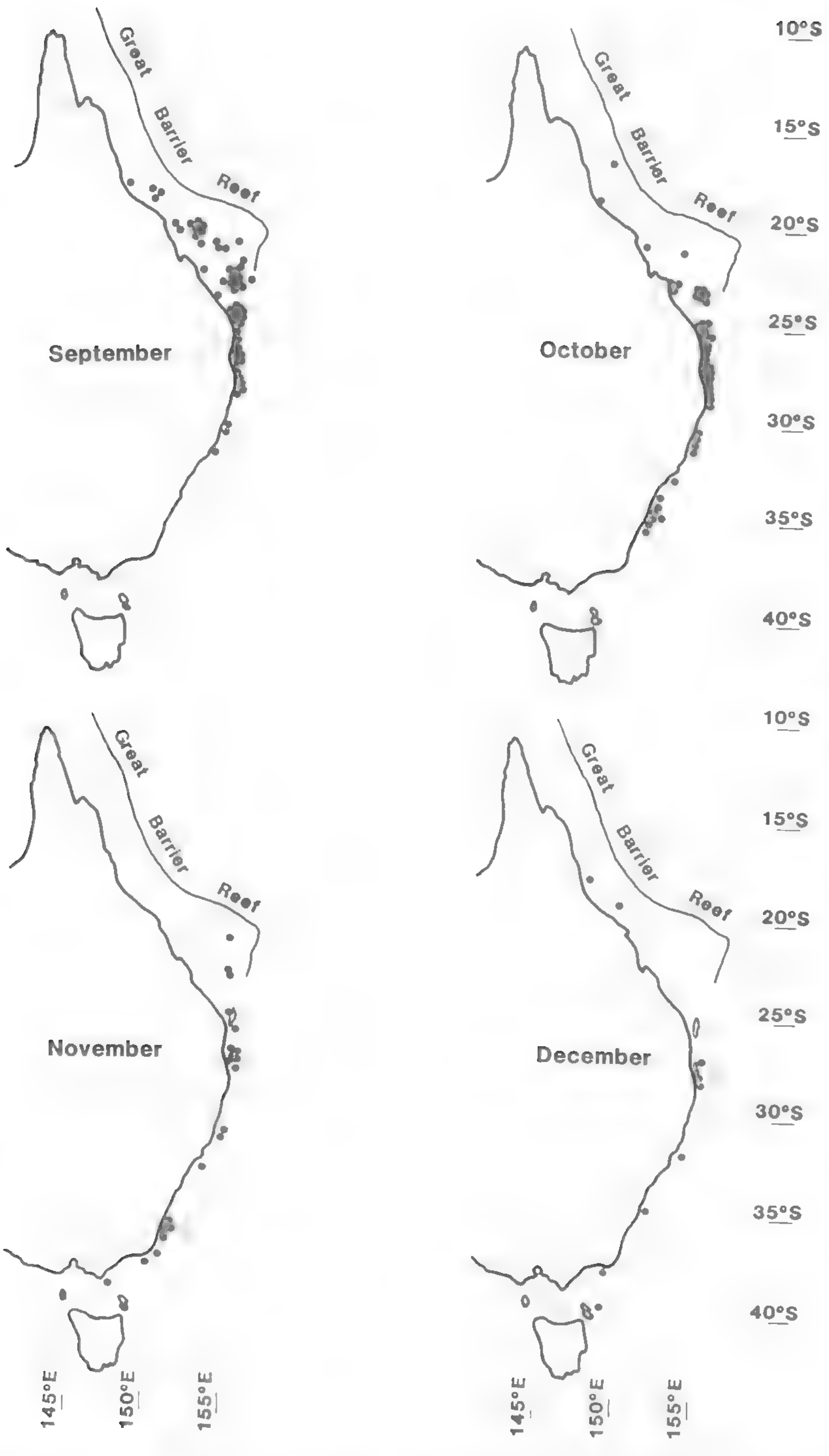

FIG. 7. Spatial distribution of Humpback Whales in east Australian waters, September-December, 1978–1989. Each marking represents one or more Humpback Whale Groups seen during a particular month in one or more years.

Area V Humpback Whales during 1952–63 resulted in a population decline extreme even by the standards of modern whaling (Tonnessen and Johnsen, 1982). The paucity of incidental sightings in the post-whaling decade prompted conjecture that Humpback Whales deliberately avoided the regions of the former east Australian shore-stations (Anon., 1976). However, similarity of the migration patterns for 1961 (Chittleborough, 1965) and 1987 (Fig.2) suggests that exploitation of Humpback Whales in east Australia did not affect their migratory behaviour.

Although the sheltered waters of the Great Barrier Reef are a major destination for those Humpback Whales which migrate northwards along the east Australian coast, it has not been established that those waters are the sole destination. Dawbin and Falla (1949) suggested that the Chesterfield Reefs, northwest of New Caledonia in the eastern Coral Sea, were the destination of the east Australian stock as Humpback Whales had been captured there in the nineteenth century (Townsend, 1935). However, the "Discovery" tag program failed to establish evidence of such a pathway and the present situation with regard to Humpback Whale migration in the Coral Sea east of the Great Barrier Reef remains unresolved.

Paterson and Paterson (1989) considered that the east Australian Humpback Whale stock was increasing at approximately 9.7% per annum on the basis of annual surveys at Point Lookout during 1981–87. The 1987/88 and 1988/89 data were consistent with that estimate but the low increase demonstrated in 1989/90 was almost certainly due to the "late" northern migration in 1990 (Fig.4). Such a variation notwithstanding, the evidence from Table 2 indicates that the east Australian portion of the Area V stock has doubled since the cessation of whaling in 1962 and now exceeds 10% of the pre- exploitation estimate of 10,000.

ACKNOWLEDGEMENTS

Particular thanks are due to Martin Bowerman, formerly editor of *Australian Fisheries*, who instigated the annual whale sighting appeal in 1979 and to the officers of the Great Barrier Reef Marine Park Authority who collated data obtained by Coastwatch surveillance aircrews. Numerous persons from many locations on the east Australian coast generously forwarded reports which enhanced this study.

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STUDIES OF TWO HUMPBACK WHALES, *MEGAPTERA NOVAEANGLIAE*, STRANDED AT FRASER ISLAND, QUEENSLAND

R.A. PATERSON AND S. VAN DYCK

Paterson, R.A. and Van Dyck, S., 1991 07 01: Studies of two Humpback Whales, *Megaptera novaeangliae*, stranded at Fraser Island, Queensland. *Memoirs of the Queensland Museum* 30(2): 343–350. Brisbane. ISSN 0079-8835.

In 1989 two Humpback Whales, *Megaptera novaeangliae*, stranded at Fraser Island, Queensland. One specimen was an 8.1m female yearling and the other a 4.2m male new-born calf. Skeletal material, soft tissue, baleen, blubber and external parasites were recovered. Histological examinations were made of tissues from the heart, lungs, liver, kidneys and frontal bone (calf only). The cause of death in the yearling was not determined whereas the calf probably died from shark attack. ☐ *Humpback Whale, Megaptera novaeangliae, strandings, Fraser Island, Queensland.*

Robert A. Paterson and Stephen Van Dyck, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101; 8 February, 1991.

Although Humpback Whales migrate close to Southern Hemisphere continental shores (Dawbin, 1966), records of strandings are relatively uncommon (Bannister, 1989). Prior to 1989 the Queensland Museum (QM) had records of five strandings (Paterson, 1986) but the deposited material was fragmentary apart from a skull, the collection of which was described in detail by Welsby (1931).

Material recovered from two Humpback Whales stranded at Fraser Island (Fig. 1) in 1989 was a significant addition to the QM collection. The specimens are registered JM7302 and JM7303 in the Queensland Museum Mammal Department.

SPECIMEN DESCRIPTIONS

FEMALE YEARLING,

JM7302 was 8.1m long, indicating a yearling, and stranded during good weather conditions near Brown's Rocks (24°46'S, 153°16'E) on 3 July 1989. Eye-witness accounts indicated that the animal was alive in the surf-zone but dead when washed ashore. When examined on the day following stranding, the right dorsolateral aspect of the carcass was buried due to tidal action (Fig. 2). Apart from superficial shark bites on the flukes and caudal peduncle there was no external evidence of injury. Barnacles, *Coronula diadema* and *Conchoderma auritum*, were noted particularly on the protuberance beneath the chin and on the pectoral fins, flukes and genital aperture (Figs 3,4). The majority of *C. auritum* were attached to *C. diadema*. Cyamids were not identified. The head and baleen were removed and blubber samples taken. The gastro-intestinal tract was empty.

When the site was revisited on 2 September 1989 it was discovered that the carcass had been washed 7km further north during stormy weather and the majority of the cervical and lumbar vertebrae were lost.

MALE CALF,

JM7303 was 4.2m long and stranded at Moon Point (25°14'S, 153°00'E) on 17 October 1989. Eye-witness accounts indicated that a larger (adult) Humpback Whale was present in deep water adjacent to Moon Point earlier on the same day while a calf, presumably the subsequently stranded animal, was seen swimming steadily in shallow water close to the shore. The actual stranding was not witnessed. When discovered the animal was bleeding from a large right axillary wound and died soon after. The carcass was recovered some hours later, taken to Urangan on the mainland where it was frozen, and subsequently transported to the QM. It had suffered numerous shark bites including a large, although healing, ventral wound. The humerus and large severed vessels were evident in the base of the previously noted axillary wound (Fig. 5). There were 24 ventral grooves and no evidence of external parasites. The specimen was cast and moulded for permanent display in the Queensland Museum.

The larynx was removed for separate examination (Quayle, this memoir). The pleural and peritoneal cavities appeared normal. The prin-

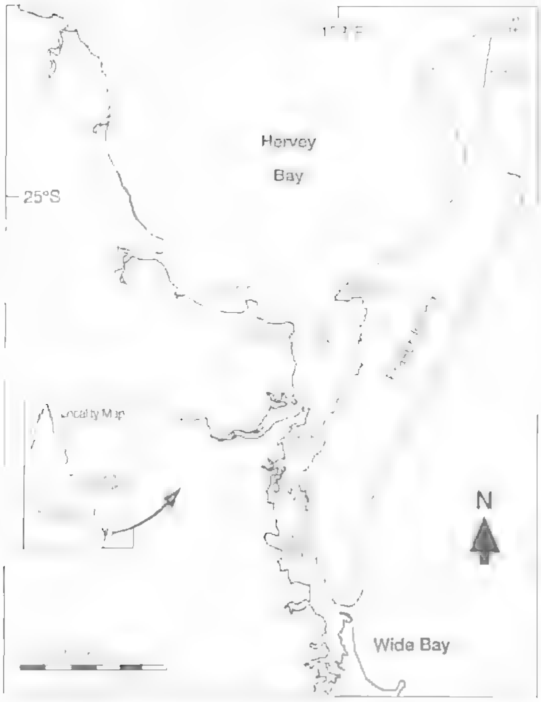

FIG. 1. Location of stranding sites on Fraser Island .

cipal gastric content was sand, possibly ingested during stranding. Faecal material was present in the intestines. Histological examination of the heart, lungs, liver and kidneys was normal apart from evidence of terminal pulmonary oedema.

There were 15 pairs of ribs and the vertebral formula was C7; T15; L11; Cd 18 = 51. Healing fractures involving the anterior aspects of the larger ribs were noted and the radiological findings (Fig. 6) suggest that the injuries had been sustained approximately four weeks previously. In addition a histologically confirmed post-traumatic pericranial reaction of similar duration to the rib fractures was noted on the supero-lateral aspect of the supraorbital process of the right frontal bone (Fig. 7). Similar pericranial injuries may occur in humans during birth and are termed cephalhaematomata (Caffey, 1973). There is no evidence that they are associated with mortality or persistent morbidity in humans and similarly the skeletal injuries suffered by JM7303 are considered to be unassociated with its death. While post-natal skeletal trauma is not entirely excluded there was no evidence of overlying cutaneous or subcutaneous injury.

FIG. 2. Partly buried carcass of JM7302 near Brown's Rocks.

FIG. 3. Barnacles, *Coronula diadema* and *Conchoderma auritum* on throat pleats of JM7302.

FIG. 4. Barnacles, *Coronula diadema* and *Conchoderma auritum* adjacent to the genital aperture of JM7302.

FIG. 5. Humpback Whale calf, JM7303, showing large right axillary wound.

FIG. 6. Radiograph of anterior aspects of the left 8th and 9th ribs of JM7303 showing healing fractures.

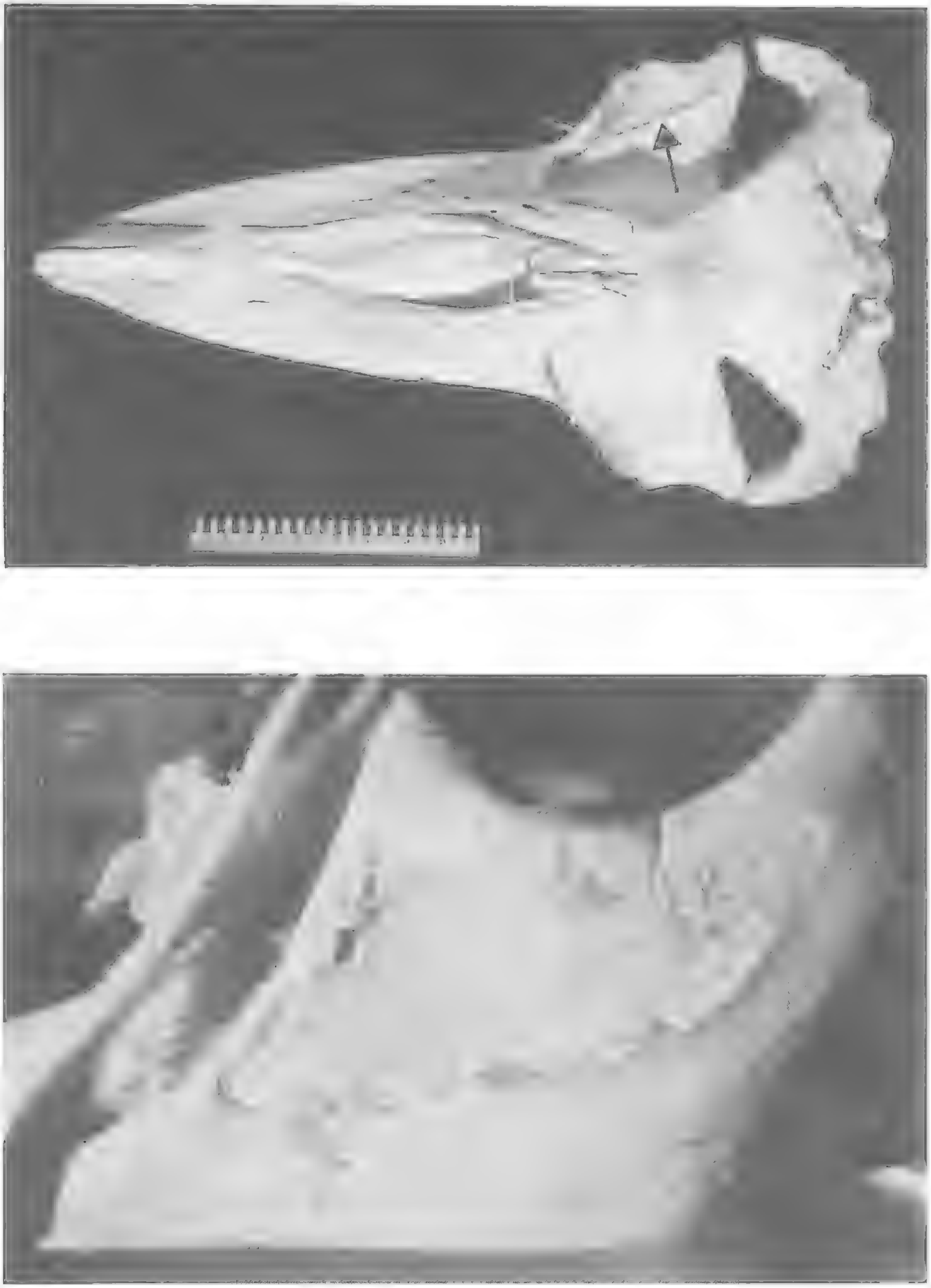

FIG. 7. Skull of JM7303 showing post-traumatic reaction to the supero-lateral aspect of the supra-orbital process of the right frontal bone.

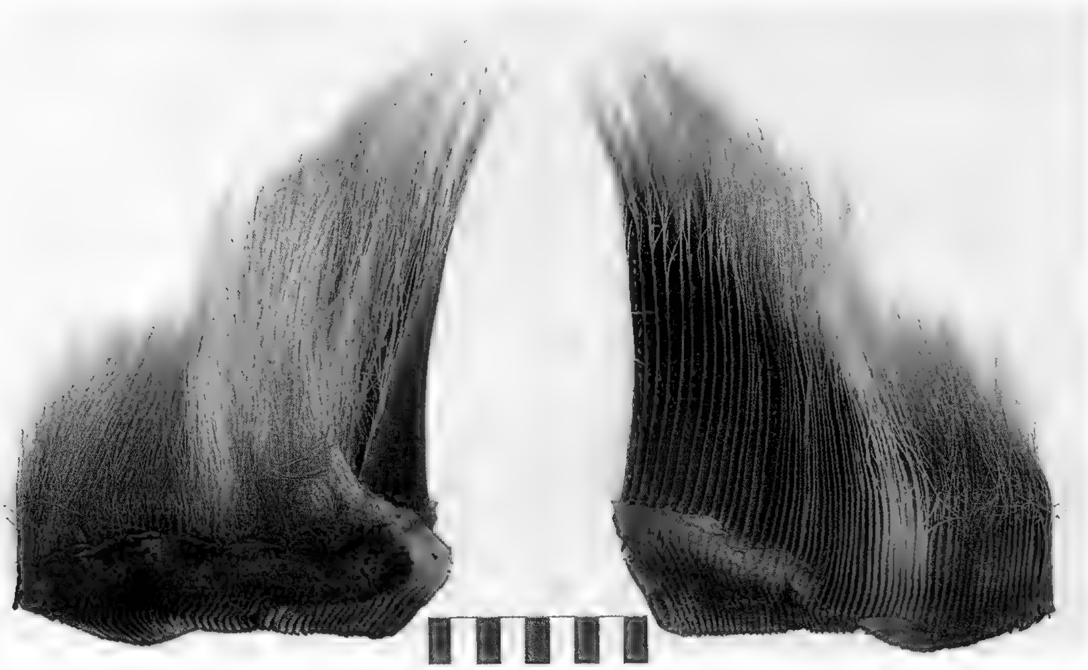

FIG. 8. Baleen of JM7302 showing band of white plates anteriorly.

BLUBBER

The mid-dorsal blubber thicknesses of JM7302 and JM7303 were 9.7cm and 4.5cm, respectively and are consistent with normal nutrition for Humpback Whales of those lengths (Matthews, 1937). It is assumed that JM7302 was northbound from the Antarctic and had been recently weaned. Accordingly its blubber would be thicker than that of JM7303 which was newborn and in the early stages of the southern migration.

BALEEN

The baleen bristles were greyish-white in both specimens. The plates were black with the exception of a few that were pale, almost white, anteriorly in JM7302 (Fig. 8). They numbered 342 and 310±5 on the left in JM7302 and JM7303 respectively (Figs 9,10). Doubt concerning the exact count in JM7303 resulted from the extremely small size of the anterior plates. The largest plates were 46cm and 9.5cm long in JM7302 and JM7303, respectively.

DISCUSSION

Given the large size of some cetaceans and the unpredictable nature of their stranding it is not surprising that recovery of useful biological material is often limited. The study of JM7302 typified those problems. Although first examined on the day following stranding, its location and available resources dictated the amount of material that could be recovered. The Queensland Museum was fortunate in the case of JM7303 in that prompt retrieval and freezing of the latter by a local fisherman provided a rare opportunity to examine and prepare an excellently preserved specimen.

Sheltered waters of the Great Barrier Reef are an important calving area for the east Australian Humpback Whale stock (Paterson and Paterson, 1984,1989; Simmons and Marsh,1986). Most Humpback Whales pass northwards along the southern Queensland coast between June and early August and pass southwards between late August and October. In the vicinity of Fraser Island they pass the eastern (oceanic) shore during both migrations but enter Hervey Bay on

FIG. 9. Lingual and buccal views of left baleen row of JM7303.

FIG. 10. Lingual and buccal views of right baleen row of JM7302.

the western shore in large numbers only during the southern migration (Paterson and Paterson, 1989). The location and timing of the strandings of JM7302 and JM7303 are consistent with those migration patterns.

ACKNOWLEDGEMENTS

We are indebted to many people who assisted with the retrieval and preparation of the specimens. JM7302 was examined and collected in accordance with a permit issued by the Minister for Primary Industries. Shamus Conway and Merv Toms of QNPWS, Wayne Kelly of Sandy Cape Lightstation, Ron Marshall, Ben Byth and Tom Paterson assisted with the retrieval of JM7302 from Fraser Island. Ken Thomas and the staff at the Brisbane City Council's Luggage Point Sewerage Station allowed us to prepare skeletal material at the Station. We are most grateful to Vic Hislop who retrieved JM7303 and transported it to Brisbane after arranging its freezing.

Bruce and Carolyn Cowell, QM, patiently applied their respective photographic and preparation skills. X-rays were taken by Sophie Kupis, Jindalee Medical Centre and John Musgrave of Sullivan, Nicolaides and Partners, kindly arranged the preparation and histological examination of numerous tissue samples. Peter Davie, QM, identified the barnacles.

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A DISSECTION OF THE LARYNX OF A HUMPBACK WHALE CALF WITH A REVIEW OF ITS FUNCTIONAL MORPHOLOGY

C.J. QUAYLE

Quayle, C.J. 1991 07 01: A dissection of the larynx of a humpback whale calf with a review of its functional morphology. *Memoirs of the Queensland Museum* 30(2): 351–354. Brisbane. ISSN 0079-8835.

The larynx of a humpback whale calf was dissected. The anatomy conformed with the general mammalian pattern with the addition of a ventral diverticulum. Some thoughts as to how the organ might function are considered. ☐ *Humpback whale, larynx, anatomy, function.*

C.J. Quayle, 79 Wickham Terrace, Brisbane 4000; 20 December 1990.

A humpback whale calf (QMJM7303) stranded at Moon Point, Fraser Island, in October, 1989 was frozen soon after death and delivered to the Queensland Museum, Brisbane. It presented an almost unique opportunity to examine a larynx of manageable size with minimal postmortem changes. The calf was 4.2 m long and estimated to be about four weeks old.

The respiratory tract began with two blowholes, slits about 5cm long on each side of the midline and inclined so that their rostral ends were closest together. The blowholes were lined with black skin which continued to the base of the skull where it became continuous with the mucous membrane.

The blowholes were surrounded by fibro-fatty tissue without obvious musculature. From their external entrance the blowholes ran almost horizontally caudally in bony grooves ending as the bony posterior choanae. The vomerine bone of the skull here separated the airway into two channels. The air passage then became a single thin-walled tube which continued, inclined ventrally, to meet the thick-walled muscular oropharynx at an acute angle. This arrangement suggests a valve. This length of tube appeared to be the equivalent of the human nasopharynx.

The larynx itself was horizontally disposed. It measured 20cm from the tip of the epiglottis to the first tracheal ring. Compared with its human counterpart it was in close proximity to the skull base with the tip of the epiglottis extending almost to the posterior choana within the conduit, I have called, the nasopharynx. In this respect elongation of the human pharynges is said to be the result of a vertical stance. The food passage passed on each side of the laryngeal opening as two pyriform fossae to become a single tube, the oesophagus, dorsal to the trachea.

The larynx was a tubular organ with a cartilaginous skeleton. There were three unpaired cartilages, the epiglottic, thyroid and cricoid, and one pair of arytenoid cartilages. Caudally the larynx became continuous with the trachea. The tube was lined with what appeared to be squamous epithelium. This was tough and closely applied particularly over the arytenoid cartilages (compare human vocal cords). The cartilages were joined by muscles most of which could be identified as following the general mammalian pattern.

The thyroid cartilage consisted of two alae or plates continuous in the ventral midline and widely deficient dorsally. There was a small rostral cornua and a long caudal one equivalent to the greater cornua of the human thyroid cartilage. The latter articulated with the cricoid cartilage on each side. There was a flat ovoid facet contiguous on each cartilage and the joint had a thick fibrous capsular membrane.

The cricoid cartilage was complete dorsally where it formed a large rectangular plate 18x12cm. It was deficient ventrally (Fig.1). The dorsal plate merged with the upper tracheal rings forming a substantial crico-tracheal plate. Caudally and laterally was the facet for articulation with the greater cornu of the thyroid cartilage. On each rostral shoulder was a large synovial joint articulating with its respective arytenoid cartilage. The lateral plates of the cricoid were narrow rostrally and broad caudally. Within the ventral deficiency lay the ventral diverticulum. A very thick band of muscle, largely transversally disposed (the thyroarytenoid muscle) filled the space between the lateral alae and covered the diverticulum.

Each arytenoid was complex in shape articulating with the cricoid cartilage as described,

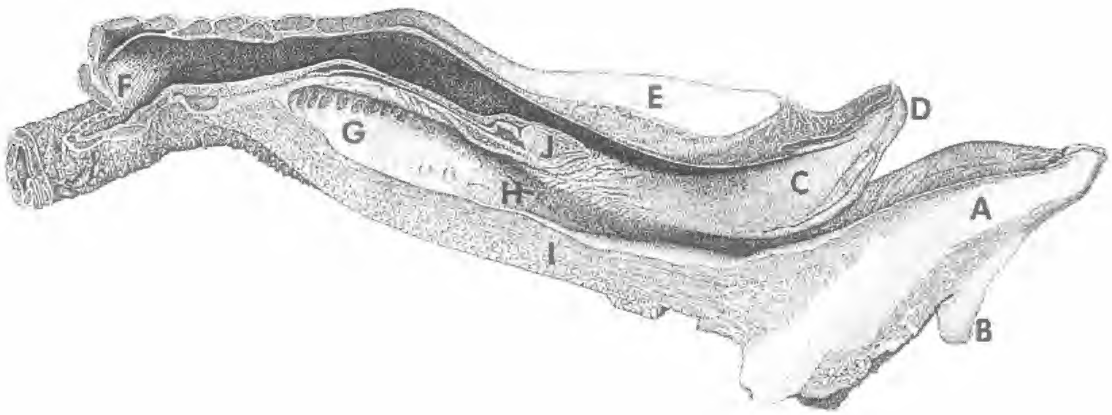

FIG. 1. Longitudinal section of Humpback Whale larynx (JM7303) in medial aspect (thyroid cartilage removed). (A) epiglottic cartilage; (B) fibrous attachment to thyroid cartilage; (C) arytenoid cartilage - corpus; (D) arytenoid cartilage - rostral end; (E) cricoid cartilage; (F) tracheal lumen; (G) fundus of the ventral diverticulum; (H) neck of the ventral diverticulum; (I) thyroarytenoid muscle; (J) interarytenoid fibro elastic connection.

The body of the arytenoid lay largely within the arch of the cricoid. A short thick process extended from the cricoarytenoid articulation to join the body of the cartilage in its middle third. The body was a banana shaped mass 15cm long with the rostral and the caudal extensions. Caudal processes were connected in the midline by a thick fibro-elastic band. The beak shaped rostral processes were concave ventrally and together were almost embraced by the epiglottis. The epiglottis together with the rostral processes of the arytenoids and the aryepiglottic folds formed the arytenoepiglottideal tube. The medial borders of the corpus were almost flat and covered with tough skin. They approximated in the midline. Some accounts refer to part of this body as the cuneiform cartilage (Hosokawa, 1950:28). A partial cleft in this specimen suggests that the cuneiform and arytenoid cartilages may be fused, the rostral process representing the cuneiform cartilage.

The epiglottis was 15 cm long and roughly spoon-shaped concave dorsally. It was relatively elastic and attached by a thick fibrous band to the thyroid cartilage near its cranial notch. The integument on the luminal side had thick longitudinal grooves which seemed almost to interdigitate with those on the adjacent surface of the arytenoid.

The trachea was comparatively short being approximately 4cm long from the cricoid plate to the bifurcation. Dorsally the proximal cartilages were not fused but "jumbled". The cartilages were deficient ventrally where they had rounded ends. The ventral diverticulum was recessed into the defect between these ends, the tracheal lumen being effectively divided into two passages.

A pouch (ventral diverticulum) opened into the laryngeal lumen by a longitudinal slit on its floor between the medial borders of the arytenoid cartilages. There is no human counterpart. It was 10cm long and was 3 cm in diameter at the fundus. The wall was fibrous and appeared nondistensible. There were some shallow pockets in the fundus and the whole was covered by a thick muscular mass. The fundus invaginated into the tracheal lumen on its ventral side and appeared to all but obliterate that lumen.

INTERPRETATION

1, the aryteno epiglottideal tube appeared to form a conduit to carry the air stream from the posterior choanae to the laryngeal inlet.

2, the airstream appeared to be directed into the ventral diverticulum (Fig. 2). The opening into the diverticulum may well be closed during normal inspiration.

3, air passing into the trachea must pass between the flattened margins of the bodies of the adjacent arytenoid cartilages.

4, the ventral diverticulum seemed unlikely to

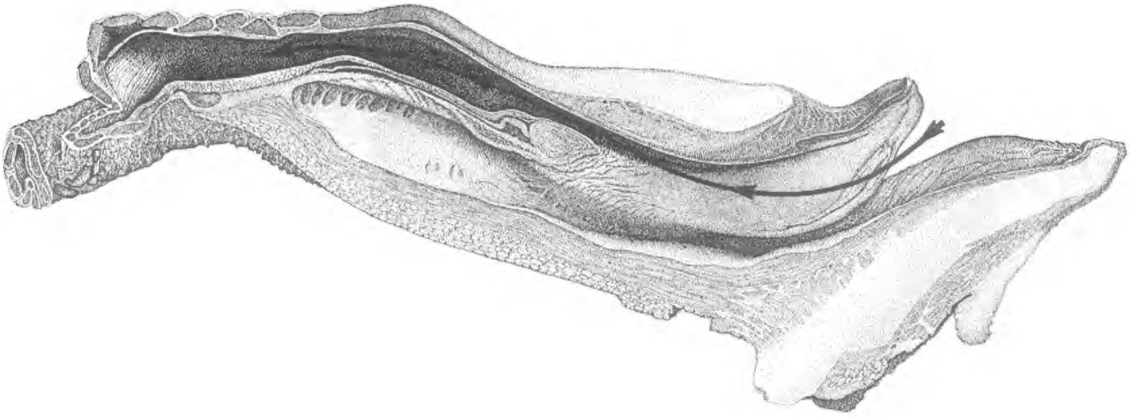

FIG. 2. Longitudinal section of Humpback Whale larynx (JM7303) in medial aspect to show course of air stream into trachea.

be distensible and as a reservoir would have been of relatively small size.

5, air expelled from the diverticulum would apparently pass over the free margins of the arytenoids and through the arytenoepiglottideal tube into the nasopharynx.

6, the ventral diverticulum could apparently function as a valve able to isolate the supraglottic air space from that in the thorax.

7, among cetaceans ventral diverticula have been described only in baleen whales (Slijper,1962:147).

8, baleen whales produce sounds organised into a complex form and distinct from the repeti-

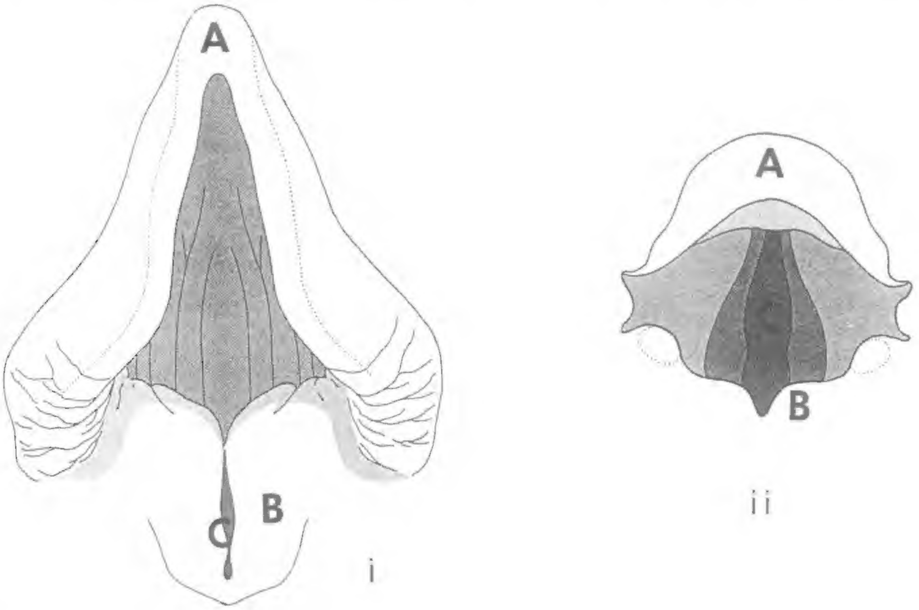

FIG. 3. Schematic drawing laryngeal inlet (i) humpback whale; (ii) human. (A) epiglottis; (B) arytenoid; (C) glottic chink.

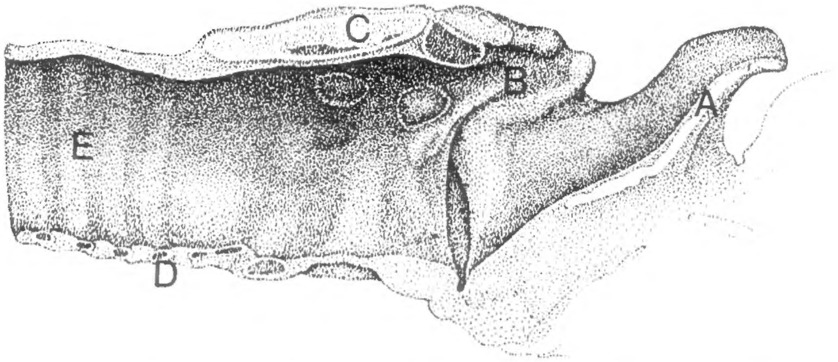

FIG. 4. Human larynx (displayed horizontally). Longitudinal section in medial aspect. (A) epiglottic cartilage; (B)aryteno-epiglottideal "tube"; (C) cricoid cartilage; (D) tracheal rings; (E) tracheal lumen.

tive clicking sounds produced by toothed whales (Schevill,1964:308).

FUNCTION

As in the human the larynx is almost certainly a valve to stop food and water going down into the trachea. In this respect it may have an added burden as the whale forces enormous amounts of water from its mouth through the baleen plates during feeding.

The larynx seems too complicated a structure to be a simple valve and the remarkable similarity between the human and whale glottic inlets (Figs 3,4) suggests that it is morphologically capable of phonation. There are no vocal cords as such, but phonation could occur between the apposing arytenoids.

In physical terms an air cavity with fluctuating volume is an efficient source of sound in water. Perhaps forcing air from the ventral diverticulum between the adducted arytenoids would make the air column both within the diverticulum and the nasopharynx vibrate.

The concept of a whale singing with sound bubbles coming out of its mouth is almost certainly incorrect. The similar physical characteristics (i.e.acoustic impedances) of the soft tissue of the whale and the surrounding sea water would mean that sound generated would pass through the body of the whale into the surrounding water in all directions with little attenuation.

I postulate that air forced from the ventral diverticulum between the arytenoids causes the air column in the diverticulum and perhaps the nasopharynx to vibrate. The resulting pressure fluctuations are transmitted through the soft tissues of the whale into the surrounding water. The air stream does not transmit the sound waves but generates pressure fluctuations in the column of air which bear on the enclosing tissues and pass through the body into the water.

The same muscle action would compress the diverticulum and adduct the arytenoids. Although the volume of air in the diverticulum is small in this specimen (which may not have been vocal) it is known that the diverticulum may be large in an adult whale. This would provide sufficient air for the relatively short bursts of phonation characteristic of the humpback whale song. While the diverticulum was compressed the trachea would be occluded and gas exchange could presumably continue uninterrupted in the lungs. Conceivably the diverticulum could be refilled from the thoracic air while the whale remained submerged.

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