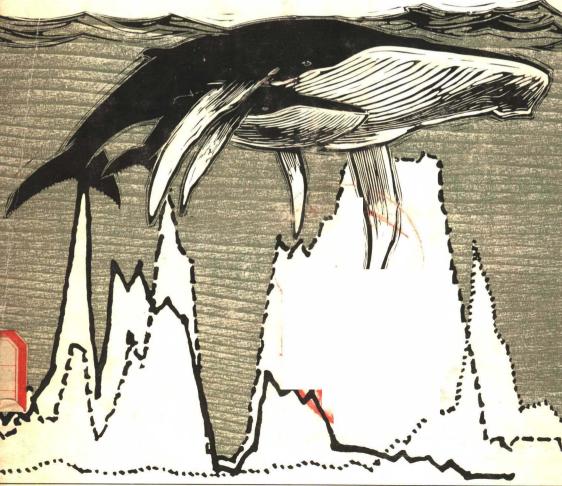
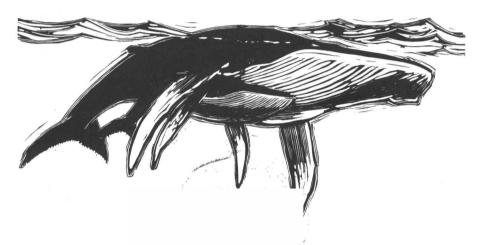
K. Radway Allen

CONSERVATION AND MANAGEMENT OF WHALES



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FOREWORD

In our modern societies, the organization of scientific endeavors leaves insufficient time for many, if not most, scientists from capitalizing on their accumulated experience and acquired wisdom. Few are successful in integrating long series of events and developing a more timeless and unified perspective of the biological world which they have been exploring. From time to time, despite these organizational constraints, such a scientist does emerge and share his wisdom with us, and such a man is K. Radway Allen.

Thus, the College of Fisheries of the University of Washington, under sponsorship of the Washington Sea Grant Program, is most fortunate in having been able to sponsor a lecture series given in May 1978 by Dr. Allen. Now, the Washington Sea Grant Program extends Dr. Allen's local audience to interested readers worldwide by publishing these lectures.

Dr. Allen's interest in whales did not develop in a slow and systematic way. Rather, its beginning in 1961 was abrupt—like the birth of a nova—coinciding with an all time low in the world's stock of the large baleen whales in the Antarctic. Although a population decline had been evident for almost a decade, the economic interests of the whaling nations were too strong to allow a rational settlement and much needed reduction of the commercial harvests in the Southern Seas. In this year a special committee was set up composed of: Dr. Douglas G. Chapman, presently Dean of the University of Washington's College of Fisheries; Dr. Sidney J. Holt, at that time with the U.N.'s Food and Agricultural Organization in Rome; and Dr. Allen, then Director of the Freshwater Fisheries Department in New Zealand, to review the problem and make recommendations.

This in itself was a new and innovative development in resource management where a panel of neutral observers was appointed, selected strictly for their expertise and acknowledged leadership in the international scientific community. It was during a large international meeting at the University of Washington in 1962 that this scientific committee attempted with all modern techniques to solve a knotty international resource problem, and which in time lead to a moratorium on catching or a much needed reduction in harvest.

Up to the formation of this Committee of Three, later expanded to a Committee of Four, none of the members had been involved to any extent in cetacean research. Afterward, all sustained deep involvement in the development of the population dynamics and management of whales. Thus, nearly two decades later it seems appropriate that this volume is being published on the accomplishment of Dr. Allen, his colleagues on the Committee of Three and Four and the many scientists who have worked within the framework created by these two committees.

O. A. Mathisen October 1979

PREFACE

The study of the population dynamics of whales began in the 1930s, but for a long time progress was very slow. It is only since about 1960 that real advances have been made, and in recent years it has been developing in an almost exponential manner. It has been my good fortune to be involved in much of this work since 1961. Like most people who have attempted to keep in touch with it, I have been disturbed by the scattered and incomplete nature of much of the literature. I have long wanted to try to bring together at least the main outlines of the concepts and techniques which have gradually evolved in the study of whale populations; and to review their application to the difficult problem of managing these resources.

I am very grateful to Dr. Douglas G. Chapman, Dean of the College of Fisheries of the University of Washington, for providing an opportunity and support for me through the Sea Grant Program so that I could at last undertake this review.

The present very rapid growth of whale population studies makes it impossible for any review to be completely up to date, and to include all the most recent data and techniques. The contents of this book were originally prepared as a series of lectures, delivered in April and May, 1978, and were as up to date as possible at that time. However, while they were being prepared for publication, important new data became available, and additional ideas were put forward, at the Special Meeting of the International Whaling Commission Scientific Committee on minke whales at Seattle in May 1978, and at the annual meetings of the IWC and its Scientific Committee in England in June 1978. As far as possible, these data and ideas have been included in the present publication.

I should like to express my sincere thanks to Dr. Chapman and to Dr. Ole A. Mathisen for all the help and encouragement they gave me in the preparation and presentation of these lectures. Also I would like to express my thanks to my many friends and colleagues on the Scientific Committee of the IWC who are the real originators of most of the contents of this book, and who have rarely failed to be vigorous and stimulating in their discussions.

My sincere thanks are also due to my wife, not only for typing and retyping the manuscript, but also for her enduring support and encouragement during the writing of these lectures and their subsequent preparation for publication.

K. Radway Allen

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1 BIOLOGY AND HISTORY OF WHALES AND WHALING

INTRODUCTION

The question as to whether whales should be exploited at all has been the subject of much vigorous and worldwide debate over the last decade. The level of popular interest in this question would greatly exceed that concerning any other group of exploited animals. Even apart from the ethical problem of whether it is wrong to kill whales at all, there are also questions as to whether any of the whale populations are sufficiently abundant, and whether our knowledge of the effects of exploitation on them is sound enough to ensure that exploitation can be undertaken without endangering their survival, and the preservation of healthy ecosystems of which they form part. Study of the population dynamics of whales, and of those aspects of their biology which directly affect their population dynamics, is therefore of particular importance as providing a basis for our judgments as to whether exploitation of whales may safely be continued.

However, quite apart from the special questions associated with whales, there are a number of factors which make study of their population dynamics particularly interesting as a component of the

general study of marine living resources.

As a group, the large whales have a worldwide distribution, and this applies also to many of the individual species. Although most of these species may be divided into a number of localized stocks, there are many advantages to be gained from overall studies, which cover many of the stocks and species.

The large whales include a fairly small number of species, most of which occupy quite similar ecological niches. Thus useful insight can be gained both from comparative study of the various species, and from consideration of the interactions between them. The marked differences in the history and in the current levels of exploitation of the various

species also provide useful material for comparative studies.

The worldwide distribution of most of the whales, and the fact that many of the principal whaling grounds are on the high seas, has led many nations to establish whaling industries at some time. It has also led to the creation of an international regulatory system. This was one of the earliest attempts at international fisheries regulation, and

still is the most comprehensive.

The wide international interest and the well-established regulatory system have, in turn, stimulated a great deal of cooperative research, particularly in the analysis of the effects on the stocks of management procedures, and the resulting catches. In association with this, the need for good catch statistics was perceived very early. For most of the major fisheries quite good data on the numbers and species of whales taken annually are available back to about 1868. Since the 1930s, the data—especially for the great Antarctic fisheries—have been extended to include the sizes and sexes of the whales caught, and often their reproductive condition. Some data on the effort expended in catching

the whales are also available as far back as the 1930s, and these have become more comprehensive, and more detailed, in recent years.

The current development of a strong popular interest in whales and whaling has undoubtedly led to an extremely critical examination of everything that is being done to regulate whaling and conserve whales. The quality of the data and the methods of analysis employed are probably being much more critically examined for whales than for any other marine animal resources.

BIOLOGY OF WHALES

Classification

Whales form part of a single group of mammals, the Cetacea. These are one of the three major groups of marine mammals, the other groups being the Pinnipedia or seals, and the Sirenia, which now comprise the manatees and dugongs. The Sirenia once included also Steller's seacow, which is probably the only species of marine mammal which has been rendered extinct by man.

Whales probably consist phylogenetically of one single stock which first appeared about the Oligocene, but which split very early into two main groups, the Odontoceti, or toothed whales, and the Mysticeti, or baleen whales. The odontocetes include one large whale and a great number of smaller species under the general names of porpoises and dolphins. The mysticetes are nearly all large whales. These talks are concerned only with the large species of cetaceans which are subject to commercial whaling. Commercial whaling in this sense refers only to operations in which animals are hunted individually with harpoons, and now mainly with harpoons fired from a gun. The smaller species of cetaceans, such as some porpoises, which are also commercially harvested although by other methods, are not considered here.

The only species of odontocete which is considered here is the sperm whale, although some medium-sized species, such as the killer and bottlenose whales, have been subject to some small-level fisheries. Virtually all the mysticetes are, however, commercial whales in this sense, the only species not in this category being the pygmy right whale; it reaches only about twenty feet in length, and is one of the least numerous whales. Thus, the large whales included here as commercial whales are one species of odontocete and nine species of mysticetes. These are—

Sperm whale
Right whale
Bowhead whale
Gray whale
Humpback whale
Blue whale
Fin whale
Sei whale
Bryde's whale
Minke whale

The principal characteristics of each of these species are summarized in Table 1.1.

The sperm whale, which occurs throughout the oceans, is a medium-sized animal. The males reach physical maturity at about 50 feet, and sometimes grow to 60 feet or more. The females only grow to about 38 feet.

The baleen whales can be conveniently divided into three groups: the right and bowhead whales, the gray and humpback whales, and the remaining five species, all belonging to the genus *Balaenoptera*.

The closely related right and bowhead whales are medium-sized, slow-swimming animals, which are commonly found close to the coastline (right whale) or to the edge of the ice (bowhead whale). The right whale is, or was, widely distributed in the temperate regions of both hemispheres, but the bowhead has always been restricted to the high latitudes of the northern hemisphere. It is not now believed that there is any major taxonomic difference between the right whales of the northern and southern hemispheres, although it seems unlikely that any mixing occurs.

The gray and humpback whales are also medium-sized and relatively slow-swimming species. They undertake major migrations between breeding grounds in warm-temperate and subtropical regions, and feeding areas in high latitudes. These breeding grounds are generally in shallow or coastal waters or, for the gray whale, often in coastal lagoons. In their migrations they generally follow paths close to the coasts, as far as possible. The humpback whale is worldwide in its distribution, but the gray whale has been restricted to the northern hemisphere. It is now found only in the North Pacific, although there is some evidence that it occurred in the past in the North Atlantic.

The remaining five species are fast-swimming whales, all essentially oceanic in their distribution. Most species undertake extensive latitudinal migrations between warm-water breeding grounds which, unlike those of the preceding group, are in the open ocean, and feeding grounds in colder but more productive areas. The extent of these migrations varies greatly in the different species. The whales range in size from the blue whale, which is the largest animal that has ever lived, usually growing to 80-90 feet in length and exceptionally to over 100 feet, to the small minke whale of 25-28 feet. They are all widely distributed throughout all the principal ocean areas. The blue whale, however, includes a relatively small race or subspecies, the pygmy blue whale, only about 70 feet in length, which is largely confined to a single small area in the southern hemisphere.

In all the baleen whales, unlike the sperm whales, the adult females are larger than the males. The difference ranges from about 5 feet in the blue whale down to about 2-3 feet in the minke whale.

Social Structure

There is a very great difference in the social structure between the sperm whale and the baleen whales. The sperm whale is essentially a polygynous animal and forms breeding herds, sometimes called

Table 1.1 Principal characteris: catches. The maximu	tics of the large im sizes given h	Principal characteristics of the large commercial whales. The usual size given is the range covered by most of the commercial catches. The maximum sizes given have generally been taken from Mackintosh (1965).	usual size giver from Mackintosh	is the range cov (1965).	rered by most or	t the commercial
	Distr	Distribution	Breeding Grounds	Breeding Behavior	Usual Size (ft.)	Food
ODONTOCETES:						
Sperm Whale Physeter macrocephalus	Worldwide	Breeding herds in tropical/temperate	Oceanic	Polygynous	M 35-60 F 30-38	Squid, fish
MYSTICETES:						
Right Whale Eubalaena glacialis	Worldwide	Cool temperate	Coastal	Mixed breed- ing herds	40-60	Copepods, other plankton
Bowhead Whale Balaena mysticetus	Arctic	Close to edge of ice	1	Mixed breed- ing herds	40-60	Krill
Gray Whale Eschrichtius robustus	North Pacific	Large N-S migrations along coasts	Coastal	Mixed breed- ing herds	35-46	Benthic inver- tebrates
Humpback Whale Megaptera novaeangliae	Worldwide	Large N-S migrations along coasts	Coastal	Mixed breed- ing herds	35-50	Krill, fish
Blue Whale Balaenoptera musculus	Worldwide	Large N-S migrations	Oceanic	Mixed breed- ing herds	70-100	Krill
Fin Whale Balaenoptera physalus	Worldwide	Large N-S migrations	Oceanic	Mixed breed- ing herds	58-85	Krill, other plankton, fish
Sei Whale Balaenoptera borealis	Worldwide	Large N-S migrations	Oceanic	Mixed breed- ing herds	45-57	Copepods, other plank- ton, fish
Bryde's Whale Balaenoptera edeni	Worldwide	Tropical/warm temperate	Oceanic	Mixed breed- ing herds	40-50	Krill
Minke Whale Balaenoptera acutorostrata	Worldwide	N-S migrations	Oceanic	Mixed breed- ing herds	23-33	Krill

harems, in which a number of females are associated with a single large male. The number of females in a harem is commonly between ten and fifteen. While there may sometimes be one or more additional large males in the vicinity of a harem it seems unlikely that these take an active role in breeding.

Juvenile animals are associated with the breeding herds, but as the males get larger, they leave the breeding herds, and form aggregations of their own. The numbers in these male groups get smaller as the animals grow, until the fully mature animals are generally solitary. Because of the harem structure, the number of socially mature males in undisturbed populations greatly exceeds that required, at any one time, to form harems.

There are also important differences in the geographical distribution. The breeding herds and the aggregations of younger males remain within the warmer waters between about 45°N and 40°S, but most of the excess mature males are found in the colder waters of higher latitudes. While it is likely that, in unexploited populations, only about 15% of the socially mature males hold harems at any one time, very little is known about either the proportions of the surplus which remain in the breeding area, or move to higher latitudes, or about the rate of interchange between the three categories.

The baleen whales, on the other hand, do not show any harem structure. They generally move in groups in which the sexes are more or less evenly balanced, and there also seems to be little age segregation. In the minke whale, however, a marked imbalance of the sexes may occur in certain areas at certain times, although even here, as far as is known, there is no indication of a harem structure.

In baleen whales, very large herds of up to 1,000 animals have been reported, but most of the herds are very much smaller, generally of the order of a few tens of animals. Blue whales apparently often travel in groups of only two or three animals. It is very likely that in all the whales the individual composition of groupings changes from time to time.

Food

The sperm whale again differs greatly from the baleen whales in the nature of its food and feeding habits. As might be expected of a toothed animal, it feeds on quite large and active prey. These are mainly cephalopods (squids), although quite large fish are also taken. It dives deeply in search of food, and is known to go down to at least 500 fathoms. It commonly stays submerged for as long as fifty minutes.

The baleen whales on the other hand are essentially filter-feeders, taking mostly the larger forms of zooplankton and small fish. In feeding the animal takes a mouthful of water which includes its prey, and then raises the tongue against the baleen plates, so that the water is forced out and the food retained on the baleen and subsequently swallowed.

In most areas, but particularly in the Southern Ocean, the principal food of the baleen whales is krill, shrimp-like crustaceans, about 5 cm long, belonging to Euphausia and related genera. Blue and

minke whales concentrate particularly on krill, whereas right and sei whales feed to a greater extent on the relatively small copepods.

Fin and humpback whales are more varied in their diet. In the North Pacific, and still more in the North Atlantic, all the baleen whales seem to take a greater variety of food, and quite large local differences are reported for most species. Even in these areas, blue whales, however, feed mainly on krill and similar organisms.

The only major exception to the plankton-feeding habit of the baleen whales is the gray whale, which feeds on or near the bottom, principally on Crustacea, which it probably dislodges from the seabed.

Distribution; Migration and Stock Separation

The sperm whale breeding herds, living chiefly in the warmer waters between 45°N and 40°S, probably show some north and south movement with the seasons, and move into equatorial waters during the winter for their hemisphere. In the Pacific, nineteenth century whalers identified a longitudinal zone close to the Equator in which they could hope to catch sperm whales at almost all times of year; this zone they called the "on the Line" grounds. Probably, however, the animals they encountered there changed with the seasons, being from the northern hemisphere stock during the northern winter, and from the southern stock during the southern winter. Quite extensive marking experiments have not yet identified any sperm whales which have crossed the Equator, and it seems likely that the northern and southern hemisphere stocks remain separate. The socially mature male sperm whales probably also undertake some degree of north-south migration between the breeding grounds and higher latitudes, but there is very little good evidence as to the timing and extent of this.

Most of the baleen whales also undertake north-south migrations with the season, breeding in the warmer waters during the winter, and going south or north to feed in the summer. These migrations occur in all the main ocean areas but they are best known in the southern hemisphere. The blue, fin, and humpback whales undertake the longest migrations; they all go south of the Antarctic Convergence (approximately 50°S) to feed, and up into at least subtropical waters in the breeding season. The sei whale does not go so far south, and generally stays in the vicinity of, or even north of, the Antarctic Convergence. Bryde's whale, as far as is known, undertakes only small, if any, north-south migrations, and remains usually in tropical and subtropical waters. The minke whale also goes far south to feed, but it is not known how far the north migration of most of the stocks extends, although the animals are common off the coast of Brazil during the southern winter. It is not yet sure, however, whether these whales belong to the same stock component that goes right down to the iceedge in summer. Little is known about the migrations of the right whale, but some movement between breeding grounds in bays and other coastal waters and feeding grounds in the open ocean probably occurs.

The migrations of the whales in the northern hemisphere are generally similar to those in the southern hemisphere. Of the two species peculiar to the northern hemisphere, the bowhead is one of the least migratory whales, and only moves north and south seasonally with the ice-edge. The gray whale, however, carries out very extensive north-south migrations. The eastern North Pacific stock migrates between winter breeding grounds in the lagoons of northern Mexico and its feeding grounds in and around the Bering Sea.

The summer range of the species of large whales in the southern hemisphere is shown in Figure 1.1.

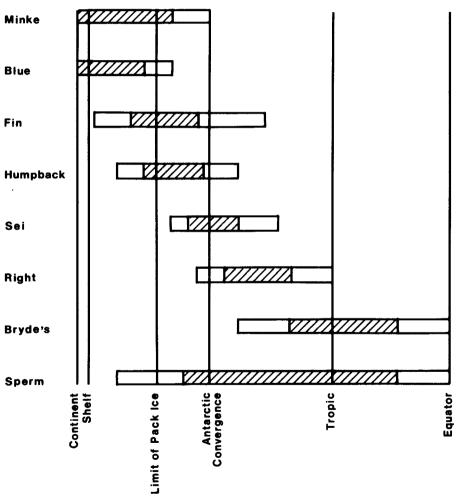


Figure 1.1 Diagrammatic latitudinal distribution of the large whales on the southern hemisphere feeding grounds, after Laws (1977) and with data on Bryde's whale from Ohsumi (1978a, 1979a).

Stock Separation. Attempts to separate the whale populations into separate stocks immediately raise problems as to how a stock should be defined. The appropriate definition to use depends on the purpose for which the separation is required. Probably the two most useful kinds of stock separations are into management stocks and into genetic stocks. Genetic stocks can be defined as subpopulations which have an insignificant degree of genetic exchange with adjacent stocks. They may thus be regarded as representing an incipient stage of speciation. In the whales it is impossible at present to identify any genetic stocks.

For management purposes, however, some division into subpopulations is essential. For this purpose stocks may usefully be defined as groups which are sufficiently isolated from neighboring groups for major changes to occur in them without affecting the adjacent stocks. This implies that the rate of interchange between such groups should be slow compared to the rate at which their size or structure may change in response to external forces such as exploitation. The International Whaling Commission has adopted a variant of the management stock—the management unit—which is defined simply as "a population unit most conveniently managed." This is, of course, a purely operational unit.

In view of its importance for management purposes, the Scientific Committee of the International Whaling Commission has devoted a good deal of attention to trying to separate the major whale populations into smaller units. Relevant data can be derived from a number of sources. Two of the most important of these are marking and recapture data and study of density distribution. If relatively high concentrations of animals are consistently found in certain areas, separated by regions containing few animals, there seem good practical grounds for regarding the areas of concentration as representing, at least, management units. Migratory and feeding behavior can also help in defining the probable grouping of populations. Thus, since humpback whales remain close to the coast in their north and south migrations. the main routes along which these migrations pass can be fairly easily identified, and may be regarded as representing nuclei of stock distribution. Sperm whales also, due to their feeding habits, tend to be concentrated along the edges of continental shelves, and thus their distribution can be related to submarine geography. There is hope that. in addition to marking and distributional data, biochemical and morphometric methods may help to throw light on the stock separation among the whales. So far the few such studies which have been made have given rather disappointing results.

The southern hemisphere sperm whales are at present divided into nine management units. In the North Pacific the situation is more uncertain. Distributional data suggest that the breeding stocks should be divided longitudinally into two or possibly three units. However, it seems likely that the mature males from these units may mingle in the Bering Sea area. Marking data are insufficient to give much help in clarifying the situation. Few data are available for the North Atlantic

but so far only one stock has been recognized here.

Probably each species of baleen whale in the southern hemisphere has its own distributional pattern, and therefore should be subdivided into an individual set of population units. At present, however, our knowledge is insufficient to enable us to do this, and the same series of population units is used for all of them. These units are based on geographical areas separated by meridians of latitude and were originally established to fit in with the concentrations of blue and fin whales observed by whalers, and they were later found to correspond quite well with the migratory patterns of the humpbacks.

In the North Pacific no general scheme of stock units for baleen whales has seemed to be appropriate. The sei and fin whales can probably be each divided into separate eastern and western stocks. The minke whale seems to have at least two substocks in the west, one in the Okhotsk Sea and along the western coast of Japan, and the other in the Sea of Japan; but in the rest of the North Pacific little is known of its stock units. The gray whale, in which stock separation can be fairly easily determined on the basis of its breeding grounds in bays and coastal lagoons, was clearly separable originally into American and Asiatic stocks. No stock separation has been attempted for the other species.

In the North Atlantic, where the geographical situation is more complex despite the smaller area, distributional data and a few marking results suggest that a greater degree of stock separation may occur. Tentatively, seven stocks have been identified for fin whales.

Reproduction

Almost invariably whales produce a single young at a birth, and twinning is very rare. The gestation period is about sixteen months for sperm whales. For baleen whales it varies between species, but in all it is less than one year. Lactation lasts for four to seven months for most of the baleen whales, and rather under two years for sperm whales. The duration of both pregnancy and lactation in the different species of whales tends to increase with their size.

In most of the baleen whales, impregnation occurs in midwinter—May or June in the southern hemisphere—and calving takes place in the following autumn or early winter, when the animals have returned to warmer waters after the feeding migration. The calves then travel back to the feeding grounds with their mothers and are weaned some time during the feeding season.

Natural Mortality Rates

The natural mortality rate of adult whales seems to tend to decrease in the different species of whales as their size increases. Thus, for the minke whale it is probably about 9-10% per annum; for sei whales, 7.5%; and fin whales, 4%. Ohsumi (1979b) has shown that this relationship is consistent also with known mortality rates for small cetaceans. The common assumption that the juvenile mortality rate would be higher than the adult rate of the same species has generally

been based on a belief that the life of a young animal would be more hazardous. Recently, however, the two species which have been most carefully examined in this respect, the sei and sperm whales, have both given evidence suggesting that there is little difference between the juvenile and adult rates. For the sperm whale the adult mortality rate is about 6% per annum.

HISTORY OF WHALING

Early European Whaling

The earliest European whaling of which we have any record seems to have been done by the Norsemen of northwestern Europe between about 800 and 1000 A.D.; slightly later the Basques were also hunting whales in the Bay of Biscay quite extensively. Both the Norsemen and the Basques were probably hunting right whales, but it is possible that they were also taking some gray whales from an Atlantic stock which may have existed at that time. From the Bay of Biscay whaling gradually spread northwards and eastwards up the European coast, and also across to Greenland, where there is a record of thirty Basque ships being present in 1578 (Slijper, 1962). By this time whaling had become a major commercial operation, as distinct from a subsistence activity, and from about 1600 onwards the Dutch and later the British whalers spread northeastwards and reached Spitzbergen about 1611.

Up to about this time whaling had probably been concentrated on right whales, but when the whalers reached the Arctic ice they found bowhead whales in great abundance. During the next two centuries they followed these whales westward along the ice-edge to Greenland and up into Davis Strait. For a time very large numbers of vessels were engaged in this fishery, but it gradually collapsed as the whales were depleted. A few vessels however hung on, and the last British whaler working in the North Atlantic returned to Dundee in 1912.

During all this time, the whalers used small sailing ships and pursued the whales in rowing boats with hand harpoons. The whales were cut up and processed either in the sea alongside the ships or on the ice. The main products were baleen and oil. Prices were so high that a whaler did not need to take more than a few whales to have a successful voyage.

American Whaling

Some local whaling on the east coast of North America began quite soon after the original settlements were established in the 1600s, and these early whalers mainly took right whales and humpback whales as they migrated along the coasts. In about 1712, a major advance took place when the American whalers turned their attention to sperm whales, and found that these could profitably be pursued in the open ocean. Over the next hundred and fifty years the New England whalers, joined later by whalers from other countries, particularly the British, gradually spread their activities first of all southwards in the Atlantic and then round Cape Horn (1789) into the Pacific. In the first half of