HUMPBACK WHALES IN THE HAWAIIAN BREEDING WATERS: POPULATION AND POD CHARACTERISTICS

LOUIS M. HERMAN AND RONALD C. ANTINOJA
Department of Psychology, University of Hawaii

ABSTRACT

Aerial, shipboard, and underwater observations were made during Spring 1976 of the population of humpback whales, *Megaptera novaeangliae*, breeding in Hawaiian waters. Animals were found around all of the major islands, almost always within the 100 fathom contour, with the bulk of the population concentrated in regions having the greatest contiguous extent of such water. Breeding and calf rearing were not confined to any given area. Survey results yielded estimates of from 200 to 250 animals. The birth rate was estimated as less than 10%, a low figure of some concern. Coloration characteristics of the Hawaii population differed considerably from the eastern North Pacific population of humpback whales, suggesting little genetic exchange with that group. Differences from the western North Pacific group were less clear, in part because of sparsity of data. Approximately 18% of the animals were alone when observed; the remainder were in pods of 2 to 9 animals. Overall there were considerably fewer singletons and considerably larger-sized pods than has been observed in feeding ground aggregations. A calf was typically found in a multiple-animal pod, consisting of the mother and, most frequently, one other adult " escort " whale. The escort seemed to serve a protective function. The large majority of the pods were swimming in fairly regular formations in apparent local migratory movements. Milling pods, with animals contacting one another, or engaging in other behaviors seemingly consistent with sexual courtship or advertisement, was observed in 16% of the cases. The possibly adverse effects of increasing public and commercial on-water and in-water whale-watching activites on the reproductive success of the whales was noted.

INTRODUCTION

Each year, during the winter breeding/calving season, a population of humpwhales (*Megaptera novaeangliae*) migrates into waters adjoining the major Hawaiian islands. The first arrivals may appear as early as November; peak numbers occur during February and March, and the last stragglers depart as late as May or June. From Hawaii, the animals return to summer feeding grounds along the Alaskan peninsula or elsewhere in the high-latitude regions of the North Pacific. This report focuses on the description of this population while in Hawaiian waters, based principally on observations carried out during the Spring of 1976. The study goals included the determination of areas of principal aggregation and their function, the estimation of population abundance and of the rate at which calves

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were recruited into the population, the description of some of the principal demographic and phenotypical characteristics of the population, the analysis of the organization of pods of whales, and the documentation of behaviors of the animals. The study was carried out using aerial, shipboard, and underwater visual observations, and included extensive photographic documentation. The analysis of behaviors is reserved for a separate paper.

The humpback whale is part of the family of Balaenopterid whales, or rorquals, which principally include the blue (*Balaenoptera musculus*), fin (*B. physalus*), sei (*B. borealis*), Bryde's whale (*B. edeni*), and piked whale (*B. acutorostrata*). Rorquals are cosmopolitan species, generally found in all oceans of the world. They are distinguished from other mysticete whales by multiple longitudinal ventral grooves extending from the throat to as far as the navel. These grooves can distend greatly, like the lower jaw of a pelican, when feeding on the small marine crustacea or small, schooling fish that are their main diet. Additional rorqual characteristics are a small, posteriorly-placed dorsal fin, and a generally slim, tapered body well adapted for rapid swimming. Unlike the other rorquals, *Megaptera* has extremely long (e.g., 3.5 to 4.5 m), highly mobile, pectoral fins; rounded knobby tubercles on the upper jaw and portions of the lower jaw, possibly sensory in function; irregular protruberances along the leading edges of the pectoral fins; moderately fine serrations or scalloping along the trailing edge of the caudal fin (tail flukes); and an irregularly shaped dorsal fin. It has been described as stouter of body than other rorquals, but those seen in Hawaiian waters seem generally slim and graceful in form. The slender form apparently reflects the reduced or even absent food intake, characterizing breeding migrations of humpback whales and other rorquals (Dawbin, 1966; Tomilin, 1967). We occasionally observed some Hawaiian humpback whales engaging in what appeared to be feeding behaviors.

According to Rice's (1963) data on eastern North Pacific stocks, physically mature female *Megaptera* average slightly longer in body length (14.8 m) than do males (13.6 m), though Tomilin (1967) reports somewhat smaller differences. Sexual maturity occurs when the animals are 2–3 m shorter. Newborn calves may range from 4 to 5 m in length (Nishiwaki, 1972), but in Hawaii some appear to be smaller than the minimum stated. Following sexual maturity at 6–12 years, females calve generally only every other year, giving birth almost always to a single young. The gestation period is close to 12 months and the lactation period lasts from 10 to 11 months. Some additional aspects of reproductive biology of humpback whales are discussed later in this paper. More detailed discussions of general and reproductive biology of *Megaptera* are available in a number of sources (e.g., Chittleborough, 1959, 1965; Mackintosh, 1972; Matthews, 1937; Nishiwaki, 1959; Omura, 1953; Rice, 1963; Symons & Weston, 1958; Tomilin, 1967; Wolman, 1972).

Megaptera, like most other rorquals, engages in long-distance annual migrations between higher-latitude summer feeding grounds and lower-latitude winter breeding grounds. Dawbin (1966) described sexual and maturational temporal segregation during migration and discussed some of the physical and ecological conditions possibly triggering and guiding migration of Southern Hemisphere humpback whales (also see Chittleborough, 1965; Nishiwaki, 1959, 1960). Unlike other rorquals, *Megaptera* prefers breeding grounds in the nearshore, shallow waters around continents or islands at approximately 10° to 20° latitude. In many cases, near-shore preference increased the vulnerability of *Megaptera* to whaling.

DISTRIBUTION AND ABUNDANCE OF THE NORTH PACIFIC STOCK

The Hawaiian population is part of the highly-exploited stock of North Pacific humpback whales. The distribution of this stock has been discussed, directly or indirectly, in a number of sources (e.g., Kellogg, 1929; Mackintosh, 1947; Nishiwaki, 1966; Omura, 1955; Rice, 1974; Tomilin, 1967; Townsend, 1935). Charts prepared by Omura (1955) and Nishiwaki (1966) and material provided by Tomilin (1967) reveal the orginal feeding range as extending from the Sea of Okhotsk on the far western rim of the upper North Pacific to the Gulf of Alaska on the eastern rim. Within this broad range, the whales were concentrated along the Kuril Islands and on both sides of Kamchatka Peninsula in the western North Pacific, within the Bering Sea and northward to the Bering Straits and the Chukchi Sea, and along the northern and southern shores of the Aleutian chain and the Alaska Peninsula down through S.E. Alaska.

Three breeding populations are generally recognized according to their separate migration loci each winter in the tropical zones of the North Pacific. An eastern Pacific, or American group, migrates southward past the west coasts of Canada and the United States to calving/breeding grounds in the bays and outlying islands along the west coasts of Baja California and the Mexican mainland (Kellogg, 1929; Rice, 1974). A western Pacific, or Asiatic group, seemingly follows a southwesterly route along the east coasts of Japan to calving/breeding areas near Taiwan, or further east in the Bonin Islands, the Mariana Islands, and reportedly, the Marshall Islands. According to Kellogg (1929) and Tomilin (1967) some whales may penetrate into the Sea of Japan on their way to the Yellow Sea. Finally, the central Pacific, or Hawaiian group, migrates into the Hawaiian waters by a route which is still unknown. Also unknown is the degree to which the three populations disperse and comingle in their summer feeding grounds, and whether there is any significant genetic exchange across breeding populations. Ivashin and Rovnin (1967) believe that dispersed groups return to their original breeding grounds and that genetic exchange is negligible. Coloration data for the different groups, discussed in a later section of this paper, tends to support this contention.

Historically, the humpback whale was hunted in the North Pacific as early as the 17th century by Japanese shore whalers using spears and arrows and, later, nets (Omura *et al.*, 1953). However, major exploitation did not occur until the 19th and 20th centuries when the stock of North Pacific humpback whales was extensively hunted throughout its summer feeding grounds by Japanese and Russian pelagic whalers (20th century); along its migratory routes in the eastern and western North Pacific by American and Japanese shore whaling stations; and in many of its tropical calving/breeding areas, principally by American and

Japanese whalers (Omura, 1955; Tomilin, 1967; Townsend, 1935). Its hunting was finally banned in 1966. At that time there may have been 200–300 animals remaining in the American population, based on extensive surveys in 1965 of the winter breeding grounds of this population (Rice, 1974). There were probably similar numbers remaining in the Hawaiian population, judging from the recent survey reported in this paper. There appear to have been no formal surveys of the Asiatic population since 1966. However, the rarity of sightings even before 1966, as noted by Tomilin (1967) and the fact that western North Pacific concentrations were always smaller than eastern North Pacific concentrations (Omura, 1955, Appendix 17) suggests that very few animals remained in the Asiatic population by 1966. Optimistically, it would seem that the North Pacific stock in 1966 numbered at most 1000 animals. Stock assessments by Wada (1972) suggested only 1200 animals. Thus, there are no indications of any substantial recovery of the North Pacific stock since 1966.

Wolman's (1972) brief review of humpback whales included an estimate of original abundance of the North Pacific stock as 4000 animals and Nishiwaki (1959) suggested 5000–6000 animals. These estimates seem low given the 3037 humpback whales caught in the North Pacific in the three-year period 1925–27 (International Whaling Statistics, 1931) and the 3455 caught by Russian pelagic whalers in the two-year period 1962–63 (International Whaling Statistics, 1966). Also, the catch statistics for 1925–27 apparently did not include the take off Kamchatka Peninsula in the western North Pacific (Omura, 1955). If we assume the estimates of Wolman and Nishiwaki are reasonable, then current abundance may be no more than 15–25% of the original stock. Worldwide figures for humpback whale populations are correspondingly low. The original abundance of the Antarctic stock may have been as much as 90,000–100,000 animals, but census data between 1965–70 revealed, on the average, a maximum of 2800 animals, or roughly 3% of the original stock (Chapman, 1974). The Antarctic stock has been protected since 1964. The eastern North Atlantic stock was decimated before the end of the 19th century and is extremely rare today (Tomilin, 1967). The western North Atlantic group currently numbers roughly 1200 animals (Winn *et al.*, 1975). It has been protected since 1955, and according to Winn et al. (1975) may not be much below its numbers at the end of the nineteenth century just before major exploitation began. Based on the slow recovery rates in other areas (Myers, 1975) and the small catch in the North Atlantic of only 22 whales in 1969/70 under a special permit to take 40, as compared with the total catch of 729 humpback whales in that area in 1903/04/05 (Mitchell, 1974), it seems more likely that full recovery of the Atlantic group lies considerably in the future. Chittleborough (1965), for example, estimated that recovery of portions of the Antarctic stock to original levels could take more than 65 years, while increases of world stocks to " significant " levels could take 50 years (Anon., 1975). The worldwide protection currently given the humpback whale by member nations of the International Whaling Commission hopefully will someday enable its reclassification upwards from an endangered species.

BACKGROUND OF THE HAWAIIAN POPULATION

The Hawaiian Island region nicely meets the preferred ecological requisites for breeding grounds of *Megaptera*. The eight main Hawaiian Islands (Fig. 1), around which the whales predominately aggregate, comprise the southeastern portion (Leeward chain) of a linearly arranged archipelago extending some 1300 nm from Kure atoll in the northwest (178° 30' W, 28° 25' N) to the island of Hawaii in the southeast. Figure 1 shows some extensive areas surrounding the main islands

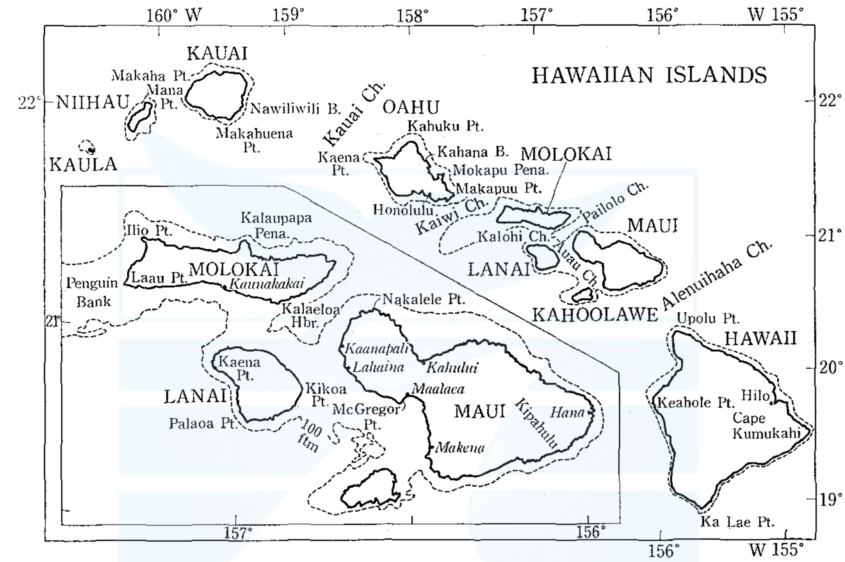

Fig. 1. The main islands of the Hawaiian Archipelago. The inset expands the four-island region of Molokai, Lanai, Maui and Kahoolawe. The dotted lines are the 100-fathom contours. Penguin Bank is the entire region within the 100-fathom contour extending southwesterly from Laau and Ilio Points, Molokai.

in which the water depth is 100 fathoms or less, especially within the four-island region of Molokai, Lanai, Maui, and Kahoolawe, and within Penguin Bank extending some 25 nm southwest of Molokai. Between November and March, surface water temperatures remain close to 25° C (77° F), with a near-isothermal layer extending downward to 50–80 m (Gosline, 1965). Zooplankton is fairly uniformly distributed throughout the coastal waters, though in markedly lesser concentrations than in equatorial waters or in waters further to the north and northeast of the islands (King and Demond, 1954; King and Hida, 1954). The relatively low zooplankton abundance and that runoffs from land have little permanent effect on the nearshore environment make for clear waters. The water clarity and the concentration of the whales near shore make for ideal surface and underwater study conditions. Strong northeast trade winds or southern storms occasionally restrict viewing opportunities, but the majority of the time the whales may be readily observed from a number of key shore points or easily accessed by ship or light aircraft.

Prior to the 1976 season, the Hawaiian population had not been studied in any detail. In fact, it seems to have gone almost unnoticed in the scientific literature until relatively recently, as illustrated by a number of compendia on the zoogeography of cetacea that failed to record the population (e.g., Marcuzzi and Pilleri, 1971; Tomilin, 1967). Bryan (1915), in his review of Hawaiian ethnology, geology, and natural history, seems to be the first to give mention of the population, but as noted by Tomich (1969) Bryan's documentation is sparse. Unfortunately, the situation improved little thereafter, being limited mainly to occasional newspaper reports of sightings (see summary in Tomich, 1969). This historical neglect seem paradoxical given that Hawaii was the commercial hub of North Pacific whaling in the early and mid-nineteenth century, offering rest, recuperation and reprovisioning to the hundreds of vessels hunting sperm whales in equatorial waters or in the seas adjacent to Japan, or else searching for right whales in the Bering Sea, the Sea of Okhotsk, and in adjacent waters. Apparently, the whalers had little interest in catching or even logging the presence of the seasonally resident humpback whales in Hawaii, which were of lesser economic importance at the time than were sperm or right whales. Minor exploitation of the Hawaiian humpback whale population (and of a few sperm whales) did occur from the late 1840's through to the late 1860's by shore whaling stations operating mainly from the island of Maui (Anon. 1848, 1856, 1866; Baldwin, 1958; also see Jones, 1938), but the records seem too fragmentary to allow for any estimates of nineteenth century abundance of the humpback whale in Hawaii. The 19th century exploitation by shore stations appears to have begun just about the time when whales, in general, were diminishing in economic importance worldwide. Combined with the apparent difficulty encountered by the Hawaiian shore stations in capturing the animals, each operation seems to have petered out only a few years after it began. Exploitation of the at-large North Pacific humpback whale stock in its higher latitude summer feeding grounds, which certainly must have included portions of the Hawaiian population was, as noted, a continuing process from the latter part of the nineteenth century, when Japanese and, apparently, Russian pelagic whaling began (H. Omura, personal communication), through to the end of 1965.

There is no evidence of any exploitation of the humpback whale by native Hawaiians prior to the nineteenth century. The antiquities of the Hawaiians, including their petroglyphs, contain no record of humpback whales, or indeed of whales of any type, and there are no Hawaiian whale legends other than a very few obviously imported from the South Pacific, where native whaling did occur (Beckwith, 1970; Kirtley, 1971; Malo, 1951). The Hawaiian language seems to contain no special word for humpback whale, though a general word for whale, *kohola*, exists, as does a special term, *palaoa*, for sperm whale teeth or products derived from the teeth, such as whale-tooth pendants (Malo, 1951; Pukui and Elbert, 1971). Sperm whales and other toothed whales were apparently washed ashore on occasion, and their teeth became the valued property of the royalty. No similar names for derivatives from baleen whales (such as baleen plates) appear in recorded Hawaiian history or in the language. The sum of the evidence thus suggests that the humpback whale was either of little interest to the pre-nineteenth century Hawaiian natives, or else that the whales were inhabiting different breeding grounds than those used today, grounds which were not observable from the island shores or the nearby waters. The resolution of those two hypotheses poses an interesting challenge to marine mammalogists and archaeologists.

CURRENT OBSERVATIONS: FIELD METHODS

We began the study at the end of February 1976, while the migratory season was in progress, and concentrated our efforts principally in the regions of suspected highest whale density, the waters within the four-island region and on Penguin Bank (Fig. 1). Other areas were also surveyed, but in less detail. Table 1 summarizes dates, times, and whale spotting conditions for the various aerial and ship surveys. Aircraft surveys used a high-winged Cessna 172, flying at 152-m (500 ft.) altitude at air speeds of approximately 100–120 knots. During an aerial survey, a predetermined transect over an area of interest was flown untill sighting of a whale or pod of whales. The aircraft then diverted from its path and orbited the pod at 152-m altitude for close-range visual observation and photography. We used

TABLE 1. AERIAL AND SHIPBOARD SURVEYS OF HUMPBACK WHALE POPULATION IN HAWAII (1976)

Date	Time	Region	Method[a)]	Spotting Conditions[b)]
29 Feb.	1130–1454	Hnl to W. Maui	A	E
29 Feb.	1617–1833	W. Maui to Hnl	A	E (F after 1745)
1 Mar.	0926–1222	Hnl to W. Maui	A	G
1 Mar.	1456–1737	W. Maui to Hnl	A	G
13 Mar.	0840–1801	Hnl to Molokai	S	E
14 Mar.	0910–1810	Kalohi Channel	S	E
14 Mar.	1110–1420	Hnl, Lanai, to W. Maui	A	E
14 Mar.	1600–1735	W. Maui to Hnl	A	G to F
15 Mar.	0800–1640	Kalohi Channel	S	G
16 Mar.	0730–1615	Molokai to Hnl	S	G (P after 1000)
19 Mar.	1000–1056	S. coast Oahu to W. Kauai	A	E
19 Mar.	1231–1627	Circle Kauai, Niihau, Oahu	A	G to F
9 Apr.	0853–1137	Hnl to W. Maui	A	F
9 Apr.	1333–1651	N. & E. Maui, circle Hawaii	A	F
9 Apr.	1745–1840	N. Hawaii to E. Maui	A	F
15 Apr.	1353–1517	Circle Oahu	A	E to G

a) A = aircraft. S = ship

b) E = Excellent; weather fair and seas calm to slight; no whitecapping (Beaufort Scale No. 0–2).
G = Good; weather fair or cloudy and seas moderate with minor whitecapping (Beaufort Scale No. 3).
F = Fair; weather fair or cloudy and seas moderate with more frequent whitecapping (Beaufort Scale No. 4); or reduced visibility due to poor light but sea state 3 or less.
P = Poor; reduced visibility and sea state 4 or more; or greatly reduced visibility in any sea state; or sea state 6 or greater.

Nikon F2 and Canon FTB cameras equipped with 105, 200, and 300 mm lenses. Visual observations were recorded in real-time on audio cassettes. The position of the aircraft over whales was obtained by reference to land-based VORTAC radio stations, if in range, or to landmarks using USCG navigational charts. The swimming direction of the whales was determined through use of the aircraft's onboard compass. Three personnel in addition to the pilot accompanied each flight.

Shipboard surveys between Oahu and Molokai were made on March 13th and 16th. The boat followed approximately the same path as the aircraft within a surveyed region, but did not divert from its path following a spotting. Three observers were positioned along the port side, and another three along the starboard side. Whales observed beyond the stern of the boat were not counted unless obviously not a previously-seen spot. The swimming direction of the whales was estimated by handheld compass and their distance from the boat gauged by visual estimation. The position of the boat was determined by reference to visibly charted landmarks or by dead-reckoning using time and distance data.

The ship remained in the Kalohi Channel area between Molokai and Lanai on March 14th and 15th for close-range observation of the whales and for launching of underwater observations. Divers equipped with Nikonos II 35-mm underwater cameras dropped off the stern of the moving ship at positions which hopefully would intercept the path of whales observed swimming astern. Scuba gear was not used because it was felt that bubble emissions might prove aversive to the whales. A surfboard was thrown into the water for the diver's use immediately after his departure, while the ship continued on its path. The diver was recovered by the ship after completing observations or on failing to contact the whales. Divers made tape recorded notes of their visual observations immediately after returning to the vessel.

The aerial, shipboard, and underwater photographs obtained, in conjunction with notes on visual observations, were used to refine the numerical counts of pod size, to describe pod composition and organization, to identify morphometric characteristics of individual animals and to categorize behaviors.

RESULTS AND DISCUSSION

Population Parameters

Distribution and Concentrations: *Four Island Region*. Figures 2–4 show representative data, giving the locations of pods and numbers of whales per pod during aerial surveys between Honolulu and W. Maui on February 29th and March 14th and during a ship survey between Honolulu and Molokai on March 13th. Each pod is numbered serially, in the order seen, and the movement characteristics of the pod, if obtainable, are shown. Calves are noted as cross symbols. The remaining animals were almost always classified as adults, though a few of seemingly juvenile status were also seen, but are not identified separately in this report. Table 2 summarizes pod and whale counts for all surveys within the four-island region. Figures 2–4 show that whales were principally found within the 100-fathom contour. Air-

TABLE 2. FOUR-ISLAND REGION: NUMBERS OF PODS, WHALES PLUS CALVES, AND CALVES OBSERVED DURING AIRCRAFT AND SHIP SURVEYS

	Region	Pods	All Whales	Calves	Whales/Pod
Aircraft					
Feb. 29	Hnl-Maui	22	43	4	1.96
	Maui-Hnl	20	52	5	2.60
Mar. 1	Hnl-Maui	23	56	0	2.43
	Maui-Hnl	22	54	4	2.45
Mar. 14	Hnl-Maui	22	55	5	2.50
	Maui-Hnl	15	27	1	1.80
Apr. 9	Hnl-Maui	6	15	3	2.50
	Totals:	130	302	22	2.32
Ship					
Mar. 13	Hnl-Mlk	38	48	0	1.25
Mar. 14	Kalohi Ch.	10	31	3	3.10
Mar. 15	Kalohi Ch.	18	30	3	1.67
Mar. 16	Mlk-Hnl	16	18	0	1.13
	Totals:	84	127	6	1.51

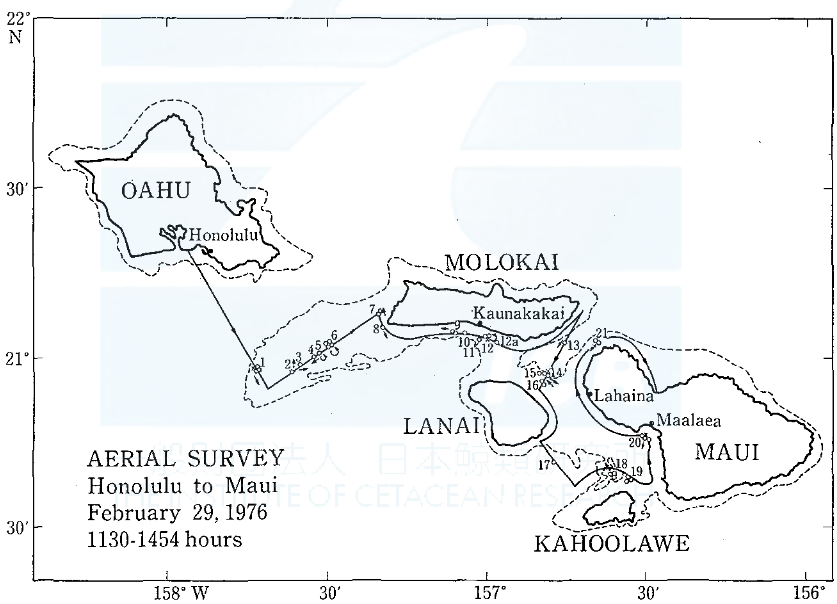

Fig. 2. Aerial survey results, showing path of aircraft (solid line), pod numbers in the order seen, and the number of whales per pod. Adults are shown as open circles and calves as cross symbols. Straight arrows show movement direction of swimming pods; arrows with a cross-hatch indicate a resting pod oriented in the direction shown; curved arrows indicate milling pods. Not all pods were classifiable because of observation difficulty. The 100-fathom contour is shown as a dashed line.

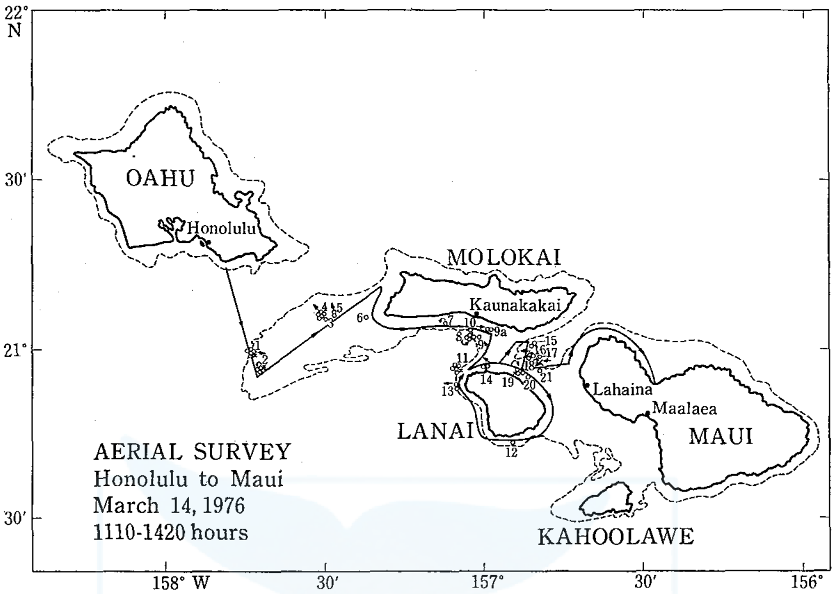

Fig. 3. Aerial survey results keyed as in Figure 2.

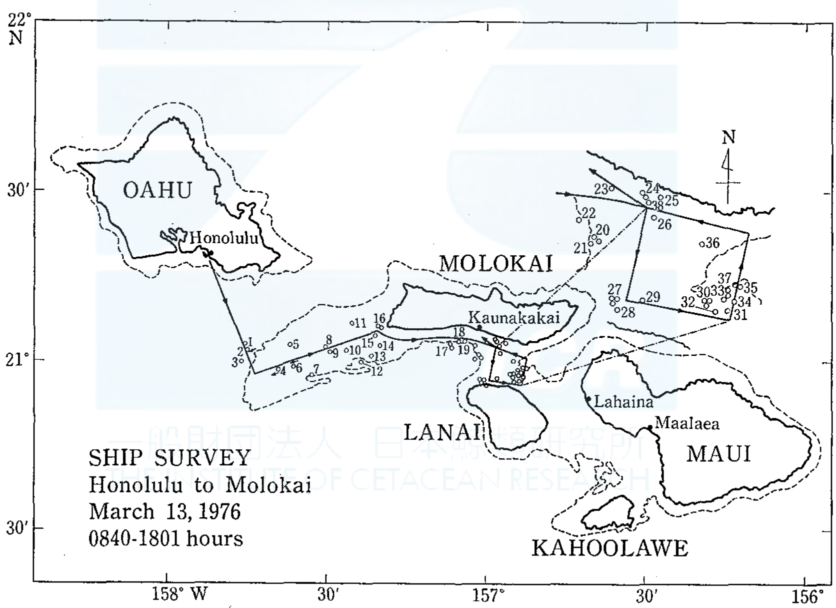

Fig. 4. Ship survey results keyed as in Figure 2. The Kalohi Channel area is expanded in the upper right of the chart to show details of the pods.

craft data gave the relatively greatest numbers of whales, on the average, in Kalohi Channel (13.7 whales/flight). This was followed by Penguin Bank (11.7 whales/flight), the Auau channel area southeast of Kalohi Channel (9.6 whales/flight) and the south coast of Molokai from Laau Point to Kaunakakai (6.3 whales/flight).

Other regions yielded much smaller numbers. The relative numbers of whales seen in the various regions remained reasonably consistent across successive flights, although some anomalies were evident. On the flight of February 29th from Maui to Honolulu, especially heavy concentrations were seen along the south coast of Molokai, and on April 9th no whales at all were seen in Kalohi Channel. Though spotting conditions were only fair on April 9th (Table 1), possibly accounting for some reduction in the counts, as on the return flight of March 14th from Maui to Honolulu, it is more likely that by this date many whales had already left on their return migration to the summer feeding grounds. Kalohi Channel, especially the south and southeast portions, seems to be an important breeding area and as these activities diminish over the season it would be one of the earliest areas expected to show a population decline. With respect to the south coast of Molokai, ten of the twenty-two whales seen on February 29th were actually located near the beginning of Penguin Bank. Though moving towards southwest Molokai, a survey perhaps an hour earlier might have placed them within the usually more densely populated Penguin Bank.

The ship survey of March 13th verified the aircraft data showing large concentrations of whales in Penguin Bank and Kalohi Channel. The fewer numbers of whales per pod, as compared with aircraft data reflects the difficulty in estimating the numbers of whales without approaching pods closely. On March 13th (and on March 16), with but one exception, the ship did not divert from the planned transect to inspect pods. In contrast, on March 14th in Kalohi Channel, the ship frequently diverted from its transect for the close-range inspection of pods, yielding an elevated count of 3.1 whales per pod (as compared with the overall estimate of 2.7 whales per pod from aircraft data in Kalohi Channel). It is significant that calves were seen from the ship only during close-range inspection. On March 15th, less time was spent on close-range inspection from the ship than on the 14th and more on general survey, resulting in an elevated pod count, but less whales per pod. Three of the pods approached on the 15th had calves, as was the case on the 14th. In general, it seems that pods with calves are easier to approach than those without, in part because the latter are capable of more rapid locomotion and prolonged diving.

On March 16th, during the ship survey, large swells and considerable whitecapping were encountered in the Penguin Bank region. Nevertheless, the pod count in that area (9 pods) was not much reduced over that found on March 13th (13 pods) under better weather conditions. Spotting of the pods on March 16th was almost entirely through seeing the large splash resulting from the breaching of an animal, whereas on the 13th blows and the animals themselves could be spotted in the absence of breaching. It may be, as has been suggested by others, that breaching is more common in rough water, perhaps serving to maintain acoustic and/or visual contact between whales.

Distributions and Concentrations: Other Regions and Islands. We cannot draw strong conclusions about concentrations of whales in the areas outside of the four-island complex or Penguin Bank, since the outlying areas were surveyed less frequently and sometimes beyond the peak of the migratory period. Nevertheless, it seems apparent from the available data that outlying concentrations in no way approached those observed within the four-island region and Penguin Bank. Table 3 shows that on March 19th, presumably still at or near the peak period of concentration of whales in the four-island complex and Penguin Bank, a total of only ten whales (four pods) was seen around the entire island of Oahu, along the north and northeast coasts; six whales (three pods) around the entire island of Kauai, between Nawiliwili Bay and Makaha Point; and no whales at all around the island of Niihau or nearby Kaula Rock. The island of Hawaii was not surveyed until April 9th, and judging from our results on that same date in the four-island region (Table 2), this was already past the peak migratory period. The two pods of whales seen near Hawaii on April 9th were at or just south of Upolu Point. The pod of six whales seen in Alenuihaha Channel was approximately 8–10 nm NW of Upolu Point heading north-northeasterly. It was one of the few pods found considerably outside of the 100-fathom contour and possibly was on the beginning of a return migration to higher latitudes.

TABLE 3. OUTLYING REGIONS: NUMBERS OF PODS (P), WHALES PLUS CALVES (W), AND CALVES (C) OBSERVED DURING AIRCRAFT SURVEYS

	Mar. 19			Apr. 9			Apr. 15		
	P	W	C	P	W	C	P	W	C
Oahu	4	10	0	—	—	—	1	3	1
Kauai Ch.[a)]	0	0	0	—	—	—	—	—	—
Kauai	3	6	0	—	—	—	—	—	—
Niihau	0	0	0	—	—	—	—	—	—
Kaula Rock	0	0	0	—	—	—	—	—	—
E. Maui	—	—	—	1	1	0			
Alenuihaha Ch.[b)]	—	—	—	1	6	0			
Hawaii	—	—	—	2	4	0			

[a)] Survey path was a straight line between Kaena Pt. Oahu and Nawiliwili Bay, Kauai.
[b)] Survey path was a straight line between Kipahulu Gulch, Maui and Upolu Pt., Hawaii.

The survey around the island of Oahu on April 15th revealed only a single pod of three whales, including a calf. No further surveys were conducted after that date, though as late as mid-May the authors observed several pods from peaks overlooking the south coast of Oahu. Also, reports were received of a few whales lingering around the island of Oahu in June.

The last departures on the northward migration seemingly would tend to be pods with calves, judging by the relatively high proportion of such pods (three of six) seen on April 9th and 15th. The delayed departure of calves would allow for attainment of sufficient growth and blubber deposit before encountering the rigors of migration and the colder waters of the higher latitudes, and typifies migratory characteristics of Southern Hemisphere populations of humpback whales (Dawbin, 1966).

Our data showing that concentrations of whales outside of the four-island region and Penguin Bank are relatively small are consistent with sighting reports from commercial hydrofoil craft during the 1976 season (Shallenberger, 1976).

Population Estimates. The combined data from the ship and aircraft surveys can be used to estimate population numbers in selected areas. Gulland (1972) suggested that counting all whales for two miles on each side of a ship's path through an area yields accurate estimates of whale density (whales/nm^2) in the four-mile wide strip covered, which may then be extrapolated to the entire region of interest. Gulland's model assumes that nearly all whales in the strip will be seen. Our data suggest, however, that it is simpler to estimate pod density (pod/nm^2) than whale density by ship survey. Our ship, transecting an area at ten knots, probably missed very few of the pods actually present within the 4-nm wide sighting strip. But, our aircraft surveys over the same region revealed that the number of whales per pod was underestimated, unless the ship approached the pods closely. Aircraft, from their favorable vantage point, count whales per pod with great accuracy, but unless surveying a region in fine detail, miss some proportion of the pods actually present. It would seem, then, that nearly all whales present in a region could be accounted for by using ship data to estimate pod density in the region, and aircraft data to estimate mean whales per pod. Multiplying the two estimates should yield highly accurate population counts. This simple model was used to estimate the number of whales present in the three main regions surveyed by ship on March 13th. The results were 63 whales for Penguin Bank (.22 whales/nm^2), 9 for the south coast of west Molokai within the 100-fathom contour (.2 whales/nm^2), and 47 for Kalohi Channel (.57 whales/nm^2), for a total of 119 whales. To this we can add seven more in the small region just north of the NW tip of Penguin Bank, where the ship encountered three pods, and aircraft data yielded an average of 2.5 whales per pod. Other than this small region, the number of whales in the area between Honolulu and Penguin Bank appears negligible. The estimates given suggest that aircraft surveys sampled from one-third to two-thirds of the population present. The larger sample size was obtained when the region was well covered by the aircraft, such as the restricted coast-line areas of Molokai.

The remaining major concentration of whales present on March 13th in the four-island region would have been in the Auau Channel region east of Kalohi Channel between Maui, Lanai, and Kahoolawe, and within the 100-fathom contour. This region was not surveyed by ship. If we assume the whale distribution on March 14th was not significantly different from that on the 13th, we can use the aircraft flights of the 14th to add to our population estimates. Five pods were spotted by the aircraft in the Auau Channel region on March 14th, but all dove before they could be approached closely. We can, however, use the mean value of 2.0 whales per pod, based on all aircraft flights over that region, to estimate the number of whales in those pods as ten. Applying the sampling ratio for aircraft, previously discussed, of from one-third to two-thirds of the population, gives a final estimate of from 15 to 30 whales actually present in Auau Channel. The assumptions made in these calculations should be treated with caution but appear reasonable in view of our overall data.

In summary, the overall estimate of population size on March 13th in the four-island region, and including Penguin Bank and the area immediately adjacent to its NW tip is thus 141–156 whales (119+7+15 to 30). There were undoubtedly whales in other regions, but likely in considerably smaller numbers than in the four-island region and Penguin Bank. On March 14th, for example, only six whales were seen along the northeast coast of Molokai and the south and west coasts of Lanai, and on March 19th, only 16 whales were found around all of Oahu, Kauai, Niihau and Kaula Rock (Table 3). East Maui and the island of Hawaii, surveyed on April 9th, yielded only 11 whales (Table 3). Concentrations in these latter two regions were likely greater three weeks earlier, and our uncertainty in estimates for the period near March 13th is, accordingly, greatest for these regions. For the present, it seems best to bracket our estimates for all combined outlying regions and islands as perhaps 50 animals as a lower bound and 100 as an upper bound. The total population on or about March 13th might then have numbered from close to 200 animals to as many as 250 animals. The March 13th period was apparently within the peak of the migratory cycle, judging by our aircraft data (Table 2). However, we do not know how long individual whales remain in the islands, and it is possible that some animals might have already departed the Hawaiian waters and that others were still in-migrating, which would add to our population counts somewhat. It would be desirable to extend the census work in the future, so that all major areas within the islands could be surveyed in parallel on given dates, and in- and out-migration studied in detail.

Nursery Grounds and Numbers of Calves. Tables 2 and 3 gave data for the number of calves seen during each aerial survey. Calves were typically accompanied by more than one adult, as discussed more fully in a later section, but in no case was there more than one calf in a pod. With the one exception of a pod of two adults and calf observed off north Oahu on April 15th, all pods with calves were found within the four-island region and on Penguin Bank. For all flights combined, the areas of greatest concentration were Kalohi Channel (9 calves), especially along the north coast of Lanai, and Penguin Bank (8 calves). Additionally, two calves were seen south and southwesterly of Lahaina, Maui. No other area yielded more than a single calf. Though the north coast of Lanai is clearly the most densely concentrated nursery region and should be protected, there is considerable dispersion of nursery areas throughout the regions surveyed.

The numbers of calves seen relative to total whales provides a basis for estimating gross recruitment rate (Seber, 1973). As a first approximation we can assume that the Hawaiian population is similar demographically to populations of humpback whales elsewhere having characteristics known through whaling operations. Normal sexual maturity for humpback whales, as for some other baleen whales, occurs from 6–12 years (Anon, 1975) for both males and females. Earlier average onset may be recorded in highly exploited stocks due to the more rapid growth rates in such cases, or the selective depletion of larger (older) animals (Chittleborough, 1965). Mackintosh (1972) states that given the two-year reproductive cycle of female baleen whales, and that 99% of the births are single calves with the sex ratio approximately equal, the expected birth rate would be 50% of the sexually mature female population. Rice (1963) calculated a pregnancy rate of 43% based on examination of 168 humpback whales caught by shore stations near San Francisco. The number of females was not specified. Nishiwaki's (1959) data on humpback whales caught in Ryukyuan waters in the western North Pacific gives the annual percentage of ovulating females as 60% and pregnancy rates as 40%. Chittleborough (1965), using catch-effort statistics from the whaling station of Albany in southwest Australia, estimated that 37% of the female humpback whales were pregnant. Of a small sample of 13 female humpback whales collected in the northwest Atlantic in 1969 and 1970, 7 (54%) were pregnant (Mitchell, 1974). The collective data from these sources suggest that the normal birth rate could be somewhat lower than 50% of the mature females; 43% may be a reasonable best estimate.

According to Nishiwaki (1959) approximately half of a normal humpback whale population are sexually mature animals, with half of these males and half females. This places the normal limit on calf recruitment rate as $.5 \times .5 \times .43 = .108$ or 10.8% of the entire population. Applying this recruitment rate to the Hawaii population, conservatively estimated as 200 animals, would yield an expected calf population of 22.

Across all of our aerial surveys, there were some obvious vagaries in our calf counts (Table 2). Low counts can generally be attributed to unfavorable spotting conditions or to the abbreviated nature of a survey, though in the case of the morning flight of March 1st, the reasons for the zero count were unclear. The largest number of calves seen on any flight was five, on the second flight of February 29th and then again on the first flight of March 14th. In each case, spotting conditions were excellent for all or nearly all of the survey. The most optimistic estimates of recruitment rates are obtained by considering the calf to adult ratios on these two flights. (Calf to adult ratios obtained after the peak migratory period, such as that of April 9th, are biased because mothers with calves remain longest in the breeding grounds, cf. Dawbin, 1966). On the second flight of February 29th, 9.6% of the total of 52 whales seen were calves, and on the first flight of March 14th 9.1% of the 55 whales were calves. These percentages can be considered the upper limits of the current calf recruitment rate for the Hawaiian population, but both are somewhat below the discussed expected rate of 10.8%. More importantly, since the four-island region and Penguin Bank appear to contain the major nursery grounds, birth rate samples from these areas may not be representaative of other areas, and would overestimate rates for the population at large. Hence, the rates of 9.1% and 9.6% should be regarded as optimistic.

The apparent low birth rate is disturbing and calls for additional assessment. The reasons for the apparent low rate are unclear. In a small unexploited population, presumably below the carrying capacity of the environment, one would, in fact, expect higher than normal rates of birth (Wilson, 1975). It seems doubtful that our sampling of the calves was disproportionately low, since pods with calves are typically slow moving or even resting, seldom diving deep or for long periods, and hence are relatively easy to spot from aircraft. It may be that a demographic analysis of the Hawaiian population would show, for reasons unknown, a smaller than usual number of mature whales, explaining the low recruitment rate. Or, it may be that the low rate reflects unfavorable biological or ecological conditions, or a response to continued harassment from the ships, aircraft, and divers passing close to the whales, intentionally or otherwise. Whatever the cause, the apparent low recruitment rate underscores the potential fragility of the population and the pressing need for its careful protection and management.

Pod Characteristics

Pod Size. Table 4 summarizes the findings on sizes of pods for all aerial surveys combined. There is generally an orderly decrease in the frequency of occurence of successively larger pod sizes, though the majority (59%) of the pods were comprised of two or more animals. The largest pod size, nine, was observed on February 29th in Kalohi Channel and on March 1st near Laau Point, Molokai. The percentage of singletons is very probably an overestimate, since we conservatively estimated one whale for all spots for which a single blow, breach, or body part was seen at a distance but the animal could not be relocated on closer approach. There were 23 such cases out of the total of 59 singletons.

TABLE 4. SIZE COMPOSITION OF PODS FOR ALL AERIAL SURVEYS

	Pod Size									
	1	2	3	4	5	6	7	8	9	Totals
No. of Pods	59	37	18	11	8	6	1	0	2	142
% Total	41.5	26.1	12.7	7.8	5.6	4.2	0.7	0.0	1.4	100.0

Note: Pod size includes both adults and calves.

The data of Table 4 may be contrasted with that of Nemoto (1964) who reported on pod sizes for the humpback whales in their summer feeding grounds in the upper North Pacific. Of 92 pods encountered by Nemoto, 50% were singletons, 43% pairs, 3% threesomes, 2% foursomes, and 1% fivesomes. There was also a single group of seven (1%). The largest difference between our data and that of Nemoto occurs for groups of three or more: 32% of our groups were three or more animals but only 7% of Nemoto's. Dispersal in the feeding ground and clustering in the breeding ground appear obviously adaptive. Grouping in baleen whales may stimulate and facilitate reproductive activities as it does for other species (Wilson, 1975) and is consistent with the presumed promiscuous mating behaviors of female baleen whales in which multiple males appear to attend a single female (e.g., see Payne, 1976). Apparent polyandrous mating bouts were observed in a number of our aerial surveys, but we cannot be sure of the sex of the participants. The counts by Winn *et al.* (1975) of the humpback whales in the West Indies breeding grounds seem discrepant in that only 23% of their sightings were groups of two or more as compared with 49% for Nemoto and 59% for our data. The Winn *et al.* counts were based on shipboard transects which apparently did not approach the whales closely. Their data may thus underestimate whales per pod, as did similar ship surveys we conducted on March 13th and 16th. The data of Nemoto (1964), though based on shipboard observation, relied on catch statistics in which boats necessarily pursued and approached whales very closely, allowing for highly accurate counts of pod size.

Pods With Calves. Table 5 shows that calves are typically found in pods with multiple adults, most often two adults, the mother and an " escort " whale. This is in contrast to other Balaenopterid whales in which the mother and calf often travel unescorted (Nemoto, 1964). The Southern Hemisphere mother-calf humpback whale pairs, like the Hawaiian group, do tend to school with other whales.

TABLE 5. NUMBER OF PODS WITH CALF (C) AND THE NUMBER OF ACCOMPANYING ADULTS (A)

Flight	1A-1C	2A-1C	3A-1C	4A-1C	5A-1C	Totals
Feb. 29 (1)		2	2			4
Feb. 29 (2)		5				5
Mar. 1 (1)						0
Mar. 1 (2)	3	1				4
Mar. 14 (1)		1		2	2	5
Mar. 14 (2)				1		1
Mar. 19						0
Apr. 9	1	1		1		3
Apr. 15		1				1
Totals	4	11	2	4	2	23

Chittleborough (1953) reported that all nine mother-calf humpback whale pairs seen in Antarctic waters were accompanied by other whales. Four of the nine were accompanied by a single additional whale. In some contrast only two of nine mother-calf humpback whale pairs seen in North Pacific waters by Nemoto (1964) were accompanied by other whales. It may be that schooling with other whales occurs principally in the terminal breeding and feeding areas rather than enroute. Thus, Chittleborough (1953), observing migrating Southern Hemisphere humpback whales near the western Australia coast, reported that the calf was usually accompanied only by the mother. Also, in Exmouth Gulf, on the Australian west coast, all seventeen calves seen by Chittleborough were accompanied only by the mother. Exmouth Gulf does not seem to be a terminal point, since migrations north and south of the Gulf were observed. Since mother-calf pairs do depart the breeding grounds last, there are few other whales for them to school with on the return migration, except for other cow-calf pairs. But, as noted for the Hawaiian population, multiple calves in a pod were never seen, and may indicate a self-imposed segregation of mothers from calves which are not their own.

The escort whale or whales may serve a protective function, as discussed in a later section. Here we may note that Southern Hemisphere humpback whale trios with calf have been observed defending themselves against killer whales. In one case cited by Chittleborough (1953), one adult of the two present kept the calf very close while the second charged the pack of 4–5 killer whales, successfully beating them off with its flukes.

Gross Activity of Pods. The gross activity of a pod was classified as swimming, milling, or resting (Table 6). Swimming behavior was defined as movement in a fixed direction during the aircraft's approach. Milling was defined as spatially undirected activity occurring within a small area. Milling animals might be lolling about, rolling on their backs, or contacting one another in the case of multiple animal pods. For singletons, the animal was classified as milling using a similar criterion of area-restricted activity, though contactual behavior was of course absent. Resting animals were lying quietly in the water, dorsal surface up, barely moving at best, usually stationary. Gross activity data was available for 97 (68.3%) of the total of 142 pods seen on all flights. The remaining pods either dove when closely approached and before they could be classified or else we could not locate the animal on close approach.

TABLE 6. GROSS ACTIVITIES OF PODS CLASSIFIED BY TYPE AND SIZE

Activity /Size	Singleton	Multiple-Adult Pods					Pods with Calf[a]						Totals
	1	2	3	4	5+	All	1	2	3	4	5+	All	
Swimming	20(83.3)	19	5	4	10	38(76.0)	1	6	2	2	2	13(56.5)	71(73.2)
Milling	4(16.7)	3	0	4	1	8(16.0)	0	2	0	2	0	4(17.4)	16(16.5)
Resting	0(0.0)	2	1	1	0	4(8.0)	3	3	0	0	0	6(26.1)	10(10.3)
(Subtotal)	24	24	6	9	11	50	4	11	2	4	2	23	97
No Data	35	9	1	0	0	10	0	0	0	0	0	0	45
(Total)	59	33	7	9	11	60	4	11	2	4	2	23	142

Note: Percentages, given in parentheses, are based on subtotals.
[a] pod size refers to number of adults accompanying calf.

It is clear from Table 6 that for multiple-adult pods, and for single adults as well, active swimming was the most common gross activity, with milling considerably less common but still more frequent than resting. It is the milling multiple-adult pods that are engaging in mating behaviors. There are no obvious relations between pod size and pod activity.

For pods with calves, swimming was relatively less frequent though still the most common behavior, while resting was more common than milling. It is probable that the young calf tires easily and tends to require that the mother be stationary while nursing. Whalers in the past have taken advantage of the lesser stamina of the calf to catch and kill the mother who remains nearby the tiring calf throughout the pursuit.

The breakdown of activity by size of pod having calves reveals a tendency for swimming and milling activities to be associated with larger-sized pods, while resting seems common when the calf is accompanied only by the mother. The data base is very small so these trends must be interpreted with caution. If they are indicative of the population at large, it may be that calves accompanied only by the mother are quite young, and that as they mature the pair either joins other whales, who tend to be active, or else are attractive to other whales who join them.

Spatial Organization of Pods. The spatial formation of swimming pods, when observable, was classified into eight different categories as described in Table 7: line astern (file); diagonal; line abreast (rank); wedge-shaped with animals spread out symmetrically behind a leading animal or animals (simplified echelon); vee-shaped with multiple leading animals abreast and one or more additional animals centered and behind; T-shaped; diamond shaped; and x-shaped. In many cases, the formation was clean-cut, as in the case of a pod of five whales observed line astern, each animal nearly touching the flukes of the one ahead, or the neatly staggered diagonal array of a pod of four whales observed on another occasion. More often, the formation was broken by one or two animals, so that three might be tightly astern while a fourth swam off to one side. In such cases, the formation of the majority of the animals was used to categorize the pod's organization. Only formations actually seen are listed. There are obviously other possibilities.

TABLE 7. SPATIAL ORGANIZATION OF SWIMMING PODS GROUPED BY POD SIZE

Formation /Pod Size	All-Adult Pods					Pods With Calves[a]					Totals
	2	3	4	5+	All	2	3	4	5+	All	
Astern	2	1	5	2	10(38.5)	2	1	0	0	3(27.3)	13(35.1)
Diagonal	2	0	2	1	5(19.2)	3	0	0	1	4(36.4)	9(24.3)
Abreast	5	0	0	0	5(19.2)	1	0	0	1	2(18.2)	7(18.9)
Wedge	—	0	2	0	2 (7.7)	—	1	0	0	1(18.2)	4(10.8)
Vee	—	2	0	0	2 (7.7)	—	0	0	0	0 (0.0)	2 (5.4)
Tee	—	—	0	1	1 (3.8)	—	—	0	0	0 (0.0)	1 (2.7)
Diamond	—	—	0	0	0 (0.0)	—	—	0	1	1 (2.7)	1 (2.7)
X	—	—	—	1	1 (3.8)	—	—	—	0	0 (0.0)	1 (2.7)
(Subtotal)	9	3	9	5	26	6	2	0	3	11	37
No information	9	3	0	0	12	0	0	0	1	1	13
(Total)	18	6	9	5	38	6	2	0	4	12	50

Note: Dashes in columns mean that spatial organization of the type specified is not possible for the given number of animals. Numbers in parentheses are percentages of subtotals.

[a] Organization based on adults in pods only. One swimming pod of the total of 13 in Table 6 was a single adult with calf and hence is not classified here.

Among the all-adult pods, the line abreast formation was observed only for paired animals, swimming side by side. For larger pods, the adults arranged themselves most commonly in the line astern formation or what may be simply its variant, the diagonal. The function of these "follow-the-leader" formations is not apparent, nor is it clear whether specific animals maintain leadership positions in the swimming pod. More protracted observations are necessary to answer these questions.

For pods with calf, only the spatial organization of the adults was classified, since the calf typically remained close to a given adult, presumably the mother. The number of swimming pods having calves was small, so generalizations are difficult. In pods with a single escort whale, the escort tended to remain behind the mother-calf pair. If multiple escorts were present, one or more might remain ahead of the mother-calf pair while the others remained behind or abreast. Invariably, we noted that when a pod with calf shifted its formation in response to the orbiting aircraft, it was to tighten the formation and move the calf to a more central position between the adults, a clearly protective behavior. In contrast, for all-adult pods, shifts of formation occurring in response to overhead aircraft were predominantly dispersals of the pod, the animals moving further apart or temporarily going in different directions. Another defensive response of a pod to the aircraft was deep diving (sounding). This tended to occur more commonly for singletons and for pods of two but rarely for larger groups.

Underwater observations of milling or stationary pods revealed that vertical dispersion was often greater than horizontal dispersion. In pods with calf, the escort would typically appear from well beneath the near-surface mother-calf pair, presumably in response to the presence of the diver. The pod would then depart from the area of the diver.

Coloration: A Clue to Population Identification

Most humpback whales are predominantly black on their dorsal surface, excluding the pectoral fins and tail flukes which may have extensive white coloration. White coloration is common on the ventral surface of the pectoral fins, flukes, and portions of the body from the throat region to the navel. In earlier whaling days when humpback carcasses could be examined, investigators studying coloration focused on the description of ventral surfaces as these seemed to show the most variability. Lillie (1915), working with carcasses of Southern Hemisphere humpback whales, devised a seven category classification scheme for ventral surface coloration, ranging from extensive white to all or nearly-all black. Later invesigators generally continued to use Lillie's categories (Chittleborough, 1965; Matthews, 1937; Omura, 1953; Nishiwaki, 1959; Symons and Weston, 1958). The major interest was in whether coloration differences could predict demographic characteristics of the population, in particular sex and body length (age). No stable, clear-cut relationships were found within or across studies, but a by-product of the research was the observation that geographically isolated groups often demonstrated different coloration characteristics. In the Southern Hemisphere, Matthews (1937) found that humpbacks from the South Georgia and South Africa regions were on the average darker in color (84.8% of 53 animals fell in the darkest two of Lillie's categories and 1.8% in the lightest two) than humpbacks from the New Zealand area (26% of 30 animals were in the darkest two categories and 26.7% in the lightest two). Symons and Weston (1958) reported that 24.1% of 58 animals captured in the Bellinghausen Sea adjoining Antarctica fell in the darkest two color categories while 36.2% were in the lightest two. Omura (1953) provides an excellent summary of differences among all five Antarctic groups and Chittleborough (1965) gives additional data on coloration differences between east and west coast Australian populations.

In the North Pacific, Pike's (1953) data for 184 British Columbia humpback whales reveal that all fell into the darkest two coloration categories. Nishiwaki (1959), examining 237 western North Pacific whales captured in Ryukyuan waters, classified 92.2% as being black or mostly black and none as being predominantly white. These results were very similar to another 164 animals subsequently captured in the same waters (Nishiwaki, 1962), leading Nishiwaki (1965) to conclude that North Pacific humpback whales are darker in coloration, having only a few small white areas, than Southern Hemisphere humpback whales, which often have large white areas.

Our coloration data for the Hawaiian population, based principally on aerial observations, must rely on coloration of dorsal, not ventral surfaces. We have found considerable variation in dorsal surface coloration of the pectoral fins. Past literature on humpback whale coloration has in a few cases reported dorsal surface coloration of the pectoral fins. These data suggest considerable color variation in the dorsal surfaces of the pectoral fins between geographically isolated breeding groups.

In Table 8 dorsal surface coloration of the pectoral fins for the Hawaii population is classified into four categories: all black; slight white (leading or trailing edges white, or a few small spots of white seen elsewhere on the surface); moderate white (mottled, piebald, speckled, or patchy areas of white); and extensive white (solid white or mostly white). Classification was based on detailed examination of aerial photographs and on supplemental notes made while circling a pod. Coloration data were available for 189 of the total of 332 whales spotted during the various aerial transects. Many of these whales were undoubtedly the same animal seen on different occasions, but assuming that whales are sampled on a random basis (with replacement in the population) the percentages should estimate population parameters closely. Table 8 shows that 37% of the whales were classified in the extensive white category and 35% in the all black category. The data reveal very close correspondence in percentages for mothers, calves, and adults, suggesting that phenotypical color characteristics are stable in the population.

TABLE 8. COLORATION OF DORSAL SURFACE OF PECTORAL FINS: COMBINED AERIAL TRANSECTS

Coloration	Mother		Calf		Adult[a]		Total	
	N	%	N	%	N	%	N	%
All Black	7	33.3	6	31.6	53	35.6	66	34.9
Slight White	3	14.3	3	15.8	27	18.1	33	17.5
Moderate White	3	14.3	3	15.8	14	9.4	20	10.6
Extensive White	8	38.1	7	36.8	55	36.9	70	37.0
Subtotal	21	100.0	19	100.0	149	100.0	189	100.0
Undetermined	2		4		137		143	
Grand Total	23		23		286		332	

a) Includes six animals classified as juveniles, two with all black coloration, one with slight white coloration and three undetermined.

These characteristics could prove useful in identification of the Hawaiian population in its summer feeding grounds, if dispersal and intermingling of populations is minimal.

From the limited data available on Southern Hemisphere stocks, it appears that white coloration on the dorsal surface of the pectoral fins was rare. Lillie (1915) made no mention of all-white pectoral fins; neither did Omura (1953) or Symons and Weston (1958). Matthews (1937) stated that of the groups in the darkest two categories, 7% had white pectoral fins. Unfortunately, data for other coloration categories was not given. In the eastern North Pacific, Pike (1953) reported that only 14.7% of the British Columbia whales had predominantly white coloration on the dorsal surface of the pectorals. This is considerably below the 37.0% value we find for the Hawaiian group. Scammon (1874) described the eastern North Pacific population as all black above, or nearly so. Very recent observations of humpback whales in the southeast Alaska region describe them as having all black pectoral fins above and as numbering 60–61 animals (M. Tillman, personal communication). From these combined data, we can infer that the Hawaiian population is reproductively isolated from the eastern North Pacific stock and that it does not summer in the feeding grounds of that region.

Tomilin (1957) provided only qualitative data on coloration of the western North Pacific stock, presumably in the area of the Kamchatka Peninsula. He described the dorsal surface of the pectorals as ranging from black to piebald or even completely white. He also described a group from the Chukchi Sea and the Bering Sea as having dusky flippers with an exceptionally white border. This was not a characteristic observed in the Hawaiian group, suggesting reproductive isolation of the Hawaiian group from at least portions of the Asiatic population. It is difficult to say whether significant intermingling of the populations occurs in common feeding grounds in the Aleutian Island regions or further to the west and north.

Chittleborough (1953), using aerial surveys to study the New Zealand humpback whale population, reported that calves were born light and darken rapidly with age. How rapidly was not specified. All of the calves we saw in Hawaii were dark above, except for pectoral fin coloration as noted and, occasionally, some white coloration on the dorsal surface of the tail flukes. We cannot say whether the calves we saw had already darkened, or whether the light color of the newborn does not occur in the Hawaiian population. Other than Chittleborough's observations on newborns, investigators seem to agree that coloration and age are not related.

The extensive color variation among individuals within the Hawaiian population, and here we include ventral as well as dorsal surfaces, may function in individual recognition among conspecifics. Color patterns may also serve as signals communicating movement intention or direction, as in the exposure underwater of the white surface of a raised pectoral or caudal fin to a school-mate swimming nearby. Additionally, light ventral surfaces and darker dorsal surfaces provide for cryptic coloration important for predators, such as *Mageptera*, which at least in part feed on schooling fish (A.V. Yablokov, in Sokolov, 1971).

SUMMARY AND CONCLUSIONS

The Hawaiian population of humpback whales may number between 200 and 250 animals, though more detailed surveys of outlying islands and study of migratory patterns is necessary to refine the bounds of these estimates. Our estimates concur with Shallenberger's (1976) data on peak population size, peak population periods, and that the population numbers are much reduced by or after the first to second week of April. A ship survey from Kauai to Hawaii from 23 February to 7 March 1976 by the National Marine Fisheries Service counted 373 whales (M. Tillman, personal communication). The bases for this somewhat larger count have not yet been clarified.

Almost all of the whales were found within the 100-fathom contour surrounding the islands, a trait noted also for other breeding groups of humpback whales (Chittleborough, 1953; Winn *et al.*, 1975). The principal areas of aggregation were within the four-island region of Molokai, Lanai, Maui, and Kahoolawe, and within Penguin Bank extending 25-nm southwesterly from Molokai.

No unique nursery area was found, though the greatest numbers of calves were in two areas: Kalohi Channel between Molokai and Lanai, particularly on the Lanai side, and on Penguin Bank. Since these two areas are also regions of maximum whale density, it is not clear whether the greater number of calves simply reflects that fact. The number of calves recruited into the population was numerically small, and the recruitment rate, at its most optimistic, appeared to be somewhat below normal expectations. Given the small population size, this seems an unusual occurrence and leads to concern for the recovery of the stock. High priorities should be given to further investigations of recruitment rate.

Calves were typically found with multiple adults, most usually two (including the mother). The additional adults seemed to serve a protective function as noted from the tightening of calf groups versus the dispersal of all-adult groups on approach of aircraft. Over the entire population, pod size was on the average larger than that noted by investigators of humpback whale populations in other waters, either in breeding or feeding areas. Accurate determination of pod size seems heavily dependent on close approach by ship or aircraft, and unless this is done the number of animals in a pod may be underestimated. Also, calves are often difficult to detect without close approach. Our data were in most cases based on close-range observations.

The amount of migration between subregions within the island waters is unclear, though the 76% of the all-adult pods seen swimming on "determined" courses suggested considerable local migration, but without any obvious pattern. The remainder of the all-adult pods were milling about within some small area often in great activity (16%), or else simply stationary or nearly so (8%). Milling pods appeared to be engaged in courtship and mating activities, though actual mating was not seen. Pods with calves were more frequently resting (26%) than were all-adult pods, possibly reflecting the lesser stamina of the calf (or mother) and/or a requirement for nursing.

The most common formation for swimming pods was line astern (file), noted in 38% of the cases. Diagonal arrays and line abreast (rank) each typified 19% of the swimming pods. The functions of the various formations were not clear.

Most of our data were obtained within the peak period of the migratory cycle, from the end of February through to the third week of March. Therefore, we have no information on changes in local aggregations over time. Data collected by E. Shallenberger (1976), particularly those based on daily observations made by the crews of hydrofoil craft transiting between the various islands of Hawaii, suggest that the earliest immigrants may arrive in the four-island region. As the season progresses, the population appears to extend itself easterly and westerly, in comparatively small numbers, from the four-island region.

The routes by which the whales arrive at or leave the islands are unknown, as is their migratory loci in northern waters. A survey we made in November 1976 of the Northwest Hawaiian Islands, the small atolls and islands extending 1,200 nm northwesterly to Midway and Kure from the main Hawaiian Islands, revealed no whales. Coast Guard flights over this region by others in November 1975 and March 1976 (Shallenberger, 1976) also found no whales. However, in late December 1976, a report was received of two pods of whales in the eastern portion of the Northwest chain, moving southeasterly. It may be that the Northwest Hawaiian Islands are used as a migratory route by only a few whales, or only during portions of a season. Further studies of this area are necessary. Currently, there seems to be no evidence that any humpback whales breed in this chain. Our discussions with personnel based on the Midway Islands indicate that no humpback whales are ever seen there, nor heard there by underwater listening stations. Nishiwaki's (1972) statement that humpback whales are frequently seen around the Midway Islands in winter is therefore puzzling.

Based on their early arrivals in the four-island area, it may be that the principal migratory route to the main Hawaiian Islands is due south, south-southeasterly, or south-southwesterly from the higher-latitude feeding grounds along the northern rim of the North Pacific. The major return migration may simply be in the reverse direction, as suggested for example, by the northerly heading of a pod of six adult whales we observed in deep water on April 9th 10 nm off the west coast of Hawaii. Direct observations of these possible migratory routes needs to be implemented.

Coloration characteristics of the dorsal surfaces of the pectoral fins of the Hawaiian whales strongly suggest that the population is not that observed in the feeding areas near southeast Alaska. The coloration also appears to differ from some subpopulations observed near Kamchatka in the upper western Pacific, though this is less certain. The degree to which there may be dispersal of the Hawaiian population in the feeding grounds should be studied, and its degree of intermingling with other populations ascertained. If the three North Pacific populations are like the Southern Hemispere humpback whales, little migration between populations would be expected (Ivashin and Rovnin, 1967; Mackintosh, 1947). However, ecological conditions vary widely in the higher latitudes of the two hemispheres. In particular, feeding areas are more restricted in the North Pacific, so generalizations are difficult to make.

It was also noted that color variations within the Hawaiian population and displays of coloration could function in individual identification among conspecifics and as signals for movement intention and direction. Additionally the ventral-dorsal variations provide cryptic camouflage.

Finally, the potential fragility of the Hawaiian population, given its small numbers and apparent low recruitment rate, should be stressed. The annual migration of the population into Hawaii has been receiving increasing popular attention, and the number of people observing or wanting to observe the whales seems to be increasing annually at an exponential rate. The generally good weather in Hawaii and the nearshore clear-water regions favored by the whales makes their observation easy. While this is a scientific boon, and vitally important to the description and understanding of the natural behaviors and dynamics of a breeding population of mysticete whales, the rare spectacle of the whales is an attraction to all. Increasingly, commercial and pleasure ships and small boats are launched to watch the whales, divers enter the water to observe, photograph, and perhaps touch the animals, planes and helicopters on tourist runs circle the animals. All of this unregulated activity constitutes a potential source of major harrassment to the whales, and some controls on this activity are needed which will, first, protect and conserve the whales and, secondly, allow the expression of their benefit to humans as an educational and aesthetic experience.

Harmer (1928) long ago warned that whales may abandon their preferred grounds under harrassment, a warning that has been realized too often in whaling history. When driven from a given locality, whales rarely return to it, selecting instead secondary and likely less favorable grounds. Harmer's warning should be well heeded in the case of the Hawaiian humpback whale.

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