Baker 1985

THE POPULATION STRUCTURE AND SOCIAL ORGANIZATION OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) IN THE CENTRAL AND EASTERN NORTH PACIFIC

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IN ZOOLOGICAL SCIENCES

DECEMBER 1985

By
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Abstract

Humpback whales throughout the world's oceans undertake seasonal migrations between summer feeding grounds in near-polar waters and winter breeding and calving grounds in tropical or near-tropical waters. The influences of this seasonal migration on the social organization and population structure of humpback whales in the central and eastern North Pacific were studied through repeated observations of naturally-marked individuals. These whales form a single "structured stock" consisting of several geographically-isolated "feeding herds" which intermingle on one or more wintering grounds. Mark-recapture analyses indicate that the Hawaiian wintering congregation is four to six times larger than the southeastern Alaska feeding herd. Some genetic isolation between feeding herds is suggested by a longitudinal cline in the coloration of humpback whale tail flukes.

Migratory movement between seasonal habitats is accompanied by marked changes in social behavior and group structure. In Hawaii, most groups of whales are transient aggregations of males competing for access to sexually mature females, including cows with newborn calves. Aggression between competing males follows a roughly hierarchical scaling of intensity, progressing from apparent threat displays to physical displacement and charge-strikes. The mating system of humpback whales is proposed to be polygynous or promiscuous. Humpback whales do not form stable pair bonds during the winter season; females are seen serially and simultaneously with multiple males, and males are seen serially with multiple females.

In contrast to the mating system, the foraging strategies of humpback whales in southeastern Alaska are generally non-competitive. Although intrasexual associations predominated, adult pods can be all male, all female, or mixed sex. The majority of cow-calf pairs are unaccompanied by other adults. Most pods are transient and associations between individuals are fluid. Some whales, however, form stable associations that endure across a summer season and reoccur across years. Cooperative feeding among stable groups is evidenced by closely coordinated behavior, and, possibly, leadership by older experienced individuals. It is proposed that the structure of humpback whale populations has evolved to enhance the probability of feeding cooperatively among closely related individuals within feeding herds, while competing with distantly related individuals for breeding partners on the wintering ground.

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General Introduction

Overview

"Since man first hunted animals he has been
a student of animal behavior." Cowan (1974)

Through the course of its lifetime, each individual in a population attempts to maximize its inclusive fitness (Hamilton 1964). The social organization of a species, in turn, reflects the sum total of each individual's attempts to maximize its inclusive fitness through cooperation and competition with other conspecifics. While broadly limited by phylogenetic inertia, social organizations are remarkably labile in responding to specific ecological pressures (Eisenberg et al. 1972; Eisenberg 1981). E.O. Wilson (1975) has expressed the phylogenetic key to mammalian sociobiology in one word -- lactation. From this single conservative trait flows the two common features of most mammalian societies including such diverse assemblages as prides of lions, herds of elephants, and, as will be shown in this dissertation, pods of whales.

First, because adult females are committed to gestation and nursing, they are a limiting resource in sexual selection (Trivers 1972). Males are thus free to maximize their fitness by attempting to mate with many females. As a result, mammals show a strong tendency for polygynous mating systems and intrasexual competition between males (Orians 1969). The specific form of a polygynous mating system is further influenced by the effects of predation and the ability of males to control access to females or to some resource to which females are attracted (Bradbury 1980; Eisenberg 1981).

Second, because young mammals depend on their mother during a substantial part of early development, the mother-offspring group is the nuclear unit of mammalian societies (E.O. Wilson 1975). Consequently, when defense against predation or exploitation of some resource requires cooperative foraging or rearing, these strategies usually develop between females through the formation of matrilineal kinship groups (E.O. Wilson 1975; Eisenberg 1981).

In this dissertation, I describe the seasonal changes in the social organization of humpback whales in the central and eastern North Pacific. I show that the extensive yearly migration of humpback whales creates a unique situation for the evolution of social behavior (Chapter 1); the forces of sexual selection may shape their mating system in one seasonal habitat, independently of the ecological forces determining their foraging strategies in the other. The form of the social organization in each seasonal habitat is strongly influenced by the conservative trends common to all mammals, particularly the large cost to females of reproduction (Chapter 2) and the absence of parental care by males. On the Hawaiian wintering grounds, the social organization can be described as a polygynous or promiscuous mating system involving male-male competition for access to females (Chapter 3). On the southeastern Alaska feeding grounds, the social organization is characterized by a non-competitive foraging strategy involving, in some cases, cooperative behavior between mature females (Chapter 4). The different social and ecological pressures in each seasonal habitat are reflected in the size, composition, and stability of humpback whale groups (Chapter 5). Finally, I propose that the structure of humpback whale populations may have evolved as a novel solution to one of the universal problems of group living (Summary and Synthesis).

Background

Although systematically hunted to near extinction during the last two centuries, baleen whales remain the least understood of the major groups of mammals (E.O. Wilson 1975). Historically, the study of baleen whales was limited to parameters considered important to the management of exploited species. The examination of thousands of carcasses provided a wealth of information on morphology, growth rates, and reproductive cycles (True 1904; Lillie 1915; Mathews 1937; Chittleborough 1965; MacIntosh 1965). The study of free-ranging animals, however, was limited primarily to anecdotal and often fanciful accounts by commercial whalers. In only a few cases were observations of whale behavior objective and quantitative (Gunter 1949). Even the recent interest in the comparative study of mammalian social organization and behavioral ecology has, with some notable exceptions (Gaskin 1980; Herman 1980), largely ignored cetaceans, particularly the baleen whales (E.O. Wilson 1975).

Several factors compound the difficulty of studying the behavior of baleen whales in the wild. First, baleen whales have adapted to an entirely marine existence and are isolated from our normal modes of observation. Second, baleen whales are relatively long-lived and iteroparous. By necessity, any study of their life history must be a protracted endeavor. Finally, baleen whales are relatively inaccessible. Although baleen whales are found in all oceans and seas of the world, only three species regularly inhabit near-shore waters: the California gray whale (*Eschrichtius robustus*), the southern right whale (*Eubalaena glacialis*), and the humpback whale (*Megaptera novaeangliae*). A fourth species, the bowhead whale (*Balaena mysticetus*), is found near shore in some seasons but this seems to be an artifact of polar ice conditions rather than a real preference for coastal waters. Of these species, only the humpback whale inhabits coastal waters at both ends of its yearly migration, thus making it the most suitable species of baleen whale for comparative study.

In spite of these difficulties, baleen whales present a compelling challenge to our understanding of mammalian sociobiology. In their adaptation to an entirely marine habitat, baleen whales, as a group, have diverged extensively from other mammals in their morphology and ecology. The possible impact of these divergences on the social organization of baleen whales has remained largely unexplored. In addition to the potential trends common to all baleen species, there may also be interspecific or even intraspecific grades or scales of social organization similar to those found in other mammalian groups (Eisenberg et al. 1972).

The following sections briefly review aspects of baleen whale biology that may be pertinent to the social organization of humpback whales.

Taxonomy

The order cetacea includes all species commonly referred to as whales, dolphins, and porpoises. Cetaceans are divided into two suborders: the odontocetes, or toothed whales, and the mysticetes, or baleen whales. The mysticetes, Latin for "mustached", have no teeth. Instead they have evolved a specialized filtering system consisting of hundreds of stiff keratinaceous plates known as baleen (Lambertsen 1983). The length and number of plates differ from species to species but essentially consist of a double series of elongated horny plates which descend, at approximately right angles, from the roof of the mouth (Gaskin 1982). The inner side of the baleen plates are frayed, forming a bristle resembling coarse hair. The fringes of one baleen plate overlap those of the next, forming a fibrous mat that efficiently filters zooplankton and small fish from seawater.

It is generally agreed that the mysticetes consist of ten extant species forming three families (Herman 1980; Gaskin 1982): the Balaenidae or right whales, the Eschrichtiidae or gray whale, and the Balaenopteridae or rorqual whales. The humpback whale is the sole member of the genus Megaptera of the family Balaenopteridae.

Distribution and Migration

The humpback whale migrates each year from summer coastal feeding grounds in high-latitude waters to breeding and calving grounds near islands or shallow banks in low-latitude waters. Encompassing nearly 10,000 km round-trip, this journey is second in length among mammals only to that of the California gray whale.

The North Pacific population of humpback whales feeds in the summer and fall along the upper rim of the North Pacific Ocean (Figure 1). Known summering grounds include sites along the coast of British Columbia, the Alexander Archipelago (southeastern Alaska), the Gulf of Alaska, and the Aleutian Islands (Andrews 1916; Nemoto 1957; Pike and MacAskie 1969; Jurasz and Jurasz 1979; Rice and Wolman 1982; Baker et al. 1985). Humpback whales also feed in the southern Bering Sea, the waters near the Kamchatka Peninsula, and the Farallon Islands of central California (Omura 1955; Tomilin 1957; Nasu 1963; Dohl 1983).

In winter, North Pacific humpback whales assemble to breed and give birth in three geographically isolated tropical areas:

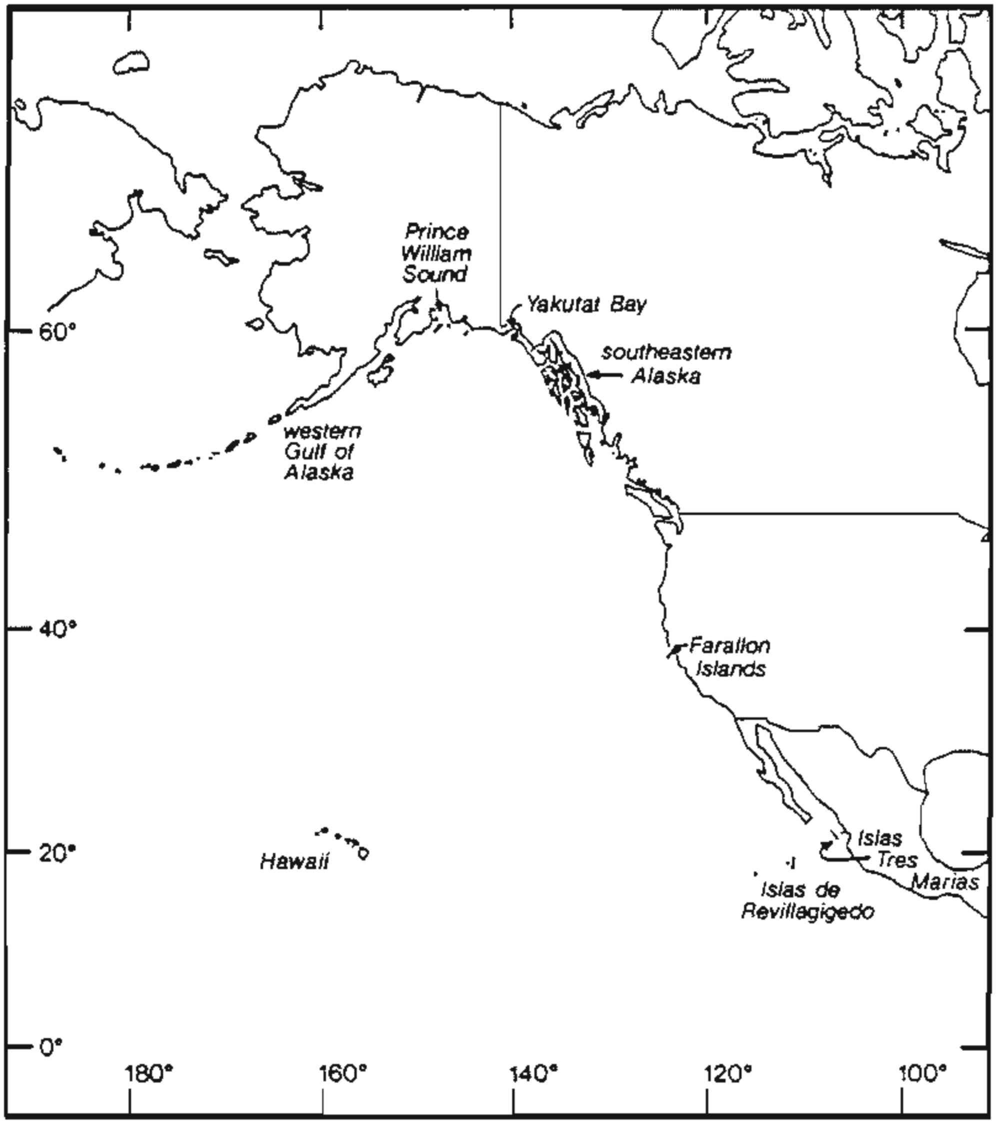
1) the Islas de Revillagigedo off Baja California and adjacent regions;
2) the western North Pacific along the Ryukuan, Bonin, and Mariana Islands; and
3) the windward islands of the Hawaiian archipelago.

The Hawaiian assembly is believed to be the numerically largest of the three (Herman and Antinoja 1977; Wolman 1978; Darling et al. 1983).

Reproductive Cycles

The reproductive cycle of humpback whales is inextricably linked to their seasonal migrations. Extensive data collected by commercial whaling biologists show that humpback whales are reproductively active only during winter months (Nishiwaki 1959; Chittleborough 1965). Based on the anatomical examination of carcasses, female humpback whales are

Figure 1: The central and eastern North Pacific ocean.


Prince William Sound
Yakutat Bay
southeastern Alaska
western Gulf of Alaska
Farallon Islands
Hawaii
Islas Tres Marias
Islas de Revillagigedo
60°
40°
20°
0°
180°
160°
140°
120°
100°

thought to ovulate once or at most twice in a winter season and to give birth once every two years following sexual maturity (Chittleborough 1965). Typically, a female will conceive on the breeding grounds one winter and, following an 11 to 13 month gestation (Mathews 1937), give birth during migration to or on the breeding grounds the following winter. Based on the presence of milk in the stomachs of calves returning to the wintering grounds, whaling biologists believed that a calf nurses for nearly a year and is weaned on its return to the wintering grounds with its mother (Chittleborough 1958; Dawbin 1966).

There are two alternatives to the "typical" two-year calving cycle in female humpback whales. A female may "rest" a year following the weaning of a calf, resulting in a three-year calving cycle. Or, a female may conceive immediately following parturition and carry the fetus to term while nursing the calf, resulting in a one-year cycle. The frequency of post-partum conception and one-year calving cycles among females in a population has remained controversial (Chittleborough 1955; Chittleborough 1965; Herman and Tavolga 1980; Glockner 1984).

Male humpback whales also undergo a seasonal sexual cycle (Chittleborough 1955; Lockyer 1984). During the winter breeding season, testes enlarge and there is an increase in spermatozoa in the seminiferous tubules (Nishiwaki 1959; Chittleborough 1955).

Sexual Maturity and Lifespan

Determining the age of first reproduction or sexual maturity for humpback whales remains problematic. Whaling biologists judge the age of mysticete whales based on the number of laminae or "growth rings" in the ear plugs (Purves 1955; Nishiwaki 1957). Roe (1967) discovered that one pale and one dark lamina together form an annual growth ring in fin whales (Balaenoptera physalus). It is uncertain, however, if this formation rate is consistent for all species of mysticetes (Lockyer 1984). From limited evidence, Chittleborough (1960; 1965) suggested that two growth layers form annually in the ear plug of humpback whales. Thus, while it is known that male and female humpback whales reach sexual maturity when between 8 and 12 growth rings are formed, it is unclear whether this indicates an age of 4 to 6 or 8 to 12 years (Symons and Weston 1958; Nishiwaki 1959; Chittleborough 1965; Lockyer 1984). A similar confusion exists about the age of physical maturity and the lifespan of humpback whales. As many as 58 growth rings have been counted in the ear plug of a humpback whale (Symons and Weston 1958), suggesting a minimum lifespan of either 29 or 58 years.

Energetics

The energetic requirements of humpback whales are poorly understood. Baleen whales have rarely been kept in captivity where these parameters are easily measured (for exceptions see Wahrenbrock et al. 1974). Instead, energetic requirements of whales have been estimated indirectly by measuring their average seasonal weight loss (Rice and Wolman 1971; Brodie 1975) or stomach contents and capacity (Lockyer 1976). Some species of baleen whales are known to undergo prolonged periods of anorexia or fasting during their yearly migration to tropical or near-tropical waters. During these periods, the whales rely on lipids stored in their blubber to meet their energetic demands.

The consequences of this ecological strategy were well known to whalers who found that whales returning from tropical waters were "dry" or low in renderable oils compared to whales returning from polar feeding waters. The differences in the renderable oil of whales of the same length on their way to and from the feeding grounds has been used to estimate the total energetic requirements during the intervening period (Rice and Wolman 1971; Brodie 1975).

In an extensive evaluation of growth and energy budgets of large baleen whales, Lockyer (1976) concluded that they need a daily ration of prey equal to 4% of their body weight during the 120-day feeding season of the southern hemisphere and about a tenth of this (0.4% of body weight) during the remainder of the year. Averaged across the entire year, her estimates of daily rations range from 1.5 to 2% of the whale's body weight. Other researchers have tried to reconcile available prey densities with the estimated energetic demands of four whale species: the fin (Brodie 1975; Brodie et al. 1978); the gray (Rice and Wolman 1971; Nerini 1984; Oliver et al. 1984); the bowhead (Griffiths 1981); and the humpback whale (Baker 1984). Each study concluded that baleen whales must find and feed in "patches" where prey densities are at least an order of magnitude greater than the average in surrounding waters.

Feeding

Nemoto (1959) categorized baleen whales as "skimmers" or "gulpers", based on their predominate feeding technique and prey size. Skimmers feed by filtering water, more or less continuously, as they swim slowly through the water. Their primary prey are the smaller zooplankton, particulary copepods. Nemoto considered the sei (Balaenoptera borealis), right, bowhead, and gray whales to be skimmers. Gulpers, or more accurately "lungers", feed by engulfing a vast volume of water and filtering the prey as they push the water back out through their baleen (Pivorunas 1979). The greater speed of the lungers allows them to feed on both macroplankton and small fish. Nemoto (1959) considered the humpback, minke (Balaenoptera acutorostrata), and fin whales to be lungers.

Humpback whales are well known for two characteristic surface-feeding strategies -- lunge feeding and bubble netting (Ingebrigsten 1929; Jurasz and Jurasz 1979; Watkins and Schevill 1979; Hain et al. 1982). Surface-lunge feeding is associated primarily with feeding on near-surface patches of euphausiids or schools of small fish. The whale's trajectory may be the result of its attempt to trap prey against the surface (Jurasz and Jurasz 1979). During bubblenet feeding, a humpback whale forms a spiral-shaped curtain of bubbles, apparently to concentrate or contain patches of euphausiids or schooling fish. Bubblenets a few meters in diameter are generally associated with feeding on euphausiids. Bubblenets as large as 25 m are associated with feeding on larger schooling fish such as herring (Jurasz and Jurasz 1979).

Exploitation and Abundance

Intensive 20th-century whaling has reduced populations of humpback whales to a small fraction of their original abundance. The entire North Pacific population is currently estimated to number less than

1,200 animals, or roughly 5% of the estimated 15,000 to 25,000 in the unexploited stock (Rice 1978; Wolman 1978). Among the baleen whales, only the right whale is rarer in the North Pacific (Herman et al. 1980).

Having survived the direct threat of extinction at the hands of commercial whaling, humpback whales now face a more insidious threat -- the loss of their seasonal habitats. As a primarily near-shore species, the humpback whale is partioularly susceptible to the impacts of coastal and continental-shelf development. Humpback whale feeding areas in the Gulf of Alaska and Bering Sea are presently leased or scheduled to be leased for petroleum exploration and exploitation. In the Hawaiian Islands, planned projects that may impact humpback whale breeding and nursing areas include deep-water mining and ocean thermal energy conversion stations (OTEC).

This near-shore developement has the potential to directly destroy habitat or to contaminate the local biosphere. Gaskin (1982) considers that cetaceans are most vulnerable to three broad categories of contaminants: the chlorinated hydrocarbons such as DDT (dichlorodiphenyltrichloroethane); compounds containing heavy metals such as mercury; and petroleum hydrocarbons. Significant levels of these man-made contaminants are presently reported in most species of cetaceans that have been examined (Gaskin 1982).

Loss of habitat can also occur indirectly through the displacement of animals away from sources of human activity. In both feeding and breeding habitats, dramatic increases in vessel traffic are a source of disturbance to humpback whale behavior (Baker et al. 1982; Baker et al.

1983; Bauer in preparation). While documented disturbance has generally been of a short-term nature, the long-term consequences of repeated, behavioral disturbance are unknown. Attempts by the Office of Coastal Zone Management to establish parts of Alaska and the Hawaiian Islands as a Marine Sanctuary for the humpback whale have been repeatedly rebuffed by special interest groups and local governments. Unless protection of its seasonal habitat is insured, the potential for recovery of the North Pacific humpback whales remains uncertain.

General Methods

Study Regions

As a migratory species, the humpback whale occupies two distinctly different seasonal habitats: winter breeding or calving grounds and summer feeding grounds. A fundamental component of this dissertation is the comparative analysis of humpback whale social organization in Hawaii, an insular wintering ground (Herman and Antinoja 1977), and southeastern Alaska, a coastal feeding region (Rice 1978).

Hawaii

Physical and Biological Characteristics. Humpback whales in both hemispheres prefer to winter over shallow ocean banks or near islands in tropical or near-tropical waters near 20 degrees latitude (Herman and Antinoja 1977). The availability of shallow, warm water seems to be the main characteristic determining selection of winter habitats. Shallow waters, less than 200 m, may provide some protection against pelagic predators which could threaten new-born calves. Warm water, greater than 22 degrees C, is presumably sought by humpback whales in order to conserve energy during the winter period of fasting (Brodie 1975).

The waters surrounding the main Hawaiian Islands satisfy both of these requirements. During winter months, the surface water temperature of the main Hawaiian Islands remains close to 25 degrees C with a near-isothermal layer extending downward to 50-80 m (Gosline 1965). A shelf of shallow water is found around each of the main Hawaiian Islands. More extensive areas of shallow water are found over the Penguin Bank off the southwest tip of Molokai and between the islands of

Maui, Kahoolawe, Lanai, and Molokai. Although occasional sightings of humpback whales are reported near the leeward islands of Hawaii, this area is not regularly habited by humpback whales (Herman and Antinoja 1977). The absence of humpback whales near the leeward islands may be explained by the somewhat cooler waters or the apparently greater number of sharks.

Food availability is not an important factor determining humpback whales' choice of wintering grounds. It is unlikely that humpback whales feed to any significant degree, if at all, in Hawaiian waters. Zooplankton are fairly uniformly distributed throughout coastal waters but are present in markedly lesser concentrations than in equatorial waters or in waters further to the north and northeast of the main islands (King and Demond 1954; King and Hida 1954). The remarkable clarity of Hawaiian waters further attests to it low productivity.

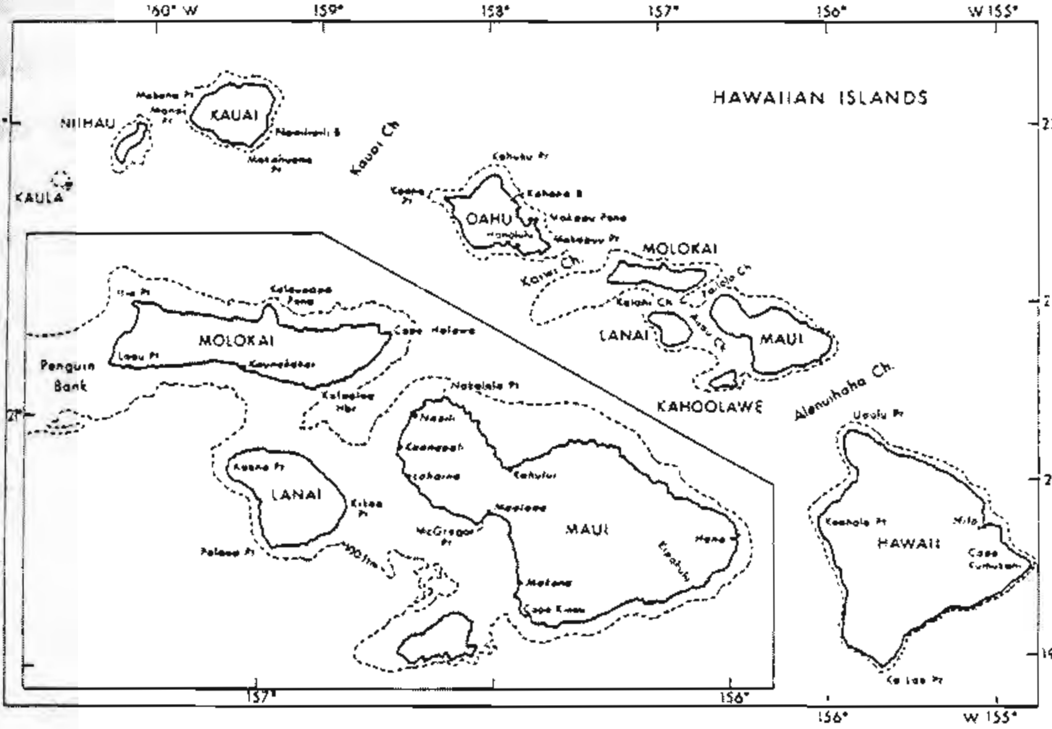
During the months of February and March there is a general clockwise pattern of the main surface currents in the North Pacific just north of the twenty degree latitude (Sverdrup et al. 1942). Currents in the eastern North Pacific tend to run southerly and turn southwesterly as they approach 20 degrees latitude. This results in a weak, predominantly westerly surface current through the main Hawaiian Islands. In the central Pacific region to the north of Oahu and Kauai, the current begins to gyre, moving north and eventually easterly. Baker and Herman (1981) suggested that humpback whales migrating to and from Hawaii could take advantage of this current pattern. For whales departing for Hawaii from the eastern Gulf of Alaska, a known feeding ground of some Hawaiian whales (Chapter 1), the southerly and southwesterly currents could provide an energy saving tail-current.

Abundance and Distribution. The results of vessel-based and aerial surveys (Wolman and Jurasz 1977; Herman and Antinoja 1977; Herman et al. 1980; Baker and Herman 1981) as well as mark-recapture analyses of photo-identification data (Darling et al. 1983), indicate that between 500 and 1000 humpback whales visit the Hawaiian Islands each winter. Humpback whales are found in the waters around all the major islands during the winter months (Figure 2). The largest number of whales are generally found in the shallow waters between Maui, Kahoolawe, Lanai, and Molokai (the "Four-Island Region") and on Penguin Bank, an approximately 33 km-wide shoal extending 46 km southwest of west Molokai. Other areas of relatively high density include the leeward coasts of the Big Island (the island of Hawaii) and Kauai, as well as the waters surrounding Niihau (Wolman and Jurasz 1977; Herman et al. 1980).

Although humpback whales are reported in Hawaii as early as October and as late as June, the largest numbers of whales are found during February and March. The seasonal population increases rapidly in late January and early February, reaches a peak in late February or early March, and declines through late March and early April. Although the rapid influx and eflux are consistent in all years, the timing of peak relative abundance may shift by several weeks from year to year (Baker and Herman 1981).

Primary study areas within Hawaii included the leeward coast of the Big Island and the leeward coast of west Maui. In 1980 and 1981

Figure 2: The main Hawaiian Islands. The 182-m isobath is shown by the broken line. The inset expands the "four island" region where study effort was concentrated in most years.


160° W
159°
158°
157°
156°
W 155°
22°
21°
20°
19°
HAWAIIAN ISLANDS
NIIHAU
KAUAI
KAULA
Mana Pt
Nonopapa Pt
Nawiliwili B
Makahuena Pt
Kauai Ch
Kahuku Pt
Kaena Pt
Kahana B
OAHU
Mokapu Pen
Honolulu
Makapuu Pt
Kaiwi Ch
MOLOKAI
Pailolo Ch
Kalohi Ch
LANAI
Auau Ch
MAUI
KAHOOLAWE
Alenuihaha Ch.
Upolu Pt
Keahole Pt
Hilo
HAWAII
Cape Kumukahi
Ka Lae Pt
Ilio Pt
Kalaupapa Pen
Cape Halawa
MOLOKAI
Laau Pt
Kaunakakai
Penguin Bank
Kalaeloa Hbr
Nakalele Pt
Napili
Kaanapali
Lahaina
Kahului
Keomuku Pt
LANAI
Kikoa Pt
Maalaea
McGregor Pt
MAUI
Hana
Kipahulu
Palaoa Pt
100 fm
Makena
Cape Kinau
157°
156°
156°
W 155°

identification photographs were also collected around all other islands, including Niihau. Focusing the research on the Big Island and Maui took advantage of the seasonal shifts in regional abundance. The peak in relative abundance tends to occur first in the southeasterly areas of the islands, suggesting a tendency for some animals to "parade" through the island chain in a southeasterly to northwesterly direction (Baker and Herman 1981). By moving northwesterly through the islands from the Big Island to Oahu or Kauai before returning to the feeding grounds, whales could take advantage of the northerly and northeasterly gyre.

History. The history of humpback whales in Hawaii is poorly documented. Native Hawaiians have few words for whales, no legends concerning baleen whales, and no history of aboriginal whaling (Herman and Antinoja 1977; Herman 1979). Although Lahaina is now popularly associated with the whaling industry of the 19th century, it was primarily a port for provisioning sperm whalers on their way to hunting grounds north or south of Hawaii. Only a few humpback whales were taken commercially by native Hawaiians under the direction of missionaries between 1840 and 1860. The decline in the value of whale products at this time seems to have put an end to this venture. The absence of historical records and anthropological evidence led Herman (1979) to propose that humpback whales only began migrating to Hawaii in the last two hundred years. Herman (1979) suggests that humpback whales dispersed or were displaced from other winter grounds because of chronic whaling pressure or long-term changes in water masses affecting surface temperature characteristics.

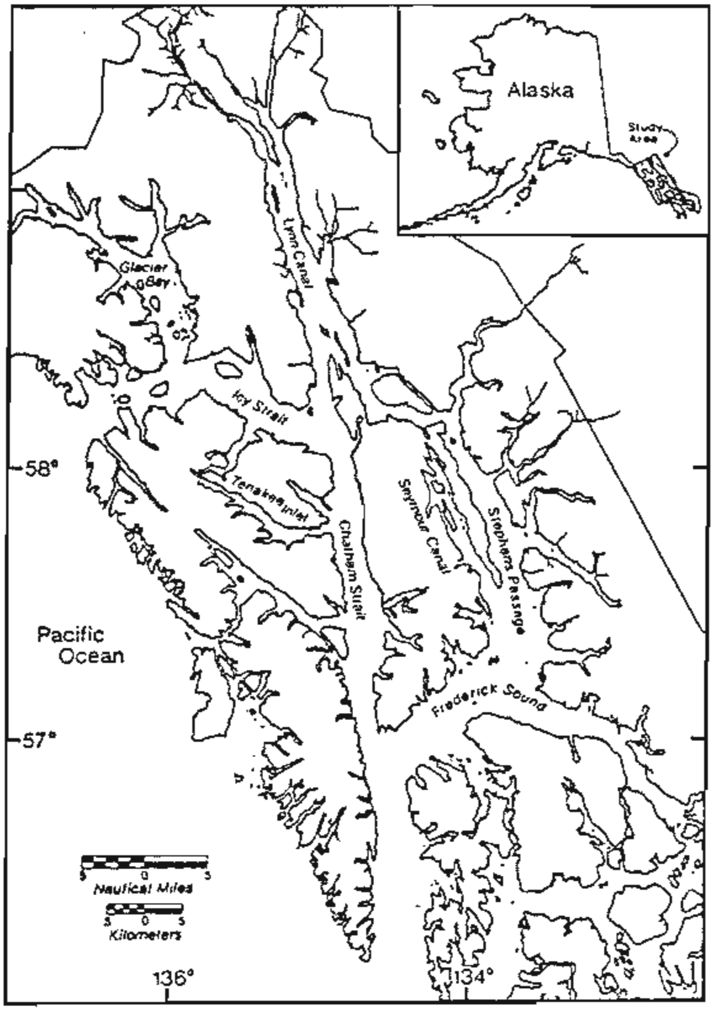
Southeastern Alaska.

Physical and Biological Characteristics. Southeastern Alaska includes the Alexander Archipelago and adjacent mainland between 50 and 60 degrees latitude north (Figure 3). This region is characterized by an intricate system of protected bays, channels, and inlets. Often refered to as the "Inside Passage", these calm waters are an ideal area for the study of feeding humpback whales. Mark-recapture analyses of photo-identification data indicate a summer population of 270 to 372 humpback whales in the waters of southeastern Alaska (Baker et al. 1985).

Like other feeding grounds of humpback whales throughout the world, southeastern Alaska is an area of high seasonal productivity. The waters are rich in both vertebrate and invertebrate species. Fish thought to be taken by humpback whales in southeastern Alaska include adult Pacific herrring, *Clupea harengus*, capelin, *Mallotus villosus*, Pacific sandlance, *Ammodytes hexapterus*, and larval or juvenile walleye pollock, *Theragra chalcogramma* (Wing and Krieger 1983; Krieger and Wing 1984). The primary invertebrate prey is thought to be euphausiids including at least four species: *Thysanoessa raschii*, *T. longipes*, *T. spinifera*, and *Euphausia pacifica* (Andrews 1909; Bryant et al 1981; Wing and Krieger 1983; Krieger and Wing 1984).

The high productivity of the inside waters of southeastern Alaska during the summer months is the result of high nutrient levels, good tidal circulation, long daylength, and moderate temperatures. Freshwater runoff from rivers, melting snow, and glaciers is nutrient

Figure 3: The primary study areas in southeastern Alaska.


Alaska
Study Area
Glacier Bay
Lynn Canal
Icy Strait
Tenakee Inlet
Chatham Strait
Seymour Canal
Stephens Passage
Frederick Sound
Pacific Ocean
58°
57°
136°
134°
5 0 5
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5 0 5
Kilometers

rich and results in variable surface salinities (Wing and Krieger 1983). Surface water temperatures ranges from about 5 to 14 degrees C during summer months.

Tidal range is large, up to about 8 m, and water circulation is complex. Tidal currents vary considerably throughout the many inlets and bays. Average current velocities are 2 to 3 km/hr but may exceed 14 km/hr in narrow passages (Hale and Wright 1979). Water clarity is variable and dependent upon tide and freshwater runoff. In near-glacial areas, such as upper Glacier Bay, visibility is only a few centimeters. In the open areas of Frederick Sound visibility may reach about 8 m during a rising tide. Daylight lasts for up to 20 hours during late June and declines to about 16 hours by the end of August. Air temperature during the summer ranges from 5 to 27 degrees C and precipitation is common.

Abundance and Distribution. Seasonal changes in the abundance and distribution of humpback whales in southeastern Alaska are complex. Whales probably begin arriving in substantial numbers during May and June, although this period has not been well studied. The largest numbers of whales are generally found in late August and early September but the timing of seasonal influx and patterns of regional occupancy changes somewhat from year to year (Baker et al. 1985). The factors controlling these yearly shifts are not understood.

Although southeastern Alaska is primarily a summer habitat, feeding aggregations are also found during fall and early winter (Dawson and Taylor 1982; Baker et al. 1985). In Seymour Canal alone, as many as 60 whales were feeding until at least mid-December of 1982. In other years, a few whales remained in Seymour Canal until at least early February. These "late-season" whales include adult males, adult females, and calves nearly a year old (Baker et al. 1985).

Observations of late-season whales have often been used to suggest that humpback whales overwinter in northern waters (Berzin and Rovnin 1966; Cuccarese and Evans 1981). However, this suggestion should be viewed with caution. Humpback whales can be found in Hawaii as early as October or as late as the first week in June. Given this broad range of sighting dates on the wintering grounds, it cannot be assumed that whales seen in northern waters during late fall, winter, or early spring have not or will not travel south that year. Although humpback whales are sighted in southeastern Alaska during all months of the year, no single individual has yet been documented to remain throughout the winter (Baker et al. 1985). If overwintering occurs in southeastern Alaska, it is probably not as common as late-season sightings would suggest.

Primary study areas within southeastern Alaska included Glacier Bay and the adjacent waters of Icy Strait, and the confluence of Frederick Sound and Stephens Passage. Separated by approximately 160 km by water, these two areas are distinctly different humpback whale habitats. Humpback whales may establish preferred ranges in either Frederick Sound or Glacier Bay, but the two area are not discrete. The same whales have been found in both areas in alternate years and at different times within the same season (Jurasz et al. 1980; Baker et al. 1982; Baker et al. 1983). Whales from Glacier Bay frequently move to Frederick Sound towards the end of the summer, possibly tracking seasonal changes in the abundance of prey (Baker 1984; Perry et al. 1985).

History. When the English explorer George Vancouver passed through Icy Strait in 1794 Glacier Bay was entirely glaciated (Bohn 1976). Subsequently, the rapid retreat of these glaciers left behind a narrow fjord more that 90 km in length. Tidal velocities are extreme in the narrow, shallow entrance to the bay and in the adjacent waters of Icy Strait. In contrast, the confluence of Frederick Sound and Stephens Passage (referred to as Frederick Sound) is a broad, open stretch of water bordered by many inlets and bays. Tidal currents are mild (2 - 3 km/hr) and glacial activity is restricted to the upper reaches of a few of the adjoining inlets.

In the years 1972 to 1978, as many as 24 whales entered Glacier Bay and remained there to feed for most of the summer. In 1978, however, 17 of the 20 whales that entered the bay abruptly departed soon after entering. Since 1978, the number of whales entering and remaining in Glacier Bay has been variable and generally lower than previous years. Two hypotheses were advanced to explain this sudden departure. The first asserted that the exponential increase in vessel traffic in Glacier Bay during the years prior to and including 1978 forced the whales to "abandon" the bay. The second hypothesis proposed that the whales' departure was the result of a natural decline in the availability of their prey. In 1981 the National Park Service, with the assistance of the National Marine Fisheries Service, initiated a multidisciplinary study of the behavior of humpback whales (Baker et al. 1982; Baker et al. 1983), the distribution of their prey (Wing and Krieger 1983; Krieger and Wing 1984), and their acoustic environment

(Malme et al. 1982; Miles and Malme 1983).

The behavioral studies documented a number of predictable short-term responses of whales to vessel traffic. In view of these results, it is not possible to conclude that vessel traffic did not contribute to the whales' departure from Glacier Bay (Anonymous 1984). At the same time, the studies of humpback whale prey documented significant yearly differences in the availability of prey in Glacier Bay and other regions of southeastern Alaska. During the 1970's humpback whales in Glacier Bay were reported to commonly feed on euphausiids near the surface (Jurasz and Palmer 1981a). From 1981 to 1984, however, humpback whales appeared to feed primarily on schooling fish and little or no surface feeding was observed. This apparent shift in prey availability, although not well documented in the years prior to 1981, could also have accounted for or contributed to the whales' sudden departure in 1978.

From 1981 to 1984 the number of whales entering Glacier Bay varied from 11 to 24 (Perry et al. 1985). The number that remained in the bay for substantial periods of time (three to four weeks) varied from one to six. The entire Glacier Bay - Icy Strait area may be visited during each July and August by as many as 36 whales or as much as 9-12% of the total estimated southeastern Alaska population of humpback whales.

Frederick Sound is generally considered the "center" of humpback whale abundance in southeastern Alaska. In 1907, a shore-based whaling station was established at Murder Cove, Admiralty Island, near the confluence of Frederick Sound and Chatham Strait (Andrews 1909; Brockstoce 1978). The station harvested several hundred humpback whales in its first few years but catches quickly declined and the station was abandoned in 1913. At its peak, the station operated a fleet of six catching vessels. A second whaling station was established at Port Alexander, Baranof Island, in southern Chatham Strait. This second station exploited off-shore species of whales in addition to humpbacks but also proved to be unprofitable after a few years. The Port Alexander facility was abandoned in 1922 and there was no further inshore whaling of humpback whales in southeastern Alaska (Bockstoce 1978; Rice 1978).

Little is reported about humpback whales in Frederick Sound again until the 1970's, when vessel-based and aerial surveys estimated 40 to 60 humpback whales in the area (Rice 1975). In more recent years, over 100 individual whales have been photo-identified in Frederick Sound during just a few weeks of late summer (Jurasz et al. 1980; Baker et al. 1982; Baker et al. 1983; Baker et al. 1985). It is not clear if this apparent increase in the number of humpback whales in Frederick Sound, and southeastern Alaska in general, is the result of improved censusing effort and methods, or the result of a true population increase.

Unlike Glacier Bay, the predominant humpback whale prey in Frederick Sound seems to be euphausiids (Andrews 1909; Bryant et al. 1981; Wing and Krieger 1983; Krieger and Wing 1984). In some years euphausiids in Frederick Sound are found in large near-surface "swarms" which are intensively exploited by humpback whales. When humpbacks are feeding on these swarms, bubble-netting and surface-lunging are commonly observed (Jurasz and Jurasz 1979; Baker et al. 1983).

Individual Identification

Humpback whales were individually identified from photographs of the ventral surface of their tail flukes and, in some cases, the profiles of their dorsal fins. The uniqueness of coloration, shape, and scarring pattern of flukes and dorsal fins allows for the reliable identification of individuals across many years (Katona et al. 1979; Jurasz and Palmer 1981a; Baker and Herman 1981). Photographs were taken with 35 mm cameras equipped with telephoto lenses and motor drives or power winders. Photographs were usually taken from small vessels which were quick and maneuverable, but at times were also taken from larger research vessels and even shore stations. A variety of films was used over the years but from 1980 to 1984 most photographs were taken with high-speed black and white negative film. This film has several advantages: 1) it can be used under a broad range of light conditions in the field; 2) selected frames can be printed and stored separately from the negatives; and 3) repeated use of the prints does not degrade the original negative.

Photographs from each observation of a whale or pod were examined and the best photograph of each individual was selected. Each photograph was then assigned a unique "Fluke Observation" number. If that photograph was then matched with another, both photographs were assigned an "Animal" number which was used for all subsequent sightings of that individual whale. The record of each Fluke Observation included sighting date, location, and sequence, as well as the behavioral role of the whale and its group size (Table 1). This information forms a "library" of sighting histories that was used in nearly every aspect of the dissertation.

Fluke photographs were graded according to their proportion of pigmentation. Following a modification of the system used by Pike (1953), an individual's flukes were placed into one of three color phases (Figure 4): 1) predominantly white, with white extending across more than 50% of each fluke; 2) moderately white, including all flukes with some discernable white covering less than 50% of each fluke; 3) dark, with no white pigmentation except for what appeared to be scarring. The color phases of humpback whale flukes were used in the analysis of geographic variation (Chapter 1) and sexual dimorphism (Chapter 2).

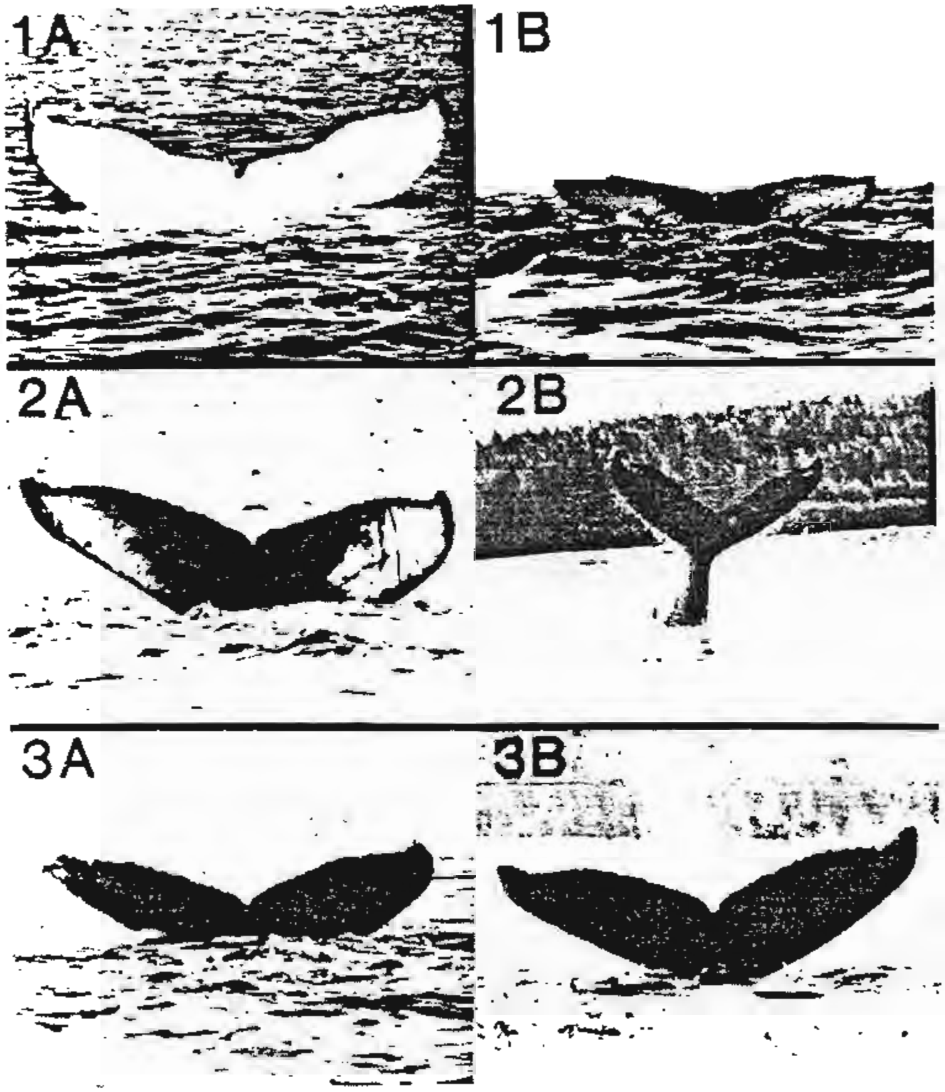
All fluke photographs were judged to be of either good, fair, poor, or insufficient quality. Good and fair quality photographs showed at least 50% of both flukes at an angle sufficiently vertical to distinguish the shape of the flukes' trailing edge. Poor quality photographs showed at least some distinctive feature of the flukes. Insufficient quality photographs did not show enough information to make an unambiguous match to another photograph. Insufficent quality photographs were excluded from all analyses. In some of the statistical comparisons of fluke photographs, poor quality photographs were also eliminated.

Table 1

Examples of the primary variables stored with each "fluke observation" record in the database library.

Observation Number	Animal Number	Region	Date	Pod Number	Pod Size	Role	Color	Qualty
0101	022	HI	02Feb80	4	4	None	1	Fair
0104	—	HI	02Feb80	4	4	None	3	Good
0388	—	HI	19Feb81	5	3	Cow	3	Good
0398	022	HI	19Feb81	5	3	Escort	1	Good
1149	045	HI	20Mar81	1	1	Singer	1	Fair
0727	599	AK	03Jul81	2	1	None	3	Good
0728	022	AK	03Jul81	3	2	None	1	Good
0730	506	AK	03Jul81	3	2	None	1	Good

Figure 4: Representative flukes of each color phase: 1A) and 1B), predominantly white; 2A) and 2B), moderately white; 3A) and 3B), no white pigment except for scarring.


1A
1B
2A
2B
3A
3B

Study Platforms

In Hawaii, data were collected from three observational platforms: aerial, shorebased, and shipboard. In Alaska data were collected only from shore and shipboard.

Shipboard

In all years whales were observed, photographed, and acoustically monitored from vessels ranging in size from a 3 m inflatable to a 30 m brigantine schooner. Vessels provided the greatest access to whales in most cases and allowed for more protracted observations than were generally possible from shore or airplanes. Positions of whales under observation from vessels were determined by radar and compass triangulation to known landmarks.

Aerial

From 1977 to 1980 an extensive series of aerial surveys were conducted throughout the Hawaiian Islands (Herman and Antinoja 1977; Baker and Herman 1981). These surveys were made from single-engine, high-wing aircraft at an altitude of 152 m and a speed averaging 160 km per hour. In addition to information on abundance and distributon, aerial surveys provided data on social organization, movement patterns, and social behavior. Data collected during aerial surveys was recorded *in situ* by hand and by voice on cassette recorders.

Shore Platforms

Shore observation platforms were used most extensively in Hawaii during 1980 and Alaska during 1981 and 1982 (Baker et al. 1982; Baker et al. 1983). In general, shore platforms were elevated locations near to shore with as much unobstructed horizon as possible. Whale behavior was observed with the aid of binoculars (7 x 35 power) or high powered field telescopes. The movement of the whales was tracked with either surveyor's transits or theodolites. In Hawaii two surveyor's transits were used from elevated vantage points approximately 2 km apart. The exact position of both transits was determined from United Stated Geographic Survey topographic maps and by aligning the horizontal scales with true north. By collecting simultaneous horizontal angles (angles of azimuth) to the whales with both transits, the position of each whale could be accurately calculated. Nikon NT-2A theodolites were used in Alaska in 1981 and 1982. Like a surveyor's transit, a theodolite measures the horizontal angle to a target. In addition, the theodolite provides an accurate vertical angle (angle of depression) to a target. When used from a known elevation and position, the angle of depression and angle of azimuth provide information on the exact position of a target (Tyack 1981).

Behavioral Observations

In all behavioral observations from aerial, shore, and shipboard platforms, a focal individual or focal group approach was employed (Altman 1974). A focal individual approach can be used for singletons and, because of the small size of most humpback pods, a focal group approach can be used for most pods without undue confusion.

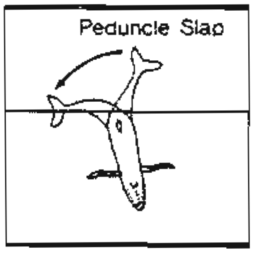
The surface behaviors of humpback whales were characterized according to an ethogram initially developed by Herman (1978, in Norris and Reeves 1978) and elaborated by Baker et al. (1982). This ethogram was supplemented by Jurasz and Jurasz's (1979) descriptions of feeding behavior in southeastern Alaska and by observations of behavioral patterns reported for the first time in this dissertation (Chapter 3). The description and inclusion of a behavioral pattern in the evolving ethogram followed the criteria suggested by Slater (1978): 1) behavioral patterns were species-typical; 2) component movements that made up the behavioral patterns occur together, simultaneously or sequentially, with a high degree of predictability; and 3) behavioral patterns were discrete and repeatedly recognizable. Some of the behavioral patterns referred to most frequently in this dissertation are illustrated in Figure 5.

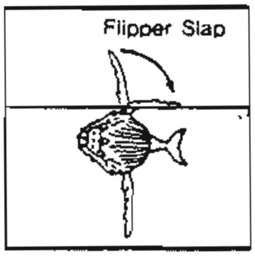
The behavior of the focal pod was recorded with one of three techniques: 1) written annotation; 2) voice annotation on cassette recorders; or 3) microprocessor time-event recorders. In Alaska during 1981 and 1982 most behavioral data were collected with the aid of microprocessor-operated, time-event recorders (MOREs). The behavioral patterns of the focal pod were entered as a two or three digit code directly into the MORE. The MORE stores each behavioral event together with the elapsed time from the start of the sampling period. The times recorded were accurate to the nearest second. "Header" information representing parameters associated with the observation were entered into the MORE at the start of the observation. This header information included the date, the starting time of the observation, and information on the identification of the whale or whales under observation.

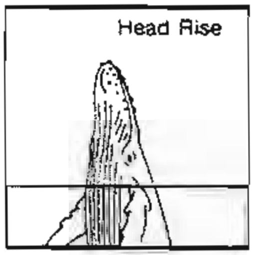
In Hawaii during 1980 and 1981 behavioral data were recorded by voice annotation on cassette recorder uing the same two and three digit codes for behaviors used with the MORE. A time base was also provided by voice with the aid of a digital clock or watch. In all years some behavioral observations were collected by written notation. Because of physical limitations, written notations of behaviors were collected synoptically in 10 or 20 minute time blocks. Within each time block, all behaviors of interest were counted. Though some information on the sequence and intervals between behaviors is lost with this approach, the use of standardized sampling periods makes these data reasonably comparable to the real-time recordings of the other two techniques.

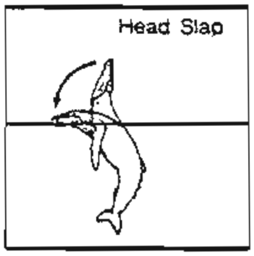
Figure 5: Some characteristic behavioral patterns of humpback whales.

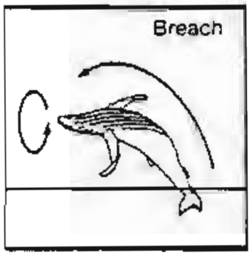

Fluke Slap


Peduncle Slap


Flipper Slap


Head Rise


Head Slap


Breach

Acoustic Recordings and Playbacks

During 1981, a preliminary study was made of the response of humpback whales to sound playback. For these experiments, recordings of humpback whale songs from 1979 to 1981, as well as synthetic control sounds, were played to whales from a stationary, 30-m long research vessel with its engine off. All recordings were made using an H-56 hydrophone, obtained from the Underwater Sound Reference Division, Naval Research Laboratory, and a Uher 4200 Report Stereo IC tape recorder. Playbacks were made from the same Uher tape recorder, amplified by a Crown DC amplifier, and projected underwater through a J-13 speaker, also obtained from the Naval Research Laboratory. Both the recording and playback systems were low-noise, high-fidelity, and flat in the frequency response from 40 to 20,000 Hz. This covers the known frequency range of humpback whale vocalizations (Winn and Winn 1978). In southeastern Alaska, whale vocalizations were monitored with a Clevite CH-13A hydrophone and a Sony TC D5M cassette recorder. This system was also flat in response to frequencies between 40 and 16,000 Hz.

Study Effort

Data employed in this dissertation were collected primarily in Hawaii during the winters of 1979 to 1982 and in southeastern Alaska during the summers of 1980 to 1984. Data from additional study regions and years were used when available. A brief methods section at the beginning of each chapter outlines the specific database and additional methods unique to that chapter.

Study effort in Hawaii and southeastern Alaska is best reflected by the length of the field season and the number of fluke observations collected in each year (Table 2). In most years, the database available for many of the analyses in this dissertation was augmented by fluke photographs from other researchers. The contributions of these researchers are acknowledged in Table 2 and elsewhere (Chapter 1).

The field season in Hawaii usually encompassed the months of February and March. In some years the season also extended into late January and early April. The number of fluke observations collected grew rapidly from 1977 to 1980 and leveled off from 1981 to 1984. A decline in the number of fluke observations collected during 1982 was the result of a shorter season and poor weather. The largest number of fluke observations, 270, was collected in 1983.

The field season in southeastern Alaska usually extended from early July to early September (Baker et al. 1982; Baker et al. 1983; Baker 1983; Baker 1983). Photo-identification data of late-season studies from November to January or February were also available for 1979 to 1982 (Baker et al. 1985). The largest number of flukes observations was collected in 1982. In 1983, research was restricted to the Glacier Bay - Icy Strait area, except for a brief survey of Frederick Sound and Stephens Passage in mid-September.

Table 2

Study periods, fluke observations, and contributing sources of photo-identification data on humpback whales in Hawaii and Southeastern Alaska.

Year	Study Period	Fluke Observations Good	Fair	Poor	Total	Source
			Hawaii			
1977	Jan - Mar	5	4	1	10	a
1978	Jan - Mar	11	10	2	23	a
1979	Feb - Mar	43	17	9	69	a
1980	Jan - Apr	108	48	17	173	a & b
1981	Jan - Apr	158	44	44	246	a, b, & c
1982	Mar - Apr	105	17	12	134	a, b, & c
1983	Jan - Mar	172	65	33	270	d
1984	Jan - Mar	117	57	31	205	d
			Southeastern Alaska			
1979	Jun - Feb	77	14	2	93	e & f
1980	Jul - Jan	119	31	13	163	a, e, & f
1981	Jul - Dec	210	55	12	277	a, b, & f
1982	Jul - Dec	314	150	26	490	a, b, & f
1983	Jul - Sep	43	44	6	93	b
1984	Jul - Sep	284	102	24	410	b

a) Herman, L.M. Director, Kewalo Basin Marine Mammal Laboratory, University of Hawaii.

b) Baker, C.S. Kewalo Basin Marine Mammal Laboratory, University of Hawaii.

d) Kaufman, G.D. Pacific Whale Foundation, Kehie, Hawaii.

e) Bauer, G.B. Kewalo Basin Marine Mammal Laboratory, University of Hawaii.

f) Lawton, W.S. Global Naturalists, Seattle, Washington.

g) Straley, J.M. and J.H. Straley, Sitka, Alaska.

Chapter I

Migratory Movement and Population Structure of Humpback Whales in the Central and Eastern North Pacific

Abstract

Photographs of individually identified humpback whales were collected in regions throughout the central and eastern North Pacific during the years 1977 to 1983. A comparison of individual identification photographs revealed a complex pattern of migration. Whales found wintering in Hawaii traveled to feeding regions throughout Alaska. Whales wintering in Mexico were found in Alaskan feeding regions and near the Farallon Islands of California. Little exchange was found between the two wintering grounds or among the five summering grounds. Fidelity to a given feeding region was demonstrated by a high proportion of migratory return. Evidence of fidelity to a given wintering ground was less conclusive. Mark-recapture analyses of resighting data indicate that the Hawaiian wintering congregation is four to six times larger than the summering population in southeastern Alaska. The coloration of humpback whale flukes showed a longitudinal cline across the five feeding regions. Flukes of whales from the eastern-most feeding regions were, on average, darker than those from the western-most feeding regions. Whales in Hawaii and Mexico were similar in fluke coloration and the average coloration on both wintering grounds was intermediate between the extremes of the feeding regions. I propose that humpback whales in the eastern and central North Pacific form a single "structured stock" consisting of several geographically-isolated "feeding herds" which intermingle on one or more wintering grounds.

Within this structured stock, sets of whales interact with different probabilities in each seasonal habitat. This, in turn, has important implications for the social organization and management of these whales.

Introduction

Humpback whales, in most oceans of the world, form sub-populations referred to in the whaling literature as "stocks". In the southern hemisphere, Mackintosh (1965) recognizes six stocks distributed around the Antarctic continent during the austral summer. During the winter, each stock migrates towards the equator to its own coastal or insular breeding ground in tropical or near-tropical waters. Chittleborough (1965) reviewed the results of discovery-tag marking and recovery from the two stocks which feed in the Antarctic Ocean south of Australia. He concluded that these stocks show strong fidelity to breeding grounds on opposite sides of the Australian continent even though some intermingling may take place during the feeding season.

Variation in the coloration of humpback whales has also been used to characterize different stocks in the southern hemisphere (Lillie 1915; Mathews 1937). Omura (1953) summarized Japanese whaling data showing a clinal decrease in the proportion of darkly pigmented animals among the South Atlantic stock eastward to the eastern Australian and New Zealand stock. Chittleborough (1965), in examining Australian whaling data, agreed with Omura in differentiating the western and eastern Australian stocks based on color differences as well as discovery-tag marking and recovery.

The recent use of natural markings and photographic documentation to identify individual humpback whales (photo-identification) has provided considerable data on migratory movement and populational structure in the North Atlantic (Katona et al. 1979; Katona and

Whitehead 1981). These data indicate that humpback whales segregate during the summer in several geographically-isolated feeding regions of the North Atlantic but congregate during winter on the Silver and Navidad Banks near Puerto Rico (Katona and Whitehead 1981; Whitehead 1982; Martin et al. 1984). Some North Atlantic humpback whales also winter near the Cape Verde Islands off Africa, but this group is not well-documented (Winn et al. 1981). No systematic differences in the coloration of North Atlantic humpback whales are reported (True 1904).

The migratory movement and stock segregation of humpback whales in the North Pacific is poorly described. Kellogg (1929), using only the observations of early whalers (Scammon 1874; Andrews 1916) suggested that humpback whales in the North Pacific are divided into an American stock and an Asian stock. He proposed that the American stock breeds in the waters off the west coast of Mexico and travels northward along the coast of North America to feeding grounds in the Gulf of Alaska, the Bering Sea, and near the Aleutian Islands. The Asian stock was thought to winter near the Ryukyu and Bonin Islands, south of Japan, and to travel north to feeding areas in the Sea of Okhotsk and along the Kamchatka peninsula. Although Rice (1978) suggested that animals from the Hawaiian wintering grounds are part of an extended American stock, Kellogg (1929) did not consider this group and may have been unaware of its existence (Herman 1979).

Discovery-tag marking and recovery has provided little data to clarify Kellogg's (1929) proposal. Of the 514 whales tagged in the North Pacific, only 22 were recovered and only nine of these showed long-range migratory movement (Ivashin and Rovnin 1967; Nishiwaki 1967;

Ohsumi and Masaki 1975; Rice 1978). All of this movement was between the Ryukyu and Bonin Islands to the south of Japan and feeding areas in the eastern Bering Sea. Although a number of authors comment on the coloration of whales from different regions of the North Pacific (Pike 1953; Tomilin 1957; Nishiwaki 1959, 1962; Herman and Antinoja 1977; Glockner-Ferrari and Venus 1983), their methods are not sufficiently similar to allow reliable comparisons.

Photo-identification of humpback whales in the North Pacific has been used to document the movement of humpback whales between the following seasonal habitats:

1) Hawaii and southeastern Alaska (Baker et al. 1982; Baker et al. 1983; Darling and Jurasz 1983);
2) Hawaii and Prince William Sound, Alaska (Baker et al. 1983; Darling and McSweeney 1983);
3) Hawaii and the Gulf of Alaska west of Prince William Sound (Baker et al. 1983);
4) Mexico and southeastern Alaska (Lawton et al. 1979; Baker et al. 1985); and
5) Mexico and Hawaii (Darling and Jurasz 1983).

Short-range movement through the Hawaiian Islands and within southeastern Alaska has also been demonstrated through photo-identification (Baker and Herman 1981; Baker et al. 1982; Baker et al. 1983).

Here I report the results of an extensive comparison of individual identification photographs collected in known feeding and breeding grounds of the central and eastern North Pacific. The photographs were taken as part of eight independent research projects. The combined data provide a more complete picture of the migratory movement and population structure of the North Pacific humpback whales than would have been possible from any single study. The final results of these comparisons is in preparation for publication with the joint authorship of the contributors.

Methods

Each of the eight studies summarized in this paper provided information from different years or regions of the North Pacific across the seven-year period from 1977 to 1983. Although the regions and study periods differed, the methods of data collection were similar in each project. As described in the General Methods, idividual identification photographs from all regions were graded according to their quality. For the purposes of the analyses in this chapter, only good and fair quality photographs were included.

Study Locations and Periods

Research effort was concentrated in seven regions of the central and eastern North Pacific. Two of these regions are winter habitats or breeding grounds (Table 3):

1) the main Hawaiian Islands; and
2) the west coast of Mexico, including the Islas Tres Marias and the Islas de Revillagigedo.

Table 3

Study periods and data sources for the wintering regions.

Year	Study Period	Identified Whales	Source
	Hawaii		
1977	Jan - Mar	9	a
1978	Jan - Mar	19	a
1979	Feb - Mar	56	a
1980	Jan - Apr	130	a & b
1981	Jan - Apr	175	a, b, & c
1982	Mar - Apr	115	a, b, & c
1983	Jan - Mar	209	d
	Mexico		
1978	Mar	28	e
1980	Mar	15	f

a) Herman, L.M. Director, Kewalo Basin Marine Mammal Laboratory, University of Hawaii.

b) Baker, C.S. Kewalo Basin Marine Mammal Laboratory, University of Hawaii.

c) Kaufman, G.D. Pacific Whale Foundations, Kehiea, Hawaii.

d) Bauer, G.B. Kewalo Basin Marine Mammal Laboratory, University of Hawaii.

e) Winn, H.E. Graduate School of Oceanography, University of Rhode Island.

f) Lawton, W.S. Global Naturalists, Seattle Washington.

Five of the regions are primarily summer habitats or feeding grounds (Table 4):

1) the Farallon Islands off the coast of central California;
2) southeastern Alaska, including the Alexander Archipelago;
3) Yakutat Bay, Alaska;
4) Prince William Sound, Alaska; and
5) the Gulf of Alaska west of Prince William Sound (subsequently referred to as the western Gulf of Alaska).

Photographs were collected in Hawaii during 1977 to 1983 from late January to early April, the period of peak seasonal abundance on the Hawaiian wintering grounds (Herman and Antinoja 1977; Herman et al. 1980; Baker and Herman 1981; Baker and Herman 1984a). Whales were photo-identified in the Islas de Revillagigedo during March of 1978 and near the Islas Tres Marias during March of 1980. Photographs were collected in southeastern Alaska during the summers of 1979 to 1983 and during the "late seasons" (November to February) of 1979 to 1982 (Baker et al. 1985). Whales were photo-identified in Yakutat Bay and the western Gulf of Alaska during the summer of 1980 (Rice and Wolman 1982) and in Prince William Sound during the summers of 1977 (Hall 1979), 1980 (Rice and Wolman 1982), and 1982. Photographs were collected in the Farallon Islands on 18 days between June and October of 1983.

Table 4

Study periods and data sources for the feeding regions.

Year	Study Period	Identified Whales	Source
	Southeastern Alaska		
1979	Jun - Feb*	83	a & b
1980	Jul - Jan*	122	a, b, & c
1981	Jul - Dec	147	b, c, & d
1982	Jul - Dec	175	b, c, & d
1983	Jul - Sep	45	d
	Yakutat Bay		
1980		5	e
	Prince William Sound		
1977		25	f
1980		31	e & g
1982		8	f
	Western Gulf of Alaska		
1980		15	e
	Farallon Islands		
1983		8	h

Table 4 (continued)

*Study period extended into the early part of the following year.

a) Lawton, W.S. Global Naturalists, Seattle Washington.

b) Straley, J.M. and J.H. Straley. Sitka, Alaska.

c) Herman, L.M. Kewalo Basine Marine Mammal Laboratory

d) Baker, C.S. Kewalo Basine Marine Mammal Laboratory

e) Wolman, A.A. and D.W. Rice. National Marine Mammal Laboratory, Seattle, Washington.

f) Hall, J. D. Solace Enterprises, Anchorage, Alaska.

g) Reinke, J.H. Seattle, Washington.

h) Ostman, J. Gulf of Farallones Research Group, California.

Results

Regional Return

Fluke photographs were compared hierarchically beginning with those taken in the same region and year (General Methods, Table 2). Within-year-and-region resights were then deleted from each sample leaving only one sighting of each individual in any given year and region (Tables 3 and 4). The yearly sightings from each region were next compared to determine the number of years an individual was seen in a given region. Individual whales were sighted repeatedly in most of the regions where photographs were collected in more than one year (Table 5). Subtracting the resights of whales seen in more than one year resulted in the total number of individuals seen in that region. In southeastern Alaska, 154 of the 326 individuals (47.2%) were sighted in more than one of the study years. Three whales were seen in all five study years. In Hawaii, 83 of the 604 individuals (13.7%) were sighted in more than one study year. No whales were seen in all seven of the study years. In Prince William Sound, 8 of the 55 individuals (14.5%) were seen in more than one study year. Mexico was the only region sampled in more than one year that did not have some resights across years.

Table 5

The number of years individual whales were sighted in each regional habitat.

Regional Habitat	Years Sighted 1	2	3	4	5	Total Whales
Hawaii	521 (86.3)	65 (10.8)	11 (1.8)	6 (1.0)	1 (0.2)	604
Mexico	43 (100.0)					43
Southeastern Alaska	172 (52.8)	88 (27.0)	43 (13.2)	20 (6.1)	3 (0.9)	326
Yakutat Bay	5 (100.0)					5
Prince William Sound	47 (86.0)	7 (12.2)	1 (1.8)			55
Western Gulf of Alaska	15 (100.0)					15
Farallon Islands	8 (100.0)					8
All Regions						1056

Note: Percentages of total whales are shown in parentheses.

Regional Exchange

A comparison of photographs among the five feeding regions and between Hawaii and Mexico revealed very little exchange within a seasonal habitat (Table 6 and Figure 6). One whale was sighted in the Islas de Revillagigedo. Mexico, during the winter of 1978 and in Hawaii during the winter of 1981. One whale was photographed in Yakutat Bay during 1980 and in southeastern Alaska, in 1982. No movement was found between the feeding regions of southeastern Alaska. the Farallon Islands. Prince William Sound. and the western Gulf of Alaska during the studies reported here. A more recent study, however, found that two whales sighted in Prince William Sound during 1977 and 1980 were sighted in southeastern Alaska during the summer of 1984 (Baker 1984). The movement between southeastern Alaska and Prince William Sound is shown in Figure 6, but these matches were not included in the table of resights or the following statistics.

If humpback whales randomly assorted among the five feeding regions or between the two wintering grounds in alternate years, the chance of resighting a whale in a different region of a seasonal habitat should approximately equal the chance of resighting it across years in a single region. For example. a whale sighted in Hawaii one year should have an equal probability of being resighted in either Hawaii or Mexico in alternate years.

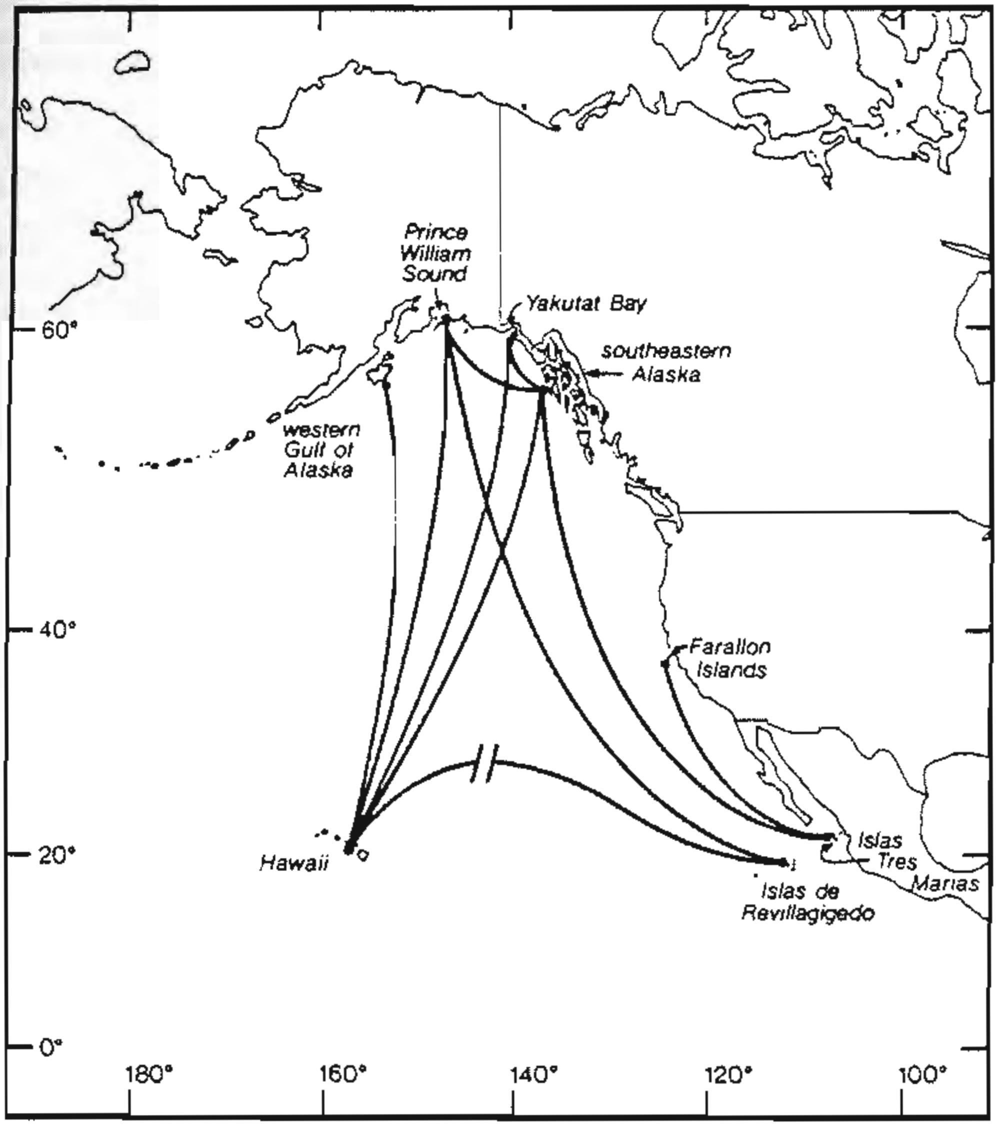
Table 6

The regional exchange and migratory movement of humpback whales in the central and eastern North Pacific.

Sighting Region	Resighting Region HI	ME	SEA	YB	PWS	WGA	FI
Hawaii	(604)	1	65	3	8	4	0
Mexico		(43)	1	0	1	0	1
Southeastern Alaska			(326)	1	0*	0	0
Yakutat Bay				(5)	0	0	0
Prince Williams Sound					(55)	0	0
Western Gulf of Alaska						(15)	0
Farallon Islands							(8)
Total Individuals							971

Note: The number of whales sighted in each regional habitat is shown in parentheses.

Figure 6: The migratory movement of humpback whales in the central and eastern North Pacific. Lines connect seasonal habitats visited by individually identified whales. Lines do not indicate migratory routes.


Prince William Sound
Yakutat Bay
southeastern Alaska
western Gulf of Alaska
Farallon Islands
Hawaii
Islas Tres Marias
Islas de Revillagigedo
60°
40°
20°
0°
180°
160°
140°
120°
100°

Following the logic of mark-recapture analyses. the probability of an across-years resighting for a given region was calculated as

$$p = 1/(N + 1.96\ (SE))$$

where N and SE are the weighted mean and standard error of the Petersen population estimate (Begon 1979). The weighted mean was calculated as

$$N = \frac{\sum M_i n_i}{(\sum m_i) + 1}$$

where M_i is the number of whales sighted prior to year i (whales at risk in year i), n_i is the number of whales sighted in year i, and m_i is the number of individuals resighted in year i. The standard error is given by

$$SE = N \sqrt{\frac{1}{(\sum m_i + 1)} + \frac{2}{(\sum m_i + 1)^2} + \frac{6}{(\sum m_i + 1)^3}}$$

Using the cumulative sightings across all years. rather than only contiguous pairs of years. should result in an inflated estimate of the population since births and deaths in the population cause a general decline in resights acoss years (Seber 1982). An inflated population estimate will provide a conservative estimate of the across-years-within-region resighting probability. The use of the upper 95% confidence limit of the population estimate is further assurance that the across-years-within-region resighting probability is conservative.

Among the feeding regions, only southeastern Alaska provided a sufficient sample size to estimate abundance and the probability of across-years-within-region resightings (Table 7). The weighted mean of the Petersen estimate suggested a seasonal "population" of 374 (+/- 47 at the 95% confidence interval) animals in southeastern Alaska. Using the inverse of the upper confidence limit as the across-years-within-region resighting probability, it was then possible to determine the expected number of resights between southeastern Alaska and the other feeding regions (Table 8). For example, the expected number of resights between southeastern Alaska and Prince William Sound (42.6) was calculated by multiplying the number of photo-identified whales from southeastern Alaska (326) by the number of whales in Prince William Sound (55) and by the estimated across-years-within-region resighting probability (1/421). A Chi-square test showed that the observed values clearly differed from the expected values under the null hypothesis that whales randomly assorted among the feeding regions (Chi-square [3] = 105.9; P < 0.005).

This process was repeated for the wintering grounds, using the across-years resighting data from Hawaii (Table 9). The weighted mean of the Petersen estimate suggested a "population" of 1,627 (+/- 307 at the 95% confidence interval) animals that have visited Hawaii across the study period. Based on this across-years-within-region resighting probability (1/1.934), the number of identified whales from Hawaii (604), and from Mexico (43). the expected number of between region resightings was 13.4; significantly greater than the single observed resight between Hawaii and Mexico (Chi-square [1] = 16.6; P < 0.005).

Table 7

The across-year resighting of whales in southeastern Alaska.

	Study Year					
	79	80	81	82	83	Sum
Whales Sighted (n_i)	83	122	147	175	45	—
Whales Resighted (m_i)	--	33	74	105	34	246
Sighted Whales at Risk (M_i)	--	83	172	245	315	326

Note: See text for description of mark-recapture notation.

Table 8

The observed and expected number of resights between southeastern Alaska and other feeding regions.

Sighting Region	Resighting Region YB n = 5	 PWS n = 55	 WGA n = 15	 FI n = 8
SEA n = 326	1 (3.9)	0* (42.6)	0 (11.6)	0 (6.2)

Note: Expected number of matches, shown in parentheses, were calculated from the between-seasonal-habitat resighting probability. See text for details.

* Two resightings were found between Prince William Sound and southeastern Alaska in 1984.

Table 9

The across-year resighting of whales in Hawaii.

	Study Year							
	77	78	79	80	81	82	83	Sum
Whales Sighted (n_i)	9	19	56	130	175	115	209	---
Whales Resighted (m_i)	--	1	5	7	23	31	42	109
Sighted Whales at Risk (M_i)	--	9	27	78	201	353	437	604

Note: See text for description of mark-recapture notation.

Migratory Destinations

The photographs of individual whales from the two wintering grounds were compared to those from the five feeding regions in order to determine the migratory destinations of humpback whales in the central and eastern North Pacific. The comparison revealed extensive interchange between seasonal habitats (Table 6). Whales from Hawaii traveled to all of the feeding grounds in Alaska. The only feeding area where Hawaiian whales were not found was the Farallon Islands. Whales wintering in Mexican waters traveled to at least three of the five feeding grounds included in the study: southeastern Alaska, Prince William Sound, and the Farallon Islands. The whale that traveled to southeastern Alaska and the whale that traveled to the Farallon Islands were photographed near the Islas Tres Marias during 1980. The whale that traveled to Prince William Sound was photographed in the Islas de Revillagigedo during 1978.

Following the procedure described earlier, the overall probability of resighting between seasonal habitats was determined from the total number of photographs from the wintering grounds (647), the total number from the summer feeding regions (409), and the total number of resights (83). This resighting probability (1/3188) was used to calculate the expected number of resights between each of the two wintering grounds and the combined sample of whales from the five feeding regions (Table 10). Based on the results of a chi-square test, it was not possible to reject the null hypothesis that the combined sample of whales from all feeding regions was equally represented on each of the two wintering grounds (Chi-square [1] = 1.22; $P > 0.25$).

The between-seasonal-habitat resighting probability was also used to calculate the expected number of resights between each of the two wintering grounds and each of the five feeding grounds, separately (Table 10). Although the expected number of resights in some of the table's cells were too small (less than 1) to make a chi-square test appropriate, the table does suggest some trends. The observed number of resights between Hawaii and Yakutat Bay was unexpectedly high and the number between Mexico and southeastern Alaska was unexpectedly low. Given the small sample sizes from both regions, the single resight between Mexico and the Farallon Islands was unexpected. Given the large sample from Hawaii, the absence of any resightings with the Farallon Islands was unexpected.

Migratory Transits

Many of the photo-identified whales traveled between seasonal habitats more than once. The 65 whales seen in both Hawaii and southeastern Alaska made a total of 115 one-way transits between these two regions. A one-way transit was considered to be any pair of sequential, though not necessarily consecutive, sightings in two different seasonal habitats uninterrupted by a sighting in a third region. The most extensive migratory transiting was shown by whale #022, an individual seen during four years in southeastern Alaska and during four years in Hawaii (Figure 1.2). The eight regional sightings indicated at least six transits (three round-trips) between Hawaii and southeastern Alaska. Although it is likely that animal #022 completed

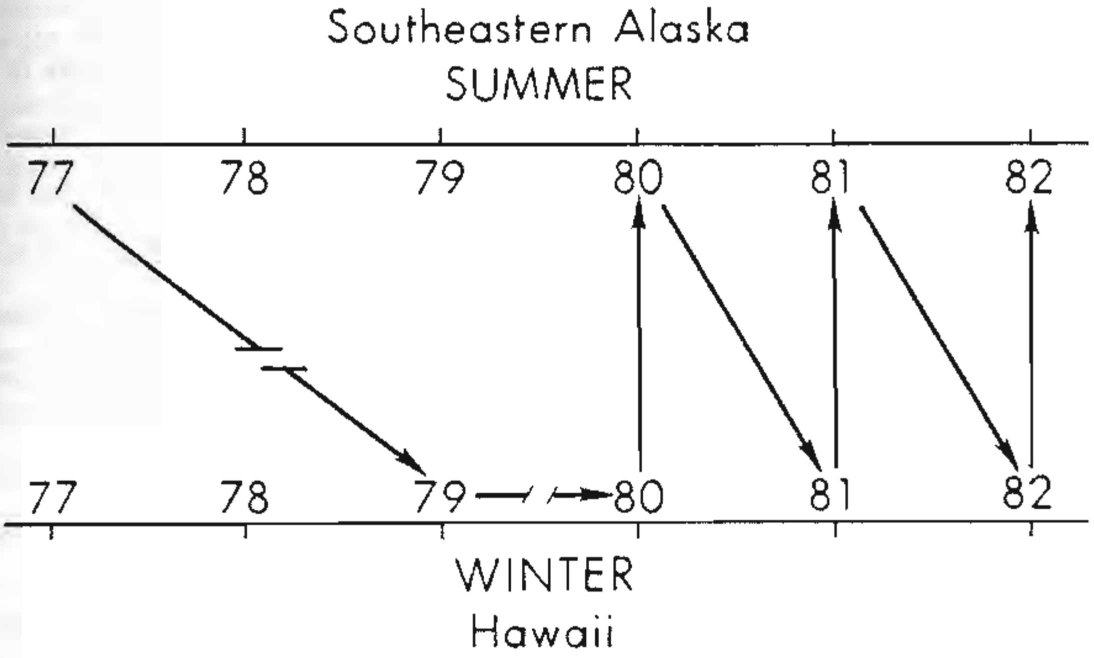
Table 10

The observed and expected number of photographic resightings between seasonal habitats of the central and eastern North Pacific.

Wintering Grounds	Summering Grounds SEA n = 326	YB n = 5	PWS n = 55	WGA n = 15	FI n = 8	Total Resights
Hawaii n = 604	65 (61.8)	3 (1.0)	8 (10.4)	4 (2.8)	0 (1.5)	80 (77.5)
Mexico n = 43	1 (4.4)	0 (0.1)	1 (0.7)	0 (0.2)	1 (0.1)	3 (5.5)

Note: Expected number of matches, shown in parentheses, were calculated from the between-seasonal-habitat resighting probability. See text for details.

Figure 7: The migratory transits of Animal #022 between Hawaii and southeastern Alaska. Broken lines indicate the probable presence of undocumented transits.


Southeastern Alaska
SUMMER
77
78
79
80
81
82
77
78
79
80
81
82
WINTER
Hawaii

the migration between summer and winter grounds each year, only confirmed transits were included in this analysis. The only other repeated migratory returns were found between Hawaii and Prince William Sound, where three whales made round-trips.

Two whales were seen in three regions. Animal #232 was sighted in Glacier Bay, southeastern Alaska during the summers of 1974, 1975, 1976, and 1977 (Jurasz and Palmer 1981a, b). It was next sighted in Yakutat Bay during the summer of 1980 and then returned to Glacier Bay in 1982. Finally, it was seen in Hawaii during the winter of 1983. Animal #301 was seen in Prince William Sound in 1977 and 1980 and in Hawaii during the winter of 1983. Animal #301 was next seen in southeastern Alaska during the summer of 1984. Animals #232 and #301 are both thought to be mature females based on their close association with a calf in one or more years (Chapter 2).

Migratory Rates

Five whales were found in southeastern Alaska during the fall or winter and in Hawaii later that same winter (Table 11). The most rapid migratory transit was recorded for animal #203, last seen in southeastern Alaska on December 8, 1982, and first seen in Hawaii on February 25, 1983. Using the minimum distance between Hawaii and southeastern Alaska (about 4500 km) and the shortest period of transit (79 days) yielded a minimum migratory speed of 2.38 km/hr, traveling 24 hours a day. The average migratory speed of the five whales was 1.88 km/hr (SD = 0.29).

Fluke Coloration

Fluke photographs used in the previous comparisons were analyzed for regional differences in color phases (General Methods). Because the categories of fluke coloration were an ordered classification of an attribute along a continuous scale, parametric statistics were used to analyze differences between regions (Snedecor and Cochran 1967). For these analyses, each pair of flukes was assigned a score corresponding to its color phase (Table 12): 1 for predominantly white, 2 for moderately white, and 3 for dark. To prevent a bias from frequently sighted whales, an individual was counted only once in each region that it was sighted.

Considering the total number of whales from all regions of the central and eastern North Pacific combined, the largest proportion of flukes were moderately white (39%) and nearly equal proportions were predominantly white (31%) or dark (30%). The proportion of flukes in each color phase, however, changed markedly from one region to another. The coloration of flukes differed significantly among the seven regions (analysis of variance; F [6/1049] = 6.99, p = 0.0001). Multiple comparisons between the means suggested two basic groups differing at the 0.05 level of probability. The darker group included the Farallon Islands, southeastern Alaska, and Yakutat Bay. The lighter group included Mexico, Prince William Sound, Hawaii, and the western Gulf of Alaska.

The mean color scores from the feeding regions suggested a longitudinal trend, ranging from lighter in western-most regions to darker in eastern-most regions (Figure 1.3). A regression of fluke coloration on longitude of the feeding region where the whale was sighted showed this relationship to be significant ($F\ [1/407] = 24.32$; $p = 0.0001$; r-square $= 0.055$; $Y' = 6.806 - 0.0342(\text{longitude})$). A longitudinal analysis of fluke coloration in the two breeding regions was not significant ($F\ [1/645] = 0.11$; $p = 0.74$; r-square < 0.001).

Yearly differences in the color phases were also examined for Hawaii and southeastern Alaska, the two regions with large sample sizes in more than one year. Using the two years with comparable effort and similar research methods (1980 and 1981 in Hawaii, 1981 and 1982 in southeastern Alaska) a nested analysis of variance confirmed the differences between regions ($F\ [1/2] = 434.63$; $p = 0.005$) but showed no differences between the yearly samples within each region ($F\ [2/620] = 0.10$; $p = 0.75$).

Table 11

Migratory transits of late-season whales.

Animal number	Last sighting Southeastern Alaska	First sighting Hawaii	Migratory transit (days)	Minimum speed (km/hr)
#553	Nov 24, 1981	Mar 21, 1982	117	1.60
#542	Nov 24, 1981	Mar 15, 1982	111	1.69
#232	Nov 29, 1981	Mar 15, 1982	106	1.77
#547	Nov 29, 1982	Mar 7, 1983	98	1.92
#203	Dec 8, 1982	Feb 25, 1983	79	2.38

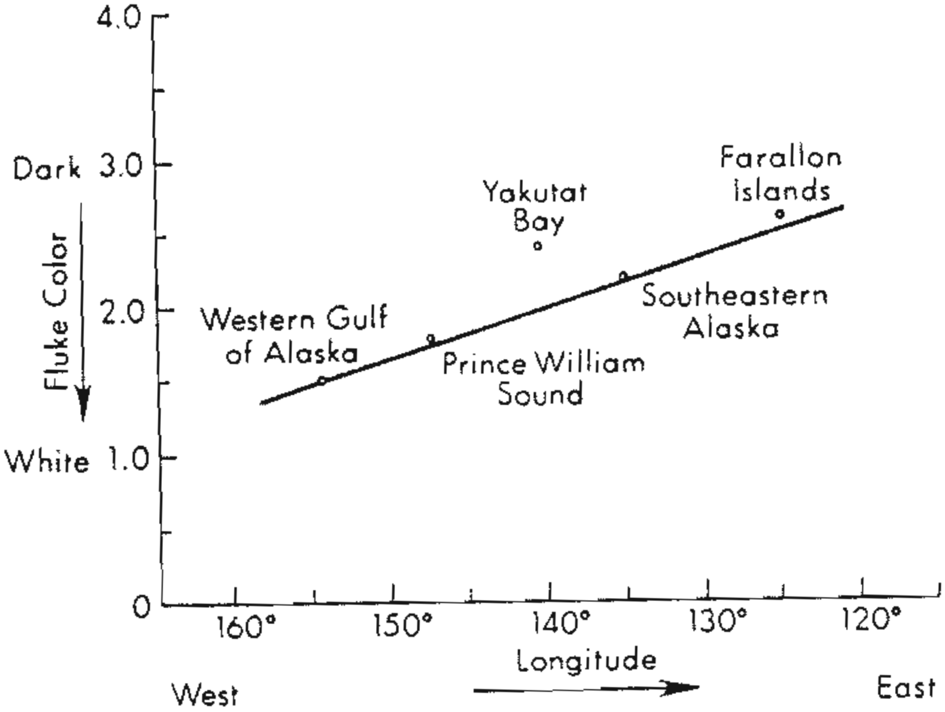
Table 12

The fluke coloration of humpback whales in each regional habitat.

Sighting Region	Color Phase 1	Color Phase 2	Color Phase 3	Mean Color Phase
Hawaii	199 (33)	252 (42)	153 (25)	1.92
Mexico	18 (42)	12 (28)	13 (30)	1.88
Southeastern Alaska	79 (24)	110 (34)	137 (42)	2.18
Yakutat Bay	1 (20)	1 (20)	3 (60)	2.40
Prince William Sound	21 (38)	24 (44)	10 (18)	1.80
Western Gulf of Alaska	9 (60)	6 (40)	0 (00)	1.40
Farallon Islands	0 (00)	3 (37)	5 (63)	2.63
All Regions	327 (31)	408 (39)	321 (30)	1.99

Note: Percentages of flukes in each color phase are shown in parentheses.

Figure 8: The regression of average humpback whale fluke coloration from each feeding region on the region's longitude.


4.0
Dark 3.0
2.0
White 1.0
0
Fluke Color
Yakutat Bay
Farallon Islands
Western Gulf of Alaska
Prince William Sound
Southeastern Alaska
160°
150°
140°
130°
120°
Longitude
West
East

Discussion

Migratory Movement

Humpback whales in the central and eastern North Pacific demonstrated a complex pattern of migratory movement. Whales from Mexico traveled northwesterly to the Farallon Islands, southeastern Alaska, and Prince William Sound. Whales from Hawaii traveled northeasterly to southeastern Alaska, Yakutat Bay, and Prince William Sound, and due north to Chirikof Island in the western Gulf of Alaska. These observations contradict Darling and Jurasz's (1983) proposal that the predominant migratory direction in the North Pacific is along a southwest to northeast axis. Darling and Jurasz's (1983) observation appears to be an artifact of sampling primarily in Hawaii and southeastern Alaska. which fall along a southwesterly to northeasterly axis. In any case, the axis between migratory destinations reflects only the vectoral sum of migratory movement, not the actual path of humpback whale migration in the North Pacific.

Migratory Rates

Chittleborough (1953) estimated a migratory rate of 8 km/hr for humpback whales based on short-term observations of swimming speed. Dawbin (1966) used the time delay between seasonal peaks in the catches of shore-based whaling stations at different latitudes to estimate an average rate of 2.28 km/hr (15 degrees per month) for the entire migratory transit. The fastest documented migratory rate of southeastern Alaska whales, 2.38 km/hr, agrees closely with Dawbin's estimate. However, my estimates, like that those of Dawbin, make the unlikely assumption that the migrating whales followed a straight-line path between southeastern Alaska and Hawaii. It is also unlikely that these whales were photographed on their last day in southeastern Alaska or on their first day in Hawaii. The actual time in migratory transit may be considerably less than implied by the photographic data.

Population Structure

Humpback whales in the eastern and central North Pacific do not appear to form two reproductively isolated stocks with separate feeding grounds corresponding to the Hawaiian and Mexican wintering grounds. Neither are they entirely nomadic, assorting randomly among different regions of each seasonal habitat in alternate years. Instead, the analysis of migratory return. migratory movement, and fluke coloration indicated that these whales. like humpback whales in the North Atlantic (Whitehead 1982; Katona et al. 1983; Martin et al. 1984), form several geographically-isolated "feeding herds". Individuals from these feeding herds intermingle in either Hawaii or Mexico during the breeding season but show little tendency to alternate between the two wintering grounds in different years. In most cases, the segregation or intermingling of whales from different regions was not absolute, but a matter of degree.

Strong site fidelity to a given feeding region was indicated by the large proportion of migratory returns to southeastern Alaska. Of the 326 photo-identified whales from this region, 47.2% were sighted in more than one of the five study years. Long-term studies of whales in Glacier Bay, southeastern Alaska. show that individual whales have returned to this locale for at least ten separate seasons across a twelve year period (Jurasz and Palmer 1981a,b; Perry et al. 1985). Site fidelity, as demonstrated by photographic resightings, is also reported for whales that summer in Prince William Sound (Hall 1979; Matkin and Matkin 1981) and other parts of the Gulf of Alaska (Rice and Wolman 1982).

Geographic segregation of feeding herds was indicated by the analysis of regional exchange. The comparison of photographs among the feeding regions resulted in only one match; southeastern Alaska to Yakutat Bay. Some movement or exchange between southeastern Alaska and Prince William Sound was shown by photographs from a 1984 study (Baker et al. 1985), but the number of matches was still far less than expected from the across-years-within-region resighting probability. Other comparisons of photo-identified whales from the North Pacific also revealed little or no exchange among summer habitats (Jurasz et al. 1981; Darling and McSweeney 1983). Although the waters of southeastern Alaska seem to encompass the primary range of a single feeding herd (Baker et al. 1985), the exact geographic boundaries of each feeding herd are unknown and may involve some overlap.

The coloration of humpback whale flukes showed systematic difference across the five feeding regions. The clinal increase in the proportion of darkly pigmented flukes from the Gulf of Alaska eastward to the Farallon Islands was similar to that observed among stocks in the southern hemisphere (Omura 1953; Chittleborough 1965). Presumably, humpback whale coloration is genetically controlled, and coloration differences of whales in the southern hemisphere are the result of some genetic isolation (Gaskin 1982). Although feeding herds in the North Pacific intermingle to breed, a genetic cline could be maintained in one or more of the following ways:

1) mating within a feeding herd while still in the feeding region or during migration;
2) assortative mating between like-colored whales on the wintering grounds, similar to the assortative mating found among color phases of the lesser snow geese (*Anser caerulescens*) (Cooke et al. 1976); or
3) maternal inheritance of coloration and maternally-directed fidelity to a feeding region.

The intermingling of different feeding herds in Hawaii and Mexico was clearly demonstrated by the analysis of migratory movement and fluke colorations. Whales from different feeding regions traveled to the same wintering ground and whales from the same feeding region traveled to different wintering grounds. The average fluke coloration of whales from Hawaii and Mexico was similar and intermediate between the extremes of the feeding regions. The distribution of color phases in Hawaii and Mexico may reflect the intermingling of different feeding herds.

Although not statistically significant, a tendency for whales from feeding regions in the central North Pacific to travel to Hawaii and for whales from the eastern North Pacific to travel to Mexico is suggested by the migratory movement data. No whales from Hawaii were found near the Farallon Islands and no whales from the western Gulf of Alaska were found in Mexico. A longitudinal trend in selecting wintering grounds would be energetically economical if migratory travel follows a straight-line path between seasonal habitats.

The analysis of migratory return was inconclusive in determining the strength of fidelity to a single wintering ground. Only 13.7% of the whales photo-identified in Hawaii were resighted across years and no whales were seen in both of the small samples of photographs from Mexico. However, the proportion of resightings across years is a function of both sample size and the true abundance of animals in a region. Consequently, it is not strictly comparable between regions unless standardized by an independent estimate of abundance.

Some exchange between the Hawaiian and Mexican breeding grounds was confirmed by the resighting, across years, of at least one whale. However, this single match was far less than expected if whales alternated randomly between the two wintering grounds. A greater degree of interchange between wintering grounds is suggested by Darling and Jurasz's (1983) report of two resightings among a much smaller sample of photographs from Hawaii and Mexico. Further photographic data from Mexico will be necessary to determine, with confidence. the extent of exchange among wintering grounds.

Several authors have suggested that the recent analyses of humpback whale song provide additional evidence for populational exchange across the wintering grounds of the central and eastern North Pacific. Winn et al. (1981) and Payne and Guinee (1983) found that the structure of humpback whale songs from Hawaii and Mexico was essentially identical in a given year, but clearly different from the structure of songs shared by whales from other oceans. Because humpback whale song changes. to some degree, from year to year (Winn and Winn 1978; Payne et al. 1983), whales that travel to Hawaii and Mexico presumably must be in acoustic contact at some point to learn the new song. Although the data presented here show that whales which winter in Hawaii and Mexico are found together in southeastern Alaska and Prince William Sound, singing is rarely heard during the summer season when most whales are found in these feeding regions.

Payne and Guinee (1983) suggest that song change may be transmitted by singers that visit both wintering grounds during a single winter season or by a 4,800 km long "string" of migrating singers maintaining acoustic contact between the two regions. An alternative hypothesis is suggested by observations of whales singing in southeastern Alaska during late fall and winter (Baker et al. 1985). Whales found in southeastern Alaska late-season groups are known to migrate to both Mexico and Hawaii and some individuals complete the southerly migration even after remaining in northern waters until as late as December. If the new song is established by late-season singers in northern latitudes and these singers later travel to different wintering grounds, they could act as the vectors of song exchange. In this case, no direct interchange between wintering grounds would be necessary.

Payne and Guinee (1983) conclude that the analysis of song structure provides an accessible method of delineating stocks or reproductively-isolated groups of humpback whales. However, neither Winn et al. (1981) nor Payne and Guinee (1983) demonstrate geographic variation in the songs of different sub-populations of humpback whales in the same ocean. only differences in the songs of populations in different oceans. Until differences between the songs of sub-populations are found, the validity of this method remains in question. Additionally, the potential for whales to exchange songs while still in northern latitudes cautions against reliance on this technique to distinguish breeding groups.

A whale stock is generally considered to be a relatively homogeneous sub-population which remains segregated from other stocks throughout the year and within which individuals have the potential to freely interbreed (Chapman 1974). This traditional definition is not adequate for the complex population structure of humpback whales in the North Pacific and the North Atlantic. Instead, both groups are best described as "structured demes" (D.S. Wilson 1975; 1977) or, in keeping with whaling terminology, "structured stocks". Each structured stock consists of several feeding herds or "ecological demes" which intermingle to breed on one or more wintering grounds. Within a structured stock sets of whales associate with different probabilities in each seasonal habitat. These seasonal changes in associations have important implications for the evolution of social organization in humpback whales.

Recent observations of humpback whale behavior indicate that sexual selection and ecological forces have acted independently in each seasonal habitat to create contrasting social systems (Baker and Herman 1984b). On the wintering grounds, the social organization of humpback whales can be described as a polygamous mating system involving male-male competition for sexually mature females (Chapter 2; Chapter 3). In some feeding regions, the social organization is characterized by non-competitive and, at times, cooperative feeding behavior involving long-term associations between individuals (Baker et al. 1982; Baker et al. 1983; Weinrich 1983; Baker and Herman 1984b; Chapter 4).

In a competitive mating system, an individual will decrease its inclusive fitness by competing with related individuals. In a cooperative feeding system, an individual will increase its inclusive fitness by cooperating with related individuals. For humpback whales, the inclusive fitness of individuals could be optimized by forming a structured stock in which individuals feed among related individuals but breed among unrelated individuals. Matrilinial kinship within feeding herds could be maintained if fidelity to a feeding region is established when a calf first travels to the feeding grounds with its mother (Baker and Herman 1984b; Martin et al. 1984). Observations of several individuals, first identified as calves, repeatedly returning to the same feeding region as their mothers, suggests that this is the case (Jurasz and Palmer 1981a,b; Mayo and Clapham 1983). Baker and Herman (1984b) suggest that the hypothesis of a structured stock could be further tested by determining the relatedness of individuals in feeding groups and breeding groups with immunological or isozymatic techniques.

The formation of a structured stock also has consequences for the management of humpback whales. In recent years, the abundance of humpback whale populations has been estimated by applying mark-recapture models to photo-identification data (Baker et al. 1982; Whitehead 1982; Darling et al. 1983). These models assume that all individuals within a population have an equal probability of being marked and recaptured (Seber 1982). A structured stock, however, is composed of sets of whales with different probabilities of associations. This suggests that mark-recapture models must be applied with caution if they are to yield valid results. Geographically-isolated feeding herds can be estimated by sampling within their respective feeding regions where the probability of capture is equal for all members of the herd (Whitehead et al. 1980; Baker et al. 1982; Whitehead 1982; Baker et al. 1983; Baker et al. 1985). The weighted mean estimate of 374 animals (+/- 47 at the 95% confidence limit) in the southeastern Alaska feeding herd is surprisingly close to Baker et al.'s (1985) estimate based on Petersen estimates from contiguous years. Estimating the abundance of an entire structured stock, however, may be more difficult. Although the weighted mean estimate of 1,627 animal (+/- 307 at the 95% confidence interval) for the Hawaiian wintering congregation is also in close agreement with another recent estimate (Darling et al. 1983), both estimates should be considered with caution. If alternating between wintering grounds is common, whales must be marked and recaptured in all wintering grounds to assure an unbiased estimate.

Exploitation of a structured stock could have a differential impact depending on its seasonal timing. Local harvesting during the feeding season could quickly deplete a feeding herd. This may have been the case in southeastern Alaska where the harvests of shore-based whaling stations declined rapidly after only one or two good seasons (Bockstoce 1978; Rice 1978). On the other hand, shore-based whaling stations along migratory routes or near the wintering grounds were able to take greater numbers of humpback whales over many seasons (Nishiwaki 1959; Pike and MacAskie 1969; Rice 1974; Rice 1978).

Why does the apparent population structure of humpback whales in the northern hemisphere differ from that in the southern hemisphere? I can suggest two answers. First, the differences in the ecological conditions between the two hemispheres could be large enough to influence the animals' social structure. The coastal diversity of the North Pacific and the North Atlantic offer a fine-grained habitat in which prey distribution may be relatively predictable due to topographic upwellings and coastal runoff. This could facilitate the establishment of site fidelity by feeding whales. The pelagic feeding grounds of the Antarctic, by comparison, seem featureless. The distribution of prey is thought to be determined by dynamic upwellings (Gaskin 1982) resulting from shifting cyclonic weather patterns (Chittleborough 1965). Prey type may also influence social organization. Humpback whale diet in the northern hemisphere is extremely varied and consists of both macroplankton and schooling fishes (Mitchell 1975). Baker and Herman (1984b) report that cooperative behavior among North Pacific humpback whales is associated primarily with feeding on schooling fishes. On the feeding grounds of the southern hemisphere, the diet of humpback whales consists almost entirely of euphausiids (Gaskin 1982). This monotypic diet may not have encouraged the development of cooperative feeding strategies.

Second, structured stocks may also exist undetected in the southern hemisphere. Stocks in the southern hemisphere were delineated primarily through discovery-tag marking and recovery. Because the recovery of a discovery tag was a terminal event for the whale, information collected from a single whale was usually limited to only the time and position of first marking and the time and position of recovery. Only in rare cases was a whale tagged more than once before it was recovered. As a consequence, discovery tagging could not reveal repeated migratory return or individual associations among whales, both of which are important in describing a structured stock.

What is the relationship between whales from the Asian wintering grounds and those which winter near Mexico and Hawaii? Is there enough intermingling of feeding herds and exchange between wintering grounds to consider all whales in the North Pacific a single structured stock? Whaling biologists agree that humpback whales throughout the North Pacific have darkly pigmented bellies and flanks (Pike 1953; Tomilin 1957; Nishiwaki 1959, 1960, 1962). Glockner-Ferrari and Ferrari (1984) suggest that this is evidence for the existence of only one stock in the North Pacific. The uniformity of flank and belly coloration is puzzling given the diversity of fluke coloration. Unfortunately, whaling biologists, with the exception of Pike (1953), provide little quantitative data concerning the relationship between ventral body coloration and fluke coloration. This absence of data is probably attributable to the whalers' practice of removing the flukes while at sea, before the whales were examined by biologists (Pike 1953). The limited data presented by Pike (1953) indicate that fluke coloration is not highly correlated with belly or flank coloration. Similarly, the data on variation in flipper coloration indicate little correlation with belly and flank coloration among the humpback whales which winter in Hawaiian waters (Herman and Antinoja 1977; Glockner-Ferrari and Venus 1983).

Discovery tag marking and recovery showed that whales traveling to winter grounds south of Japan were found summering in the Bering Sea as far east as Unimak Island (Nishiwaki 1967). This eastern-most documented feeding area of Asian whales is only a few hundred kilometers west of Chirikof Island, the western-most documented summering ground of whales from Hawaii. The proximity of these sightings suggests some overlap in the summering grounds of whales from Hawaii and the western Pacific. However, observations from the southern hemisphere (Chittleborough 1965) indicate that overlap of the summer range is not necessarily evidence of significant exchange between stocks.

Speculation aside, available data does little to confirm or deny Kellogg's (1929) original hypothesis of an American and an Asian stock in the North Pacific. The population structure of humpback whales in the eastern and central North Pacific, as described by individual movement, coloration, and song structure, is complex. Without comparable data from the western North Pacific, the relationship between these two groups remains unknown, and our knowledge of humpback whale abundance, migratory behavior, and social organization remains incomplete.

Chapter II

The Reproductive Histories of Humpback Whales in Hawaii and Southeastern Alaska

Abstract

A total of 1230 whales were photo-identified in either southeastern Alaska or Hawaii during the years 1977 to 1984. 119 of these whales were inferred to be reproductively mature females based on their close association with a calf in one or more years. 154 whales were inferred to be males based on their roles as singers or escorts in Hawaii. An additional three whales, sighted only in southeastern Alaska, were inferred to be males based on the absence of an accompying calf across sighting histories of five or more years. Differences in the fluke coloration of males and females may suggest either sexual dimorphism or sex-based differences in migratory movement. Reproductive histories of males corroborate the hypothesis that singing and escorting are interchangeable male roles. Interbirth or "calving" intervals were determined from multiple sightings of individual females and ranged from one to six years in length. In Hawaii, sightings of seven females across contiguous years gave an estimated reproductive rate of 0.60 (calves per mature female per year). In southeastern Alaska, sightings of 30 females across contiguous years gave an estimated reproductive rate of 0.349. The survival of a calf through at least its first year of life was documented in five cases and one incident of possible weaning was observed. The apparent loss of a calf between Hawaii and southeastern Alaska was documented in one case. Neonatal mortality of 2.6% - 8.1% during the first six months of life was estimated by comparing the observed calving rates in southeastern Alaska to reported pregnancy rates from commercial catches. I suggest that reproductive

rates estimated from sightings of females in Hawaii are inflated by an increased sightability of cow-calf pairs and the failure to account for neonatal mortality. The lower interbirth intervals observed in southeasern Alaska may more closely reflect "true" rates of population increase.

Introduction

The humpback whale, like other baleen whales, lacks any obvious sexually dimorphic traits. Although adult females are, on average, slightly larger than adult males, this difference is of little use in sexing individuals (Mathews 1937; Ralls 1976). Conclusive proof of an individual's sex comes only from full-ventral observations of the genitals (True 1904; Mathews 1937). While such observations are easily obtained on the flencing deck of a whaling vessel, they are considerably more difficult to obtain from live animals in the wild. Recently, photographs of the lateral profile of the genitals have also been used to sex individuals (Glockner-Ferrari and Venus 1983). Unless a whale is inverted at the surface, however, its genitals are visible only to an underwater observer. This restricts the direct sexing of animals in many situations, including behavioral studies in northern waters.

Indirect evidence of a whale's gender can accumulate from its long-term sighting histories and documentation of social behavior. Because of the close association of a cow and her calf it is usually possible to identify a calf's mother, even when other adults are present in a group (Herman and Antinoja 1977). The fact that cow-calf pairs never associate with each other on the Hawaiian wintering grounds helps to prevent confusion about the mother of an individual calf (Herman and Antinoja 1977; Herman et al. 1980).

Data have also accumulated on the sex of individuals found in two behavioral roles characteristic of humpback whales on the wintering grounds: "escorts" and "singers". Herman and Antinoja (1977) first described the common association of an adult humpback whale with a cow-calf pair in Hawaiian waters and termed the adult companion of the pair an "escort". Herman and Tavolga (1980) later suggested that the escort may play an allomaternal role in protecting the calf or, alternatively, that it may be a male consorting with a female ovulating postpartum. Recent studies show that the duration of affiliation between an individual escort and cow-calf pair is generally only a few hours (Darling et al. 1983; Tyack and Whitehead 1983; Mobley and Herman 1985; Chapter 3). Such a brief period of association is unlikely if allomaternal behavior were involved and suggests instead the temporary affiliation of a courting male. Glockner (1983) sexed 14 individual escorts from photographs of their genitals and found all to be males.

Payne and McVay (1971) and Winn et al. (1971) first described the song of the humpback whale and commented on its possible functions. Winn et al. (1973) reviewed whaling literature and used cytological techniques to suggest that only mature males sing. Tyack (1981) reported observations of singers involved in aggression and in behavior he believed to be associated with mating. Glockner (1983) determined that four singers were males based on the lateral profiles of their genitals. The repeated observations of individually identified whales acting as escorts or singers over several winter seasons provides further evidence that these roles are interchangeable and sex-specific to males (Darling et al. 1983; Chapter 3).

In addition to providing information on the sex and social roles of individual humpback whales, long-term sighting histories are the only method currently available for studying the reproductive cycle of female humpback whales. Based on the examination of carcasses in commercial catches, humpback whales are generally thought to give birth once every two or three years after reaching sexual maturity (Chittleborough 1965; Lockyer 1984). Pregnancy rates are reported to be 0.43 (calves per mature female per year) in the coastal eastern North Pacific (Rice 1963), and 0.40 in the western North Pacific (Nishiwaki 1962). Based on aerial censuses of Hawaiian waters during the peak of the winter season, Herman and Antinoja (1977) report that 9.1 - 9.6% of all whales observed were calves. This suggests a calving rate of 0.40 - 0.42, very close to the pregnancy rates reported by Rice (1963) and Nishiwaki (1962). Observations of individually identified cows in Hawaii indicate that some cows give birth every year (Glockner-Ferrari and Ferrari 1984), confirming earlier reports of post-partum ovulation in a small percentage of females (Chittleborough 1965). However, the proportion of the female population on a yearly birth cycle and the viability of these "yearly" calves remains in question.

Here I present data from which I infer the sex and age-class of individual humpback whales based on sighting histories and behavioral roles. The sighting histories of escorts and singers provide further evidence that these roles are sex-specific to males. Sighting histories of cows provide information on their reproductive cycles and, in a few cases, document the survival or death of calves during their first year of life.

Methods

Field studies of humpback whales were conducted in Hawaiian waters during the winters of 1979 to 1984 and in southeastern Alasks during the summers of 1980 to 1984 (General Methods). Whales were observed and photo-identified from small vessels on a daily or near-daily basis (General Methods) Additional data from years previous to 1979 are presented when available and relevant (Herman and Antinoja 1977; Herman et al. 1980).

Results

Females

Of the 1230 whales individually identified in either Hawaii or southeastern Alaska from 1977 to 1984, 119 were inferred to be reproductively mature females based on their close association with a calf in one or more years. 46 of these females were sighted only in southeastern Alaska, 59 were sighted only in Hawaii, and 14 were common to both regions.

Calving Cycles. Sightings of females across more than a single year provided information on calving intervals of humpback whales. Because sighting histories were seldom continuous, it is useful to distinguish "determined" calving intervals from "undetermined" calving intervals. Undetermined intervals were defined as the longest continuous series of sightings of a female without a calf, regardless of whether of not those sightings were bounded by a previous or subsequent sighting with a calf. Consequently, undetermined intervals are only a minimum estimate of the true calving interval. Determined intervals were defined as consecutive sightings of a female that were bounded by previous and subsequent sightings with a calf. A determined interval can be one year or more in length. An undetermined interval, by definition, must be two years or more in length. Any sighting of a female without a calf was assumed to represent a two-year undetermined interval. For example, #530 (Case 31, Table 13). was sighted without a calf in 1981 and 1983 and with a calf in 1982 and 1984. These four sightings indicate one determined two-year interval between the birth of a calf in 1982 and the birth of the next calf in 1984. An undetermined two-year interval is indicated by the absence of a calf in 1981.

Forty females were sighted in southeastern Alaska during more than one year (Table 13). The 114 sightings of the southeastern Alaska females provided information on 55 calving intervals. Only 3 calving intervals were determined; 2 intervals were two-year and 1 was one-year. The 52 undetermined intervals included 40 two-year, 8 three-year, 2 four-year, 1 five-year, and 1 six-year intervals.

Eighteen females were sighted in Hawaii during more than one year (Table 14). The 40 total sightings of the Hawaiian females showed 16 undetermined two-year intervals, 1 determined two-year interval, and 1 determined one-year interval.

Table 13

Reproductive histories of female humpback whales sighted on more than one year in southeastern Alaska.

Case	Animal Number	Sighting Year 80*	81	82	83	84	Total Sightings	Total Calves
1.	154	C		A		A	3	1
2.	235	A	C			C	3	2
3.	508	A	C	C			3	2
4.	573	C	A		A	C	4	2
5.	161	A	A	A	C	A	5	1
6.	166**	A	A	A	A	A	5	0
7.	539	A	A	C	A	A	5	1
8.	587	A	A	A	A	C	5	1
9.	229		C	A			2	1
10.	289		A	C			2	1
11.	501		A			C	2	1
12.	510		C	A			2	1
13.	535		C			C	2	2
14.	540		C		+	A	2	1
15.	554**		A	A			2	0
16.	555		A	C			2	1
17.	561		A			C	2	1
18.	569		A	C			2	1
19.	595		A	C			2	1
20.	599		A	C			2	1
21.	155		A	C		A	3	1
22.	258		A		A	C	3	1
23.	277		A	A		C	3	1
24.	519		A	C		A	3	1
25.	541		A	A	C		3	1
26.	556		A	C		A	3	1
27.	580		A	A	+	A	3	0
28.	600		C	A		C	3	2
29.	741		C	A		A	3	1
30.	193		A	C	A	A	4	1
31.	530		A	C	A	C	4	2
32.	581		A	A	A	C	4	1
33.	593		A	A	C	A	4	1
34.	114			C		A	2	1
35.	216			C		A	2	1
36.	231			A		C	2	1
37.	232			A	+	A	2	0
38.	268			A		C	2	1
39.	404			A		C	2	1
40.	236			C	A	C	3	2
Total							115	43

Table 13 (Continued)

Note: The letter C indicates the presence of calf in that sighting year. The letter A indicates the absence of a calf.

* Some sighting data taken from Jurasz et al. 1981.

** Reported to be a female by Jurasz and Palmer 1981a.

\+ Sighted with a calf in Hawaii during indicated year.

Table 14

Reproductive histories of female humpback whales sighted more than one year in Hawaii.

Case	Animal Number	78	79	80	81	82	83	84	Total Sightings	Total Calves
1.	062	C			C				2	2
2.	424	A				C			2	1
3.	075		C		C				2	2
4.	370		A					C	2	1
5.	011			C			C		2	2
6.	100			A			C		2	1
7.	183			A		C			2	1
8.	071			C	A	C		A	4	2
9.	082				A		C		2	1
10.	114				A	+	A		2	0
11.	117				A			C	2	1
12.	245				C	A			2	1
13.	346					A	C		2	1
14.	354					C		A	2	1
15.	432					C		A	2	1
16.	355						A	C	2	1
17.	365						C	A	2	1
18.	442						C	C	2	2
19.	540						C	A	2	1
Total									40	23

Note: The letter C indicates the presence of calf in that sighting year. The letter A indicates the absence of a calf.

+ Sighted with a calf in southeastern Alaska during indicated year.

<u>Calving Rates</u>. Several different estimates of calving rates can be derived from the sighting histories of females in Hawaii and southeastern Alaska. If resight histories were complete, calving rates would be a direct function of birth intervals. Unfortunately, the number of determined calving intervals is presently too small to estimate calving rates. Using undetermined calving intervals would require making the unlikely assumption that all females gave birth in years that they were not sighted.

It seemed a better strategy to estimate calving rates by dividing the number of yearly sightings with calves by the total number of yearly sightings of females. This estimate makes no assumption about the presence or absence of a calf during years when a female was not sighted. However, it will be inflated if females with calves are over-represented in the sighting histories, or deflated if females with calves are under-represented in the sighting histories. The calving rate based on all sightings of females was 0.575 for Hawaii and 0.374 for southeastern Alaska.

A more conservative estimate of calving rates can be derived from the inclusion of only the sightings of a female in two or more contiguous years. This requirement should help to control any bias introduced by the conspicuous presence of a calf, unless the female was calving yearly. Using contiguous sightings also helps to guard against any cyclical bias in the presence or sightability of a female in a given region or year. Like the previous estimate, however, this assumes that the observed calving intervals were a representative sample of all intervals in each region. In Hawaii only seven females had contiguous sightings, giving a calving rate of 0.60. In southeastern Alaska, 29 females had one or more cases of contiguous sightings. From these 83 sightings there were 29 calvings giving a rate of 0.349.

Calf survival and mortality. The survival of a calf through at least its first year of life was documented in four cases (Table 15). Three calves, identified by their flukes or distinctive dorsal fins, were observed as yearlings in Hawaiian waters. Animal #72 was first observed as a newborn with its mother (#71) near Maui on March 6, 1980. Animal #72, then a yearling, and its mother were seen the following year near the Big Island across a three day period. On the first two days the yearling was sighted with the female and another adult. Behavioral observers did not recognize #72 but did note that it was small and suggested that it might be a yearling. On the second day the yearling, female, and adult "escort" were observed for over five hours during which they repeatedly tail-slapped, flipper-slapped, and breached, sometimes in tandem. The third day the female was seen alone.

Animal #416 was first observed as a calf with its mother (#541) on September 4, 1983 in southeastern Alaska. They were next seen traveling together on February 3, 1984, near Maui, unaccompanied by other adults. Behavioral observers did not recognize the yearling and assumed that it was an adult.

Animal #1072 was sighted with its mother, #245, near Maui during the winter of 1981. The cow-calf pair were next sighted in southeastern Alaska the following summer (1981). Animal #245 and #1072, then a yearling, returned to Maui and were sighted on March 9, 1982,

Table 15

The documented survival of humpback whale calves during their first year of life.

	Calf #	Cow #	First Sighting Date	First Sighting Region	Last Sighting Date	Last Sighting Region	Interval (Days)
1.	072	071	Mar 6, 1980	HI	Feb 14, 1981	HI	345
2.	1072	245	Mar 3, 1981	HI	Mar 9, 1982	HI	371
3.	198	539	Jul 10, 1982	SEA	Dec 5, 1982	SEA	148
4.	416	541	Sep 4, 1983	SEA	Feb 3, 1984	HI	152

accompanied by a male, #022, also from southeastern Alaska (Chapter 5), and an adult of unknown sex. Once again, behavioral observers did not recognize the yearling and assumed that it was an adult. All of the animals accompanying the female, including the yearling, were involved in surface activity associated with aggression (Chapter 3).

The fourth yearling, #198, was observed as a calf with its mother, #539, in southeastern Alaska throughout the summer of 1982. Observations of late-season whales in southeastern Alaska showed that #198 was still accompanied by its mother at least until December 5, 1982. The female, #539, was subsequently seen in southeastern Alaska during 1983 and 1984 unaccompanied by #198 or a new calf. Animal #198 has not been resighted since the late-season of 1982.

One incident of apparent calf mortality was documented. Animal #183 was sighted with a newborn calf on March 15, 1982 near Maui. She was next sighted in southeastern Alaska the following August and September, 1982, unaccompanied by a calf.

Males

A total of 154 whales were inferred to be mature males based on their roles as escorts or singers in Hawaii. Twenty-five of these males were sighted in both Hawaii and southeastern Alaska. An additional three whales, sighted only in southeastern Alaska, were inferred to be males based on the absence of an accompanying calf across sighting histories of five or more years.

Many of these males were sighted in either Hawaii or southeastern Alaska across more than one year. Of the 157 males, 3 were sighted in six years, 9 in five years, 9 in four years. 13 in three years, and 18 in two years. No animal identified as an escort or singer in one year was observed as a cow with a calf in any alternate years.

Continuity and interchange of behavioral roles. The 154 males were sighted in Hawaii on 269 occasions, including multiple sightings within years. The animals were acting as escorts in 159 of these sightings, as singers in 27 sightings, and in two sightings the whales were escorting and singing simultaneously. In the remaining 81 sightings, no behavioral role was determined.

Several males were observed acting repeatedly as escorts or singers and a few were observed interchanging roles (Table 16). The most extensive resighting histories are available for #13 and #51. Animal #13 was observed escorting a cow-calf pair or female on five separate occasions and both singing and escorting a cow-calf pair on a single occasion during the years 1978 to 1984. Animal #51 was observed as an escort on five occasions, as a singer on two occasions, and with no known role on three occasions during 1979 to 1984. Further details of the behavior of these and other individual males are presented in Chapter 3.

Table 16

The behavioral roles and role transitions of individually identified males in Hawaii.

	Observations									
Frequency	1	2	3	4	5	6	7	8	9	10
				Escorting Only						
87	E									
6	E	E								
16	E	N								
2	E	E	E							
6	E	N	N							
2	E	E	N	N						
1	E	E	E	E	N	N				
				Escorting and Singing						
1	E	S								
1	E	E	E	E	E	ES				
1	E	ES	N	N	N	N				
1	E	E	S	S	N	N	N	N	N	
1	E	E	E	E	S	S	N	N	N	N
				Singing Only						
16	S									
3	S	N								
1	S	N	N							
3	S	N	N	N						
Total 154										

Note: The letter E indicates escorting, S singing, ES escorting and singing simultaneously, N no observable behavioral role. The role transitions are grouped into sighting categories, not listed by chronological order. Thus 87 individuals were sighted as escorts only once, six were sighted twice as escorts, 16 were sighted once as escorts and once without a known role, etc., irrespective of the order of the sightings.

Coloration of males and females

Fluke photographs were used to examine differences in the coloration of males, females, and animals of unknown sex from Hawaii and southeastern Alaska. Each fluke was assigned a score corresponding to its color phase (General Methods): 1 for predominantly white, 2 for moderately dark, and 3 for dark (Table 17). An individual was counted once in each region that it was sighted. Because some individuals were seen in both regions, this resulted in a loss of independence in regional samples but allowed for the simultaneous analysis of differences between all sexed animals as well as differences between sexed animals in each region.

Overall, animals from southeastern Alaska were darker than those from Hawaii and females were darker than males or unknowns (ANOVA region $F[1/1269] = 29.51$, $p < 0.001$; sex $F[2/1269] = 3.37$, $p < 0.035$; Tukey pair-wise comparisons $p < 0.05$). Females from southeastern Alaska were the darkest group followed by unknowns from southeastern Alaska and females from Hawaii. Males from southeastern Alaska and Hawaii were almost identical in coloration and slightly darker than unknowns from Hawaii. The average coloration of unknowns from southeastern Alaska was nearly midway between the average of females from southeastern Alaska and males from both regions.

Table 17

The fluke coloration of sexed whales in Hawaii and southeastern Alaska.

Southeastern Alaska

Sex	Color Phase 1	2	3	Mean Color Phase
Females	8 (13)	19 (32)	33 (55)	2.42
Males	9 (32)	12 (43)	7 (25)	1.93
Unknowns	84 (24)	127 (37)	137 (39)	2.14

Table 17 (continued)

Hawaii

Sex	Color Phase 1	 2	 3	Mean Color Phase
Females	20 (27)	34 (47)	19 (26)	1.99
Males	54 (35)	63 (41)	37 (24)	1.89
Unknowns	205 (33)	263 (43)	145 (24)	1.90

Note: Percentages of flukes in each color phase are shown in parentheses.

Discussion

Females

The sighting histories of female humpback whales in southeastern Alaska indicate that the reproductive rate of this population was 0.349 - 0.374 during the study years. Calving cycles of individual females were variable, ranging from one year to five years. If the observations of Jurasz and Palmer (1981a) are correct, one female, #166, seen with a calf in 1974, was without a calf in five consecutive years of observations.

Why were reproductive rates of females in southeastern Alaska lower and more variable than estimated rates based on commercial catches, survey counts, and other individual animal studies? The answer can be found in the potential biases of each technique. Pregnancy rates based on the presence of fetuses in commercial catches do not account for stillbirths or neonatal deaths and may be biased by international regulations which prohibit taking females with calves, effectively excluding these females from catch statistics. Differences in the migratory timing of age-sex classes may also result in differential exploitation (Mizroch 1983).

Counts of calves on the wintering grounds may be affected by the sightability of cow-calf pairs and seasonal changes in the relative abundance of other age-sex classes (Herman and Antinoja 1977; Perrin and Donovon 1984). Individual animal studies may suffer from the problems of discontinuous sighting records and the conspicuousness of females when accompanied by a calf. Studies confined to the wintering grounds will not account for neonatal mortality unless the studies are able to document the calves' return the following year. The estimates, reported here, of calving rates in Hawaiian waters (0.527 - 0.600) are probably inflated for these reasons.

Many of the biases affecting other techniques did not affect the estimates of reproductive rates based on sighting histories of females from southeastern Alaska. The high probability of return to the region (Chapter 1) helps assure that individuals are seen repeatedly and continuously across several years, regardless of the presence or absence of a calf. Estimates of reproductive rates from southeastern Alaska also take into account stillbirths and some neonatal mortality; a calf sighted in southeastern Alaska during July or August has already survived its first six months of life and its first long-range migration. The only bias I could not prevent was the possible inclusion of sighting years prior to a female's sexual maturity, resulting in an overly conservative estimate of calving rates. Only very long-term reproductive histories similar to those available for humans (Palmore and Gardner 1983) will assure a thorough understanding of all important reproductive parameters.

The survival of calves through the first year of life was documented in four cases. Three cases showed the migratory return to Hawaii of the yearling with its mother. In one of these cases the yearling disaffiliated from the cow following a strenuous episode of aerial behavior lasting over five hours. It is possible that the calf's departure was an instance of weaning and that the preceding aerial activity was the result of the cow's refusal to nurse. Similar parent-offspring conflicts are common during weaning in some ungulates (Leuthold 1977). If this interpretation is correct, it supports the earlier conclusion of whaling biologists that humpback calves nurse for nearly a full year (Chittleborough 1965; Lockyer 1984). Behavioral observations of right whales (Eubalaena glacialis) also indicate that yearlings are weaned after their return with their mother to the wintering grounds (Taber and Thomas 1982).

One case of neonatal mortality was documented by the loss of a calf between Hawaii and southeastern Alaska. An overall neonatal mortality of 2.6 - 8.1% during the first six months is suggested by comparing the observed calving rate in southeastern Alaska (0.374 - 0.349) to the pregnancy rates from commercial catches in the western (0.40, Nishiwaki 1959) and eastern (0.43, Rice 1963) North Pacific. Although this estimate of neonatal mortality may be inflated if reported pregnancy rates from catch statistics are inflated, it is comparable to Schwartz and Jones' (1984) report of 5.3% mortality among gray whale calves in the calving lagoons.

Possible causes of mortality for humpback and gray whales include stillbirths, accidental strandings, predation, and even harassment by vessel traffic (Lockyer 1984). Evidence of non-fatal attacks by killer whales, Orcinus orca, or pelagic sharks comes from the presence of parallel scarring on the flukes of the humpback whales. These scars are found on 34 of the 1348 (2.5%) flukes in the entire photo-identification catalog (unpublished data). Like other large mammals, humpback whales are probably most susceptible to predation when they are young or sick (Caughley 1977). In one case a 6 - 9 month old calf sighted in southeastern Alaska on September 6, 1984, showed extensive scarring, apparently as the result of an orca attack (Figure 9). No adults were documented to have acquire similar scars during their sighting histories.

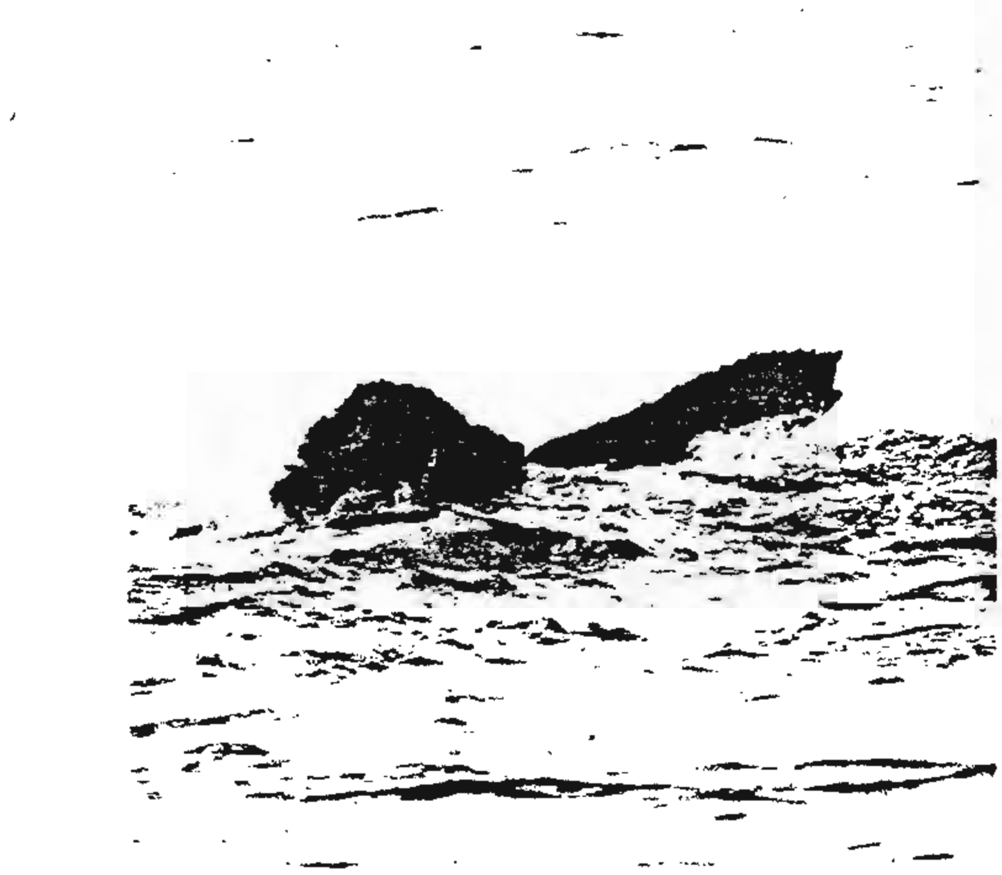
Males

The sighting histories of animals inferred to be males corroborate other reports, reviewed earlier, that escorting and singing on the wintering ground are sex-specific role of males. Some males have been sighted repeatedly acting as an escort over as many as six consecutive years. Individuals seen as escorts were also seen as singers, confirming the interchangeability of these behavioral roles. No animal sighted as a cow in one year was sighted as an escort or a singer in alternate years.

There is only one report of singing by a cow (Tyack 1982). In this single incident, singing was heard for 19 min in the vicinity of what appeared to be a lone cow-calf pair. Based on the absence of more than a single adult at the surface, the observers assumed that the cow was singing. However, the possibility cannot be excluded that a second adult was also present and surfacing alternately with the cow (Watkins and Moore 1983). Other incidents of singers in the company of cow-calf pairs initially resulted in a similar confusion (Herman and Tavolga 1980; Chapter 3).

It is tempting to assume that all adults accompanying females in Hawaii are males. In large, surface-active pods that include females without a calf, the role of the accompanying adults appears directly

Figure 9: Scarring from a killer whale attack on the fluke of a humpback whale calf, approximately 6 - 9 months old.



analogous to that of escorts (Tyack and Whitehead 1983; Chapter 3). While this may be true in most cases, the observation of a female and her yearling in a surface-active pod cautions against an uncritical acceptance of this analogy. This caveat does not necessarily apply to escorts accompanying a cow-calf pair. The chance of a cow with a calf being "escorted" by her yearling is probably vanishingly small due to the infrequency of yearly calving cycles and the likelihood that a yearling is weaned before a new birth. To date, no observations of a cow-calf pair accompanied by a yearling have been reported. Nonetheless, inferring gender from behavioral roles must continue to be evaluated and corroborated by direct sexing with genital photographs and, possibly, karyotyping or other cytological techniques.

Coloration

The analysis of fluke coloration indicates that females were darker than males and unknowns, even after attempting to account for overall differences in the coloration of whales from Hawaii and southeastern Alaska. In his study of humpback whales taken from a shore-based whaling station on Vancouver, British Columbia, Pike (1953) reported that females were generally darker than males in throat, flank, and fluke coloration. Glockner-Ferrari and Venus (1983) present data suggesting similar differences in the coloration of escorts and females from Hawaiian waters but they did not comment on this trend.

Interpreting color differences in females and presumed males as sexual dimorphism is confounded by evidence for a general cline in the coloration of humpback whales across the feeding grounds of the central and eastern North Pacific (Chapter 1). This is further complicated by the overall differences between whales from some feeding regions, including southeastern Alaska, and whales on the Hawaiian and Mexican wintering grounds. Regional differences were also apparent in the coloration of females and unknowns from Hawaii and southeastern Alaska; only presumed males from both regions were of similar coloration. This confusing situation could be explained by the following hypotheses:

1) there is a general cline in the coloration of whales from different feeding grounds;
2) females and males from different feeding regions mix on the wintering ground, resulting in an average coloration intermediate between the extremes of the feeding regions;
3) females are more site specific to their natal feeding ground (philopatric) than males, resulting in some dispersal of males from their natal feeding ground.

Some available data are consistent with these hypotheses. The mixing of males and females from different feeding herds during the winter season and the possible mechanisms for maintaining a genetic cline in the feeding regions were discussed previously (Chapter 1). A greater degree of philopatry in female humpback whales would be consistent with the general trend among mammals (Eisenberg 1981; Greenwood 1983). In the North American black bear, <u>Ursus americanus</u>, for example, females often inherit part of their mother's territory and are tolerant of territorial overlap with related females (Rogers 1974, cited in Wilson 1975).

One testable prediction of this hypothesis is that females from Prince William Sound, the Gulf of Alaska, or other feeding grounds to the west will be lighter than females from southeastern Alaska, while males from these region will be similar in coloration. A small sample of sexed animals from Prince William Sound and the western Gulf of Alaska is suggestive but far from conclusive; the three females were all of the lightest color phase while the two males were intermediate and dark. Counter-evidence for a greater degree of philopatry among females comes from the three animals sighted in more than a single feeding region (Chapter 1); two are thought to be reproductively mature females and the third is of unknown sex.

The possibility must also be considered that the apparent difference in the fluke coloration of males and females is an artifact of the method used to sex males in southeastern Alaska. The majority of males in southeastern Alaska (25 of the 28) were also sighted in Hawaii. If only light colored males from southeastern Alaska travel to Hawaii, the results of the color analysis would be misleading. It is difficult, however, to imagine a behavioral or population mechanism that would account for such a systematic bias. The fact that, in southeastern Alaska, animals of unknown sex were mid-way in coloration between males and females is some evidence against the possibility of a systematic bias. Nonetheless, an independent method of sexing animals in northern waters and further study of the coloration of sexed animals from feeding grounds to the west of southeastern Alaska are necessary to clarify this complex situation.

Introduction

The aggressive behavior of mysticete whales remains relatively undescribed. In his early review of cetacean aggression, Norris (1967) concluded that aggression, particularly in the context of male-male competition, is apparently universal in the odontocetes but nearly absent in the mysticetes. He noted as an exception only the gray whale, *Eschrichtius robustus*, whose violent defense of its young and aggressive behavior toward whalers earned it the name "devilfish". A few other exceptions to the portrayal of mysticetes as timid and docile creatures have also been noted. The defensive use of the flukes by humpback whales (Chittleborough 1953), and by right whales, *Eubalaena glacialis* (Donnelly 1967), in response to approaches by killer whales has been reported. Right whales have been observed to jostle each other in possible competition for females and, in a manner similiar to odontocetes, to use their flukes to strike conspecifics (Saayman and Tayler 1973; Payne and Dorsey 1983). Herman and Tavolga (1980) reviewed research on the social behavior of humpback whales and concluded that aggression in this species may be more common than previously supposed. They hypothesized that humpback whales, like most mammalian species, are polygamous and that males may compete, at least through epigamic displays, for access to sexually mature females. Some reports of aggressive or competitive behavior in humpback whales have corroborated this conclusion (Baker et al. 1981; Glockner-Ferrari and Ferrari 1981; Darling et al. 1983; Tyack and Whitehead 1983).

Agonism is often defined to as the broad range of behaviors which occur between conspecifics during conflict over access or priority of access to some resource (Scott and Fredericson 1951 cited in Brown 1975) Agonistic behavior frequenty includes acts of threat, defense, attack, escape, and appeasement. In this chapter I present observations that run counter to the popular view of mysticetes as "gentle giants", indicating instead that humpback whales engage in strenuous and sometimes violent behavior toward conspecifics. Although appeasement, defense, and escape may also have occured during these observation, my descriptions are generally limited to behaviors that appeared to be threats or direct attacks. For this restricted set of behaviors that most simply resembled "fighting", I prefer to use the term aggression (Wilson 1975). This aggression occurs in predictable social contexts, in a roughly predictable scaling of intensity, and shows a seasonal increase and decrease in frequency paralleling changes in the abundance of whales in Hawaiian waters. Further data are presented on the sex of singers and escorts and on the interchangeability of these roles. The overall evidence supports the hypothesis that, as in the odontocetes, aggressive behavior in humpback whales is the result of male-male competition for access to sexually mature females.

Methods

Field observations of humpback whales were carried out in Hawaiian waters during the winter-spring seasons of 1979, 1980, and 1981. Additional observations from 1982, and from years prior to 1979, are presented where available and relevant. Whales under observation were individually identified according to methods described earlier (General Methods). If an animal has been observed more than once it is referred to by its animal number. If resighting information is not available on an individual, it is referred to by a letter indicating its spacial position in the group of whales under observation.

Observations of whale behavior were made daily or near-daily from small boats, as well as during biweekly aerial surveys (Herman and Antinoja 1977; Herman et al. 1980; Baker and Herman 1981). One of the research boats was equipped with a submerged plexiglass viewing chamber (developed by L.M. Herman) which allowed the observation and filming of whales near the vessel. Altogether, several thousand hours of observation were made over the three-year period.

Results

Results are presented in three sections: Behavioral Observations, Behavioral Continuity, and Populational Dynamics. The first section reports some exemplary observations of aggressive behavior between humpback whales. The selection of these observations was based on one or more of the following criteria: 1) the observation contained the only example of a rare behavior; 2) the observation was of sufficient duration to encompass a broad repertoire of behavior; or 3) the individuals involved have a behavioral history relevant to the topic.

The second section presents further evidence on the social roles characteristic of individuals engaged in aggression, and on the continuity of individual behavior across several years. Finally, the section on populational dynamics relates changes in the frequency of aggressive behavior across the winter season to changes in whale abundance and the composition of groups (pods) of whales.

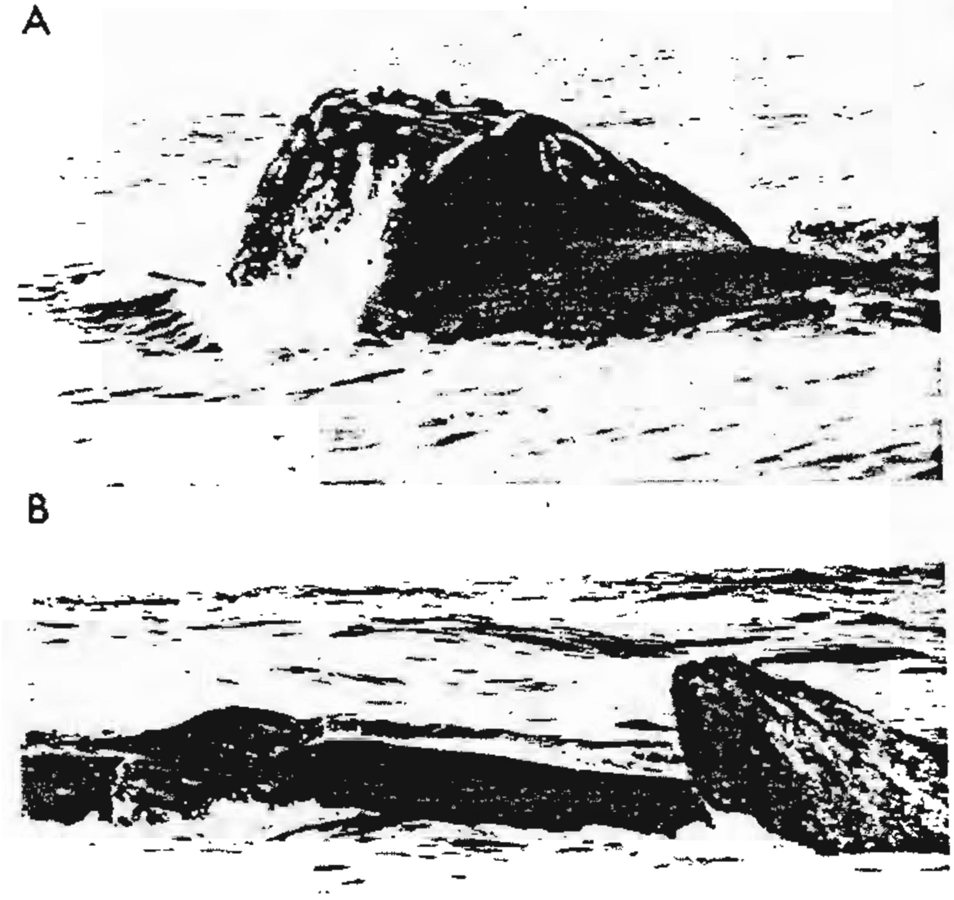
Behavioral Observations

Cow, calf, and escort pods. Observation I: On March 24, 1979, a cow, calf, and escort were seen near Lahaina, Maui. I photographically identified the cow (#172) and the escort (#13), and observed them for about one hour as they slowly moved south toward the island of Lanai. The same cow, calf, and escort were seen three hours later; at that time they were accompanied by an additional three escorts, two of which, #48 and 49, had been seen in previous years (see Behavioral Continuity). The fourth escort in the pod has not been resighted and is referred to as whale F. The whales were extremely active and remained near the surface. Consequently, we were able to record much of the next two hours of observation on videotape, through the plexiglass viewing chamber of the research vessel. The videotape records showed the ventral and lateral aspects of the escorts, allowing us to identify three of the escorts as males, #13, 48, and 49. Whale #13, the original escort, occupied a position nearest the cow-calf pair, which remained at the front of the group during the entire observation. The other three escorts repeatedly exchanged proximity to #13 and were repeatedly displaced rearwards. At each surfacing #13 lifted his jaw or rostrum above the water, exposing his ventral pleats and a partially inflated throat as he lunged ahead of the other escorts (Figure 10). This behavior has been termed an "inflated headlunging," or, more simply, "headlunging".

Viewed from below the surface the lead escort, #13, often appeared to be physically displacing the other escorts, at times actually lifting them up through the surface of the water. The escorts frequently released long streams of air from their blow-holes while swimming underwater, a behavior we have termed "bubble-trailing," and released large bursts of air just before surfacing and headlunging. The release of large bursts of air from the blow-hole either singly or in rapid sequence is referred to as "underwater blowing". Whale #13 also released an immense amount of air from both sides of his mouth. This formed a large "V"-shaped curtain of bubbles that flowed rearwards as the whale moved through the water.

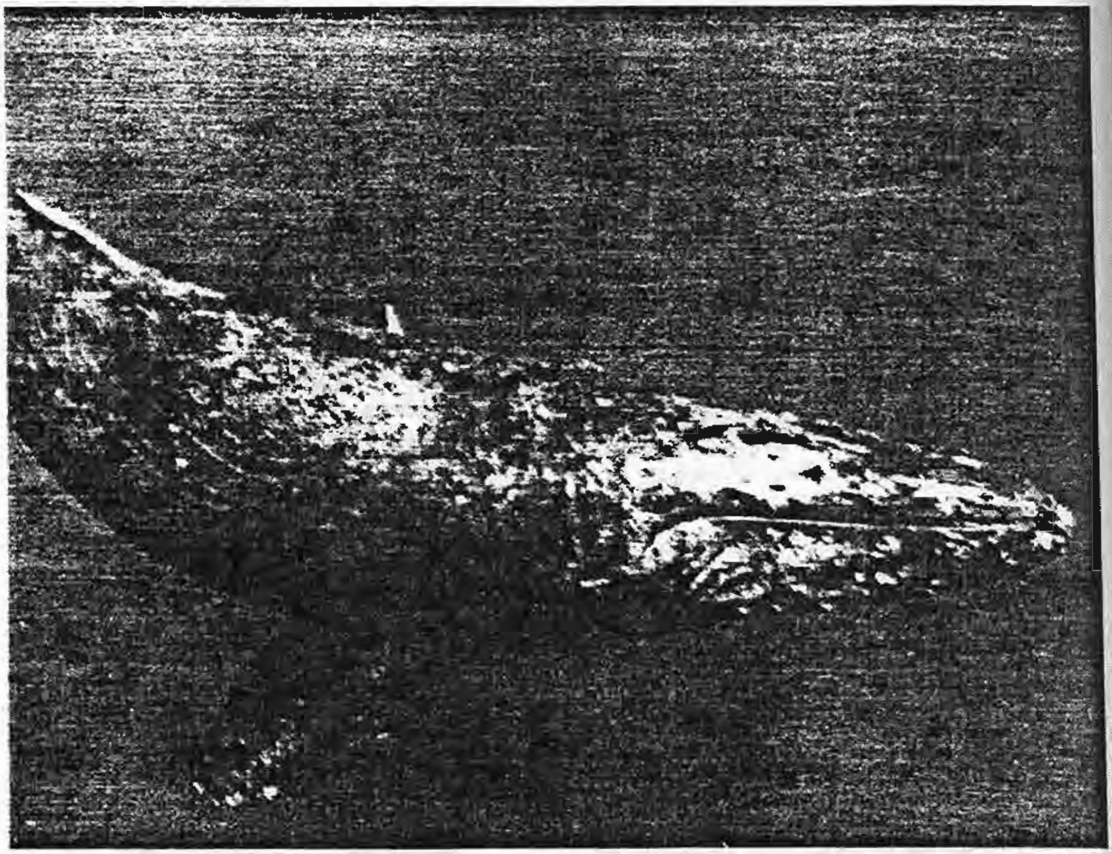
In addition to interposing himself between the cow-calf pair and the other escorts, #13 repeatedly crossed the bow of the small research vessel, showing his full lateral aspect and extending his flipper to within a few meters of the vessel (Figure 11). I have interpreted this posture as a broadside display, similar in form and function to that seen in many other mammalian species (Leuthold 1977).

Figure 10: Typical postures of headlunging humpback whales. A) The posterior to anterior aspect of whale #49 shows the engorgement of the ventral pouch. B) Lateral view of two whales headlunging. The forward whale blocked the rear whale's approach to a cow and calf in the lead of the pod. Photographs by William Stifel, Kewalo Basin Marine Mammal Laboratory.



Figu

Figure 11: A broadside threat by an escort whale. The right flipper is pointed towards the foreground resulting in its extreme foreshortening. Note parallel scars along the whale's side. Photograph by Ron Antinoja, Kewalo Basin Marine Mammal Laboratory.



The cow-calf pair remained one to two whale lengths in front of the group and was not involved in physical interactions with the escorts. The trailing escorts, #48 and whale F, were also somewhat removed from the direct competition and both disaffiliated from the pod during the latter part of the observation. Whales #13 and 49 showed the most intense interaction, and struck ventrally and laterally toward each other with their flukes. The level of activity remained high for more than two hours of observation.

Observation II: During an aerial survey conducted on April 10, 1979, a cow, calf, and escort were seen moving east along the south coast of Molokai. A fourth whale approached the trio from several hundred meters to the rear and approached the pod. On the first two approaches the escort whale changed course to diagonally intercept the "intruder" and block its approach. During the second approach the escort appeared to make body contact with the intruder and released a long bubble-trail across its path. On the third approach the escort turned around and headed towards the intruder. The intruder veered to the side as the escort delivered a violent blow with its caudal peduncle and flukes while making an abrupt 180 degree turn (Figure 12). The force of the blow lifted the posterior half of the intruder clear of the water. The original escort then moved rapidly back towards the cow and calf while the intruding whale continued to trail the trio by several hundred meters.

Figure 12: A lead escort uses its peduncle and fluke to strike the trailing escort of a cow, calf, and two-escort pod. A) The lead escort is turning just below the surface as it strikes the trailing escort with its flukes and peduncle. The force of the blow lifted the posterior third of the trailing escort out of the water. B) The lead escort completes its strike to the trailing escort and turns back in the direction of the cow and calf. Photographs by C. Scott Baker, Kewalo Basin Marine Mammal Laboratory.


A
B

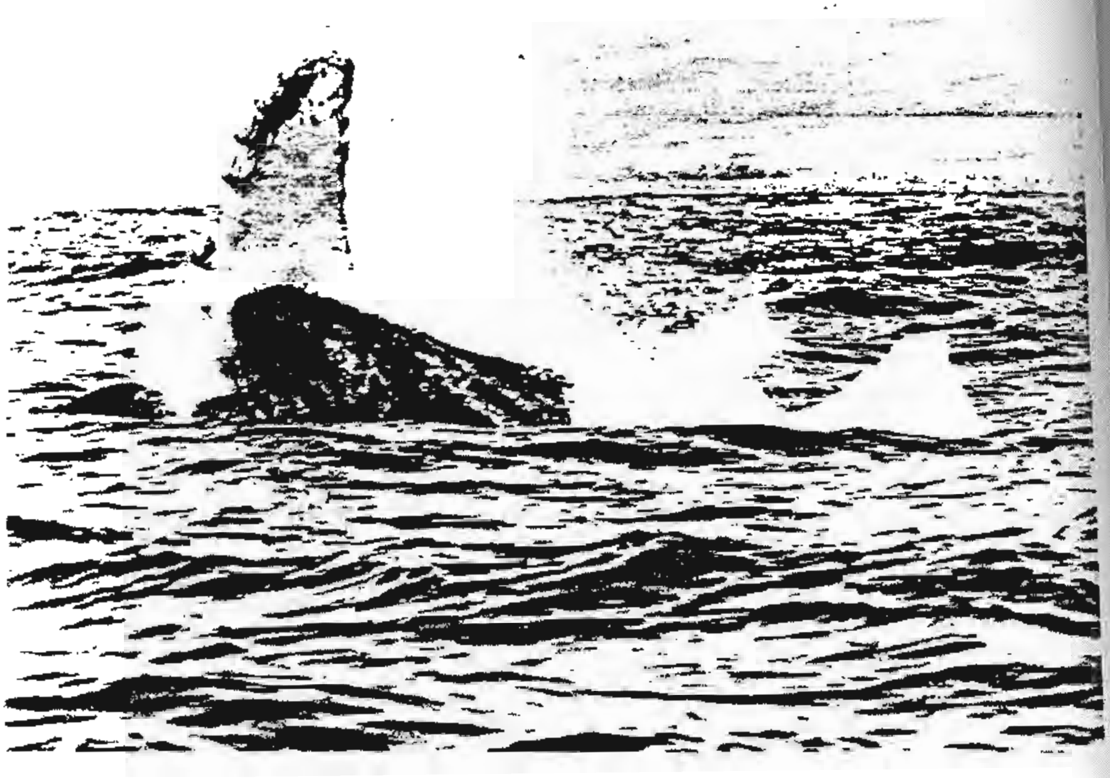
Observation III: On March 15, 1981, a cow, calf, and four escorts were observed southeast of west Maui moving rapidly and on an erratic course. One escort, #49 (see Observation I), remained nearest the cow and repeatedly displaced the other escorts rearwards by positioning itself behind the cow-calf pair and headlunging directly in the path of the other escorts. At least once he charged and butted one of the trailing escorts as the latter attempted to approach the cow-calf pair. Although the trailing escort turned sharply aside from the charge, it did not avoid a blow to its side by #49's rostrum (Figure 13). As in Observation II the animal receiving the blow rolled to one side and lifted its flipper out of the water.

Fig

After 95 minutes of interpositioning and headlunging by #49, one of the trailing escorts slapped its tail flukes on the water (flukeslapped) six times in succession. Within a few minutes the three trailing escorts disaffiliated from the pod and moved away in a northerly direction. Only one escort, #49, remained with the cow-calf pair. I followed the cow, calf, and #49 for another 40 minutes as they moved slowly and quietly to the southwest. No further surface behaviors or signs of disturbance were observed.

Observation IV: On March 20, 1980, in mid-channel between Maui and Lanai, a cow, calf, and escort were resting on the surface. Before we could photographically identify the original escort a fourth animal leaped from the water (breached) approximately 100 m away and moved rapidly toward the cow and calf. The original escort quicky moved to block the new whale's approach. I deployed a hydrophone and heard loud singing originating from one of the whales in the group. The two

Figure 13: A charge and strike between two escorts. The whale with the upraised rostrum charged the other and butted it just below the insertion of the flipper. Photograph by William Stifel, Kewalo Basin Marine Mammal Laboratory.



escorts began headlunging while the cow and calf remained quietly at the surface about two whale-lengths distant. During the observation we determined which whale was singing by correlating attenuations in song intensity with each animal's respiration at the surface (cf. Tyack 1981). The singer was the escorting whale being displaced away from the cow and calf. The singing stopped as the four animals began moving north together with the cow and calf in the lead. The two escorts continued headlunging and the escort that had been singing continued to be displaced rearwards.

Observation V: On March 11, 1981, a cow, calf, and escort were seen resting quietly in Maalaea Bay, Maui. The cow, identified as #62, had been seen previously in 1978 and 1979 (see <u>Behavioral Continuity</u> for details). The escort, #564, had not been seen before, but was identified in Southeast Alaska later, during the summer of 1981. I approached the pod to within 100 m and deployed the J-13 underwater speaker from the research vessel. A humpback whale song recorded near Maui in 1979 was played back to the pod for ten minutes. Five minutes after the playback began the escort suddenly headlunged near the cow and appeared to "herd" the cow-calf pair away from the vessel. The pod then submerged and was next seen seven minutes later, lying quietly at the surface over 500 m away. I slowly moved the vessel towards the pod to attempt a second playback. The vessel neared the pod and the engine was stopped. As we were coasting to a halt the pod surfaced ahead of us and the escort moved perpendicularly across the vessel's path, within 10 m of the bow. The escort then turned parallel to the vessel, swam approximately 15 m toward the rear of the vessel, and then turned aside. The pod moved away slowly and resumed its surface resting behavior within 100 m of the ship. During two more replications of the ten-minute playback the whales remained apparently undisturbed while maintaining their proximity to the vessel.

Pods without calves. Observation VI: On February 6, 1980, a pod of three adult whales was observed nearshore of the northwest coast of the island of Hawaii. When surfacing, the three whales maintained a constant linear order. Whale A remained in the lead some one to two whale lengths ahead of B, who in turn was ahead of the third whale, #22. At each surfacing B headlunged in front of #22, physically displacing #22 to the rear of the pod. Raw and bleeding areas on the leading edges of the dorsal fins and rostrums of B and #22 attested to the forceful contact between them. The headlunges were frequently preceded by underwater blows, and both B and #22 bubble-trailed.

The animals remained near the surface, making it possible to view some of their underwater behavior. During one underwater observation all three animals were positioned horizontally and motionless approximately 15 m below the surface; #22 was behind whale B and both were facing toward and perpendicular to whale A. Whale #22 then swam toward the surface, and making a large arc, resettled at its original depth but facing A head to head. Whale B mimicked this movement, maintaining its position between A and #22.

During most of this observation A remained quietly in place. However, at one point it rolled ventral-up at the surface and forcefully slapped the dorsal side of its flukes against the surface of the water (inverted flukeslap). Whale A later breached. These were the only aerial behaviors observed by any of the whales.

Whale A was identified as a female from photographs of its genital area taken when it was inverted at the surface. Whale #22 has been resighted extensively in both Hawaii and Southeast Alaska and is thought to be a male. Details of #22's sightings are shown in Table 18 and discussed later in the section on behavioral continuity.

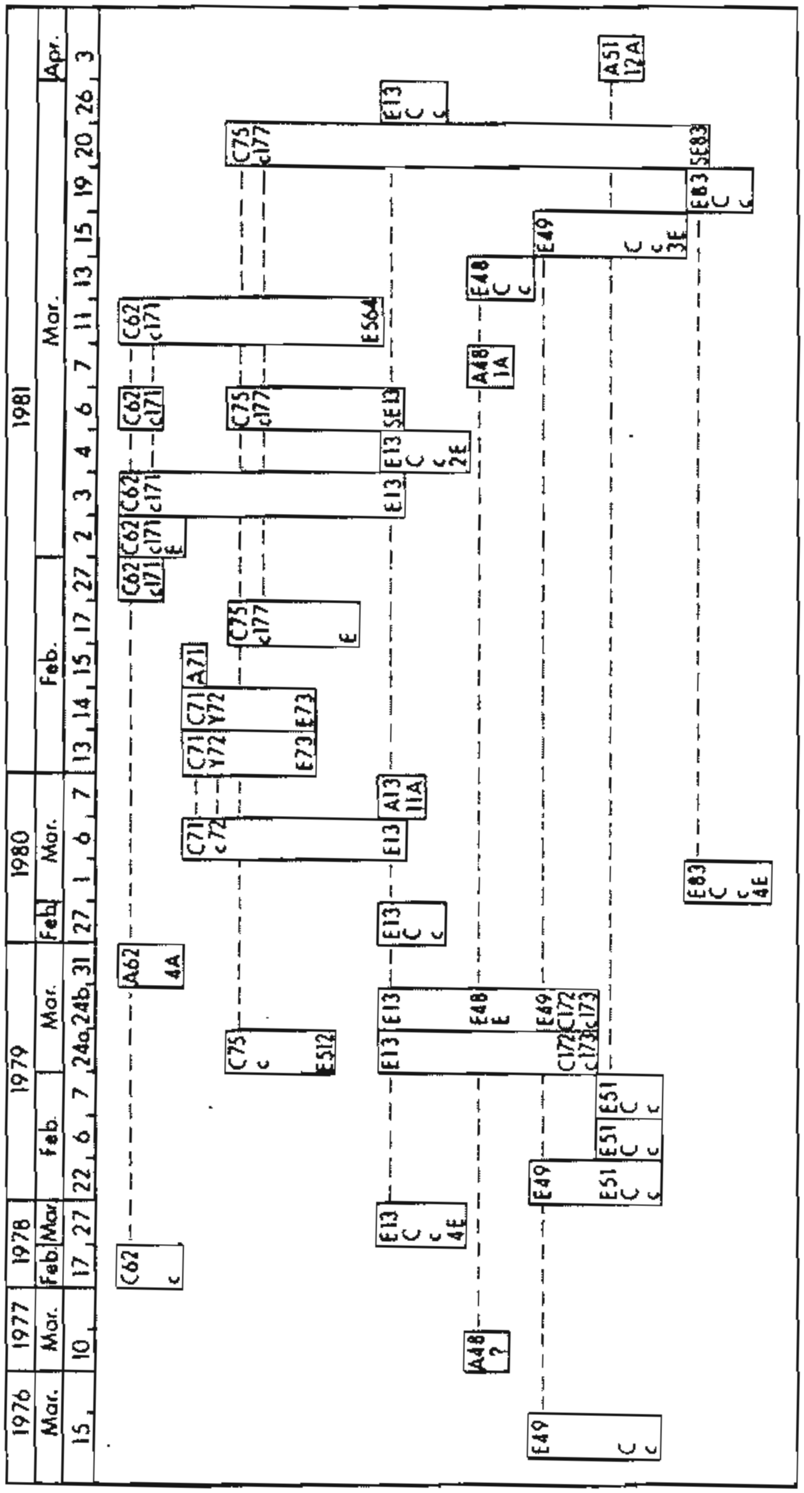
Observation VII: On March 11, 1980, a pod of three whales was sighted moving northwest offshore of Olawalu Point, Maui. As in Observation VI, the animals were moving in a line-astern formation, and are referred to by letters indicating their relative order in the pod. The position of the whales remained constant throughout the observation with A in the lead and B continuously displacing C to the rear of the formation. Both whales B and C engaged in frequent headlunging and underwater-blowing. The three whales remained at the surface during most of the observation; at one point whale A began a short series of flukeslaps and inverted flukeslaps. Forty minutes into the period of observation, whale C disaffiliated from the pod and was not resighted. The surface activity subsided and A and B moved slowly northwest for the next thirty minutes, surfacing regularly every seven to nine minutes. An unidentified animal then breached approximately 200 m away from the pair and joined the pod. The surface activity of the pod suddenly increased, and the new whale was met with a display of headlunging and interpositioning similiar to that seen earlier. Shortly after this affiliation, A again flukeslapped several times and, at one point, rolled ventral-up at the surface and repeatedly slapped its flippers against the surface of the water.

Observation VIII: On February 21, 1980, a pair of whales was observed moving slowly north near the northwest point of the island of Hawaii. A flurry of aerial behavior suddenly ensued which concluded in a breach and several flukeslaps. A third whale appeared at the surface and all three animals began moving rapidly north. As in Observations VI and VII, the second and third animal in the line-astern formation headlunged at each surfacing, with the second whale consistently displacing the third to the rear of the formation. This behavior continued for 20 minutes until the third whale turned inshore and began to sing. The original pair resumed its previous, leisurely pace and moved north out of viewing range. I continued to observe and record the lone singing whale for 40 minutes, during which time it moved less than 50 m and remained submerged, on the average, for twelve minutes between surfacings.

Behavioral Continuity

Figure 14 presents the resighting history and complex pattern of associations of some individually identified escorts and mature females resighted over six years of observations. Whale #49 was first sighted in 1976 and subsequently sighted twice in 1979 and once in 1981. In all four of these observations #49 was an escort. In Observation I, #49 was identified as a male.

Figure 14: The association of cows and escorts in Hawaii. Individually identified whales are designated by their whale number and behavioral role. Resighted individuals are shown across rows connected by dashed lines. Boxes enclose pods. A = adult, C = cow with calf or yearling, c = calf, E = escort, SE = singer-escort, and Y = yearling.


1976
Mar.
15
1977
Mar.
10
1978
Feb
17
Mar
27
1979
Feb.
22
6
7
Mar.
24a
24b
31
1980
Feb
27
Mar.
1
6
7
Feb.
13
14
15
17
27
1981
2
3
4
6
7
Mar.
11
13
15
19
20
26
Apr.
3
E49
A48
C62
E13
C75
E51
A62
C71
A13
C72
Y72
E73
A71
C171
E564
SE13
E48
A51
12A
E83
SE83
C177
C172
C173
E512

Whale #13, a male, was first sighted in 1978 and on nine subsequent occasions over the following three years. In nine of the ten total sightings #13 was escorting a cow-calf pair. Only once, over a resighting interval of about three hours, was the cow being escorted the same (see Observation I). On March 6, 1981, researchers from the Pacific Whale Foundation observed #13 escorting #75 and her calf. As one of the researchers approached the pod underwater, #13 began to sing and slowly escorted the cow and calf away from the diver (G. Kaufman, personal communication).

Whale #75 was first identified in 1979 with a calf and a single escort, #512. She was not seen in 1980, but was seen again with a calf in 1981 on three occasions, each time with different escorts. On March 6, 1981 she was escorted by #13, and on March 20 by #83 who was singing at the time (G. Kaufman, personal communication).

Whale #71 was sighted near Maui in 1980 with her calf and escorted by #13. On February 13, 1981, she was seen off the island of Hawaii with her calf from 1980, now a yearling, and escorted by #73. Underwater observations of the trio did not indicate any distention of the abdomen or other obvious signs of pregnancy in #71. On the following day #71 was still with her yearling and #73. She and the yearling were observed breaching repeatedly for nearly an hour. On the third day, #71 was sighted alone, resting quietly within a kilometer of her location on the previous two days.

Whale #62 was first seen on February 17, 1978, offshore of the southeast coast of Molokai, with a calf and unescorted. In 1979 she was seen, without a calf, in a pod with four other adult whales. She was not sighted in 1980, but in 1981 she was seen again with a calf on five occasions. She was unescorted on only the first of these five sightings. On March 3, 1981, she was escorted by #13. On March 11 she was escorted by #564 and was the subject of the playback experiment described in Observation V.

Whales #51, 83, and 48 have been seen in company with at least one of the individuals described above and have been identified as escorts on several occasions. Whale #22, discussed in Observation VI, also has an extensive resighting record, shown in Table 18, but has not been seen in the company of any of the animals in Figure 14. Whale #22 was radio tagged on July 23, 1977, in Southeast Alaska by personnel from the National Marine Mammal Laboratory (Marine Mammal Division 1977) and was seen subsequently in Southeast Alaska in 1981 and 1982. In Hawaii, #22 was observed escorting a cow-calf pair in 1979, competing for proximity to a female in 1980 (see Observation VI), singing while escorting a cow-calf pair in 1981, and in a pod of four adults in 1982. In total, #22 has been sighted twelve times in six years.

Populational Dynamics

Data from 1981 were examined in order to evaluate the relationships between seasonal changes in the abundance of whales and the frequency of aggression. During 1981, observations of pod size and behavior were made from small boats during non-systematic surveys of Hawaiian waters. Pods were approached in order to collect individual identification photographs and were observed for a minimum of 20 minutes to determine the number of whales present (pod size) and their activities. Across the three-month study we observed 331 pods totaling 726 whales.

Abundance was estimated by dividing the total number of whales observed during two-week intervals by the number of boat-days during that period; this approximates a "catch-per-unit-effort" statistic that should reflect seasonal changes in abundance. Although this statistic provides only a rough estimate of abundance, the general trends show good agreement with data from aerial surveys in past years (Herman et al. 1980; Baker and Herman 1981).

An index of aggressive activity was generated for each two-week period by reviewing behavioral records of the pods. Pods were judged to be engaged in aggression if headlunging or active displacement between whales took place. The number of pods judged to be engaged in aggression, multiplied by 100, was then divided by the total number of pods observed, to give the percentage of pods engaged in aggression. The results are presented in Figure 15 and show that both abundance and percentage of pods engaged in aggression were low early in the season and rose rapidly to a peak during the first two weeks of March. These indices declined somewhat more slowly than they increased.

The seasonal changes in pod size and composition are presented in Figure 16, based on the same two-week periods shown in Figure 15. Pod sizes of one or two predominated during January and early February and the number of calves were low. During March and early April there was a rapid increase in pod size with pods as large as nine animals observed on occasion. The peak number of calves and the largest average pod size were observed during the first two weeks of March, synchronous with the peak in abundance and peak percentage of agonistic pods. A

Figure 15: The seasonal changes in abundance and frequency of aggression during the winter of 1981. Abundance is represented by the average number of whales observed per boat per day for a given fifteen-day period. Frequency of aggression is represented by the percentage of pods engaged in aggression during each period.

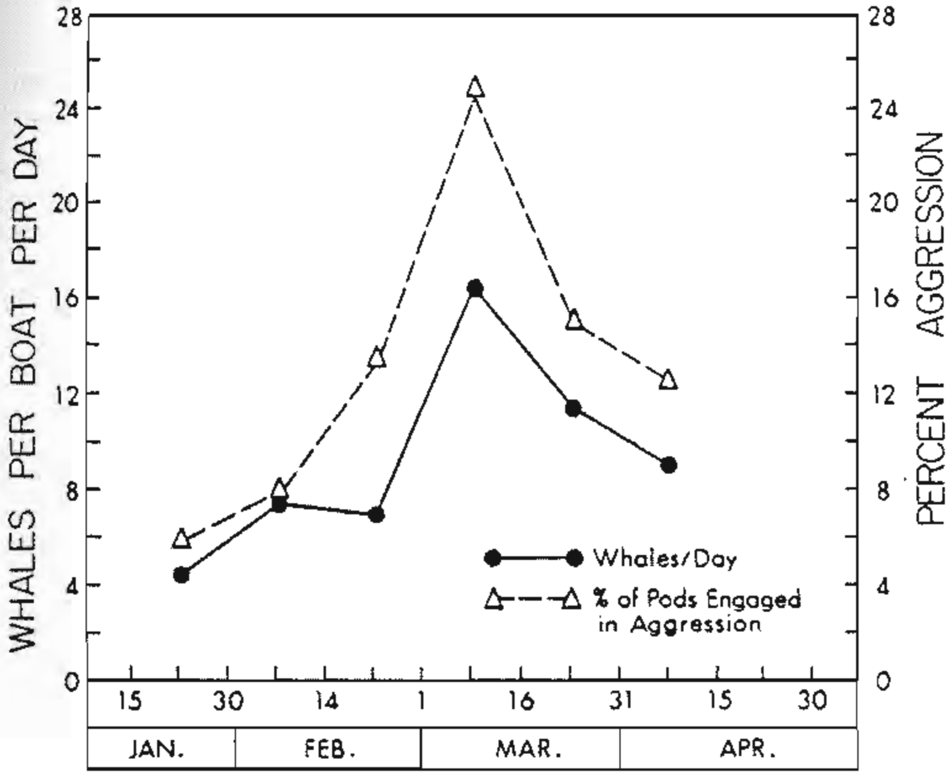
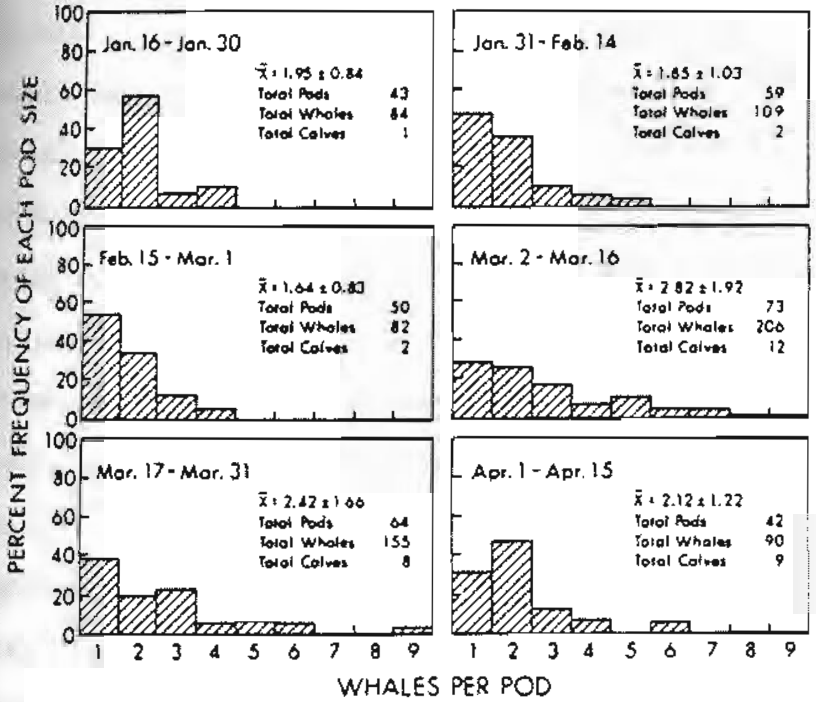

WHALES PER BOAT PER DAY
PERCENT AGGRESSION
0
4
8
12
16
20
24
28
15
30
14
1
16
31
15
30
JAN.
FEB.
MAR.
APR.
Whales/Day
% of Pods Engaged in Aggression

Figure 16: Seasonal changes in pod size and composition of humpback whales during the winter of 1981. The fifteen-day periods correspond to those shown in Figure 15. The mean and standard deviation of pod size are shown for each period.


PERCENT FREQUENCY OF EACH POD SIZE
WHALES PER POD
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
Jan. 16 - Jan. 30
x̄ = 1.95 ± 0.84
Total Pods 43
Total Whales 84
Total Calves 1
Jan. 31 - Feb. 14
x̄ = 1.85 ± 1.03
Total Pods 59
Total Whales 109
Total Calves 2
Feb. 15 - Mar. 1
x̄ = 1.64 ± 0.80
Total Pods 50
Total Whales 82
Total Calves 2
Mar. 2 - Mar. 16
x̄ = 2.82 ± 1.92
Total Pods 73
Total Whales 206
Total Calves 12
Mar. 17 - Mar. 31
x̄ = 2.42 ± 1.66
Total Pods 64
Total Whales 155
Total Calves 8
Apr. 1 - Apr. 15
x̄ = 2.12 ± 1.22
Total Pods 42
Total Whales 90
Total Calves 9

Discussion

Behavioral Contexts and Scaling of Aggression

The observations reported here indicate that aggression in humpback whales during the winter breeding season was the result of male-male competition for reproductively mature females. In cow, calf, and escort pods it is certain that a sexually mature female is present and evidence reported here and reviewed earlier (Chapter 2) indicates that, in many cases, escorts are males. Lone escorts were typically seen behind and a little below the cow-calf pair. If another whale approaches the trio, the initial escort attempted to maintain its proximity to the cow and to displace the intruder to the rear of the pod and away from the cow-calf pair. If the intruding whale persisted in its approach to the cow, it was met by an escalating series of aggressive behaviors by the initial escort. All multiple-escort pods observed in 1981 exhibited aggression that centered around the escorts' competition for physical proximity to the cow. A similar spatial relationship of escorts in large pods has been described for humpback whales wintering on Silver Bank in the Caribbean (Tyack and Whitehead 1983).

In the observations of non-calf pods, the context of the aggression appeared to be identical to that for pods having a cow-calf pair. In one reported observation of a non-calf pod (Observation VI), the individual in the lead position, the position analogous to that of the cow in cow-calf pods, was identified as a female. Other cases of mature females in the lead of non-calf pods are reported in Chapter 5. Because of the frequency of surface-lunging and the increased respiratory rate of these pods, they are often referred to as "surface-active" (Herman and Antinoja 1977; Glockner-Ferrari and Ferrari 1981; Tyack and Whitehead 1983). Several of the accompanying or trailing whales in the non-calf pods have been identified on other occasions as singers, escorts, or both. This suggests that these accompanying whales were also males and that, like the escorts accompaning a cow-calf pair, they were competing for proximity to a sexually mature female in the lead of the pod.

Aggressive behavior between escorting whales followed a roughly hierarchical scaling of intensity. An aggressive encounter between humpback whales probably began with a simple interception and broadside threat. Here the lead escort simply moved horizontally or diagonally across the path of the intruder. Unfortunately, this level of threat usually occured without any obvious surface behavior and was observable only from an aerial platform or an underwater viewing chamber (see Observations I and II). For this reason it was difficult to judge the relative frequency of such behaviors.

The headlunge was the most commonly observed aggressive behavior and appears to be indicative of a broad intermediate level of aggression. As shown in Figure 10, the whale lunged forward near the surface, engorging its ventral pleats with water or air. To the human observer, the visual effect of this engorgement was a marked increase in the size of the animal. The apparent enlargement of an animal through piloerection, abnormal inhalation, or specialized morphology is one of the most common elements of agonistic displays in vertebrate species (Darwin 1872). The feeding mechanisms of the humpback whale (Jurasz and

Jurasz 1979) may have preadapted it for this type of display. However, there is a qualitative difference in the degree of engorgement of the ventral pleats during feeding and that observed during the headlunge. In the headlunge. the ventral pleats, although enlarged, remained taut and the animal retained a generally fusiform shape. In contrast, during feeding the ventral pleats are relaxed and grossly distended as the whale engulfs its prey (Figure 17). The lesser degree of engorgement seen during aggressive encounters may represent an attempt to increase apparent size without sacrificing hydrodynamic efficiency.

The headlunge also differed from the less frequently observed "headrise" or "spy-hop". In the headrise there was no engorgement of the ventral pleats and the rostrum was raised vertically out of the water in an almost languid fashion (Madsen and Herman 1980).

If the intruding whale was not initially discouraged, the frequency and strenuousness of the headlunges increased, as did the proximity of the escorts to one another. Some degree of the range of intensity of this behavior can be seen in a comparison of Figure 10 to Figure 18. Often the headlunges of the lead escort were directly in front of the trailing animal which appeared, as a result, to be physically displaced to the rear. It also appeared, at times, that the whale being displaced to the rear of the pod was also attempting to bodily submerge the lead whale. possibly to deny the lead animal access to air. In this respect the physical contact often observed during headlunging may act to the advantage of both contestants; the lead animal maintains his lead position but must suffer vulnerability to suffocation by an intruder approaching from the rear.

Figure 17: Vertical lunge-feeding by a humpback whale. During lunge-feeding the throat is greatly enlarged and the ventral pleats are unfolded. Photograph by Thomas Kieckhefer, Kewalo Basin Marine Mammal Laboratory.

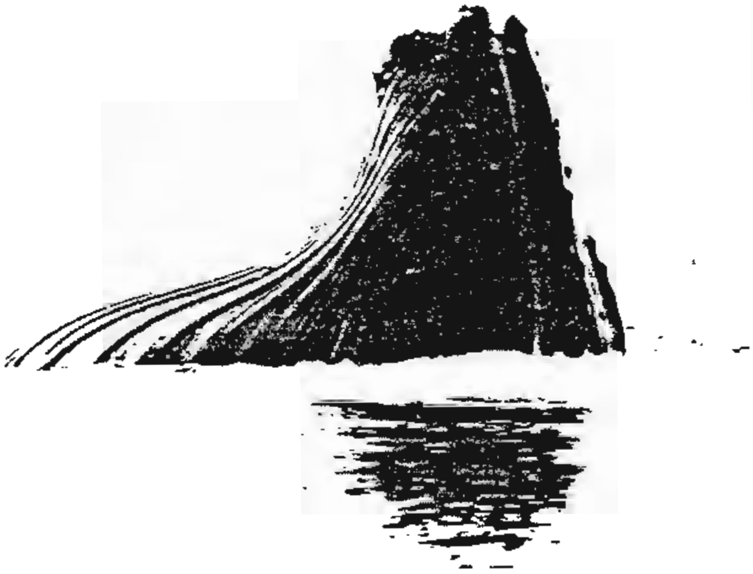
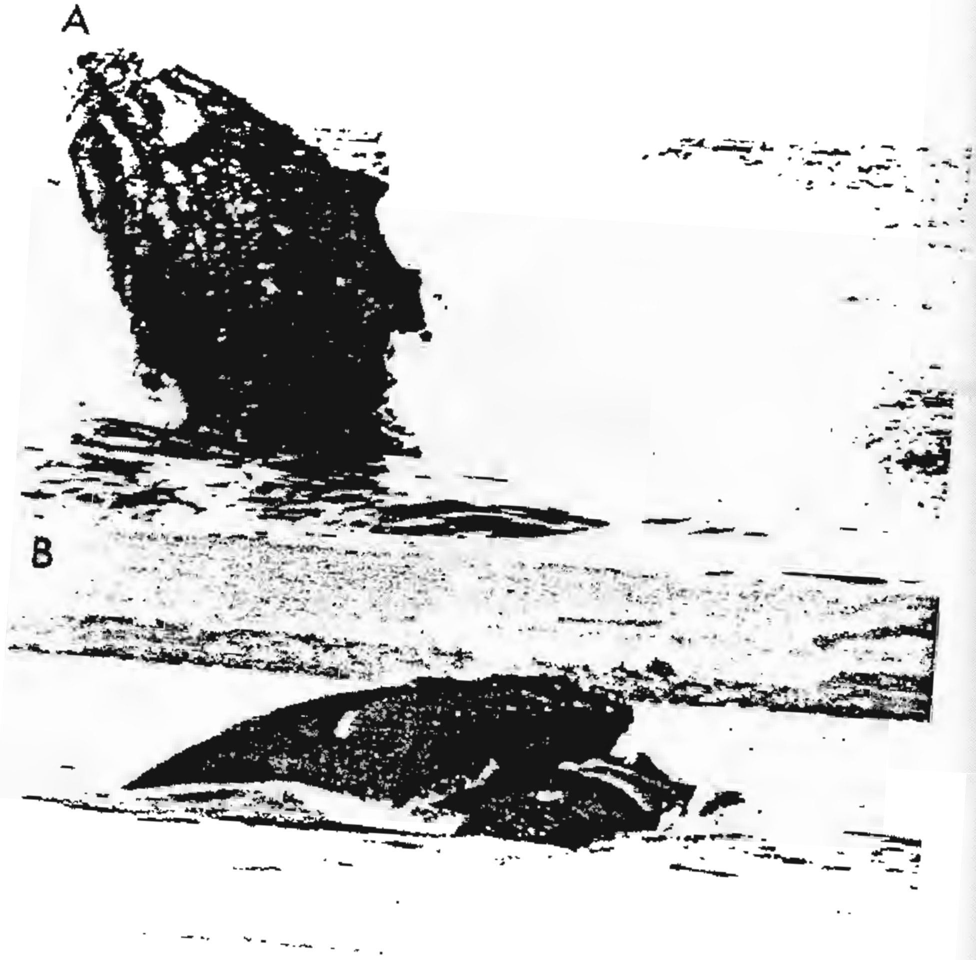


Figure 18: Headlunging whales. A) An escort lunges through the surface. Note the partially inflated throat and the open eye near the waterline. B) An escort lunges over the back of a second escort. Photographs by William Stifel and Thomas Kieckhefer, Kewalo Basin Marine Mammal Laboratory.


A
B

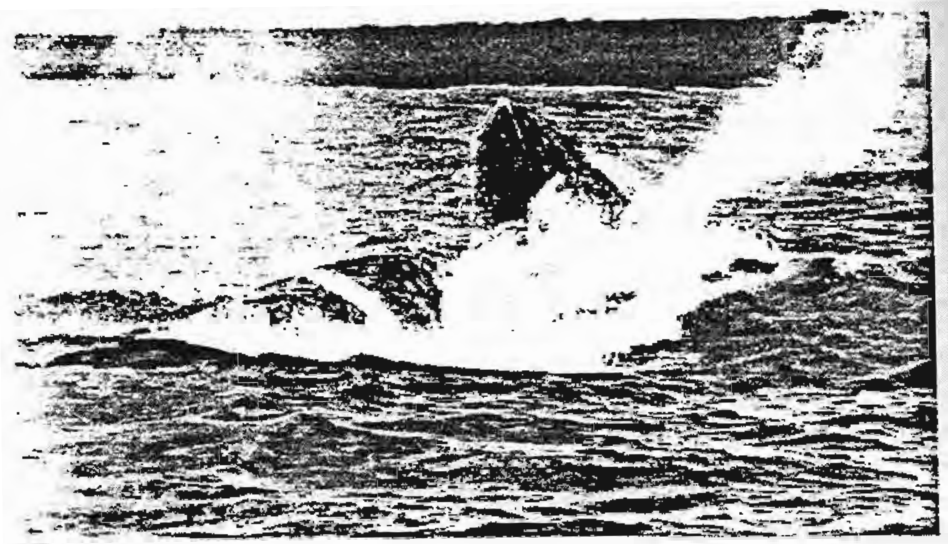
In some instances (see Observation VI) forceful contact was evidenced by raw areas on the escorts' dorsal fins and rostrums. I have also observed scarring and abrasions on the back and sides of escorts (Figure 10 and 11). Similar scars are observed on right whales and are thought to result from the use of their callosities as weapons in male-male aggression (Payne and Dorsey 1983). Humpback whales lack callosities, but the barnacles that collect on discrete parts of the flukes, flippers, and rostrum may also function as abrasive "weapons" in aggressive encounters.

The underwater release of air, referred to as "bubbling," was commonly observed in association with headlunging and characteristically took one of three forms: bubble-trails, underwater blows, and, more rarely, the release of air from the mouth. As with the headlunge, the feeding behavior of the humpback whale may have preadapted it for these displays. Like the bubblenet, which in theory disorients the schooling prey (General Introduction), the underwater exhalations observed in Hawaii may visually disorient an intruding whale. To a human observer in the water, being immersed in a bubble-trail is extremely disorienting; even a thin curtain of bubbles reduces visibility to a meter or less. Circular or spiral bubble-trails have not been observed in Hawaii and the underwater exhalations observed during aggressive encounters were always longitudinal or sinusoidal in shape. Underwater blows have been observed from humpback whales in the Northwest Atlantic (Hain et al. 1982) and also appear to be used as a feeding strategy. To my knowledge, however, the release of large amounts of air from the mouth of a whale has not been previously documented. Although air may be taken into the mouth at the surface during a headlunge, the large volume observed suggested that it was released from the lungs and into the mouth. Yablokov et al. (1972) described the respiratory system of baleen whales and proposed that the trachea may be easily dislodged from the internal nares, allowing air to be released into the mouth. A dissection of a humpback whale in which I assisted confirmed this description of the trachea.

In many observations the intruding whale or whales were discouraged enough to disengage from the pod during the intermediate level of aggression characterized by headlunging and bubbling. In a few cases, however, the violence of the contest escalated beyond the level of displacement to the level of charge-strikes. I have observed three types of charge-strikes by humpbacks: butting, lateral fluke strikes, and peduncle strikes. Butting was discussed in Observation III and is illustrated in Figure 13. The whale in the foreground of the figure charged the other and butted it with its rostrum. The whale receiving the blow rolled to its right and lifted its left flipper. The upraised flipper may be the result of the force of the blow, a defensive posture, or the result of an attempt by that whale to place itself in a position to reciprocate with a ventrally directed strike of the fluke or flipper. In some extreme cases, butting whales rose up out of the water in a near-vertical posture (Figure 19). The position of the two whales in Figure 19b closely resembles descriptions of alleged vertical copulation in humpbacks (Nishiwaki and Hayashi 1950; Slijper 1962). Possibly, early whalers misinterpreted the physical competition between males as mating.

Figure 19: Vertical posture of butting humpback whales. A) One whale rises vertically out of the water as it butts a second whale. B) Two whales butting and rising vertically out of the water in a ventral to dorsal position. Photographs by William Stifel and Thomas Kieckhefer, Kewalo Basin Marine Mammal Laboratory.

A



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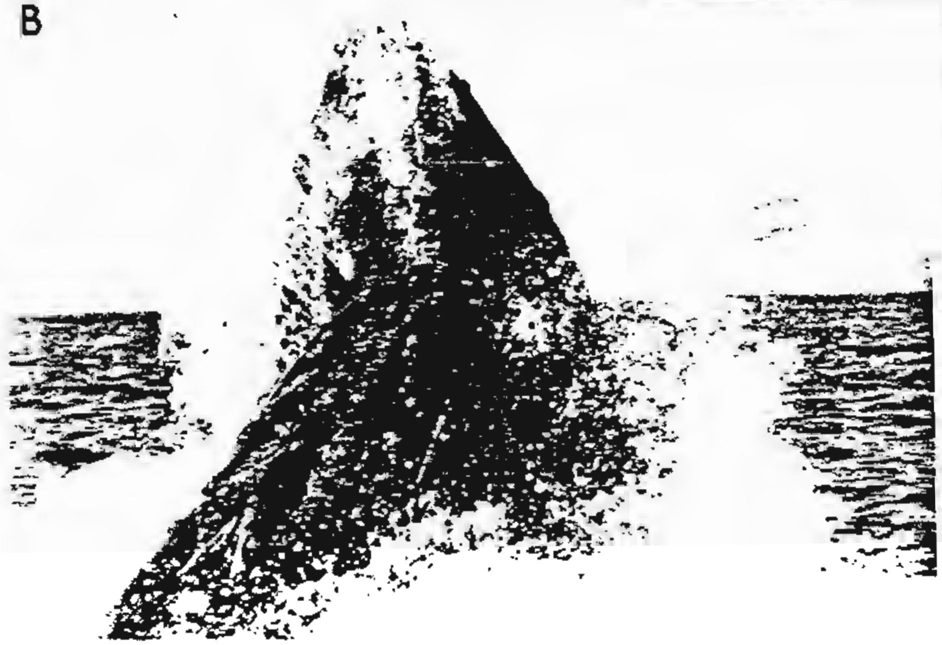


Lateral fluke strikes were observed when competing whales were swimming side by side. Here the animals jostled each other and rolled to one side while they lashed ventrally or laterally with their flukes. Similar behavior is commonly observed during aggression between dolphins in captivity (personal observation).

The third type of charge-strike was the most violent and was discussed in Observation II (Figure 12). In this instance, the lead escort turned and headed directly toward the approaching whale to deliver a forceful strike with its caudal peduncle. As in Figure 13, the whale on the receiving end turned and rolled to one side.

In observations to date, the escort initially accompanying the cow-calf pair, or the escort closest to the pair at the beginning of the observation, was always successful in maintaining its proximity during a single observation period. In protracted observations, such as those described in Observations I and III, the lead escort was also the one that remained when other escorts disaffiliated. The length of time from the first association of the challenger to its disaffiliation ranged from as little as ten minutes to as long as several hours. However, it is clear from the resighting histories that lead escorts left or were replaced over periods of only a day. Other researchers in Hawaii have observed the displacement of a lead escort during a single hour-long observation (Darling et al. 1983). On the Silver Bank in the Caribbean, Tyack and Whitehead (1983) report that lead escorts maintained their position for an average of 7.5 hours before they were replaced.

During aggressive encounters between escorts, the cow-calf pair usually remained in the lead of the pod some one to two whale-lengths removed from the activity. Aggression directed towards a cow-calf pair by an escort was rare and, when it was observed, appeared to be an attempt by the escort to herd the cow-calf pair away from a singer or a playback of a whale song (see Observation V). In pods without calves the behavior of the lead animal was also relatively stereotyped. The lead animal was most likely to engage in flipperslapping, flukeslapping, inverted flukeslapping, and breaching. Flukeslapping in odontocetes has been interpreted as an indicant of fear or stress (Defran and Pryor 1980). The inverted posture has been observed in female right whales apparently attempting to avoid copulation (Mandojana 1981). Although the humpback whale may flukeslap in other contexts as well, the combination of posture and behavior in the observations reported here suggests a response of the female to the aggression and advances of the competing males. Cows with calves may avoid such forceful displays for fear of injuring the calf, or because of the need to conserve energy at a time when they are lactating but not feeding.

Behavioral Continuity

An individual acting as an escort on one occasion was likely to be an escort in subsequent observations, both within seasons and across years (Chapter 2). Animal #49, for example, was seen four times over five years, always as an escort. Whale #13 was observed ten times over four years and was an escort in all but one observation. Both #49 and 13 were photographically sexed as males. Other animals observed as escorts have not been directly sexed but circumstantial evidence suggests that these individuals are males. Female humpback whales typically give birth once every two or three years following sexual maturity (Chittleborough 1965; Chapter 2). Consequently, an adult whale seen over several years without a calf is likely to be a male. Whales #22 and 48, not directly sexed, have resighting histories spanning four or five years each. Both whales appeared to be adults when first sighted, both have acted as escorts, and neither has been observed with its own calf. The resighting histories and behavioral roles of these two individuals parallel those of known males #49 and 13. Thus, it is likely that #22 and 48 are also males, and that escorting behavior is generally sex-specific (Chapter 2).

Data on the duration of affiliation between escorts and cow-calf pairs were reviewed briefly earlier. Additional data on the transience of the association between escorts and mature females can be found in Figure 14. With but one exception, no two adults were seen together for more than a few hours over the six years and 33 sightings. Only #73 and 71, the latter a cow accompanied by her calf of the previous year, were seen together across a two-day period, at a time when the cow was apparently weaning her yearling. If the association between the two adults was continuous, it suggests that a courting male humpback may accompany a female for as long as a few days. This is somewhat longer than the 3.5 hour maximum period of affiliation reported by Mobley and Herman (1985). However, the overall pattern of social fluidity shown in Figure 14 is in general agreement with their conclusion that humpback whales are not monogamous and do not form stable pair-bonds during the breeding season. Instead, females associate both serially and simultaneously with multiple males and males associate serially with multiple females. This suggests that humpback whales have a polygynous or promiscuous mating system. A further distinction between these two systems will only be possible with data on frequency of mating between individual males and females within a season. Such data will be extremely difficult to obtain; thus far, there appear to be no reliably documented reports of humpback whale matings.

An escort was also likely to be a singer (Chapter 2). The interchangebility of these roles supports Winn and Winn's (1978) and Tyack's (1981) conclusion that singing, like escorting, is a sex-specific behavior of males. Some of the observations documented whales singing and escorting simultaneously. In these cases it seemed that the vocalizations functioned, in part, as a threat display between escorts. In Observation IV, one of the escorts was singing as it attempted to displace another escort. Whales #13, 22, and 83 were each singing while escorting cow-calf pairs away from underwater observers. In Observation V, the escort, #564, initially responded to the playback of a song by herding the cow-calf pair several hundred meters away from the sound projector and vessel. These observations agree with earlier reports that singing whales are at times accompanied by other whales (Herman and Tavolga 1980), but are contradictory to Winn and Winn's (1978) observation that all singing whales are alone, and to Tyack's (1981) report that singers stopped singing when approached by other whales. Our observations are consistent with the hypothesis that singing plays a role in the mating system of humpback whales, but further suggest that singing is more plastic and occurs in a broader range of contexts than previously reported.

Populational Dynamics

At least two factors could have contributed to the seasonal peak in the occurrence of aggression. First, the increase in aggression occurred concomitantly with an increase in abundance or local density. A high density of conspecifics, in itself, can lead to increases in aggression. Second, if the observed aggression was primarily a result of competition between males for access to females, then its occurrence could also have been influenced by seasonal changes in the reproductive states of mature males and females.

Like many migratory species, the humpback whale is seasonally reproductive. For the South Pacific humpback whale, Chittleborough (1965) determined that the height of gonadal activity coincides with the peak overall numbers of whales in the breeding grounds. In females, the presence of corpora lutea, near-term fetuses, and a marked increase in the number of newborn calves indicate a peak in both ovulation and parturition during the two-week peak of the seasonal population (Chittleborough 1958). In males, a peak in gonadal activity at this same time is evidenced by changes in testes weight, the diameter of testes tubules, and the density of sperm in the vas deferens (Chittleborough 1955). Because the activity of male gonads is under the general control of androgens, it is reasonable to assume that the levels of these hormones are highest at this time. In addition to controlling gonadal activity, the androgens, in particular testosterone, have been implicated in the aggressiveness of males in many mammalian species (Wilson 1975).

Chittleborough (1955, 1965) also reported an annual period of quiescence in male and female gonadal activity during the feeding season. Aggressive behavior is rare during the summer feeding season, even though the local density of whales often exceeds that found in Hawaii (Baker et al. 1982; Baker et al. 1983). I have observed the behavior of a number of of the same individual whales in Hawaii during the winter and in Alaska during the summer (Chapter 1). At least three of these individuals, #22, 512, and 564, were observed singing or escorting in Hawaii; some of the aggressive behaviors of #22 and 564 are described in Observations V and VI. None of these individuals displayed aggression in Southeast Alaska. The infrequency of aggressive behavior during the summer supports the argument that the aggression seen in Hawaii was, in part, the result of increased gonadal activity of both males and females during the winter season. It seems probable that an increase in population density, ovulatory activity in mature females, and testicular activity in mature males each contributed to the observed peak in aggressive behavior.

Changes in the abundance of whales and the frequency of aggression were paralleled by changes in pod size and the number of calves in Hawaii. Consistent with findings in earlier years (Herman et al. 1980), the relative frequency of large pods increased as the season progressed. The presence of peak numbers of calves with the overall peak abundance in the middle of the season, but a greater proportion of calves late in the season, was also consistent with earlier data from aerial surveys (Herman and Antinoja 1977; Herman et al. 1980).

The changes in pod size and the numbers of calves may, in part, have reflected differences in the migratory timing of certain age-sex classes. As described by several researchers (Nishiwaki 1959, 1960; Chittleborough 1965; Dawbin 1966), humpback whales arrive on the wintering grounds in the following order: late-lactating females and immatures, mature males and females, and late-pregnant females. The return to the feeding ground follows roughly the reverse order: newly pregnant females, immatures, mature males and females, and females with newborn calves. In the data summarized in Figure 16, the proportion of pairs was large during the last half of January. Many of the early-season pairs consisted of a large whale and a much smaller one. These may have been newly arrived cows with unweaned yearlings. In February, when population numbers were still low, there was a predominance of singletons which may have been unaffiliated immature animals. The sudden increase in the frequency of large pods during March probably resulted from the same factors contributing to the increase in aggression: a high population density, the arrival of mature males and females, and the tendency for competing males to temporarily affiliate with ovulating females. Finally, in April, the large proportion of calves reflected the tendency for cow-calf pairs to remain on the wintering grounds while other age classes were beginning to leave (Dawbin 1966).

Chittleborough (1965) noted that the timing of peak ovulation in females is closely correlated with the timing of peak spermatogenesis in males and that both are in synchrony with yearly migration to the wintering grounds. However, the timing of migration in the North Pacific humpback whale is somewhat variable from year to year, with peak numbers on the wintering grounds occuring as much as three weeks apart across a three-year period (Nishiwaki 1962; Herman et al. 1980; Baker and Herman 1981). Because of the rapid increase and decrease in the numbers observed within a winter season, a small shift in the timing of migration may result in great differences in the relative abundance of whales present on any particular date from year to year. For example, aerial surveys in Hawaii showed peak numbers of whales during the last two weeks of February in 1977 and less than half that number during the same period in 1979 (Herman et al. 1980; Baker and Herman 1981).

The majority of female humpback whales are thought to ovulate only once or, at most, twice during a breeding season (Chittleborough 1965). If reproductive success is to be assured, the timing of ovulation must correspond closely with the peak abundance of mature males on the breeding grounds. The environmental factors intiating the departure of humpback whales from the summer feeding grounds are unknown (Nishiwaki 1961; Dawbin 1966; Baker and Herman 1981; Baker et al. 1985). It is not likely, however, that a migratory releaser could synchronize the reproductive states of animals on the breeding grounds; the journey is simply too long and the timing of migration is too variable. Instead, it seems reasonable that a behavioral system may have evolved to sychronize the gonadal activity of male and females despite the year-to-year shifts in migratory timing. I suggest here that this system is the song of the humpback whale. The singing of mature males, including the simultaneous chorusing of many males, could communicate the presence of adequate breeding partners and help stimulate ovulation in females. This would not only assure reproductive success, it would also help minimize the time that mature animals, males or females, need remain on the wintering grounds where the abundance of food is low (General Methods).

Reproductive synchronization of this type is not uncommon. The stimulation of reproductive activity at a social level, known as the "Fraser Darling effect," helps synchronize breeding in many colonial birds (Wilson 1975). Both visual and auditory stimuli from the male mate and the colony milieu help induce ovarian development (Lott et al. 1967). Synchronized breeding also occurs among social ungulates, e.g., the wildebeeste, *Connochaetes taurinus*, but the factors controlling this phenomenon are unknown (Wilson 1975).

I am not proposing that the humpback whale song functions solely to synchronize ovulation; only that it may be a major function. Previously, it has been proposed that the song of the humpback whale communicates an individual's species, location, sex, readiness to mate, or willingness to engage in aggression (Payne and McVay 1971; Winn et al. 1971; Herman and Tavolga 1980; Tyack 1981). However, attempts to determine, through playback studies, the specific communicative function of singing were inconclusive (Tyack 1983; Baker and Herman 1984a). Given the large investments of both sexes in the winter breeding season, synchronizing or inducing ovulation seems of paramount importance, and may be a driving force for this complex and prolonged acoustic display by males.

Chapter IV

Cooperative Feeding Among Humpback Whales in Southeastern Alaska

Abstract

Pods of up to ten humpback whales were observed feeding cooperatively in southeastern Alaska. Cooperation was evidenced by closely coordinated behavior, repeated associations between pod members, and, possibly, leadership by older experienced individuals. The ecological basis of cooperative feeding may lie in an increased ability to herd or corral agile and fast-swimming schools of fish, particularly Pacific herring, *Clupea harengus*. Membership in cooperatively-feeding pods is influenced by gender, reproductive status, and idiosyncratic partner preferences. A predominance of female members suggests some dimorphism in the prey preferences of humpback whales. A unique series of trumpet-like vocalizations, termed a "feeding call", is described. The call may help coordinate surface lunging in large pods. Duetting of the feeding call was recorded in one observation. I suggest that the complex winter song of the humpback whales may have its evolutionary origins in vocalizations from the summer feeding grounds.

Introduction

A social group differs from a simple aggregation in that its members exhibit some degree of cohesion and coordination, as well as instances of cooperation (Wilson 1975; Leuthold 1977). Coordinated behavior, particularly in hunting strategies, and group cohesion are well known among some species of odontocetes (Norris and Dohl 1980), including the killer whale, *Orca orcinus*, the bottlenose dolphin, *Tursiops truncatus* (Wells et al. 1980), the dusky dolphin, *Lagenorhynchus obscurus* (Wursig and Wursig 1980), and the sperm whale, *Physeter macrocephalus* (Best 1979). It has even been argued that dolphins are true "altruists" (Norris and Dohl 1980). For baleen whales, however, there is little evidence of these characteristics of sociality. Instead, baleen whale groups, referred to as pods, are traditionally defined simply by spacial proximity and synchrony of respiratory behavior (Gunter 1947; Herman and Antinoja 1977; Baker et al. 1982; Whitehead 1983).

Among humpback whales, only a single feeding stategy, known as "echelon" feeding, has been previously suggested as evidence of cooperative behavior. As first described by Jurasz and Jurasz (1979), echelon feeding involves two to four whales surface-lunge feeding in synchrony. During each lunge, the whales are positioned in an inverted V-formation, parallel to each other and staggered by a half a whale length. Echelon formations are also observed among skim-feeding bowhead whales, *Balaena mysticetus* (Wursig et al. 1982). The trailing animals in the echelon formation presumably benefit from a temporary increase in density of prey escaping to either side of the lead animal. The benefits to the lead animal in the echelon are unknown, however, and a non-mutualistic basis for the coordinated behavior cannot be excluded. Repeated associations between individuals feeding together in an echelon would be stronger evidence for true cooperation or reciprocation (Trivers 1971; Axelrod and Hamilton 1981). However, neither Jurasz and Jurasz (1979) or Wursig et al. (1982) document such associations. In his study of feeding humpback whales off Newfoundland, Whitehead (1983) concluded that coordinated behavior in small groups was the result of each member's attempt to avoid disrupting the prey patch, not the result of cooperative action. Whitehead et al. (1982) found no repeated associations between feeding humpback whales beyond that expected from chance.

More recently, Baker and Herman (1984b) have described two distinct modes of social organization among feeding humpback whales in southeastern Alaska. The first involves casual associations among whales in small pods or large aggregations feeding on swarming euphausiids. The second, less common mode, involves large pods of whales cooperatively feeding on schooling fish. Here I present, as evidence of a cooperative feeding strategy among humpback whales, further observations of repeated associations between individuals and the closely synchronized behavior of large pods. In some cases the association between individuals involved in cooperative feeding extended across several years. A unique series of vocalizations was recorded from some cooperatively feeding whales. This "call" occured in a specific feeding context and remained stereotyped across years.

Methods

Field studies of humpback whales were carried out in the waters of southeastern Alaska during the summers of 1980 to 1984. Some additional observations from the summer of 1985 are included where available and relevant (Baker 1985). Informal observations of whales' behavior were made daily or near-daily from small boats. Formal observations of whale behavior and movement were made from land-based observation stations (Baker et al. 1982; Baker et al. 1983). An attempt was made to individually identify all whales during both formal and informal behavioral observations.

Prey Assessment

Humpback whale prey was assessed with a chart-recording fathometer or echosounder (Whitehead 1983; Wing and Krieger 1983; Krieger and Wing 1984). A fathometer introduces short pulses of high frequency sound into the water through a hydrophone or transducer. The echos of the sound are then received by the tranducer between transmissions of the pulses and evaluated for their timing and strength. The timing of the echo's return gives the depth of an object or "target". The strength of the return provides information about the size and density of the target (Krieger and Wing 1984). The use of fathometers or echosounders to detect and evaluate biological targets is generally referred to as "hydroacoustics" to distinguish it from bioacoustics or the study of biologically generated sounds.

In 1984 and 1985, humpback whale prey were qualitatively assessed with a Ross Fineline 250-C, recording fathometer equipped with a 45-kHz or a 100-kHz tranducer (Baker 1984; 1985). The lower frequency used in 1984 was adequate for detecting nektonic targets the size of small schooling fish and larger. The 100-kHz tranducer was capable of detecting planktonic targets, including euphausiids and copepods, as well as the larger nektonic targets. Both systems were capable of observing prey in the upper 200 m of the water column.

During the summers of 1982, 1983 and 1984, quantitative surveys of humpback whale prey were conducted by Ken Krieger and Bruce Wing of the Auke Bay Laboratory of the National Marine Fisheries Service (Wing and Krieger 1983; Krieger and Wing 1984; Krieger and Wing 1985). Quantitative hydroacoustics involves use of a carefully calibrated echosounder and the confirmation of target species with net tows. Much of my interpretation of fathometer recordings is based on collaboration wih Krieger and Wing and, where possible, their results are used to substantiate my own (Baker 1984).

Bioacoustics

The vocalizations of humpback whales were monitored with a Clevite Gould CH-13A hydrophone and recorded with a Sony TC D5M stereo cassette recorder (General Methods). Recordings of whale vocalizations were analyzed with a Kay 6061-A sonograph at the University of Hawaii's Department of Linguistics.

Results

Results are presented in four sections: Behavioral Observations, Vocalizations, Group Composition, and Prey Assessment. Each section focuses on three cooperatively feeding groups distinguished by their location, group membership and characteristic behavior.

Behavioral Observations

Surface-Feeding Group. A surface-feeding group of from six to ten humpback whales was observed on three occasions during the summer of 1981 and on three occasions during the summer of 1984 (Table 19). The whales were first sighted in Frederick Sound on both July 17 and July 20. On September 7, 49 days later, they were found at the mouth of Tenakee Inlet, approximately 154 km by water from the location of the previous two sightings. In 1984 the group was found at three locations in Chatham Strait: in Chaik Bay on July 27, at the mouth of Tenakee Inlet on August 18, and near Peril Strait on September 3. On each of the three sighting dates in 1984, vessel-based surveys found few if any other whales in Chatham Strait from Point Gardner to Point Couverton, an area 90 km in length.

The details of two observations are described here to characterize the unique behavior of the surface-feeding group. On July 17, 1981, six surface-feeding whales were observed from a small vessel near the mouth of Gambier Bay in Frederick Sound. All whales remained submerged for up to five minutes before lunging through the surface in a closely-packed group (Figure 20). After surfacing, the animals milled together for

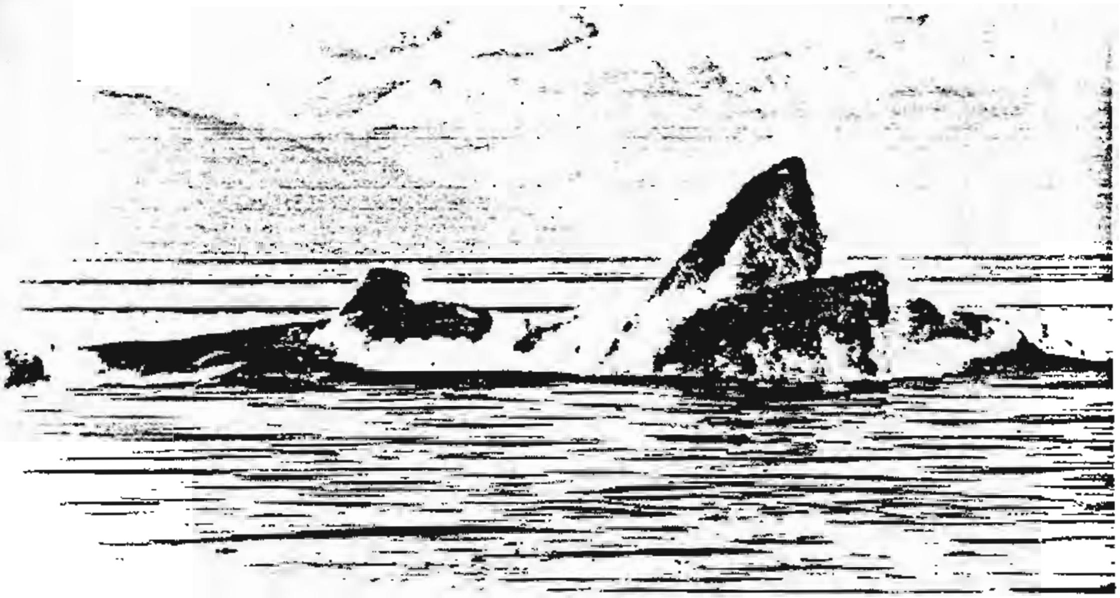
Table 19

Sightings of surface-feeding group in southeastern Alaska.

Date	Location	Pod Size	Prey Species
Jul 17, 1981	Gambier Bay	6A	schooling fish
Jul 20, 1981	Gambier Bay	10A	---
Sep 7, 1981	Tenakee Inlet	9A	schooling fish
Jul 28, 1984	Chaik Bay	6A+1c	schooling fish
Aug 18, 1984	Tenakee Inlet	7A+1c	Pacific herring
Sep 13, 1984	Peril Strait	7A+1c	schooling fish

Note: Adults are noted by the letter A and calves are noted by the letter c.

Figure 20: Surface lunge of cooperatively feeding whales. A) Seven whales lunge through the surface in the pursuit of schooling herring at the mouth of Tenakee Inlet on Aug 18, 1984. B) Six whales lunge through the surface near Gambier Bay on July 17, 1981. Note the vertical posture of the central lead whale. This animal was identified as #561, the consistent group leader, by the unique barnacle scarring on the edge of her lower rostrum.

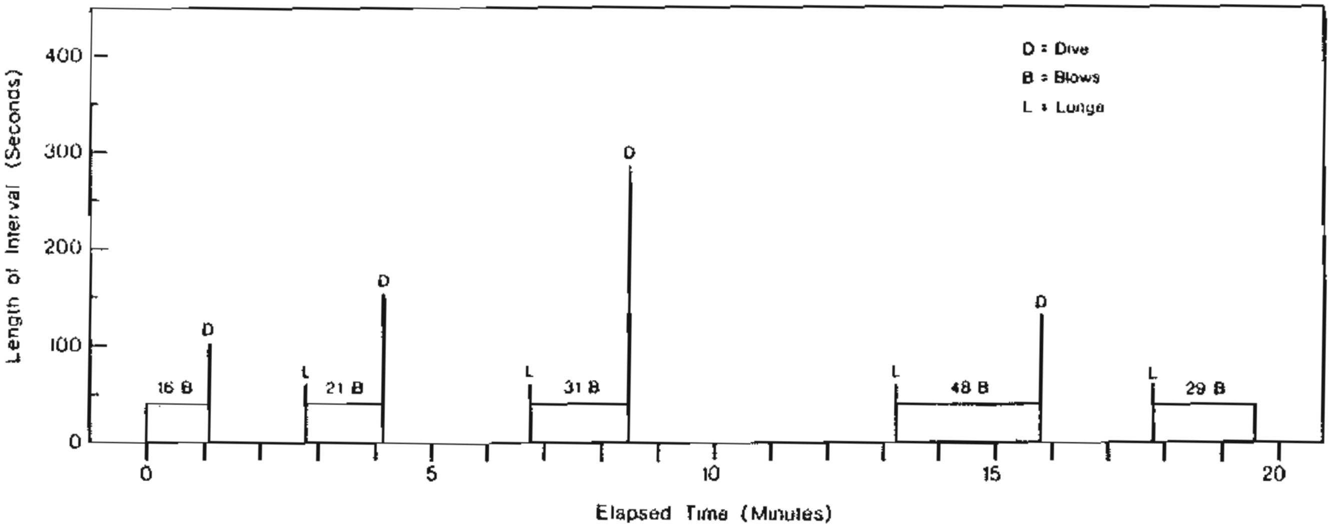


approximately two minutes before diving. From 16:00 to 17:11 that afternoon, thirteen surface lunges were observed. Two of these lunges were preceeded by a large (20 m in diameter) bubblenet formed in a counter-clockwise direction. In each lunging episode, one whale was first to surface through the water and was positioned centermost in the group (Figure 20b). The presence of a leading, central whale was characteristic of each surface lunge during this and all other observations.

On July 20, 1981, the surface-feeding pod was found within a few kilometers of its position three days earlier. An additional four whales had joined the group bringing its total size to ten. A 20 minute observation from a shore-based platform provided a complete record of four surface-lunging episodes (Figure 21). The synchronous diving and surface lunging were similar to the previous observation but no bubblenets were observed. Before each surface lunge, all whales remained submerged for two to five minutes. After each lunge, the pod divided; one subgroup traveled in a counter-clockwise arc about 50 m in diameter, rejoining the second subgroup which was traveling along a complementary arc in a clockwise direction. Following the confluence of the subgroups the whales dived. The group remained at the surface for about two minutes between dives, with longer surfacings following longer dives.

The whales' closely coordinated behavior was demonstrated by the simultaneous surface lunges, common dives, and highly clumped distribution of respirations or blows. The average interval between blows was 7.9 seconds (n = 145) with a standard deviation of 28.5

Figure 21: Behavioral record of ten whales in a surface-feeding group near Gambier Bay on July 20, 1981. L = surface lunges, D = common dive periods, B = blows (visible respirations).


D = Dive
B = Blows
L = Lunge
Length of Interval (Seconds)
400
300
200
100
0
16 B
D
L
21 B
D
L
31 B
D
L
48 B
D
L
29 B
0
5
10
15
20
Elapsed Time (Minutes)

seconds, giving a coefficient of variation of 3.61. If individual whales were acting independently, the intervals between their blows should approximate a time-homogeneous Poisson process (Fagen and Young 1978), with a resultant coefficient of variation of 1 (Snedecor and Cochran 1967).

Point Adolphus. A behaviorally coordinated pod of subsurface-feeding whales was found near Point Adolphus in Icy Strait throughout July and August of 1982 and 1983 (Baker 1983; Baker et al. 1983). In 1984, the group disbanded although individual members remained in the area (Perry et al. 1985). In 1985, the group reformed and remained together from June to mid-September. Observations at Point Adolphus in 1980 and 1981 suggested that the group also occupied the area for at least part of these years (Jurasz et al. 1980; Baker et al. 1982). The "core members" of the subsurface-feeding pod ranged from four to seven whales. Although lacking the spectacular lunges of the surface-feeding whales, the subsurface-feeding pods were equally synchronized in their movement and respiration.

Bartlett Cove. A second pod of subsurface-feeding whales was found in Bartlett Cove of Glacier Bay during the summer of 1982. This pod was observed from a shore-based platform on a near-daily basis from July 9 to August 6 (Baker et al. 1983). The core members in Bartlett Cove consisted of a cow-calf pair and two adults.

Vocalizations

Lunge-Feeding Group. The vocalizations of the surface-lunging pods were monitored during two observations. On September 7, 1981, hydrophone recordings were collected during three of the surface-lunging episodes. Vocalizations just prior to each surface lunge were stereotyped and are typified by the sonographs from one episode shown in Figure 22. The whales were silent for approximately three or four minutes following submergence. About 35 seconds prior to surface lunging a single whale began a series of five trumpeting calls of 440 Hz in frequency and 2.5 seconds in length. At the end of the fourth call a second voice joined at 500 Hz and rose to 550 Hz during its 4.5 seconds duration. Following a pause of eight seconds, the first voice began a sixth call, of 2 seconds in length, at about 500 Hz, and ended with a 3.5 seconds call that gradually rose to 550 Hz. The rise in frequency seemed to be accompanied by an increase in volume and gave the impression of a musical crescendo. The second voice joined in at 1000 Hz during the sixth call and rose abruptly to 1500 Hz at the beginning of the last call (Inset, Figure 22). The vocalizations of both whales ended just as the group erupted through the surface. With the exception of the second voice. which was not present in other episodes, the vocal series prior to all three surface lunges were nearly identical.

On September 13, 1984, vocalizations were monitored during two surface lunges. Sonographs of these vocalizations showed them to be similar to those collected three years before (Figure 23). Following the pod's submergence. the whales were silent for approximately three minutes. Fifty seconds prior to surfacing a single whale began a series of trumpeting calls at 440 Hz in frequency and averaging 2.2 seconds in duration. After 17 seconds of silence, the whale called twice more, rising in frequency to 550 Hz. The last call ended just as the whales

Figure 22: Sonograph (Kay 6061-A sonograph, 10 to 1,000 Hz scale) showing the feeding call recorded from surface feeding pod on September 7, 1981. The abrupt end of the sixth call coincided with the simultaneous surface lunge of nine whales. Inset shows expanded frequency scale (20 to 2,000 Hz scale) of apparent vocal duet.

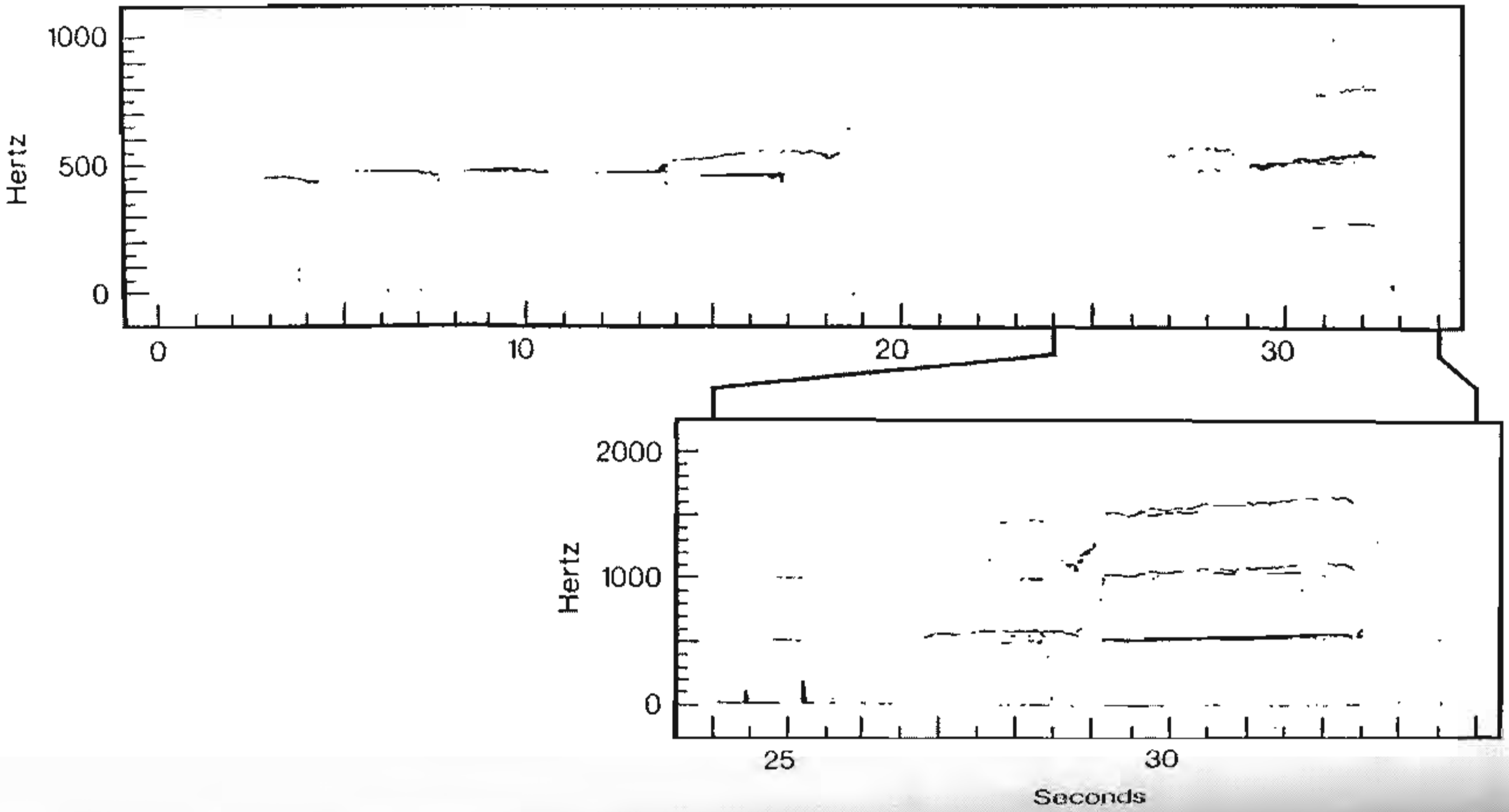
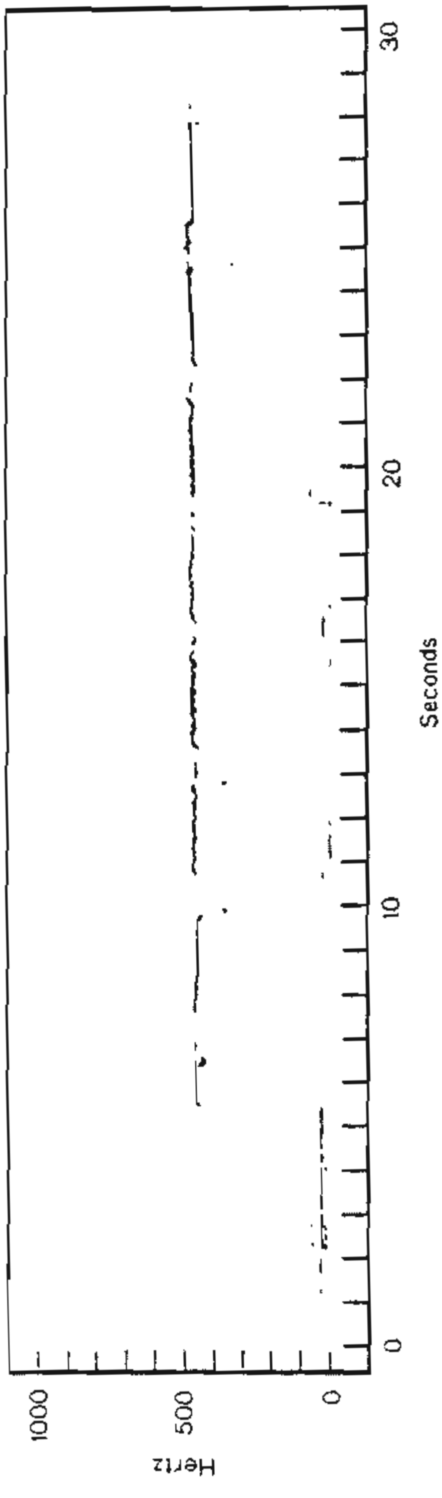
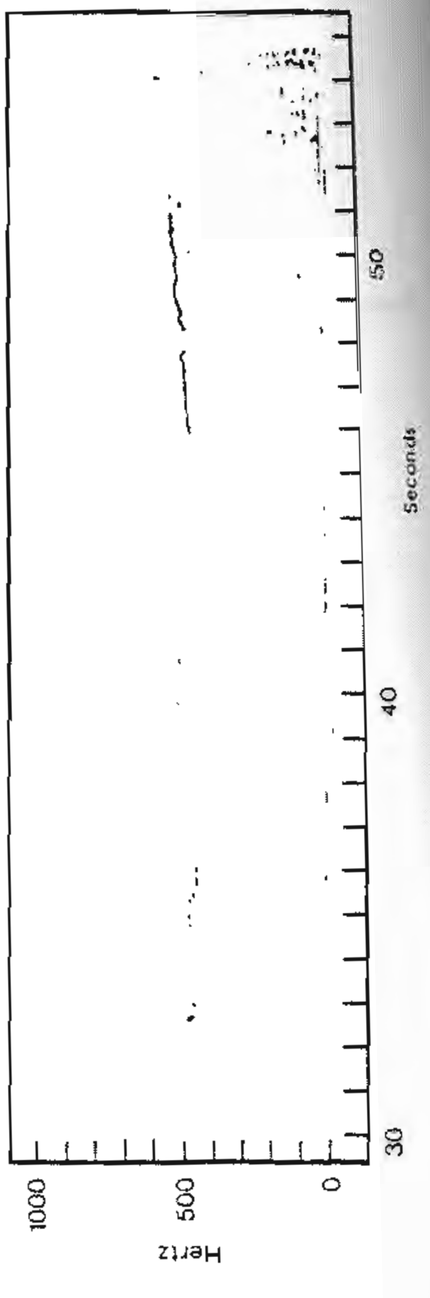

Hertz
1000
500
0
0
10
20
30
Hertz
2000
1000
0
25
30
Seconds

Figure 23: Sonograph (Kay 6061-A, 10 to 1,000 Hz scale) showing feeding call recorded from surface feeding group on September 13, 1984. The abrupt end of the ninth call coincided with the simultaneous surface lunge of seven adults and a calf. The broadband, low frequency "grunts" following the end of the ninth call were made while the whales were at the surface, after the group lunge.


Hertz
1000
500
0
0
10
20
30
Seconds


Hertz
1000
500
0
30
40
50
Seconds

lunged through the surface. No second voice joined the primary voice in this recording.

Point Adolphus. Whales near Point Adolphus were monitored by hydrophone on only a few occasions. Although sporadic low frequency grunts and moans were recorded, no structured or repeated calls were found.

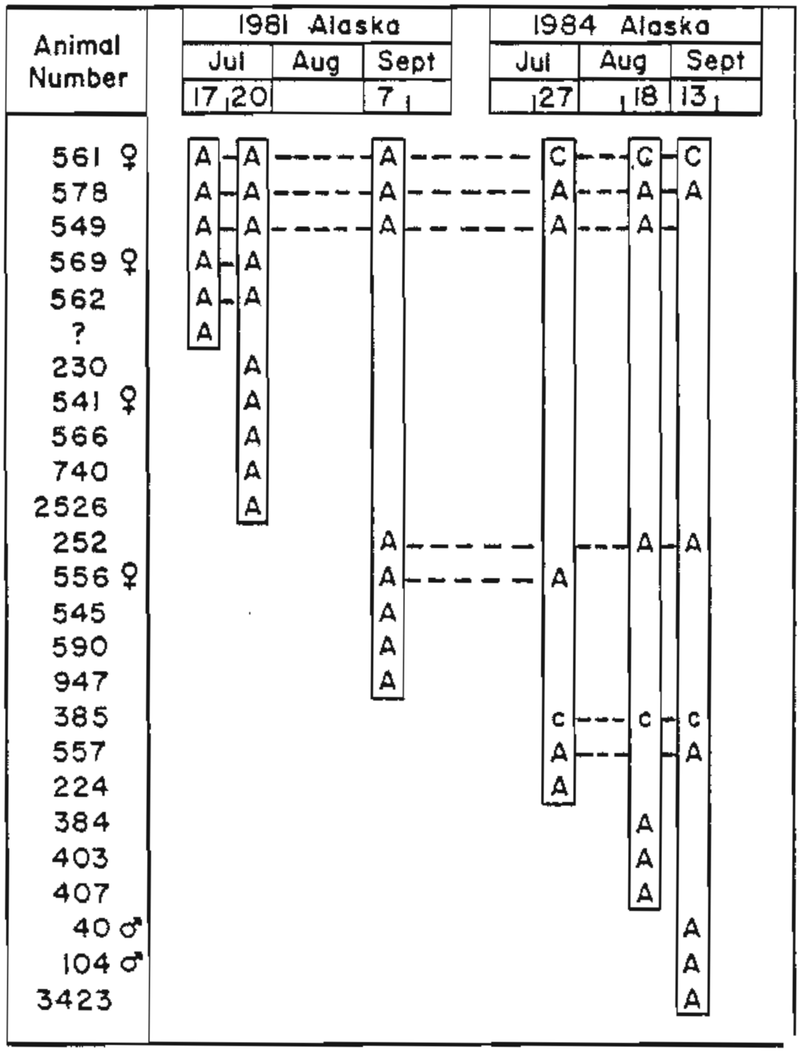
Bartlett Cove. Whales in Bartlett Cove were monitored regularly during 1982 (Miles and Malme 1982). These recordings also showed sporadic vocalizations but no structured calls.

Group Composition

Surface-Feeding Group. The analysis of individually identified whales from each of the six surface-lunging pods showed repeated associations between many of the members (Figure 24). Two individuals (#561 and 578) were common to all six pods. One whale (#549) was common to five pods, two whales (#569 and 252) were common to three, and three whales (#562, 556, and 557) were common to two pods. The calf (#385) was common to the three 1984 observations. Among the whales sighted repeatedly, four were seen in at least one observation from each year. The remaining 15 whales were sighted only once.

From the characteristic chin patch and barnacle scars along its lower rostrum, it was possible to determine that #561 was the lead animal in each of the surface lunges across all observations (Figure 20b). Based on its close association with the calf in 1984, I assumed that #561 was the mother. This conclusion is supported by the fact that only #561 and 578 were with the calf in each of the 1984 observations.

Figure 24: The sighting record and associations of whales in the surface feeding pods. Boxes enclose pods. Letters indicate behavioral role or age class: A = adult, C = cow with calf, c = calf.



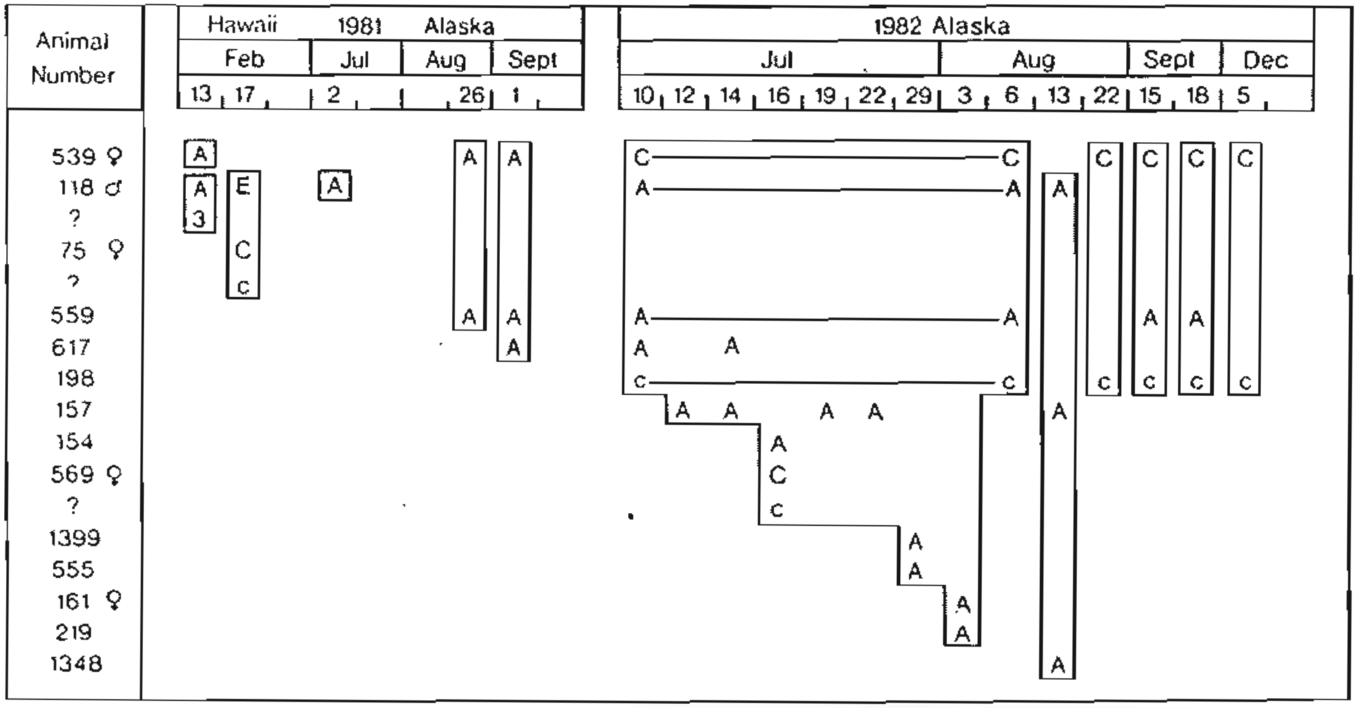
Animal Number	1981 Alaska Jul 17	1981 Alaska Jul 20	1981 Alaska Aug	1981 Alaska Sept 7	1984 Alaska Jul 27	1984 Alaska Aug 18	1984 Alaska Sept 13
561 ♀	A	A		A	C	C	C
578	A	A		A	A	A	A
549	A	A		A	A	A	
569 ♀	A	A					
562	A	A					
?	A						
230		A					
541 ♀		A					
566		A					
740		A					
2526		A					
252				A		A	A
556 ♀				A	A		
545				A			
590				A			
947				A			
385					c	c	c
557					A		A
224					A		
384						A	
403						A	
407						A	
40 ♂							A
104 ♂							A
3423							A

To determine the age-sex class of other individuals in the surface-feeding groups, I examined their complete resighting histories in Hawaii and southeastern Alaska (Chapter 2). Animals #40 and 104 are thought to be mature males based on their roles as escorts on the Hawaiian wintering grounds. Three other adults, in addition to #561, are thought to be reproductively mature females based on their close association with a calf in Hawaii or southeastern Alaska. Animal #541 was seen with a calf in southeastern Alaska in September of 1983 and with the same calf, then a yearling, in Hawaii during February of 1984. Animal #556 was seen with a calf in September of 1982 and #569 was seen with a calf during July of 1982; both sightings were in southeastern Alaska. There is no direct evidence to determine the sex of the other 18 whales in the six pods.

Point Adolphus. Long-term associations were also found among subsurface-feeding whales (Figure 25). The core members of the subsurface-feeding pod near Point Adolphus consisted of three individuals (#577, 166, and 587) during 1981, 1982, 1983 and 1985, and up to four other individuals (#236, 581, 573, and 155) that were present for most of one or more of these seasons. Other individuals associated with the core group for periods of a day or less, occasionally forming a pod of as many as nine whales.

Five of the seven whales from the core group are known to be females based on their associations with a calf in one of the study years (Figure 25): #155, 236, 573, 587, and 581. A sixth, (#166) is thought to be a cow based on observations of Jurasz and Palmer (1981a)

Figure 25: The sighting record and associations of the "core members" of subsurface feeding pods at Point Adolphus. Boxes enclose pods. Letters indicate behavioral role or age class: A = adult, C = cow with calf, c = calf.


Animal Number
539 ♀
118 ♂
?
75 ♀
?
559
617
198
157
154
569 ♀
?
1399
555
161 ♀
219
1348
Hawaii
1981
Alaska
Feb
Jul
Aug
Sept
13
17
2
26
1
1982 Alaska
Jul
Aug
Sept
Dec
10
12
14
16
19
22
29
3
6
13
22
15
18
5
A
E
C
c
3

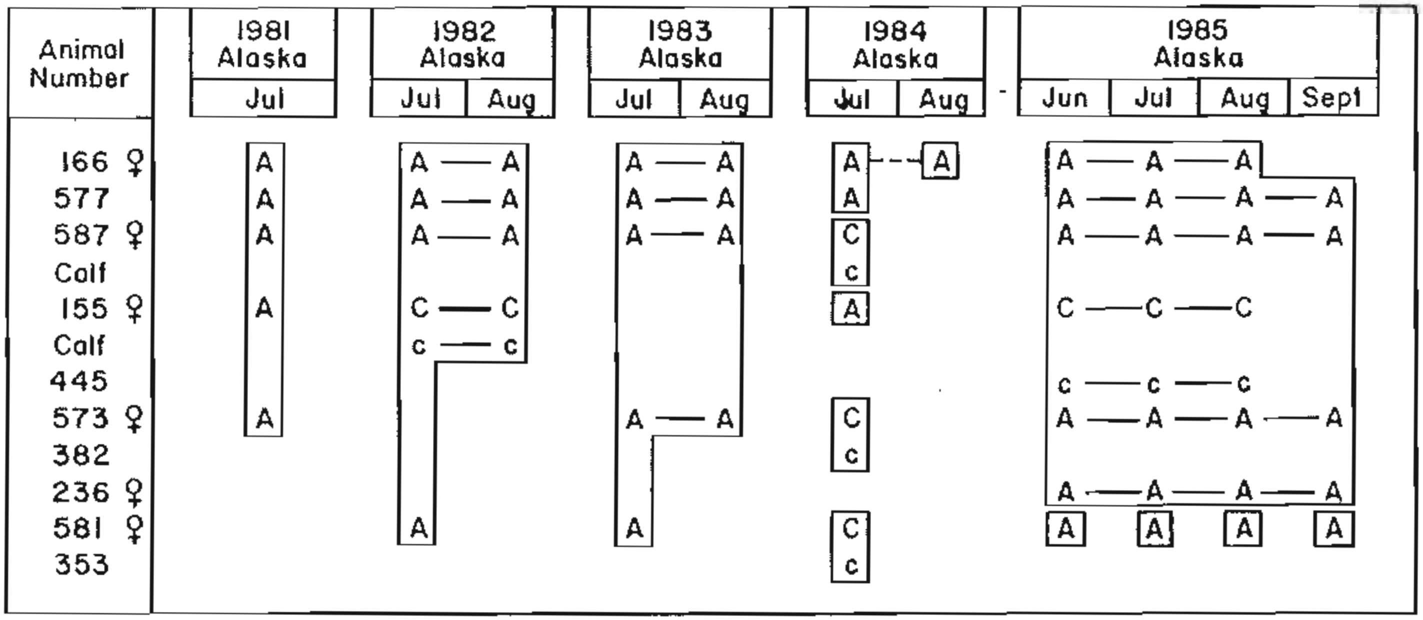
but has not been seen with a calf during the years 1980 to 1985. The sex of animal #577 is unknown.

During the summer of 1984 all seven of the animals from the core group were sighted repeatedly in the Point Adolphus area, but only a few individuals briefly associated with each other. Four of the core animals (#236, 581, 587, and 573) were accompanied by calves during 1984.

Bartlett Cove. The subsurface-feeding pod in Bartlett Cove consisted of a cow-calf pair, cow #539 and her calf #198, and two adults, #559 and 118 (Figure 26). During its residency in the cove, the pod was joined by as many as five other whales, including a second cow-calf pair (cow #569, also found in the surface-feeding pod during 1981). Of the nine other whales identified with the residents, only #157 and 565 were seen in the cove for more than one day. In some instances the presence of the transient whales appeared to disturb the resident four, resulting in aerial behavior and dissynchrony of behavior.

The three adult Bartlett Cove residents showed associations over more than a single summer season and in two seasonal habitats. Animals #118 and 539 were observed within a kilometer of each other near the island of Hawaii on February 13, 1981. Animals #539 and 559 were seen together in Frederick Sound, southeastern Alaska, on August 26, 1981, and again with #565 on September 1, 1981. After leaving Bartlett Cove in mid-August of 1982, #539 and her calf #198 were seen in Frederick Sound within a few hundred meters of #559 (Dawson and Taylor 1982). At this time, the three were surface feeding on swarming euphausiids, a

Figure 26: The sighting record and associations of whales feeding together in Bartlett Cove. Boxes enclose pods. Letters indicate behavioral role or age class: A = adult, C = cow with calf, c = calf.



Animal Number	1981 Alaska Jul	1982 Alaska Jul	1982 Alaska Aug	1983 Alaska Jul	1983 Alaska Aug	1984 Alaska Jul	1984 Alaska Aug	1985 Alaska Jun	1985 Alaska Jul	1985 Alaska Aug	1985 Alaska Sept
166 ♀	A	A	A	A	A	A	A	A	A	A	
577	A	A	A	A	A	A		A	A	A	A
587 ♀	A	A	A	A	A	C		A	A	A	A
Calf						c					
155 ♀	A	C	C			A		C	C	C	
Calf		c	c								
445								c	c	c	
573 ♀	A			A	A	C		A	A	A	A
382						c					
236 ♀								A	A	A	A
581 ♀		A		A		C		A	A	A	A
353						c					

distinct departure from their earlier feeding behavior in Barlett Cove. In 1984, animals #539 and 559 were found feeding together again on euphuasiids in Stephens Passage on September 6 and 8.

Animal #118 is thought to be a male based on his role as an escort in Hawaii during the winter of 1981 and his long history of sightings without a calf in southeastern Alaska. Animal #559 has been seen in 1980, 1981, 1982, and 1984 without a calf (Jurasz et al. 1980; Perry et al. 1985), but due to the variability of calving intervals among female humpback whales in southeastern Alaska (Chapter 2), I cannot yet confidently assume that it is a male.

Prey Assessment

Surface-Feeding Group. It was possible to determine, with reasonable certainty, the primary prey of the surface-lunging pods during four of the six observations. On July 17, 1981, hand-size fish were seen leaping out of the water just before the whales lunged through the surface. The size and color of the fish suggested that they were herring, *Clupea harengus*. On September 7, 1981, a recording fathometer aboard the research vessel showed dense traces of schooling fish in the path of the whales. The fish were at depths of about 40 m in 50 m of water. Fathometer tracings from July 23 and August 18, 1984, showed dense traces of schooling fish along the face of the rocky coastline where the whales were feeding. The shape and backscattering characteristics of the school suggested that these fish were also herring (Krieger and Wing 1984).

Point Adolphus. Humpback whale prey near Point Adolphus was determined with hydroacoustic surveys and net sampling during the summers of 1982 to 1985 (Wing and Krieger 1983; Krieger and Wing 1984; Krieger and Wing 1985; Baker 1985). Hydroacoustic surveys in the paths of the feeding whales showed dense traces of schooling fish in each year. Sampling with mid-water trawls during 1983 and 1984 confirmed that these fish were herring averaging 205 mm in length (Krieger and Wing 1985).

Bartlett Cove. A dense school of fish was found in Bartlett Cove during each of the seven hydroacoustic surveys of the cove in 1982. Net sampling with a pelagic fish trawl from the *John N. Cobb* yielded pure catches of capelin, *Mallotus villosus* (Wing and Krieger 1983). No fish schools were found in Bartlett Cove during 1983 or 1984 despite frequent hydroacoustic sampling. Few whales entered the cove during these years and none stayed for more than a few hours (Baker 1983; Perry et al. 1985).

may also function as leaders (Leuthold 1977). Among many ungulates, these animals are typically females. It is possible that matriarchs, similar to those found among elephants (Loxodonta africana), are also found among humpback whales. These animals could be important reservoirs for cultural information including migratory routes, specialized feeding strategies (such as those described here), and an understanding of the patchy distribution and seasonal changes in prey abundance.

Perhaps the most persuasive evidence that these feeding groups were acting cooperatively comes from the documentation of repeated associations between group members. In many cases, associations between individuals persisted throughout an entire summer season and extended across years. A repeated association extending from one year to another is particularly impressive considering the long migration to the wintering grounds and the dispersal of feeding herds which intervenes between summer seasons (Chapter 1). There is only one previous report of an association between humpback whales extending across seasons. Nemoto (1964) noted that a pair of whales were Discovery-tagged on the Antarctic feeding grounds one austral summer and captured together the next summer..

Ecological Bases of Group Formation

Why is feeding on schooling fish asociated with coordinated behavior and groups cohesion among humpback whales? By feeding in large, coordinated groups, humpback whales may increase the probability of controlling the movement and preventing the dispersal of large fish schools. Analogously, the pack-hunting tactics of the social canids and felids allow these animals to capture prey several times their size (Kleiman and Eisenberg 1973; Bertram 1978). For small, slow-moving prey, such as swarming euphausiids, herding and large group size is probably unnecessary.

Why bother to feed on schooling fish when swarming euphausiids are readily available and require less complex social interactions? Contrary to what is generally assumed (Andrews 1909; Bryant et al. 1981), swarming euphausiids may not be readily available every year or during all times of the season. Recent studies of humpback whale prey in southeastern Alaska show significant seasonal and yearly fluctuations in abundance and distribution of different prey types (Wing and Krieger 1983; Krieger and Wing 1984). Although only about 20% of the whales encountered in southeastern Alaska during July and August of 1984 were feeding on schooling fish (Baker 1984; Krieger and Wing 1985), little is known about the predominant prey during the spring and fall. Observations of feeding whales during late November and early December suggest that schooling fish are a primary late-season prey in some years (Baker et al. 1985). Possibly more important, the nutritional content of some species of schooling fish is far superior to that of euphausiids. A nutritional analysis of prey collected in southeastern Alaska during 1984 showed that herring have an average energy content of 2.64 kcal/gr wet weight compared to 1.72 kcal/gr wet weight for euphausiids (Baker 1984). This higher caloric value is an attractive bonus for an animal that has only a few months in which to gather its food for the entire year. As with the social carnivores, cooperative feeding may allow humpback whales to exploit an energetically rich trophic level that is unavailable to, or inefficiently utilized by, solitary feeders.

Group foraging may also result in some degree of increased feeding efficiency even in the absence of true cooperative behavior (E.O. Wilson 1975). In desert finches, group foraging within bounded areas increases the probability that the next prey patch encountered by the group has not been recently depleted or dispersed by wandering singles (Cody 1971). A similar advantage to group movement may exist for foraging whales if fish schools are most efficiently exploited by groups and if feeding singles disperse schools. Some evidence of this is suggested by the group movement of the surface-feeding pods and the absence of other whales in the Chatham Strait area during these observations.

A final factor influencing the formation of humpback whale pods could be predation. Group foraging provides superior defense against predation in many species, and is a primary force maintaining aggregations in grazing ungulates (E.O. Wilson 1975; Leuthold 1977). The only known predator of humpback whales in northern waters is the killer whale (Chittleborough 1953; Whitehead and Glass 1985). Reports of killer whale attacks are infrequent, but an analysis of scarring on the flukes of humpback whales in the central and eastern North Pacific showed evidence of nonfatal attacks on humpback whales, at some point in their lives, in 2.5% of the individuals examined (Chapter 2). In the

Northwest Atlantic, a similar analysis of scarring showed evidence of nonfatal attacks in 33% of 756 flukes examined (Katona et al. 1980).

Determinants of Group Composition

Membership in cooperatively feeding groups seemed to be influenced by gender, reproductive status, and partner preference. The predominance of mature female members may suggest some dimorphism in the prey selection of humpback whales. Undoubtedly, the energetic demands of pregnancy and lactation on female humpback whales are extreme (Lockyer 1976). Baleen whales exhibit one of the highest relative and absolute intrauterine growth rates of any group of mammals (Eisenberg 1981). Ralls (1976) suggests that the larger average size of female baleen whales, compared to males, is not due to an absence of sexual selection on males but rather the greater pressure on females to be "bigger mothers" and thus "better mothers". The energetic demands of reproduction are further exascerbated by the seasonal fasting and lengthy migration of baleen whales. The low and variable calving rate of females in southeastern Alaska indicates some resource limitation on female reproduction (Chapter 2). Cooperating to feed on an energetically superior prey could enhance a female's reproductive potential.

Females were more likely to join feeding groups in years that they were not accompanied by a calf. Cow-calf pairs are relatively solitary on the feeding grounds and the presence of a calf in a large pod is rare (Nemoto 1964; Chapter 5). In particular, cow-calf pairs are only rarely found with other cow-calf pairs (Chapter 5). The disruption of the Point Adolphus core group may have been the result of births to several of the group members during 1984 (Perry et al. 1985). The possible reasons underlying the avoidance between cow-calf pairs are discussed in later chapters (Chapter 5; Summary and Conclusions).

Partner preference, as well as gender and reproductive status, played a role in pod composition. Animals #539 and 559, for example, continued to associate after moving to different areas of southeastern Alaska and while feeding on euphuasiids. At Point Adolphus, as many as seven other whales, including some mature females without calves, were resident in some summers but repeated associations were generally restricted to only the seven "core members."

It is tempting to speculate that kinship ultimately determines partner preference and the composition of feeding groups. A tendency for neighboring whales to be matrilineally related could exist if fidelity to a feeding locale is established when a calf first travels to the feeding grounds with its mother (Baker and Herman 1984b; Martin et al. 1984; Chapter 1). The relatedness of adults in the feeding groups described here is known in only one case; #516, first observed as a calf in 1974, is reported to be the offspring of #166 (Jurasz and Palmer 1981a). Although these two animals were found near each other in most years, they were found feeding together in the same pod on only a few occasions during 1982 and 1984 (Perry et al. 1985). In many mammalian species, however, it is the relationship between cows and their female offspring that is enduring (E.O. Wilson 1975); #516 is thought to be a male.

Functions of Vocalizations

The specific behavioral context and function of humpback whale vocalizations during the feeding season have not been described. Only the function and context of the winter song and "social sounds" have been studied through playback experiments (Tyack 1981, 1982, 1983; Baker and Herman 1984a). The stereotyped series of vocalizations reported here, referred to as a "feeding call", occurred specifically though not exclusively during group feeding, and may have one or more of three functions: 1) agonism or establishing dominance in relation to individual spacing; 2) coordinating group behavior; and 3) disorienting or herding schooling fish.

The hearing capabilities of the Pacific herring have not been studied, but its close relative, the Atlantic herrring, is sensitive to sounds ranging in frequency from 30 Hz to 10,000 Hz, with greater sensitivity towards the lower frequencies (Enger 1967). Playback experiments show that Pacific herring respond with avoidance and "alarm" to some synthetic and vessel sounds (Schwartz and Greer 1984). The frequency and duration of the humpback whale feeding calls are similar to those of some synthetic sounds which elicited strong responses from the herring. Schwartz and Greer (1984) report that herring schools coalesce and become more uniform in their movement during avoidance and alarm. It is possible that humpback whales exploit these predictable responses and use vocalizations to herd or coalesce the schools of herring.

Evidence of an agonistic component to the feeding call comes from recent playback experiments in Hawaii (Joseph Mobley, personal communication). A large proportion of responses to the feeding call involved "charges" similar to those reported in playbacks of "social sound" (Tyack 1983) and agonistic behavior similar to that observed in male-male competition (Baker and Herman 1984a; Chapter 3). However, extrapolations to the function of feeding-season vocalizations based on behavioral responses on the wintering ground may be unfounded given the profound differences in motivational regimes operating in the two habitats (Baker and Herman 1984b). Whales in Hawaii, particularly males, may be motivationally potentiated to respond aggressively to any conspecific vocalization.

Counter-evidence to an agonistic function is provided by the absence of other behaviors associated with aggression. The calls did not result in dispersal of the pods and no whales disaffiliated from the pod following a feeding call. Instead, the close proximity of the lunging whales and the propinquity of the feeding call with the surface lunges are circumstantial evidence for an affiliative or coordinative function. Playbacks of the feeding calls on the feeding grounds are necessary to clarify these interpretations.

Feeding Calls and the Evolution of the Winter Song

Several characteristics of the second voice in the feeding calls recorded in 1981 (Figure 22) suggest that this was a case of vocal duetting. The second voice matched, to some degree, the first voice in both timing and frequency, though offset by one or two octaves. The tendency to be offset by one or more octaves during vocal mimicry is well known to anyone who sings and is a characteristic of vocal mimicry in dolphins (Richards et al. 1984). Although studies of yearly changes in humpback whale song show that these animals are impressive vocal mimics, no other instance of duetting has been reported (Winn et al. 1981).

The observation of stereotypic calls and vocal duetting in the context of group feeding may have important implications for understanding the evolutionary origins of the winter song. Tyack (1982) has suggested that the complexity of humpback whale song is the result of runaway sexual selection, a process which may explain the evolution of exaggerated secondary-sexual characteristics in one sex, usually the male, of some species. According to Fischer (1958), the initial phase of runaway sexual selection requires that the trait under selection must be of some survival value to the individual, as well as being attractive to some members of the opposite sex. Without some initial survival value the gene controlling the attraction of one sex to a trait of the other could not become established in the population. Although recent theoretical treatment shows that in some circumstances this requirement is not necessary, Fischer's original formulation remains the most plausible.

If humpback whale song evolved through runaway sexual selection, then its fundamental components, an impressive acoustic memory and ability for vocal mimicry, may still be important characteristics in the other could not become established in the population. Although recent theoretical treatment shows that in some circumstances this requirement is not necessary, Fischer's original formulation remains the most plausible. If humpback whale song evolved through runaway sexual selection, then its fundamental components, an impressive acoustic memory and ability for vocal mimicry, may still be important characteristics in the foraging success of males and females on the feeding grounds as well as the mating success of males on the wintering grounds. Like many of the stereotyped behaviors observed during aggressive competition in Hawaii (Chapter 3), the song may have its evolutionary origin in feeding behavior.

Chapter V

Seasonal Changes in the Size, Composition, and Stability of Humpback Whale Groups

Abstract

The size, composition, and stability of humpback whale groups were studied in two seasonal habitats of a single population. The structure of humpback whale groups, referred to as pods, was not determined solely by random processes in either habitat. On the southeastern Alaska feeding grounds there was an unexpectedly high proportion of singles and large pods of adults. Although intrasexual associations were the most common, adult pods could be all male, all female, or mixed sex. The majority of cow-calf pairs were unaccompanied by other adults. When cow-calf pairs did associate with other whales, they could be accompanied by either males, females or both sexes. Some whales formed stable associations in pods that endured for an entire summer season and re-occurred across years. Most pods, however, were transient and associations between individuals were fluid. On the Hawaiian wintering grounds the size of adult pods was significantly larger than in southeastern Alaska. The majority of cow-calf pairs were accompanied by one or more escorts, thought to be courting males. Associations between sexes seemed to follow rigid rules. No females were found with other females. Pod structure was very fluid and associations were transient. Whales seen together in a pod on one occasion were unlikely to be seen together again. Overall, the structure of humpback whales showed profound seasonal changes shaped by a competitive mating system on the wintering grounds and a non-competitive or cooperative foraging strategy on the feeding grounds.

Introduction

> "I would think the schools of baleen whales should be examined also in the breeding areas, in which the meaning of the school of baleen whales is somewhat different from that of schools in the feeding areas." T. Nemoto (1964).

Social organization is potentially the most variable structure characterizing a species (Eisenberg 1981). While broadly limited by phylogenetic inertia (E.O. Wilson 1975), the social organization of most species is remarkably labile in responding to proximate changes in environmental and populational pressures. Important ecological factors influencing social organization include the distribution of food and the effects of predation (Eisenberg et al. 1972). Other determinants of social organization are the reproductive strategies and the mating system of a species. In migratory or seasonally reproductive species, there may be distinct social systems operating during different times of the year (Leuthold 1977).

Until recently, the social organization of baleen whales remained virtually undescribed (E.O. Wilson 1975). Based on the predominance of pairs and trios on the feeding grounds, commercial whalers assumed that most baleen whales formed monogamous pair-bonds or small family units which remained together throughout the year (Nemoto 1964). In only a few cases did whaling biologists examine the group structure of baleen whales by documenting seasonal changes in group sizes or the age-sex class of group members (Nemoto 1964; Chittleborough 1965; Dawbin 1966).

Among humpback whales, recent studies argue against the traditional assumption that all baleen whales form family units. During the winter breeding season, the structure of humpback whale groups is transient and associations between individuals are fluid (Mobley and Herman 1985; Tyack and Whitehead 1983; Chapter 3). Pods of humpback whales appear to result from males aggregating in response to the presence of a mature female. Within these pods, violent aggression is observed between males competing for proximity to the female (Glockner-Ferrari and Ferrari 1981; Tyack and Whitehead 1983; Chapter 3).

The function of groups on the feeding grounds is less clear. Whitehead et al. (1982), in his study of humpback whales on the feeding grounds of the northwestern Atlantic, found no evidence of repeated associations, above that expected by chance, among adult whales. In southeastern Alaska, however, associations between some individual whales are stable and extend over seasons and years (Baker and Herman 1984b; Chapter 4). Repeated associations are also reported among humpbacks feeding on the Stellwagon Bank near Cape Cod (Weinrich 1983).

While these behavioral studies have begun to characterize some seasonal aspects of group structure and social behavior, they have not yet addressed the interaction of these seasonal components in the overall social organization of humpback whales. Here I present data on the group size, group composition, and group stability of free-ranging humpback whales from both the feeding and wintering grounds of a single population or structured stock (Chapter 1). These three attributes of sociality form the basis for a more complete model of seasonal changes in the social organization of humpback whales.

Methods

Field studies of humpback whales were conducted in Hawaiian waters during the winters of 1979 to 1984 and in southeastern Alaskas during the summers of 1980 to 1984. Whales were observed and photo-identified from small vessels on a daily or near-daily basis (General Methods). Additional data from years previous to 1979 are presented when available and relevant (Herman and Antinoja 1977; Herman et al. 1980).

Unit of Analysis

Nineteenth century whalers distinguished three levels of group size in baleen whales (Clark 1956, cited in Nemoto 1964); "pods" or "gams" numbering up to about twenty whales, "schools" or "shoals" of some twenty to fifty whales, and the "herd" or "body of whales" comprising fifty to several hundred individuals. Following this traditional nomenclature I have defined a pod as two or more individuals moving in the same direction, within two to three whale lengths of each other, and in close behavioral synchrony, particularly with respect to respiration, diving, and surfacing (Herman and Antinoja 1977; Baker et al. 1982; Whitehead 1983). For convenience, a single whale was also referred to as a pod. Although I did not attempt to quantify spatial proximity or behavioral synchrony, pods were easily distinguished. Groups characterized as pods were observed in both Hawaii and southeastern Alaska.

A shoal has been described as a dense aggregation of whales in an area of only a few square kilometers in extent (referred to as a "flock" in Baker et al. 1982; Baker et al. 1983). Whales in a shoal, though milling in a common area, do not move in a uniform direction. Individuals are separated by relatively large interindividual distances, and show no obvious synchrony of respiration, diving, or surfacing. Within a shoal, whales are sometimes found in pods of two to four, but often it is not possible to distinguish any group subunits. Presently available data suggest that shoals are transient groups aggregating in response to local concentrations of prey, particularly swarming euphausiids (Baker et al. 1983; Baker 1984; Wing and Krieger 1983; Krieger and Wing 1985). Groups characterized as shoals were observed only in southeastern Alaska.

A herd of humpback whales was defined earlier as a unit of a structured stock (Chapter 1). Southeastern Alaska seems to encompass the range of a single feeding herd which remains segregated, during summer, from other feeding herds to the north and west. The southeastern Alaska feeding herd is estimated to number between 270 and 374 animals (Baker et al. 1985). Whales in Hawaiian waters are a congregation of several feeding herds (Chapter 1).

Although social structure may exist at all three levels of group size, determining the significance of such a structure in the larger groups is problematic. It is difficult to quantify the exact extent of shoals or herds. Given their size, a very large data set would be necessary to distinguish meaningful from coincidental associations within the groups. As a consequence of these problems, the analyses of group size, composition, and stability is restricted to the level of pods. Because of their particular behavioral and populational importance, pods with a calf are examined separately as a subgroup of all pods in each seasonal habitat.

Pod Size

The initial size of humpback whale pods was determined visually during vessel-based surveys of southeastern Alaska and Hawaii. The overall analysis of pod size is restricted to data collected during surveys of Hawaiian waters in 1980 and 1981 and of southeastern Alaska waters during 1981 and 1982. These years are the most comparable in terms of study effort and area. Although vessel-based surveys were non-systematic in design, the large number of pods encountered and the large area surveyed helped assure that the sample of pod size was approximately random during each study period.

A preliminary inspection of the frequency of pod sizes in southeastern Alaska and Hawaii indicated that the distribution was skewed positively. To allow the use of standard parametric statistics in some analyses of pod size, the data were normalized with a logarithmic transformation (Snedecor and Cochran 1967). Consequently, only geometric means are reported and standard deviations are omitted. In determing the size of calf pods, only the adults were counted.

Sex Composition and Size Preference

Whale pods encountered during vessel-based surveys were approached in order to photo-identify the pod members. The sex of each member was later inferred, if possible, based on all available sighting information of that individual (Chapter 2). The data set used to determine sex-based preferences in pod size and composition included sighting records from all study years. All fluke observations were used except those of insufficient quality.

The determination of sex was usually based on extensive sighting records of an identified individual. Consequently, some sexed individuals account for a large number of sightings in the data set. For this reason, it cannot be assumed that the analysis of sex composition and size preference is based on a random sample of the population.

For the analysis of sex-based preferences for pod size, a pod was considered a female pod if it contained at least one female or a male pod if it contained at least one male. A pod was considered both a male and a female pod if it contained both sexes. Although this resulted in some loss of independence in the data set, the number of pods classified into more than one category was relatively small. The number of sexed adults found in cow-calf pods was small and did not warrant a separate analysis.

Pod Stability and Repeated Associations

Pod stability and repeated associations are related but distinct measures of social affiliations. Pod stability is defined here as the persistence of association between individuals in the same pod. Stability is reflected by the frequency of changes in pod size and membership. A repeated association is defined as the grouping of two individuals in the same pod on two or more days regardless of the intervening associations. Because individual whales were seldom under continuous observation it was not always possible to distinguish repeated associations from stable groups.

Pod stability is illustrated through case histories of frequently sighted individuals selected from the fluke library (General Methods). These case histories were chosen to demonstrate the range of pod stability in each seasonal habitat. The analysis of repeated associations was more complex. First, it was necessary to designate a focal individual and determine the identity of the focal animal's associates in each sighting. These records were then examined for common associates across sightings. To accomplish this task, a computer program was written to search through the fluke sighting library (General Methods) by iteratively treating each identified whale as the focal individual. The output of this program included the number of sightings, the number of associates, the number of repeated associations, and the identity of the repeated partner for each individual in the catalog. The search for repeated associations was conducted first within each seasonal habitat, Hawaii and southeastern Alaska, and then across seasonal habitats. Sightings from all years of the study were used and only fluke observations of insufficient quality were omitted from the search.

Group Size

Southeastern Alaska

Adult Pods. A total of 483 pods of whales were encountered during vessel-based surveys of southeastern Alaska in the summer of 1981 and 1982. Of this total, 390 pods consisted entirely of adults. Yearly differences in the sizes of adult pods were not significant (F[1/388] = 0.01, p = 0.95). In the combined sample from 1981 and 1982, 52.8% of the adults encountered were singletons, 29.7% were pairs, 10.5% were trios, and 7.0% were larger pods (Table 20).

If pod size in Alaska was determined simply by coincidental meetings or other random events, the distribution of sizes should approximate a zero-truncated Poisson distribution (Cohen 1969). To test this null hypothesis, the expected frequency distribution of pod sizes was calculated from a zero-truncated Poisson distribution (Caughley 1977) and compared to the combined data from 1981 and 1982 (Table 20). The observed frequency distribution of pod sizes in southeastern Alaska differed significantly from the predicted distribution (Chi-square[4]= 27.44, p = 0.005), with fewer pairs, trios, and quartets, but more singles and large pods than expected.

The only other data available on group sizes of feeding humpback whales, those of Nemoto (1964), come from the pelagic whaling grounds of the North Pacific (Table 21). The pods observed by Nemoto also differed from a zero-truncated Poisson distribution (Chi-square[3]= 9.7; p < 0.025) but included more pairs and fewer larger groups than expected; nearly the opposite of the trend in southeastern Alaska.

Table 20

Pod sizes of humpback whales encountered during
vessel-based surveys of southeastern Alaska
in the summers of 1981 and 1982.

Adult Pods
(mean size = 1.54)

	1A	2A	3A	4A	5A	6+A	Total
%	52.8	29.7	10.5	2.6	---4.3---		
Frequency	206	116	41	10	9	8	390
Expected	180.9	124.8	57.4	19.8	---7.1---		
Chi-square	3.48	0.62	4.69	4.85	--13.80--		27.44 (p<0.01)

Cow-Calf Pods
(mean size = 1.62 adults)

	1A-1c	2A-1c	3A-1c	4A-1c	5A-1c	6+A-1+c	Total
%	55.4	20.7	14.1	4.4	---5.3---		
Frequency	51	19	13	4	3	3	93
Expected	42.2	29.5	13.8	4.6	---1.8---		
Chi-square	1.84	3.74	0.05	0.08	---9.8---		15.51 (p<0.01)

Note: Expected number of pods were calculated from the zero-truncated Poisson distribution (Caughley 1977). Adults are noted by the letter A and calves are noted by the letter c.

Table 21

Pod sizes of humpback whales on the pelagic whaling grounds of the North Pacific in 1955 and 1956 (from Nemoto 1964).

	Total Whales*						
	1	2	3	4	5	6+	Total
%	50.0	42.4	3.3	4.3			
Frequency	46	39	3	2	1	1	92
Expected	50.2	27.9	10.3	3.5			
Chi-square	0.35	4.42	5.17	0.1			9.7 (p<0.025)

Note: Expected number of pods were calculated from the zero-truncated Poisson distribution (Caughley 1977). Adults are noted by the letter A and calves are noted by the letter c.

* It is not clear from Nemoto (1964) whether his pod sizes include total whales or adults only.

Calf Pods. Of the 194 pods observed in 1981, 32 (16.5%) included a calf. Of the 289 pods observed in 1982, 61 (21.1%) included a calf. In the combined sample of 93 cow-calf pods, 55.4% were unaccompanied by another adult, and 20.7% were accompanied by a single adult (Table 20). The remaining 23.9% of cow-calf pairs were accompanied by two or more adults. The average number of adults, including the cow, in cow-calf pods did not differ significantly from adult-only pods ($F[1/482] = 0.62$, $p = 0.43$). Like adult only pods, the number of adults in cow-calf pods was not adequately modeled by the a zero-truncated Poisson distribution (Chi-square[5] = 15.51, $p < 0.025$).

Only twice in 1981 and once in 1982 did a pod include more than a single calf. If multiple-calf pods resulted from the chance encounter of cow-calf pods their probability of occurrence should approximately equal the product of their independent probability of occurrence in the population. Given the overall percentage of cow-calf pairs in the two sample years (19.2%), multiple cow-calf pairs should occur in approximately 3.7% (0.192 X 0.192) of the observations. Thus, from the total of 483 pods, 17.9 multiple-calf pods were expected, significantly more than the three observed (Chi-square[1] = 13.10, $p < 0.005$).

Observations of two multiple calf pods suggested some behavioral disturbance associated with the confluence of cow-calf pairs. On September 3, 1981, a cow, calf, and a second adult moved toward a pod of six adults with a calf. As the pods joined, the first calf began an intense display of breaching and headslapping that lasted for approximately 20 minutes. Shortly afterwards the pod dispersed and the two cow-calf pairs separated. On July 16, 1982, a pod of five adults and a calf were joined by a second cow-calf pair. Although there was an increased level of surface activity by the pod, the two cow-calf pairs remained associated for most of the day.

Sex-Based Preferences. Sexed whales were found in 301 adult pods during the years 1980 to 1984 (Table 22). One or more males were found in 163 adult pods. One or more females were found in 115 adult pods. 23 pods included both males and females and were counted in both categories. The average size of a pod containing a male was significantly smaller than the average pod containing a female ($F[1/323] = 11.27$, $P < 0.001$).

Pod size preference, however, was not strictly determined by sex or reproductive condition. Idiosyncratic preferences for pod size were obvious in the sighting records of both sexes. Females were particularly variable in their pod size preferences. One of the most solitary animals in the sighting records, #530, was observed on 21 occasions while she was resident at Point Adolphus from 1981 to 1984. Although she was accompanied by a calf in 1982 and in 1984 she was never found in the company of another adult. Animal #530's solitary behavior could not be explained by an absence of social opportunities. As many as nine other adults were resident at Point Adolphus during these years (Chapter 4). One of these residents, #587, also a female, was sighted 15 times during 1981 to 1983. She was alone on only one occasion. In 1984, #587, accompanied by a calf, was sighted eight times in Glacier Bay. In spite of the general solitary nature of most cows, she was accompanied by other adults twice and by a second cow-calf pair once.

Table 22

The size of humpback whale pods in southeastern Alaska containing individuals of surmised sex.

	1A	2A	3A	4A	5A	6+A	Mean
				<u>Males</u>			
%	51.1	28.0	11.8	1.1	2.2	5.9	
Frequency	95	52	22	2	4	11	1.63
				<u>Females</u>			
%	33.3	32.6	14.5	7.3	3.6	7.7	
Frequency	46	45	20	10	5	12	2.04

Possibly the most gregarious animal in the sighting record, #561, also a female, was found in three pods during 1981 with six, nine, and 11 other adults, respectively (Chapter 4). During 1984 she was accompanied by a calf and four to six other adults in each of three separate sightings.

Idiosyncratic differences were apparent, though less dramatic, in the pod size preferences of males. Animal #159, for example, was generally, but not exclusively, solitary. Out of a total of 24 sightings from 1982 to 1984 he was alone 16 times (67%), with one other adult five times (21%), with two adults three times (12.5%), and once with two adults and a calf. Animal #564, on the other hand, was sighted nine time during 1981 to 1984 (see Figure 29) -- on no occasion was he alone.

Hawaii

Adult Pods. A total of 575 pods of whales were encountered during vessel-based surveys of Hawaiian waters during 1980 and 1981. Of this total, 476 pods consisted only of adults. Yearly differences in the size of adult pods were not significant ($F[1/474] = 3.86$; $p = 0.051$). In the combined sample, 33.5% of the adult pods were singletons, 42.4% were pairs, 12.2% were trios, and 11.9% were larger pods (Table 23). The observed frequency distribution of pod sizes from the combined data differed significantly from the the zero-truncated Poisson distribution with far more pairs than expected (Chi-square [4] = 37.63 $p < 0.005$). Further details of pod size in relationship to aggression and seasonal abundance are presented in Chapter 3.

Table 23

Pod sizes of humpback whales encountered during vessel-based surveys of Hawaii in the winters of 1980 and 1981.

Adults Pods
(mean size = 1.84)

	1A	2A	3A	4A	5A	6+A	Total
%	33.5	42.4	12.2	7	---4.8---		
Frequency	159	201	58	33	11	12	474
Expected	176.7	152.8	88.1	38.1	13.2	5.1	
Chi-square	1.8	15.2	10.3	0.7	0.4	9.43	37.65 (p<0.005)

Cow-Calf Pods
(mean size = 1.94 adults)

	1A-1c	2A-1c	3A-1c	4A-1c	5A-1c	6+A-1c	Total
%	23.2	52.6	16.8	4.2	---3.2---		
Frequency	22	50	16	4	2	1	95
Expected	34.3	30.5	18.1	7.8	---4.3---		
Chi-square	4.4	12.5	0.2	1.9	---0.4---		19.3 (p<0.025)

Note: Expected number of pods were calculated from the zero-truncated Poisson distribution (Caughley 1977). Adults are noted by the letter A and calves are noted by the letter c.

Calf Pods. Of the 248 pods observed in 1980, 52 (21%) included a calf. Of the 323 pods observed in 1981, 43 (13.3%) included a calf. In the combined sample of 95 cow-calf pods, 23.2% were unaccompanied by another adult, 52.6% were accompanied by a single adult, and 24.2% were accompanied by two or more adults (Table 23). No pods were observed to have more than a single calf. Although cows with calves appeared to be somewhat more gregarious than adults without calves, this difference was not significant (F[1/568] = 0.89; p = 0.347). The number of adults in Hawaiian cow-calf pods was not adequately modeled by the zero-truncated Poisson distribution (Chi-square [4] = 19.34, p > 0.005); cow-calf pairs were accompanied by one other adult far more often than expected.

Sex-Based Preferences. Sexed whales were found in 107 adult pods during 1977 to 1984 (Table 24). One or more males were found in 76 pods and a female was found in 19 pods. Five pods included both males and females and were counted in both categories (see Group Composition for further details). Although males were found alone and in large pods somewhat more often than females, the average size of male and female pods was not significantly different (F[1/109] = 0.03, p > 0.86).

Table 24

The size of adult pods in Hawaii containing individuals of surmised sex.

	1A	2A	3A	4A	5A	6+A	Mean
				Males			
%	33.3	25.3	14.5	8.1	3.5	15.0	
Frequency	29	22	13	7	3	13	2.19
				Females			
%	20.8	45.8	12.5	16.7	4.2		
Frequency	5	11	3	4	1		2.14

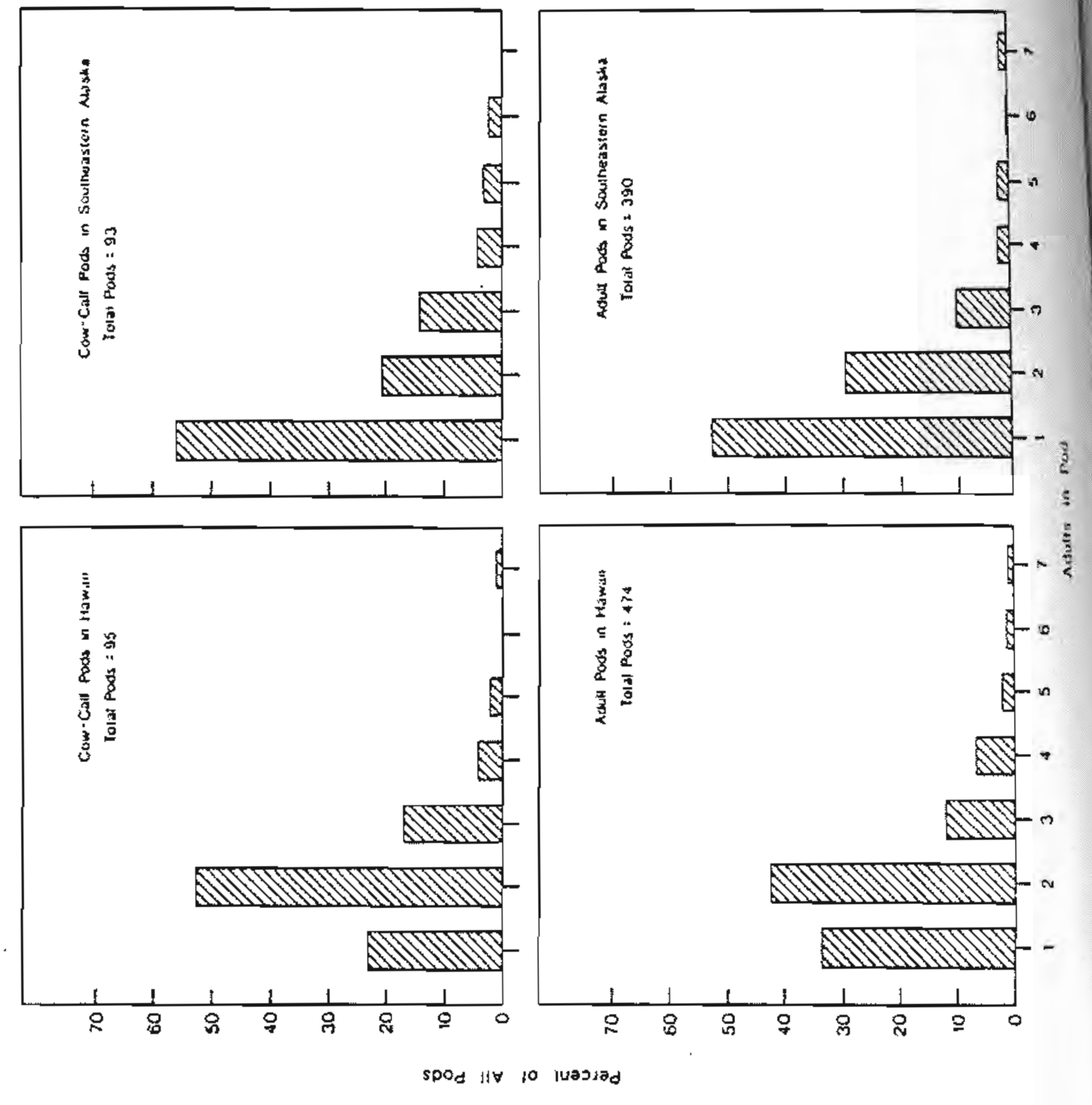
Seasonal Comparisons

Adult Pods. The sizes of humpback whale pods in Hawaii and southeastern Alaska are summarized in Figure 27 and show marked seasonal differences. In southeastern Alaska, about 30% of the adults encountered (52.8% of the pods) were alone. In Hawaii, only about 15% of the adults encountered (33.5% of the pods) were alone. The average size of adult pods in southeastern Alaska was significantly smaller than in Hawaii (F[1/862] = 24.92, p < 0.0001).

Calf Pods. Seasonal differences in the size of calf pods were even more dramatic than differences in adult pods (Figure 27). The average number of adults in calf pods was significantly smaller in southeastern Alaska than in Hawaii (F[1/187] = 5.69, P < 0.018). In southeastern Alaska 54% of the cow-calf pairs were unaccompanied by other adults while 34% were accompanied by one or two adults. In Hawaii only 23% of the cow-calf pairs were unaccompanied while 70% were accompanied by one or two adults. Cow-calf pairs accompanied by three or more adults, however, were found in nearly equal proportions in both regions.

Sex-Based Preferences. Comparing the size of male and female pods confirmed that males were more solitary in southeastern Alaska than in Hawaii (F[1/271 = 14.22, p < 0.0002). Females were more likely to be found in pairs in Hawaii but average pod size was similar in both regions (F[1/160 = 0.13, p < 0.71).

Figure 27: The size distribution of humpback whale pods in Hawaii and southeastern Alaska. Pod size information comes from vessel-based surveys of Hawaii during 1980 - 1981 and of southeastern Alaska during 1981 - 1982. The size of cow-calf pods indicates only the number of adults.


Cow-Calf Pods in Hawaii
Total Pods : 95
Cow-Calf Pods in Southeastern Alaska
Total Pods : 93
Adult Pods in Hawaii
Total Pods : 474
Adult Pods in Southeastern Alaska
Total Pods : 390
Percent of All Pods
Adults in Pod
0
10
20
30
40
50
60
70
1
2
3
4
5
6
7

Pod Composition

Southeastern Alaska

Adult pods. Sexed whales were sighted in 301 adult pods during the years 1980 to 1984 (Table 25). In 55 of these pods, two or more sexed whales were identified. In order to examine the patterns of associations between sexes within pods, all pair-wise associations were calculated between pod members. For example, a pod containing one female (F) and three males (M) contained $(4)(4-1)/2 = 6$ pair-wise associations: three FM pairs and three MM pairs.

To test the hypothesis that members of each sex associated at random within pods, the expected distribution of pair-wise associations was calculated with the binomial equation from the observed contribution of each sex class (Table 26). This distribution assumed nothing about the overall proportion of sightings of each sex or the average group size in the population. Instead, it addressed only the question of equality within the matrix of observed pair-wise associations and assumes only that sexed individuals were an approximately random sample of all members of each sex. The binomial equation predicted significantly more FM pairs and fewer MM or FF pairs than observed (Chi-square[2]= 6.95, $p < 0.05$).

Calf pods. Sexed whales were found in 125 calf pods (Table 25). In 100 of these pods, only the cow was identified. The remaining 25 pods contained 49 pair-wise associations (Table 26).

Table 25

The sex composition of humpback whale pods in southeastern Alaska.

Adult Pods

Frequency	A1	A2	A3	A4
89	F			
14	F	F		
5	F	F	F	
1	F	F	F	F
2	F	F	M	
15	F	M		
5	F	M	M	
1	F	M	M	M
148	M			
11	M	M		
1	M	M	M	

Table 25 (continued)

Cow-Calf Pods

Frequency	A1	A2	A3	A4
100	C			
1	C	C		
1	C	C	F	M
7	C	F		
1	C	F	F	
1	C	F	M	
1	C	F	F	M
7	C	M		
4	C	M	M	

Note: Letters denote sex or reproductive role: A = adult, F = female without a calf, M = male, C = female with a calf.

Table 26

Pair-wise associations between individually identified whales of surmised sex in southeastern Alaska.

Adult Pods

	Females	Males
Females	37 (30.8)	32 (44.2)
Males		22 (15.9)

Cow-Calf Pods

	Cows	Females	Males
Cows	2 (7.8)	14 (10)	21 (13.5)
Females		3 (3.2)	5 (4.3)
Males			4 (5.9)

Note: Expected frequencies of associations based on the binomial equation.

The difference between the observed distribution of pairs and the predicted binomial distribution was only marginally significant (Chi-square[5]= 10.76, $0.10 > p > 0.05$), even though CC associations were far less common than expected and CM associations were more common.

<u>Hawaii</u>

<u>Adult pods</u>. Sexed whales were found in 106 adult pods during the years 1977 to 1984 (Table 27). The majority of associations in these pods were between individuals of unknown sex. In only 11 pods were two or more sexed individuals identified. The 11 multiple animal pods yielded 11 pair-wise associations (Table 28). Although there were no observed associations between females, the sample size was too small to confidently determine that this was a trend. The distribution predicted by the binomial equation did not differ significantly from the observed distribution of associations between males and females (Chi-square [2] = 0.676, $p > 0.75$).

Females were sighted with males in five pods. In one of these pods a female was accompanied by her calf of the previous year, as well as a male, and another adult of unknown sex (Chapter 1). In two cases females were sighted in pods with males one year and with a calf the following year. Animal #355 was sighted on February 7, 1983, accompanied by #18, a male, and two other adults of unknown sex. She was sighted the following year in Hawaii, accompanied by a calf. Animal #68 was accompanied by #45, a male, and #69, an unknown, near Maui on March 7, 1981. Thirty days later (April 7, 1981) she was sighted swimming slowly with one other whale near Niihau. A few minutes into the observation four other adults joined the pair, forming an aggressive, surface-active group. Animal #68 was seen with a calf in southeastern Alaska the next summer (1982).

Females without calves were sighted in several other large, surface-active pods which probably contained males (Chapter 3). In one case the female, #346, was sighted in a surface-active pod with three other adults on February 25, 1982. She was sighted in Hawaii the following year accompanied by a calf.

Males were found together in six pods not known to contain females. In none of these pods, however, was it possible to determine that all members were males; each pod contained members of unknown sex or unidentified animals.

Calf pods. Individually identified whales were found in 170 calf pods (Table 28). In 43 of these pods only the cow was identified. The remaining 127 pods contained 224 pair-wise associations. The observed distribution of pairs differed from the predicted binomial distribution (Chi-square [2] = 73.29, p > 0.01) with far more CM and far fewer MM associations than expected. There were no CC associations and no CF associations. However, the behavioral determination of sex, if unreliable, could have biased this result (Chapter 2).

Table 27

The sex composition of humpback whale pods in Hawaii.

Adult Pods

Frequency	A1	A2
19	F	
5	F	M
76	M	
6	M	M

Cow-Calf Pods

Frequency	A1	A2	A3	A4	A5	A6	A7
43	C						
109	C	M					
8	C	M	M				
5	C	M	M	M			
2	C	M	M	M	M		
2	C	M	M	M	M	M	
2	C	M	M	M	M	M	M

Note: Letters denote sex or reproductive role: A = adult, F = female without a calf, M = male, C = female with a calf.

Table 28

Pair-wise associations between individually identified whales of surmised sex in Hawaii.

Adult Pods

	Females	Males
Females	0 (0.6)	5 (3.9)
Males		6 (6.6)

Cow-Calf Pods

	Cows	Females	Males
Cows	0 (29.7)	0 (0)	163 (103.7)
Females		0 (0)	0 (0)
Males			61 (90.6)

Note: Expected frequencies of associations based on the binomial equation.

Pod Stability and Repeated Associations

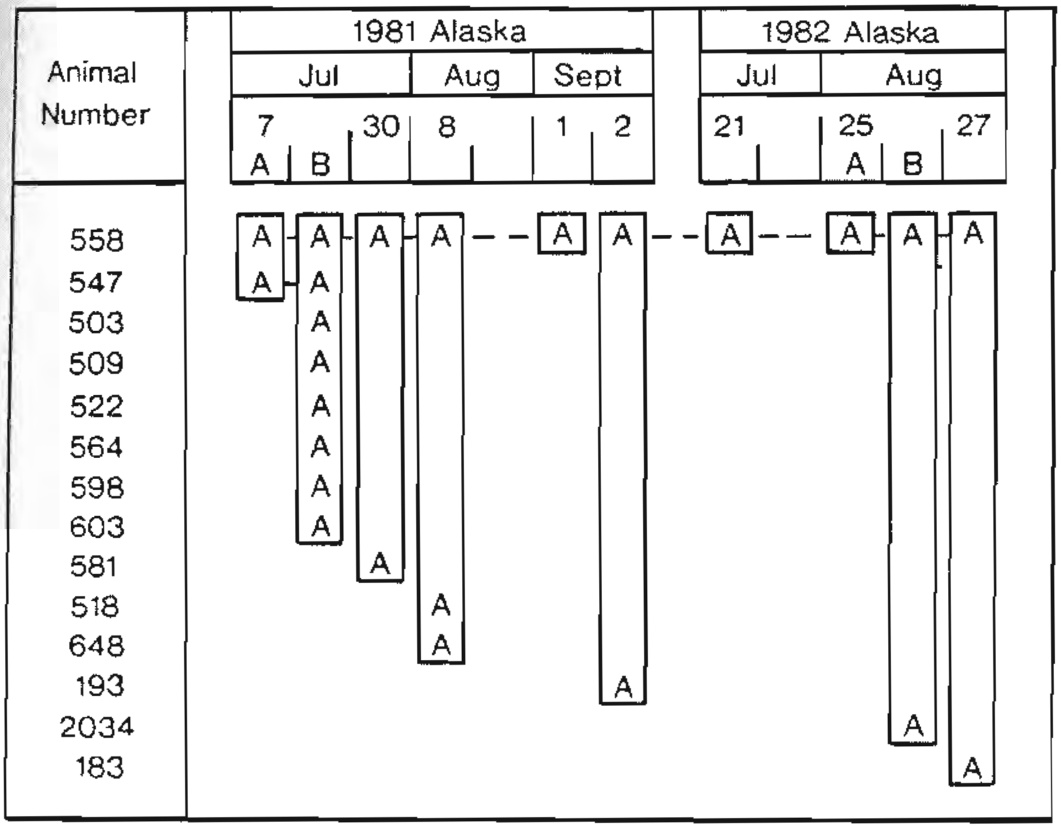
Southeastern Alaska

Pod Stability. Transient pod structure and fluid associations between individuals are illustrated by the sighting history of #558 (Figure 28), an animal of unknown sex. Animal #558 was first sighted on July 7, 1981, and sighted subsequently on four occasions during 1981 and four occasions during 1982. In total, #558 was observed with 13 other identified whales in ten pods on nine separate days during 1981 and 1982. In only one case was #558 accompanied by the same individual in two observations; with #547 in two pods on the same day, July 7, 1981. Because this association lasted only a single day it is not considered a repeated association.

Fluid, but in a few cases, repeated associations were observed in the sighting histories of #564 (Figure 29), a male (Chapter 2). Animal #564 was sighted in nine pods on seven different days during 1981 - 1984. Across these sightings he associated with 29 other whales, including at least two females and two males. He was found repeatedly with two other whales: #547, another male, on July 7, 1981, and August 28, 1982; and #503, an animal of unknown sex, on July 7, 1981, and September 1, 1981.

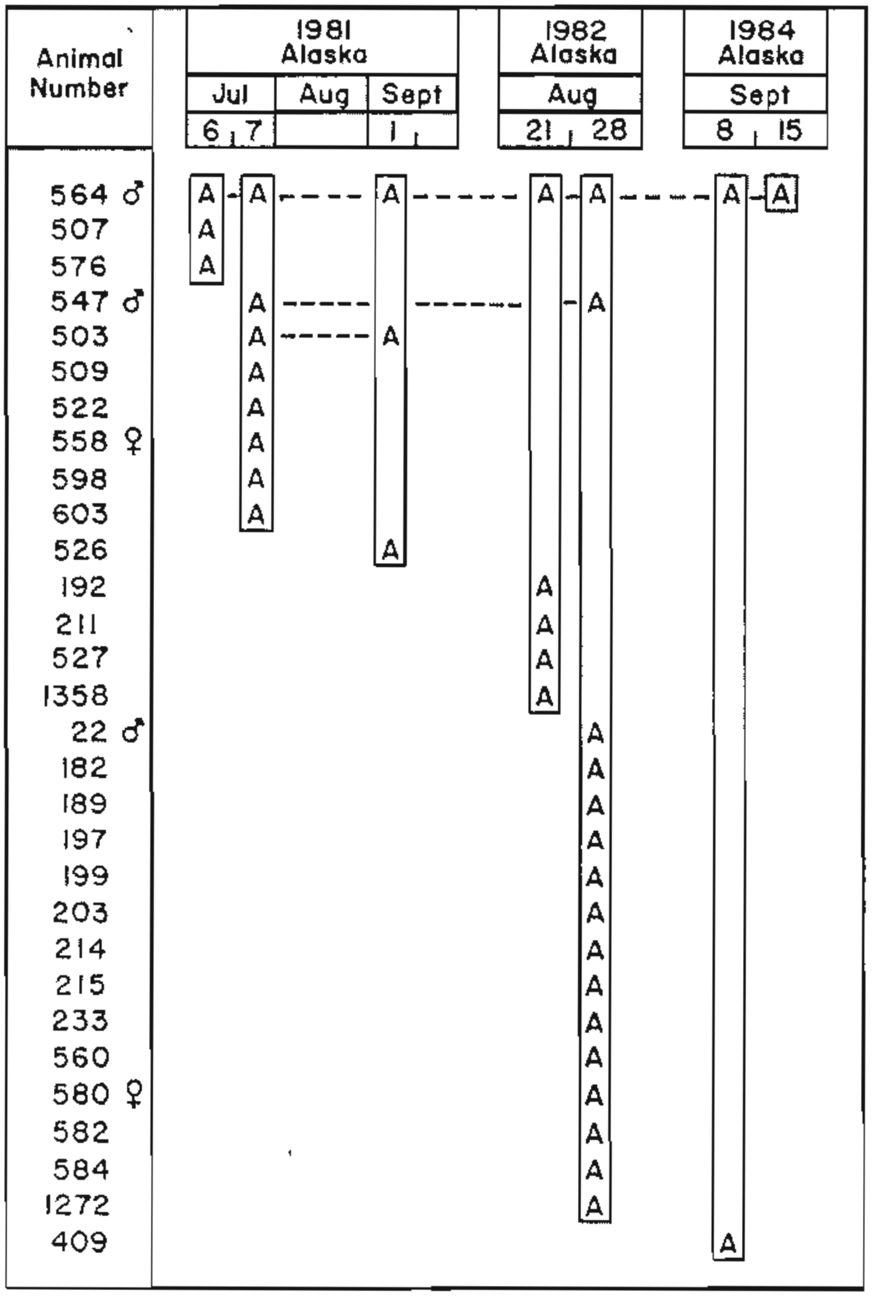
Continuous or nearly continuous associations were observed among a pod of animals found in Bartlett Cove, Glacier Bay, during 1982 and a pod of animals found near Point Adolphus during the summers of 1981 to 1983 and 1985. Details of the social stability and behavior of these pods are presented in Chapter 4.

Figure 28: The sighting record and companions of #558, an animal of unknown sex, in southeastern Alaska. Boxes enclose pods. Letters indicate behavioral role or age class: A = adult, C = cow with calf, c = calf.



Animal Number	1981 Alaska						1982 Alaska			
	Jul			Aug	Sept		Jul	Aug		
	7 A	7 B	30	8	1	2	21	25 A	25 B	27
558	A	A	A	A	A	A	A	A	A	A
547	A	A								
503		A								
509		A								
522		A								
564		A								
598		A								
603		A								
581			A							
518				A						
648				A						
193						A				
2034									A	
183										A

Figure 29: The sighting record and companions of #564, a surmised male, in southeastern Alaska. Boxes enclose pods. Letters indicate behavioral role or age class: A = adult, C = cow with calf, c = calf.



Animal Number	1981 Alaska Jul 6	1981 Alaska Jul 7	1981 Alaska Aug	1981 Alaska Sept 1	1982 Alaska Aug 21	1982 Alaska Aug 28	1984 Alaska Sept 8	1984 Alaska Sept 15
564 ♂	A	A		A	A	A	A	A
507	A							
576	A							
547 ♂		A				A		
503		A		A				
509		A						
522		A						
558 ♀		A						
598		A						
603		A						
526				A				
192					A			
211					A			
527					A			
1358					A			
22 ♂						A		
182						A		
189						A		
197						A		
199						A		
203						A		
214						A		
215						A		
233						A		
560						A		
580 ♀						A		
582						A		
584						A		
1272						A		
409							A	

Repeated Associations. Of the 414 whales individually identified in southeastern Alaska from 1980 to 1984, 189 were sighted on two or more days, the minimum requirement to engage in a repeated association. In the 895 observations of resighted whales, there were 1130 pair-wise association. Among these 1130 associations, there were 87 repeated associations, of which 56 involved two associations, 11 involved three associations, and 20 involved four or more repeated associations (Table 29). In two cases, pairs of whales consisted of the same individuals on 13 separate days. In total, 64 of the 189 resighted whales were documented to have engaged in at least one repeated association.

Most of the multiple, repeated associations (animals seen together more than twice) in this analysis were accounted for by individuals in large stable pods (Chapter 4). These multiple, repeated associations were the result of intermittent observations of essentially continuous associations between pod members.

Many of the single repeated associations could be expected from chance given the size of the feeding herd and the fluidity of associations in non-stable pods. From the sighting record of #564, for example, it is possible to calculate the size of the population from which a repeated observation could occur at random. On the first sighting day, #564 was found with two other animals. On the subsequent six sighting days, he was found with seven, two, four, fifteen, and one whales, respectively. Thus the chance of #564 associating again with either of his two companions from the first day should be

$$2(1/n-1)(29)$$

where n is the size of the population within which these animals randomly mix. On the second sighting the chance of a single association should be

$$9(1/n-1)(22),$$

the sum of the whales seen on the first and second sighting multiplied by the sum of all companions in subsequent sightings. The probability of a single resight among all of the observed associations, is the sum of each per-sighting probability

$$2(1/n-1)(29) + 9(1/n-1)(22) + 11(1/n-1)(20) + 15(1/n-1)(16) + 30(1/n-1)(1).$$

Rearranging the equation provides a population estimate of 747. This suggests that, given the number of animals with which #564 associated, a single repeated association would be expected by chance in a randomly mixing population of 747. Two repeated observations, the number observed, would be expected from chance in a population of $747/2 = 374$, very nearly the estimated size of the southeastern Alaska feeding herd (Baker et al. 1985).

Repeated associations occured among females, among males, and between males and females (Table 30). However, repeated associations predominated among members of the same sex. Based on the frequency of males and females in all repeated associations the binomial equation predicted more FM pairs than observed (Chi-square[2] = 5.88, $0.05 < P < 0.10$). This tendency was even more pronounced when the analysis was restricted to individuals sighted togther three or more times (Chi-square[2] = 8.84, $p < 0.025$).

Table 29

A summary of sighting data used to determine the repeated associations between individuls in southeastern Alaska and Hawaii.

Total Individuals	Resighted Individuals	Total Pods	Total Pairs	Pair-Wise Associations			
				1	2	3	4+
Southeastern Alaska							
414	189	895	1130	1043	56	11	20
Hawaii							
869	136	305	798	793	5	--	--

Table 30

The frequency of repeated associations between humpback whales of surmised sex in southeastern Alaska.

Pairs Sighted Togther at Least Two Times

	Females	Males
Females	33 (28.3)	23 (32.4)
Males		14 (9.3)

Pairs Sighted Together at Least Three Times

	Females	Males
Females	23 (18)	9 (19)
Males		10 (5)

Note: The predicted number of associations, shown in parentheses, was calculated with the binomial equation.

Hawaii

Pod Stability. There were no obvious cases of pod stability in Hawaiian waters. Examples of fluid pod structure were presented in Chapter 3. Additional aspects of fluid pod structure in Hawaii are discussed by Mobley and Herman (1985).

Repeated Associations. Of the 869 whales identified in Hawaii between 1977 and 1984, 136 were sighted on two or more occasions. In the 305 sightings of resighted whales there were 798 pair-wise associations. Repeated associations were observed only five times (Table 31). Two repeated associations involved pairs of animals of unknown sex. One repeated association involved a male and an animal of unknown sex. One repeated association involved an escort and a cow-calf pair and one involved a pair of escorts in two different cow-calf pods. In four of the five cases, repeated associations were documented to occur only from one day to the next. In the fifth case, the interval between documented associations was four days. A sixth repeated association (Chapter 3), between a female with her yearling and an adult of unknown sex, was based on identification of the female from unique characteristics of her dorsal fin. This association spanned from one day to the next (Chapter 3).

Seasonal Comparisons

A total of 76 whales from southeastern Alaska were sighted in Hawaii at least once between 1977 and 1984. Southeastern Alaska whales were found in 117 Hawaiian pods involving 139 pair-wise associations. Southeastern Alaska whales were found associated together in nine

Hawaiian pods. Eight associations involved pairs of whales and the ninth involved a trio giving a total of 11 pair-wise associations between southeastern Alaska whales on the wintering ground. Southeastern Alaska males were found with southeastern Alaska female four times (Table 32). Southeastern Alaska males were found together once, apparently competing for the same unidentified female in a surface active pod on March 12, 1979. A second association between southeastern Alaska males is suggested in Case 3, where #69 appeared to be competing with #45 for access to #68.

Only once were two whales which associated in southeastern Alaska sighted together in Hawaii. Animals #552 and 503, both of unknown sex, were sighted together in Hawaii on January 25, 1981, and in southeastern Alaska seven months later on September 3, 1981. Animals #552 and 503 were not sighted together repeatedly in southeastern Alaska, although both were sighted there more than once. Animal #503 was sighted ten times with a total of 37 other whales and engaged in several repeated associates. Animal #552 was sighted three times with a total of three other whales but engaged in no repeated associations.

Table 31

Repeated associations between humpback whales in Hawaiian waters.

Case	Animal	Surmised Sex	Behavioral Role	Initial/Subsequent Sighting	Interval
1.	#050	Male	None	March 30, 1979	1 day
	#047	Unknown	None	March 31, 1979	
2.	#083	Male	Escort	March 19, 1981	1 day
	#075	Female	Cow	March 20, 1981	
3.	#066	Unknown	None	February 3, 1981	1 day
	#067	Unknown	None	February 4, 1981	
4.	#329	Male	Escort	March 8, 1983	1 day
	#326	Male	Escort	March 9, 1983	
5.	#436	Unknown	None	January 31, 1984	4 days
	#366	Unknown	None	February 4, 1984	

Table 32

Associations between southeastern Alaska whales in Hawaii.

Case	Animal	Surmised Sex	Behavioral Role	Pod Size	Sighting Date
1.	022	Male	--	--	Mar 12, 1979
	045	Male	--		
2.	503*	Unknown	None	4	Jan 25, 1981
	552*	Unknown	None		
3.	069	Unknown	None	4	Mar 7, 1981
	045	Male	None		
	068	Female	None		
4.	078	Unknown	None	8	Mar 24, 1981
	169	Unknown	None		
5.	022	Male	None	4	Mar 9, 1982
	245	Female	None		
6.	505	Unknown	None	9	Mar 7, 1983
	536	Unknown	None		
7.	045	Male	Escort	4	Mar 13, 1983
	232	Female	Cow		
8.	237	Male	None	2	Feb 17, 1984
	441	Unknown	None		
9.	095	Male	Escort	5	Mar 22, 1984
	415	Female	Cow		

* Also seen together in southeastern Alaska on September 3, 1981.

Discussion

Southeastern Alaska

The size of humpback whale groups in southeastern Alaska was not determined solely by random processes. Although superficially resembling a zero-truncated Poisson distributions, the frequency of group sizes departed significantly from that expected by chance. Singles and large groups of five or more adults were unexpectedly common while pairs, trios, and quartets were unexpectedly infrequent.

There were no rigid rules for pod composition and the associations between the sexes in southeastern Alaska. Adult pods could be all male, all female, or mixed-sex. However, the predominance of intrasexual associations and the larger size of female pods suggests that associations between females were the most common. In comparison to Hawaii, cow-calf pairs were relatively solitary, and when they did associate with other whales, were accompanied by either males, females, or both sexes.

The stability of pods and the patterns of repeated associations between individual whales in southeastern Alaska were complex. Some whales formed stable associations in pods that endured for an entire summer season and reoccurred across several years. Most pods, however, were transient and associations between members were fluid. Occasional repeated associations were observed between members of transient pods but could be explained by chance given the size of the feeding herd and the frequency of social transitions. The fluidity of associations, however, was not due to aggression or overt competition. Aggressive behavior similar to that observed in Hawaii was extremely rare in southeastern Alaska. Most feeding groups seem to form and disperse casually in response to transient concentrations of prey.

The choice of prey type was a primary factor underlying variability in the social organization of humpback whale in southeastern Alaska. Humpback whales will feed on prey ranging in size from centimeter-long euphuasiids to schooling fish, 250 cm or more in length (Gaskin 1982). Exploiting this broad range of trophic levels has resulted in at least two distinctive foraging strategies in southeastern Alaska (Baker and Herman 1984b): small pods or singles feeding on swarming euphuasiids, and large pods feeding cooperatively on schooling fish (Chapter 4).

When feeding on euphuasiids, associations between whales were generally transient and pod size was unstable. In Frederick Sound, where the primary prey was euphausiids (Wing and Kreiger 1983), mean pod size was 1.6 animals and changes in pod composition occurred about once every two hours (Baker et al. 1983). In contrast, at Point Adolphus, where the primary prey was Pacific herring (Krieger and Wing 1984), a pod of six adults and a calf remained together nearly continuously for over three months (Chapter 4).

The bimodal departure of pod sizes from the zero-truncated Poisson distribution may actually reflect a compound size distribution controlled by prey type. Pods feeding on euphuasiids, probably the most common prey type in southeast Alaska during summer months (Krieger and Wing 1985), could account for the large proportion of singletons observed. Pods feeding on schooling fish could account for the unexpected number of pods larger than five adults. Pods sizes of three or four may be relatively inefficient when feeding on either prey. Neither of these distinctions, however, was absolute. The size of whale pods was also influenced by the density of either prey type. Increases in the densities of euphausiids during late summer results in some increase in the pod size of whales (Baker 1984). Similarly, single whales and small pods have been observed feeding on small schools of fish (Baker 1984; Krieger and Wing 1984; Baker 1985). Further evidence for the influence of prey type and densities is suggested by differences in the pod sizes observed in southeastern Alaska and those reported by Nemoto (1964) from the feeding grounds of the Bering Sea and near the Aleutians Islands. Unfortunately, Nemoto (1957; 1964) provides insufficient data on prey type to determine the nature of the influence.

The preference for different prey types in southeastern Alaska was, in turn, influenced by a whale's sex and reproductive status. Males were more solitary than females without calves. Females without calves tended to predominate in large pods feeding cooperatively on schooling fish (Chapter 4). Together, the size preferences of different sexes and the relationship between pod size and prey type suggest some dimorphism in the prey preferences of humpback whales (Chapter 4). The basis of this dimorphism may be the extreme energetic demands on female whales during pregnancy and lactation (Lockyer 1976; Ralls 1976). By cooperating to feed together on schooling fish, an energetically superior prey, females may increase their reproductive success. The incentive to cooperate could be enhanced by kin selection acting through matrilineal associations maintained on the feeding grounds (Chapter 1).

Although the intense competition between males on the breeding grounds (Chapter 3) must also require a considerable expenditure of energy, it probably does not approach the sustained, two-year costs of reproduction to females.

From the standpoint of energetics and the hypothesis of dimorphism in prey preference, cow-calf pairs should also cooperate with other females in seeking high energy prey. This was not generally the case. Although some cow-calf pairs were observed in large pods (see Figures 4.5, 4.6 and 4.7), they were on average more solitary than females without a calf. This suggests that other factors interfere with or outweigh the advantages to cow-calf pairs of group feeding. For example, an inexperienced calf may disrupt the coordinated behavior necessary for pods to herd schooling fish. Or, a cow may choose planktonic prey to help initiate feeding behavior in the calf. Some of the cost of lactation could be offset if the calf achieves success in capturing slow-moving planktonic prey.

Finally, humpback whale cow-calf pairs appear to actively avoid each other in both southeastern Alaska and Hawaii (Herman and Antinoja 1977; Tyack 1982; Mobley and Herman 1985). The disbanding of the "core members" at Point Adolphus coincided with births to several of the whales (Perry et al. 1985; Chapter 4). One explanation for the avoidance between cow-calf pairs is the potential danger of nursing another cow's calf (Mobley and Herman 1985). Among some pinnipeds where lactation during fasting also creates a heavy energetic cost to females, orphaned or wandering pups are sometimes killed by nursing females (Reidman and Lebouf 1982 ??). Like a two-edged sword, the energetic demands of female reproduction may cut both ways, resulting in either social affiliation or dispersion depending on the influence of other variables.

Hawaii

The modal size of humpback whale adult pods and the modal number of adults in cow-calf pods increased from one in southeastern Alaska to two in Hawaii. The major departure from the zero-truncated Poisson distribution was found in the unexpectedly large proportion of adult pairs as well as cow-calf pairs accompanied by a single adult.

The modal size and the distribution of both adult and cow-calf pod sizes was consistent with that reported in Hawaii by Mobley and Herman (1985) from comparable vessel-based surveys. Previous aerial surveys, however, reported a larger percentage of singles and pods of five or more (Herman and Antinoja 1977; Herman et al. 1980). These differences can be accounted for by the relative biases of each observation platform; vessels-based surveys accurately determine the size of relatively small pods but often underestimate the size of large pods (Herman and Antinoja 1977).

Associations between sexes in Hawaii seemed to follow rigid rules. No females were found with other females.

Whales seen together in Hawaii on one occasion were unlikely to be seen together again. Of the 789 documented pair-wise associations between adults, there were only five cases of repeated associations. A sixth repeated association was based on dorsal fin identification (Chapter 3). No repeated associations were observed to extend from one year to the next. Five of the six repeated associations spanned only from one day to the next and were probably continuous across that period. Four of these may have been temporary courting bonds, although the sex of the associates was unknown in some cases. The fifth, involving two escorts, may have been a prolonged competitive interaction (Tyack and Whitehead 1983; Chapter 3). Only the repeated association which spanned four days is difficult to explain. The period of association, if continuous, seems too long for a courtship bond or a competitive interaction. It is possible, however, that this was an observation of a cow and unweaned yearling whose age-class was not identified (Chapter 2).

It is difficult to escape the conclusion that the social organization of humpback whales in Hawaii is primarily a function of their polygamous or promiscuous mating system (Chapter 3). The modal size of adult pods, the modal number of adults in cow-calf pods, and the modal size of female pods, each two, strongly suggests an abundance of mating pairs. The predominance of intersexual associations in adult pods, although only a small sample, was further evidence for the presence of mating pairs.

The somewhat bimodal size distribution of adult male pods reflected alternative mating strategies of males. Large adult pods were almost unanimously "surface-active" aggregations of males competing for access to a lead female (Tyack and Whitehead 1983; Chapter 2; Chapter 3). Many of the single may have been singers, which are almost invariably lone males (Winn et al. 1973; Tyack 1981; Glockner 1983). Singers presumably attempt to attract receptive females rather than actively search for or compete for them in large pods (Tyack 1981; 1982; Chapter 3).

Consistent with a polygamous or promiscous mating system, associations between all adults in Hawaii were fluid. The rare association that extended from one day to the next may have indicated successful courtship between a male and a female or a prolonged competitive interaction between males. As Mobley and Herman (1985) suggest, the dynamic character of pods in Hawaii is probably due to males "prospecting" for females in estrus and the aggressive competition between males seeking access to these females (Chapter 3).

Influences of Population Structure

The seasonal migration of humpback whales has profoundly influenced their population structure in the North Pacific (Chapter 1) and the Northwest Atlantic (Whitehead 1982; Martin et al. 1984). On the feeding grounds humpback whales segregate into a number of geographically-discrete "feeding herds". Each winter these feeding herds congregate on one or more large wintering grounds. Earlier (Chapter 1), I proposed that by forming such a "structured stock", humpback whales could increase the chances of cooperating with related individuals on the feeding grounds but decrease the chances of competing with a related individual for breeding partners on the wintering grounds. At present, the relatedness of individual humpback whales in each seasonal habitat remains unknown. However, the analysis of repeated associations between individual whales provides data to evaluate two corollaries of the structured stock hypothesis: 1) repeated associations between individuals should be more common on the feeding grounds than on the wintering grounds; and 2) interactions between members of the same feeding herd should be relatively uncommon on the wintering ground.

The magnitude of difference in the patterns of associations between whales in Hawaii and southeastern Alaska corroborates the first corollary. Repeated interactions between individual whales were found in about 1 in 13 of all documented pair-wise associations in southeastern Alaska but in only 1 in 160 of all documented pair-wise associations in Hawaii. Some repeated associations between whales in southeastern Alaska were the result of whales forming stable pods which reoccurred across years. Other repeated associations were transient and may have occurred simply by chance given the size of the feeding herd. In either stable pods or fluid but repeated interactions, the opportunity exists for cooperation or reciprocation between individuals in a feeding herd. In contrast, the rare repeated interactions in Hawaii were generally the result of temporary courtship bonds or prolonged competitive interactions.

At least one southeastern Alaska whale was included in 139 of the pair-wise associations documented in Hawaii. In only 11 of these pairs were both members southeastern Alaska whales. To corroborate the second corollary of the structured stock hypothesis, the observed number of Hawaiian pairs containing two southeastern Alaska whales must be less than or equal to the number expected by chance given the number of Hawaiian pairs with one southeastern Alaska member. If the 11 Hawaiian pairs with two southeastern Alaska member is more than expected by chance, it would suggest that even though feeding herds congregate on the wintering grounds, members of different feeding herds do not intermingle.

The probability of southeastern Alaska whales co-occurring in Hawaii can be framed as follows: given that one member of a Hawaiian pair is a southeastern Alaska whale, what is the probability that both members are southeastern Alaska whales? If all whales from southeastern Alaska feeding herd travel to Hawaii, this probability should be equal to the number of individually identified whales from the southeastern Alaska divided by the total number of whales which visit Hawaii. Although some southeastern Alaska whales migrate to Mexico, this appears to be a small proportion and can be ignored in this "rough" calculation. A liberal estimate of the number of whales visiting Hawaii during the 1977 to 1983 study years was calculated in Chapter 1: 1,933 animals. Dividing this estimate by the number of southeastern Alaska whales photo-identified during a comparable period (326 animals), suggests that 1 in 5.9 of the Hawaiian pairs containing at least a single southeastern Alaska whales should also contain a second. Based on this probability and the 139 Hawaiian pairs with at least one southeastern Alaska whale, the expected number of Hawaiian pairs containing two southeastern Alaska whales is about 23.3, significantly more than the 11 observed (Chi-square[1] = 7.79; $p < 0.01$). The difference in the observed and expected co-occurrences of southeastern Alaska whales corroborates the second corollary of the structured stock hypothesis; by congregating with other feeding herds, southeastern Alaska whales decrease their chances of competing against each other on the Hawaiian wintering ground.

Influences of Calf Rearing

It is puzzling that the social organization of humpback whales in Hawaii shows so little influence of the other major winter activity -- parturition and rearing of calves. Unlike the gray whale, _Eschrichtious robustus_, (Swartz and Jones 1980; Norris et al. 1983) and the right whale, _Eubalaena glacialis_, (Gilmore 1969; Taber and Thomas 1982) there is no distinct segregation of cow-calf pairs on the wintering grounds. Instead, cow-calf pairs are found throughout the Hawaiian Islands, with only a slight preference for near-shore or shallow areas (Herman et al. 1980). Although humpback whale cow-calf pairs tend to migrate somewhat later than immatures, mature males and "resting" females without calves (Dawbin 1966), there is considerable overlap with these other age-sex classes while on the wintering grounds. Cow-calf pairs tend to be solitary early in the winter season and escorted more frequently as the season progresses (Herman et al. 1980; Mobley and Herman 1985). Herman et al. (1980) suggest that this may indicate an initial period of self-imposed isolation after parturition to insure bonding between the cow and her calf. An alternative explanation is that cows are simply anestrous shortly after birth and thus do not attract courting males early in the season. If post-partum ovulation occurs, it is delayed by perhaps a month relative to the peak period of ovulation in females without calves (Chittleborough 1958).

The only obvious trend among cow-calf pods is that they do not associate with each other (Herman and Antinoja 1977; Herman et al. 1980; Mobley and Herman 1985; this chapter). Tyack (1982), in his analysis of pod movement and orientation, showed that cow-calf pairs detect and avoid each other at some distance. As discussed previously, this avoidance is probably due to the danger of nursing another female's calf at a time when fasting and lactation impose severe energetic demands on a cow.

Are there other, less apparent, influences of parturition and calf rearing on the social organization of humpback whales in Hawaii? This question could be addressed in future studies with presently available techniques. Photogrammetry, the use of large-format aerial photographs to determine the size of animals, could provide information on the size of pod members (Ratnaswamy 1980; Scott and Winn 1980). With the age-length tables available from whaling catches, the age and possibly sex composition of pods could be determined. This may reveal more subtle temporal and spacial segregation of age-sex classes. A cytogenetic study of humpback whales is presently underway in the northwest Atlantic and the North Pacific (Richard Lambertsen, personal communication). Small biopsies of skin and blubber are collected from whales with the retrievable shaft of a cross-bow. The tissue is then cultured and karyotyped. Through the analysis of chromosomal banding it may be possible to determine, in some cases, the relatedness of individuals in pods other than the cow and the calf. With the combined use of photogrammetry, cytogenetics, and photo-identification, we could gain a thorough understanding of the social organization and population structure of humpback whales in the North Pacific.

Summary and Synthesis

Social Organization and the Evolutionary Consequences of Migration

In describing the social organization of a mammalian species it is convenient for heuristic purposes to consider several life phases (Eisenberg 1981): 1) the mating system, 2) the foraging system, and 3) the rearing system. In examining each phase it is important to account for the often conflicting interests of males and females. Among mammals, where polygyny is the rule, the mating system is most often viewed from a male perspective. Rearing systems, on the other hand, are generally viewed from a female perspective. For baleen whales, the evolution and influences of migration on social organization is an important additional consideration. In the following sections, I attempt to briefly summarize the major findings outlined in this dissertation, as they relate to each of these life phases and the evolution of migration in humpback whales.

Mating System

Male mammals do not lactate and are seldom involved in direct parental care. The greater parental investment by most female mammals makes her the limiting resource and leaves males time to increase their fitness by attempting to mate with as many females as possible (Trivers 1972). All available evidence indicates that humpback whales follow this general mammalian trend toward polygyny. Male humpback whales are seen in rapid sequence with different females. Males compete aggressively with each other to escort females presumed to be in estrus. Associations between males and females thought to be mating pairs are brief, lasting at most a few days.

Beyond the simple attributes of polygyny, the mating system of the humpback whale is difficult to categorize. Some polyandrous or promiscuous component is indicated by observations of females associating simultaneously and in rapid sequence with multiple males. Many of these associations are probably prospecting by males (Mobley and Herman 1985) and do not result in multiple matings by females. However, if a female ovulates more than once in a season, she is almost certain to mate with more than one male. The observation of female #68 sighted with a single male on March 7 and in a large surface-active group on April 7 (Chapter 5) may have been such an incident.

The operational sex ratio. The degree of competition between males of polygynous species is determined to a large degree by the operational sex ratio, defined by Emlen and Oring (1977) as the number of sexually active males divided by the number of fertilizable females. In general, highly synchronized breeders have a low operational sex ratio and thus a low variance of male reproductive success and weak sexual selection. Although seasonally synchronized in their breeding, humpback whales appear to have a very high operational sex ratio.

The percentages of male fetuses (52% of 2,063 examined) and adult males (52% of 18,136 examined) from commercial catches in the southern hemisphere (Chittleborough 1965) indicate a sex ratio slightly biased towards males in all age classes. The operational sex ratio is further biased by the percentage of non-ovulating cows with a calf. It has generally been assumed that about one third of mature females give birth each year and are thus unavailable for mating. Only a small percentage (8.5%) of cows were thought to ovulate post-parturm (Chittleborough 1965). This estimate, however, was based on the presence of a fetus in lactating females and thus indicates only the percentage of post-partum conceptions. The large percentage of cow-calf pairs accompanied by courting males suggests that the frequency of post-partum ovulation is probably much higher (Herman and Tavolga 1980; Mobley and Herman 1985; Tyack 1981; Chapter 3).

A far more important factor contributing to a biased sex ratio on the breeding grounds is the relative timing and duration of reproductive activity in each sex. The majority of female humpback whales are thought to ovulate only once or, at most, twice during a breeding season (Chittleborough 1965). Like most mammals, female humpback whales may be receptive for only a few days prior to and after ovulation. Males, on the other hand, are presumably sexually active througout the winter season, a period of possibly four to six months (Chittleborough 1955). If females come into estrus at slightly different times throughout the winter season, the ratio of the duration of female receptivity to the duration of male activity could be extreme. This would guarantee a surfeit of males available to compete with each other for access to females.

Convergence with ungulates. Based on his observations of the southern right whale, Eubalaena glacialis, Donnelly (1967) first proposed a similarity between the reproductive behavior of mysticetes and ungulates. Many of the observations reported in Chapter 3 also suggest a convergence in behavior between the two groups. The social context and pod geometry of escorting whales closely resembles that of the "tending" or "driving" males in many ungulate species. Among some ungulate species, the tending male temporarily associates with a pre-estrus female during the breeding season and defends her against intruding males (Leuthold 1977). As with the humpback whale escort and cow-calf pair, the affiliation between the tending male and the female ungulate is usually brief, ranging from less than an hour to at most a few days. The tending male's ability to remain close to the female and to dissuade intruding males seems to play a key role in his reproductive success (Leuthold 1977). If uninterrupted by intruding males, he simply follows the female until she signals her intent to mate by stopping, at which time the male mounts and copulates. Because mating has not yet been observed in humpback whales, the extent of the similarity between escorting and tending remains unknown.

The form and hierarchy of aggressive behavior in humpback whales also show similarities to those of some ungulate species, particularly the unhorned groups such as the equids. As described in Chapter 3, aggression in humpback whales follows a progression from simple interception and broadside displays, to displacement and headlunging, to charge-strikes. Many unhorned ungulates follow a similar progression from broadside threats, to parallel threats or neck-wrestling, to butting, biting, and kicking (Klingel 1974).

Do humpback whales lek? The mating system of humpback whales has several characteristics of a lek (Herman and Tavolga 1980; Tyack 1982; Whitehead and Moore 1983). Male humpback whales provide neither resource for females or parental care. Males congregate and display (sing) in large numbers on a colonial breeding ground which is separated from the feeding grounds.

Unlike most lekking species, however, male humpback whales do not defend specific territories on the breeding grounds. Most leks also involve a rank-ordering of territories implying some system of dominance between males (Eisenberg 1981). Darling (1983) has suggested that such a system exists among male humpback whales. He reports that male-male interactions occur in the absence of females in order to establish a future hierarchy of access to estrus females. Darling (1983) further proposes that the song of male humpback whales is a display of resource holding potential and functions primarily to mediates or initiate dominance disputes between males. I find it unlikely, however, that male humpback whales would devote much time and energy to establishing dominance in such a large and fluid congregation. The rarity of repeated interactions between males and the violence of their competition would make such a strategy futile and dangerous. A dominance hierarchy would also be expected to decrease overt aggression and competition for females. The observations of violent competition between multiple escorts does not indicate a prearranged ordering of access but rather, a general "free-for-all" in which each battle must be won anew.

The hypothesis that singing functions, at least in part, to communicate the resource holding potential of the singer was first considered by Tyack (1982) and is not without merit. However, an intrasexual dominance display should be relatively unambiguous, resistant to cheating, and have a strong component of individual recognition. The length, complexity, yearly changes, and mimicry of the song make it an unlikely candidate for such an display and suggest instead, an epigamic display shaped by female mate choice.

In their evaluation of the lek hypothesis, Whitehead and Moore (1982) note that male humpback whales do not establish a displaying "arena" which females visit solely for the purposes of copulation. Instead, they argue, male humpback whales, like male anuran amphibians (Arak 1983), congregate, compete, and display in an area chosen by females for parturition and rearing (Whitehead and Moore 1982). This analogy fails, however, on a critical point; male humpback whales, acting individually, do not defend specific areas with a resource value to females such as egg-laying sites for amphibians or pupping beaches for pinnipeds. Male humpback whales simply overlap with females throughout the breeding grounds.

Male or female-initiated congregations? Whitehead and Moore's (1982) argument does, however, raise one of the most interesting questions about the evolution of the humpback whale mating system -- are the lek-like congregations of humpback whales on the wintering grounds male initiated or female initiated? In other words, do males initiate congregations for their own benefit, or do females compel males to congregate in order to mate? Bradbury and Gibson (1983) outline reasons for male- or female-initiated clumping including the relative impacts of predation, signal enhancement and reception, and resource distribution. They conclude that two models, one male initiated and one female initiated, are the most consistent with available data on most lekking species: 1) Males simply clump in "hotspots" where the largest number of females are likely to pass or be found; or 2) females prefer large clumps of males because it facilitates mate choice.

For humpback whales, these two models could be distinguished by the answer to a single question: Were female humpback whales historically constrained to choose specific wintering grounds primarily for ecological characteristics conducive to parturition and calf rearing, or did they choose specific wintering grounds by convention to facilitate mate selection? I believe that circumstantial evidence supports the latter hypothesis and the general model of female-initiated congregations in humpback whales.

Although humpback whale wintering grounds throughout the world share certain common ecological characteristics such as warm, shallow water (General Introduction), there appear to be an abundance of unoccupied areas with similar characteristics. In the Caribbean, for example, the vast majority of humpback whales winter on the Silver and Navidad Banks north of the Dominican Republic (Scott and Winn 1980; Whitehead 1982; Whitehead and Moore 1982). However, neighboring areas of the Caribbean are replete with warm, calm, and protected waters. Observations of birth on the wintering grounds are rare and commercial whaling statistics indicate that a considerable number of births actually occur during migration (Chittleborough 1965). This suggests that the choice of wintering grounds with shallow, near-shore waters is not primarily for parturition. Other balaenopterid whales apparently give birth and raise calves in an entirely pelagic environment. Only the right whale, and the gray whale, Eschrichtius robustus, seek shallow near-shore areas for calving and rearing. Among gray whales, however, it is clear that the cows enter the lagoons along the coast of Baja California prior to giving birth and remain deep in the lagoons to raise their calves. Other age-sex classes, including mature males and nonparturant females, congregate at the lagoon mouths where some mating is thought to occur (Norris et al 1983; Swartz and Jones 1980). Unfortunately, the absence of documented copulation by humpback whales on the wintering ground could be considered evidence that this also takes place elsewhere. However, behavioral evidence (Chapter 3) and commercial whaling data indicate that a significant proportion of matings do, in fact, occur on the winter grounds.

Finally, there is evidence of female mate choice operating on other male courtship behavior. The elaborate song of the humpback whale may have evolved as a courtship display through runaway sexual selection (Tyack 1982). No other baleen whale is known to have such an elaborate display associated with the mating season.

Foraging System

In striking contrast to their competitive mating system, the foraging system of humpback whales in southeastern Alaska can generally be characterized as non-competitive and, at times, cooperative.

<u>Group Foraging</u>. When feeding on euphausiids, humpback whales are solitary or form small pods that are fluid and transient. When euphausiids begin to swarm and concentrate in late summer, humpback whales will form aggregations of as many as 40 individuals in an area of only a few square kilometers. Early whalers referred to these aggregations of feeding whales as "shoals". Most shoals that I have observed were transient, forming and dispersing across only a few days. Although the local density of whales within a shoal is far higher than I have ever observed in Hawaii, there is little evidence of aggression or

competition. Within a shoal, whales casually join and leave smaller behaviorally synchronized pods of four or less.

The absence of aggression or territoriality in humpback whales feeding on euphausiids is almost certainly explained by the patchy distribution of this prey. The factors controlling aerial and vertical distribution of euphausiids include light, salinity, tidal velocity, and the location of phytoplankton blooms (Mauchline 1968). The formation of swarms, particularly dense concentrations of euphausiids, also has a behavioral component that is poorly understood. Although concentrations of euphausiids tend to reoccur in certain locations of southeastern Alaska (Krieger and Wing 1984; 1985), their exact timing and position seem to be relatively unpredictable and transient. If a food source is rich but unpredictable in time and space, territorial defense is not usually an efficient foraging strategy. Instead, individuals should forage in groups (Horn 1968), which can efficiently exploit a rich but patchily distributed resource. My observations of humpback whale shoals are consistent with this hypothesis of group foraging.

Reciprocation. Within foraging groups of birds, on which Horn's (1968) model is based, the energetic advantage to individuals in the group is essentially the result of geometry. Little is demanded in the way of behavioral interactions between individuals except that they move as a group. The coordinated behavior of humpback whales in some feeding strategies suggests a more complex system of cooperation. In echelon feeding, for example, the trailing animal in the formation presumably benefits from a temporary increase in the density of prey escaping to either side of the lead animal. Although it seems unlikely that there is any immediate benefit to the lead animal, a long-term benefit could accrue through reciprocation. In a reciprocal system, each individual follows the lead some proportion of the time, thus outweighing the costs, if any, of taking the lead at other times. A primary requirement for any system of reciprocation is repeated interactions between participants (Trivers 1971; Axelrod and Hamilton 1981). Without repeated interactions, there would be little incentive against cheating. The frequency of repeated interactions between individuals in southeastern Alaska (Chapter 5) demonstrated the minimum requirement for reciprocation. In combination with a long lifespan and a reasonable degree of intelligence, the results of reciprocation in even casual associations could be a powerful force in shaping the non-competitive feeding strategy of humpback whales.

Cooperative feeding. When feeding on schooling fish, some humpback whales form large pods which remain stable across an entire summer season and reoccur across years. Cooperative behavior is evinced by closely coordinated behavior, repeated associations, and possibly leadership by older experienced individuals. By acting cooperatively, individuals may increase their efficiency at feeding on agile, fast swimming fish which are a calorically superior prey. Membership in cooperatively-feeding pods is influenced by gender, reproductive status, and idiosyncratic partner preference. Kinship relations may underlie partner preference and group formation. A predominance of female members suggests a dimorphism in prey preference. If reproduction in female humpback whales is food limited, cooperative feeding could directly enhance each group member's reproductive potential and the inclusive fitness of all related members.

The advantages to males of feeding together cooperatively could be offset by the risk of having to later compete with a former feeding partner for breeding partners on the wintering grounds. This potential disadvantage does not necessarily apply if there is only one male member in a cooperate group, especially if that male is related to the females. This disadvantage also does not apply to female group members. Given the operational sex ratio and the small parental investment of males, it is unlikely that females humpback whales ever compete with each other for breeding partners.

Rearing System

The rearing systems of mammals are usually classified by the degree of cooperation between females (Eisenberg 1981). At present, there is little evidence of such cooperation in the rearing of humpback whale calves. Cow-calf pairs on the wintering grounds seemed to be accompanied only be courting males. On the feeding grounds, cow-calf pairs are relatively solitary and when they are accompanied, may associate with adults of either sex. Single cow-calf pairs were found in large cooperatively feeding pods but this seemed to be the exception rather than the rule. Cow-calf pairs were never seen to associate with each other in Hawaii and only rarely seen together in southeastern Alaska.

What prevents female humpback whales from forming a cooperative rearing system similar to that of the African elephant, _Loxodonta africana_? Like elephants, humpback whales are long-lived and iteroparous; two characteristics considered prerequisite for developing advanced social organizations (Dublin 1983). Allomothering would seem to be particularly advantageous for defense of the calves. Like other large mammals, including elephants, humpback whales are probably most susceptible to predation when they are young (Chapter 2). Even a small risk of predation should be a powerful force inducing a group rearing system among humpback whales.

While attempting not to beg the question, I can only speculate that when a calf is present, the potential costs of cooperation between females outweighs the benefits. The most obvious cost is the danger of nursing another female's calf. Given the prolonged periods of fasting and the energetic costs of lactation in female baleen whales, this danger may be overiding. In elephants, allomothering, including the nursing of other females' calves, is encouraged by the interelatedness between females. Because female elephants breed synchronously, a single dominant bull may inseminate several females in the same herd (Dublin 1983). This results in a high degree of kinship within a cohort. A similar system of kinship seems to account for allomothering in lion, Panthera leo, prides (Bertram 1976). The mating system of humpback whales, on the other hand, seems to guarantee that each offspring of a female has a different sire. This would result in relatively weak kinship ties within and across cohorts.

Bertram (1976) also suggests that reciprocal altruism and the increased survival of cubs born with companions may contribute, in addition to kin selection, to communal suckling among lions. In humpback whales, these potential advantages are offset by the asynchronous calving intervals, the weak kinship ties, and the higher costs of lactation during the compressed nursing period.

The potential disruption of a calf in a feeding group may also be important. For the grazing elephants, there is little chance that an inexperienced calf could substantially disrupt group feeding. In the highly coordinated feeding strategy of some humpback whales this is not the case. An inexperienced animal could be a significant cost to the group. In pack-hunting carnivores, this disruption is avoided by provisioning the parent or helper that takes care of the young while the other adults hunt (Kleiman and Eisenberg 1973; Bertram 1976; 1978; Moehlman 1979). The obvious inability of baleen whales to provision each other prohibits this system from evolving.

Finally, the long-range migration of humpback whales is in itself disruptive to the social cohesion necessary to form rearing groups. Although group integrity is maintained by some species during migration, humpback whales are known to segregate by age-sex class. Arrival on the wintering grounds tends to occur in the following order: late-lactating females and immatures, mature males and nonparturant females, and late-pregnant females. The return to the feeding ground follows roughly the reverse order. The staggered migratory timing of females within and across cohorts would require that rearing groups reform in each seasonal habitat.

Migration and Population Structure

Migration is generally considered the movement between areas of greatest seasonal resource value (R. Baker 1978). Extensive latitudinal migration allows baleen whales to exploit an extremely rich source of food in northern waters during summer months and conserve energy by moving into warmer water during winter months (Brodie 1975). One author (R. Baker 1978) has even suggested that the migratory paths and destinations of baleen whales can be explained simply as movement along a seasonally-changing, latitudinal cline of greatest availability of food. This hypothesis predicts that migration should be strictly latitudinal, a slow movement towards the equator during winter, possibly terminating wherever a continental upwelling or the equatorial convergence results in some available prey. Clearly, humpback whales have carried migration one step further. Abandoning any chance of feeding, they may move longitudinally as well as latitudinally in order to seek not only a new ecological environment, but possibly more important, a new social environment.

Ultimately, the driving force behind the evolution of social organization is the attempt by each individual in a population to maximize its inclusive fitness (E.O. Wilson 1975). In a cooperative foraging strategy, an individual will increase its inclusive fitness by cooperating with closely related individuals. In a competitive mating system, an individual will decrease its inclusive fitness by competing with closely related individuals. For birds and mammals which form stable social groups with related individuals, this often leads to a conflict of interest which results in periodic fission of groups or in the permanent dispersal of either male or female offpring from their natal group (Greenwood 1983). But a migratory whale need not suffer the conflicts of cooperatively feeding and competitively breeding in the same group. Instead, humpback whales may organize into a "structured stock" (Chapter 1), consisting of segregated "feeding herds" which intermingle on one or more wintering grounds.

By forming a structured stock sets of whales can associate with different probabilities in each seasonal habitat -- individuals can feed among closely related individuals but breed among distantly related individuals (D.S. Wilson 1975; 1977). Matrilinial kinship groups can form within a feeding herd if fidelity to a feeding region is established when a calf first travels to the feeding grounds with its mother. The frequency of repeated association between some whales in southeastern Alaska is persuasive circumstantial evidence of such kinship relationships on the feeding grounds. Even in the absence of kin selection, repeated association within the relatively small feeding herds could provide the basis for reciprocal cooperation.

The congregation of several summer feeding herds on a large wintering ground would help prevent inbreeding as well as decrease the probability that closely related males would compete with each other for access to females. It would further assure females an adequate choice of breeding partners during the short reproductive season. The "free-for-all" mating system observed in Hawaii, with its intense male-male competition, rarity of repeated associations, and intermingling of feeding herds, supports the conclusion that the winter migration carries whales from each provincial feeding herd into a dynamic social milieu.

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