Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters

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Humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters engage in strenuous aggression toward conspecifics. The social context and sex of individuals involved suggest that aggression is the result of male–male competition for sexually mature females, including cows with newborn calves. Characteristic behaviors associated with aggression occur in a roughly hierarchical scaling of intensity and include broadside displays, underwater exhalations, head lunges (in which the throat is inflated and enlarged), physical displacement, and charge–strikes. Humpback whales do not form stable pair bonds during the winter breeding season; females are seen serially and simultaneously with multiple males and males are seen serially with multiple females. Repeated observations of individually identified whales indicate that escorting and singing are interchangeable reproductive roles of mature males. Incidents of aggression show a seasonal increase and decrease that parallel changes in abundance and average pod size. A seasonal peak in the frequency of aggression is probably related to an increase in population density and to changes in the reproductive physiology of mature males and females. It is suggested that singing may function, in part, to synchronize ovulation in females with the peak abundance of mature males on the wintering grounds.

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Les baleines à bosse (*Megaptera novaeangliae*) qui passent l'hiver dans les eaux hawaiennes ont des comportements particulièrement agressifs à l'égard des autres baleines de la même espèce. Le contexte social et le sexe des individus agressifs permettent de croire que ce comportement résulte de la compétition mâle–mâle à l'adresse des femelles à maturité, y compris les femelles qui ont des baleineaux nouveaux-nés. Les comportements caractéristiques de l'agression peuvent être classifiés grosso modo selon une échelle hiérarchique d'intensité: affichage de la partie latérale du corps, expirations sous l'eau, plongées tête première au cours desquelles la gorge est gonflée, déplacements et attaques avec coups. Les baleines à bosse ne s'engagent pas dans des liens de couple durables au cours de la saison de reproduction d'hiver; les femelles côtoient plusieurs mâles séparément ou simultanément et les mâles côtoient plusieurs femelles séparément. Des observations répétées d'individus identifiés indiquent que le côtoiement et les cris sont des rôles reproducteurs interchangeables joués par les mâles à maturité. Les manifestations agressives suivent une tendance ascendante puis descendante, en parallèle avec les changements dans l'abondance et le nombre moyen de baleines dans les rassemblements. La fréquence des agressions atteint un maximum saisonnier probablement relié à une augmentation de la densité de la population et à des changements physiologiques chez les mâles et les femelles à maturité. Il est possible que les cris servent, du moins en partie, à assurer la synchronisation de l'ovulation chez les femelles avec la densité maximale des mâles à maturité dans l'aire d'hiver.

[Traduit par le journal]

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." More recently, other exceptions to the portrayal of mysticetes as timid and docile creatures have been noted. The defensive use of the flukes by humpback whales, *Megaptera novaeangliae* (Chittleborough 1953), and right whales, *Eubalaena australis* (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 similar 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. Several 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).

A major obstacle to understanding the social behavior of humpback whales has been the difficulty in determining an individual's age-class and sex. Like other baleen whales, the humpback lacks any obvious sexually dimorphic traits. Consequently, sexing an individual during field observation is difficult. Only a cow, when accompanied by her calf, can be identified easily and with certainty as to her sex and age-class. Because of the very close association of the cow and her calf it is possible to identify the mother, even when other adults are present in the group. The fact that cow–calf pairs never associate with each other in the Hawaiian wintering ground (Herman and Antinoja 1977; Herman et al. 1980) prevents confusion about the mother of an individual calf.

Data have also accumulated on the sex of individuals found in two behavioral roles characteristic of humpback whales: "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

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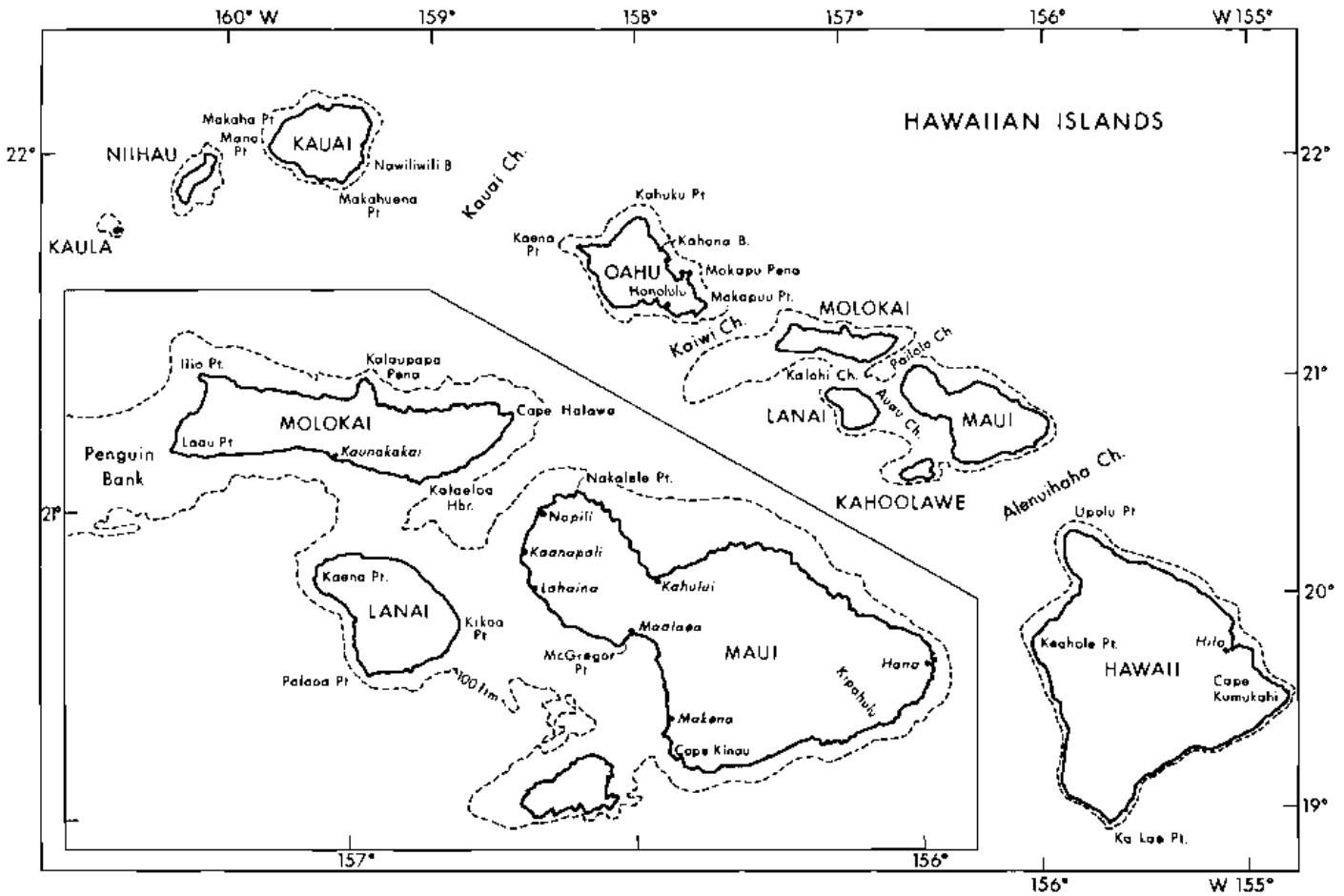

FIG. 1. The main Hawaiian Islands. The 182-m isobath is shown by the broken lines. The inset expands the major study area.

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. Mobley and Herman (1981) presented data on the photographic identification and resighting of individual escorts and cow–calf pairs during a single winter season. They found that the duration of affiliation between an individual escort and cow–calf pair was generally only a few hours. 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. (1970) 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) photographically determined that four singers were males.

This paper presents observations that run counter to the popular view of mysticetes as "gentle giants," indicating instead that humpback whales engage in strenuous and sometimes violent aggressive behavior toward conspecifics. We suggest that the aggressive behavior occurs in predictable social contexts, in a roughly predictable scaling of intensity, and that the incidence of aggression 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 and spring seasons of 1979, 1980, and 1981. Figure 1 shows the main Hawaiian Islands and our study areas. Additional observations from 1982 and from years prior to 1979 are presented where available and relevant. 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 Plexiglas viewing chamber, developed by the second author, which allowed the observation and filming of whales near the vessel. Altogether, several thousand hours of observation were made over the 3-year period. Behavioral observations were voice-recorded during real time using a cassette tape recorder; a time base was also provided by voice with the aid of a digital stopwatch. The nomenclature used to categorize whale behavior followed that developed originally by Herman and Forstell (1977) and added to later by Herman and Tavolga (1980) and by Baker et al. (1982).

Whales were photographed with 35-mm SLR cameras equipped with power winders and 200- and 300-mm lenses. Whales were individually identified from clear photographs of the ventral surface of the tail flukes and of both sides of the dorsal fins. The uniqueness of

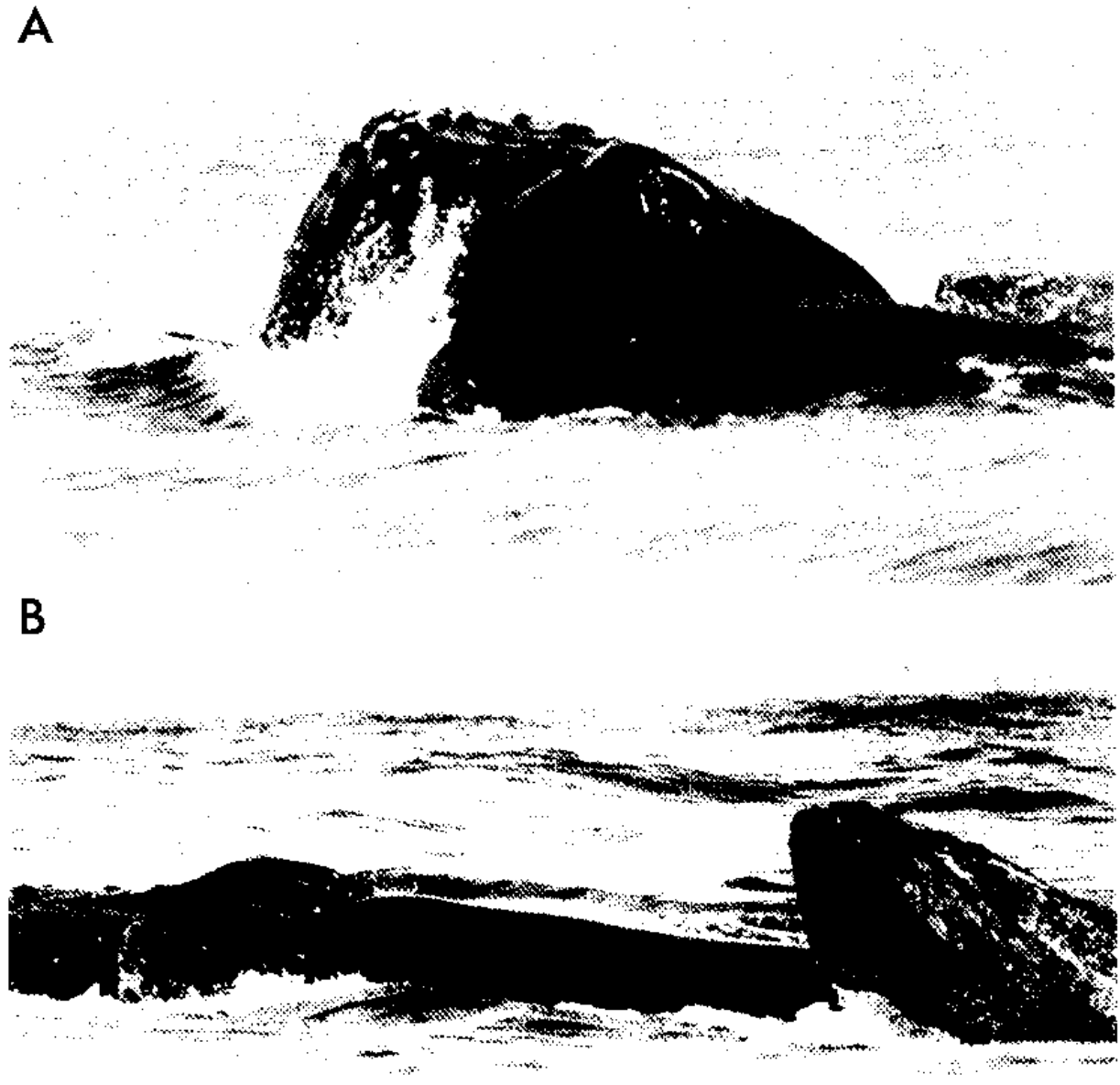

FIG. 2. Typical postures of headlunging humpback whales. (A) The posterior to anterior aspect of whale No. 49 shows the engorgement of the ventral pouch. (B) Lateral view of two whales head lunging. The forward whale blocked the rear whale's approach to a cow and calf in the lead of the pod. Photographs by William Stifel, Kewalo Basin Marine Mammal Laboratory.

coloration, shape, and scarring patterns of flukes and dorsal fins allows for the reliable identification of individuals across many years (Katona et al. 1979; Baker and Herman 1981). At present, the Kewalo Basin Marine Mammal Laboratory maintains a photographic library of 1056 individual humpback whales identified in the North Pacific. Of these, 305 have been observed on more than one occasion. Individually identified animals are assigned a "whale number" and information on location, date of sighting, and social affiliation are stored in a data retrieval file at the University of Hawaii computing center. Whale numbers are given in the text if the individual has been observed more than once. If resighting information is not available on an animal, it is referred to by a letter indicating its linear position in the group of whales under observation.

During 1981, a preliminary study was made of the responses of humpback whales to sound playback. For these experiments, recordings of humpback whale songs from years 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. Both the recording and playback systems were low noise, high fidelity, and flat in their frequency response from 40 to 20 000 Hz. This covers the known frequency range of humpback vocalizations (Winn and Winn 1978).

Results

Results are presented in three sections: Behavioral observations, Behavioral continuity, and Population 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: (*i*) the observation contained the only example of a rare behavior; (*ii*) the observation was of sufficient duration to encompass a broad repertoire of behavior; or (*iii*) the individuals involved have a behavioral history relevant to the topic.

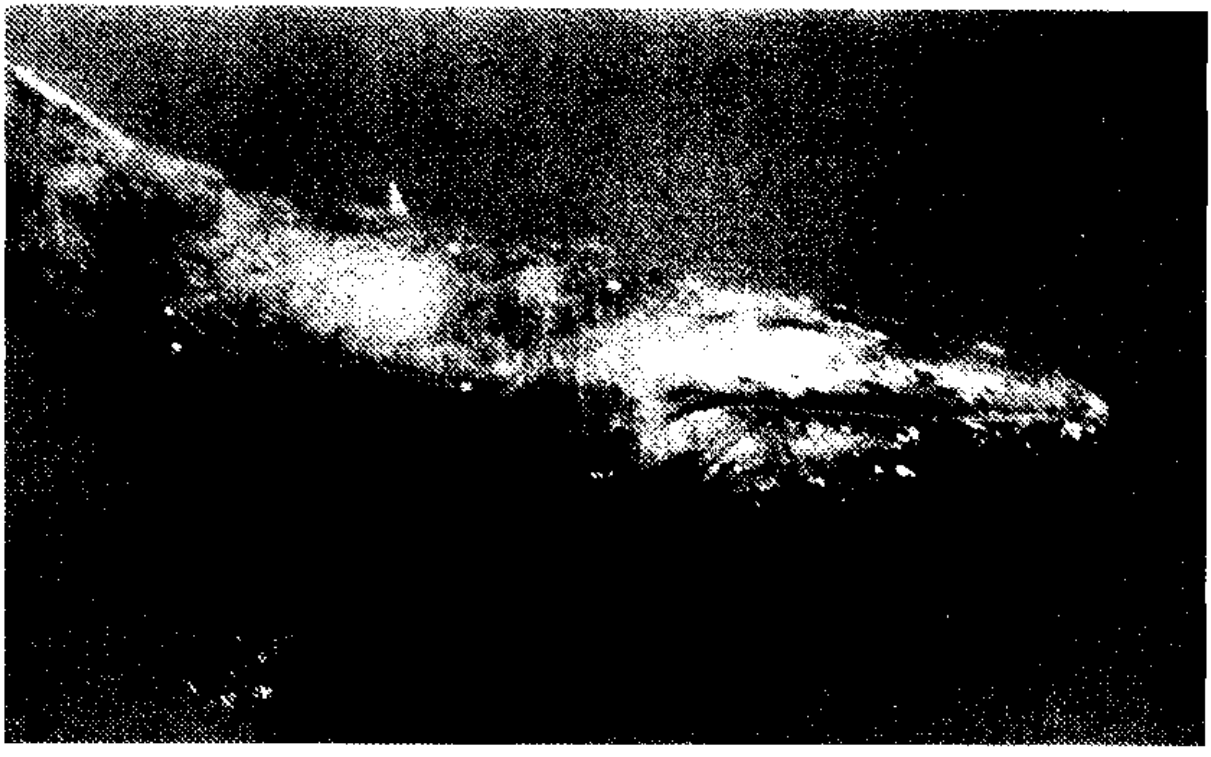

FIG. 3. A broadside threat by an escort whale. The right flipper is pointed towards the foreground resulting in its extreme foreshortening. Note parallel scars along the whale's side. Photograph by Ron Antinoja, Kewalo Basin Marine Mammal Laboratory.

The 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 population 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. We photographically identified the cow (whale No. 172) and the escort (No. 13) and observed them for about 1 h as they slowly moved south toward the island of Lanai. The same cow, calf, and escort were seen 3 h later; at that time they were accompanied by an additional three escorts, two of which, Nos. 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 2 h of observation on videotape, through the Plexiglas viewing chamber of our research vessel. The videotape records showed the ventral and lateral aspects of the escorts, allowing us to identify three of the escorts as males, Nos. 13, 48, and 49. Whale No. 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 No. 13 and were repeatedly displaced rearwards. At each surfacing No. 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. We have termed this behavior "inflated head lunging," or, more simply, "head lunging." Typical head-lunging postures are shown in Fig. 2.

Viewed from below the surface the lead escort, No. 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 blowholes while swimming underwater, a behavior we have termed "bubble trailing," and released large bursts of air just before surfacing and head lunging. The release of large bursts of air from the blowhole either singly or in rapid sequence is referred to as "underwater blowing." Whale No. 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, No. 13 repeatedly crossed the bow of our small research vessel, displaying his full lateral aspect and extending his flipper (pectoral fin) to within a few metres of the vessel. Figure 3 shows a whale in a posture similar to that of No. 13 when he crossed the path of the vessel. We have interpreted this posture as a broadside threat, similar in form and function to that seen in many other mammalian species.

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, No. 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. Whale Nos. 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 through to our leaving the pod after more than 2 h 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 metres to the rear and attempted to affil-

FIG. 4. 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.

iate with 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° turn. As can be seen in Fig. 4A, 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 metres.

Observation III: On March 15, 1981, a cow, calf, and four

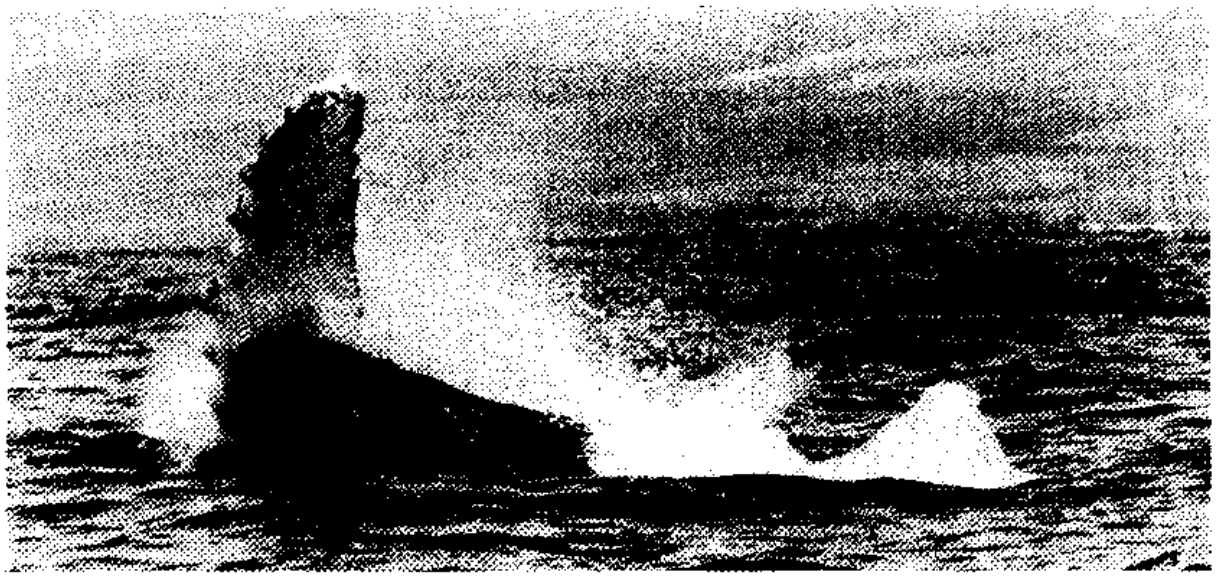

FIG. 5. A charge and strike between two escorts. The whale with the upraised rostrum charged the other and butted it just below the insertion of the flipper. Photograph by William Stifel, Kewalo Basin Marine Mammal Laboratory.

escorts were observed southeast of west Maui moving rapidly and on an erratic course. One escort, No. 49 (see Observation I), remained nearest the cow and repeatedly displaced the other escorts rearwards by positioning itself behind the cow–calf pair and head-lunging directly in the path of the other escorts. His behavior was very aggressive and at least once he charged and butted one of the trailing escorts as the latter attempted to approach the cow–calf pair. Though the trailing escort turned sharply aside from the charge, it was not able to avoid a blow to its side by No. 49's rostrum (Fig. 5). As in Observation II, the animal receiving the blow rolled to one side and lifted its flipper out of the water.

After 95 min of interpositioning and head–lunging by No. 49, one of the trailing escorts slapped its tail flukes on the water (fluke slapped) 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, No. 49, remained with the cow–calf pair. We followed the cow, calf, and No. 49 for another 40 min 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 midchannel 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 quickly moved to block the new whale's approach. We deployed a hydrophone and heard loud singing originating from one of the whales in the group. The two escorts began head lunging 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 head lunging 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 No. 62, had been seen previously in 1978 and 1979 (see Behavioral continuity for details). The escort, No. 564, had not been seen before, but was identified in southeast Alaska later, during the summer of 1981. We approached the pod to within 100 m and deployed the J-13 underwater speaker from our research vessel. A humpback whale song recorded near Maui in 1979 was played back to the pod for 10 min. Five minutes after the playback began the escort suddenly head-lunged near the cow and appeared to "herd" the cow–calf pair away from the vessel. The pod then submerged and was next seen 7 min later, lying quietly at the surface over 500 m away. We 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 our 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 10-min 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 on 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, No. 22. At each surfacing B head-lunged in front of No. 22, physically displacing No. 22 to the rear of the pod. Raw and bleeding areas on the leading edges of the dorsal fins and rostrums of B and No. 22 attested to the forceful contact between them. The head lunges were frequently preceded by underwater blows, and both B and No. 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; whale No. 22 was behind whale B and both were facing toward

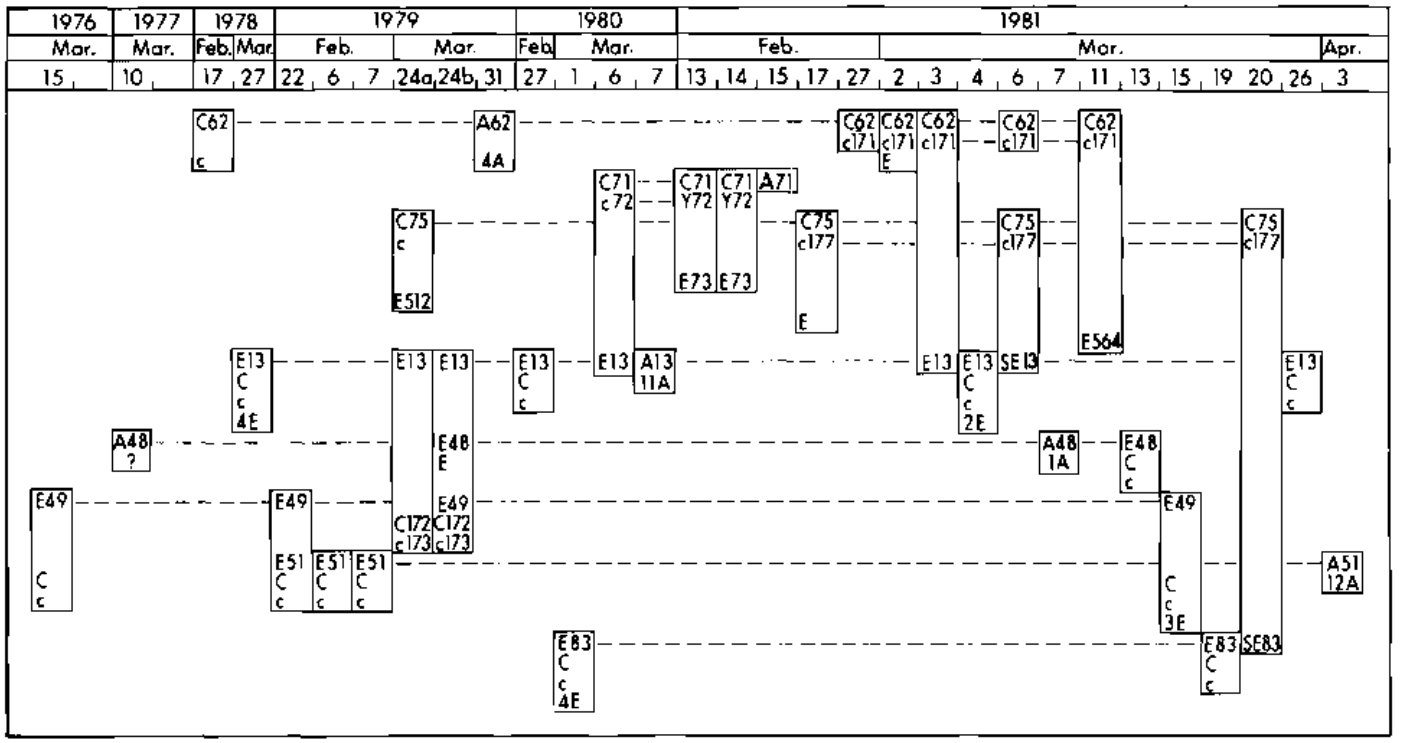

FIG. 6. The association of cows and escorts in Hawaii. Individually identified whales are designated by their whale number and behavioral role. Resighted individuals are shown across rows connected by broken lines. Boxes enclose pods. A, adult; C, cow with calf or yearling; *c*, calf; E, escort; SE, singer–escort; Y, yearling.

and perpendicular to whale A. Whale No. 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 No. 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 fluke slap). 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 No. 22 has been resighted extensively in both Hawaii and southeast Alaska and is thought to be a male. Details of No. 22's sightings are shown in Table 1 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 Olowalu 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 head lunging 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 fluke slaps and inverted fluke slaps. 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 30 min, surfacing regularly every 7 to 9 min. An unidentified animal then breached approximately 200 m away from the pair and joined the pod. The activity of the pod suddenly increased, and the new whale was met with a display of head lunging and interpositioning similar to that seen earlier. Shortly after this affiliation, A again fluke slapped 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 fluke slaps. 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 head lunged at each surfacing, with the second whale consistently displacing the third to the rear of the formation. This behavior continued for 20 min until the third whale turned inshore and began to sing. The original pair resumed its previous leisurely pace and moved north out of our viewing range. We continued to observe and record the lone singing whale for 40 min, during which time it moved less than 50 m and remained submerged, on the average, for 12 min between surfacings.

Behavioral continuity

Figure 6 presents the resighting history and complex pattern of associations of some individually identified escorts and mature females resighted over 6 years of observations. Whale No. 49 was first sighted in 1976 and subsequently sighted twice in 1979 and once in 1981. In all four of these observations No. 49 was an escort. In Observation 1, No. 49 was identified as a male.

Whale No. 13, a male, was first sighted in 1978 and on nine subsequent occasions over the following 3 years. In 9 of the 10 total sightings No. 13 was escorting a cow–calf pair. Only once, over a resighting interval of about 3 h, was the cow being

TABLE 1. The resighting history of whale No. 22

Year	Month	Day	Region	Pod size	Role
1977*	Jul.	23	Alaska	3	Adult
1979	Mar.	12	Hawaii	5	Escort
1980	Feb.	2	Hawaii	4	Adult
1980	Feb.	6	Hawaii	3	Adult
1980†	Aug.	21	Alaska	?	Adult
1981	Feb.	19	Hawaii	3	Singer–escort
1981	Jul.	3	Alaska	1	Adult
1982	Mar.	9	Hawaii	3	Adult
1982	Aug.	21	Alaska	1	Adult
1982	Aug.	26	Alaska	1	Adult
1982	Aug.	28	Alaska	4	Adult
1982	Aug.	29	Alaska	2	Adult

*Courtesy of Allen Wolman, National Marine Mammal Laboratory.
†Courtesy of Charles Jurasz, SeaSearch, Juneau, Alaska.

escorted the same (see observation I). On March 6, 1981, researchers from the Pacific Whale Foundation observed No. 13 escorting No. 75 and her calf. As one of the researchers approached the pod underwater, No. 13 began to sing and slowly escorted the cow and calf away from the diver (G. Kaufman, personal communication).

Whale No. 75 was first identified in 1979 with a calf and a single escort, No. 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 No. 13 and on March 20 by No. 83 who was singing at the time (G. Kaufman, personal communication).

Whale No. 71 was sighted near Maui in 1980 with her calf and escorted by No. 13. On February 13, 1981, she was seen off the island of Hawaii with her calf from 1980, now a yearling, and escorted by No. 73. Underwater observations of the trio by one of the authors did not indicate any distention of the abdomen or other obvious signs of pregnancy in No. 71. On the following day No. 71 was still with her yearling and No. 73. She and the yearling were observed breaching repeatedly for nearly an hour. On the third day, No. 71 was sighted alone, resting quietly within a kilometre of her location on the previous two days.

Whale No. 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 No. 13. On March 11 she was escorted by No. 564 and was the subject of the playback experiment described in Observation V.

Whale Nos. 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 No. 22, discussed in Observation VI, also has an extensive resighting record, shown in Table 1, but has not been seen in the company of any of the animals in Fig. 6. Whale No. 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, No. 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, No. 22 has been sighted 12 times in 6 years.

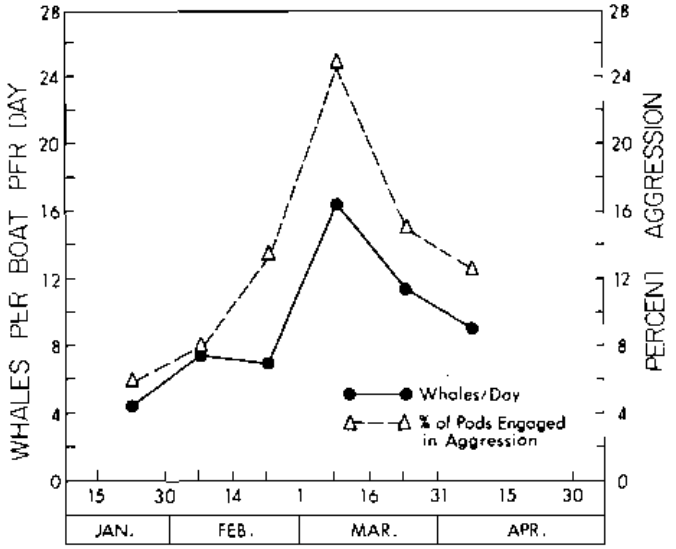

FIG. 7. The seasonal changes in abundance and frequency of aggression during the winter of 1981. Abundance is represented by the average number of whales observed per boat per day for a given 15-day period. Frequency of aggression is represented by the percentage of pods engaged in aggression during each period.

Population 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 nonsystematic surveys of Hawaiian waters. Pods were approached in order to collect individual identification photographs and were observed for a minimum of 20 min to determine the number of whales present (pod size) and their activities. Across the 3-month study we observed 331 pods totaling 726 whales.

Abundance was estimated by dividing the total number of whales observed during 2-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 2-week period by reviewing behavioral records of the pods. Pods were judged to be engaged in aggression if head lunging 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 Fig. 7 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 2 weeks of March. These indices declined somewhat more slowly than they increased.

The seasonal changes in pod size and composition are presented in Fig. 8, based on the same 2-week periods shown in Fig. 7. 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

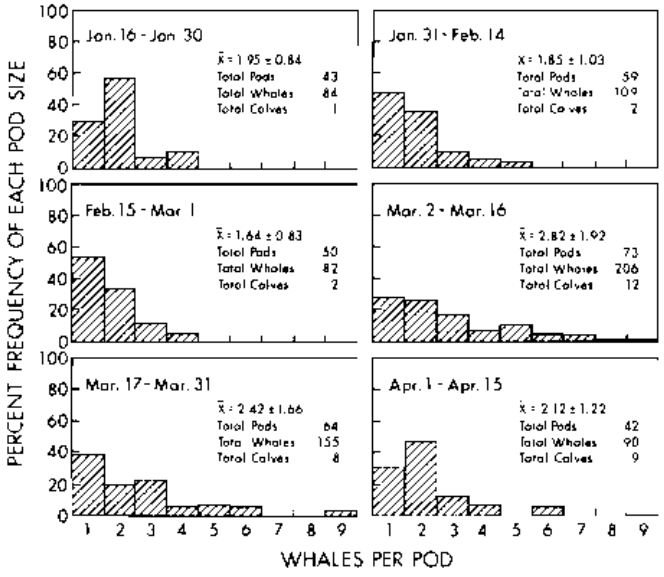

FIG. 8. Seasonal changes in pod size and composition of humpback whales during the winter of 1981. The 15-day periods correspond to those shown in Fig. 6. The mean and standard deviation of pod size are shown for each period.

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 2 weeks of March, synchronous with the peak in abundance and peak percentage of agonistic pods. A nonparametric Kruskal–Wallis test showed that differences in pod size across the six sample periods were significant ($\chi^2_{[5]} = 18.21$, $p = 0.0027$). An analysis of variance showed good agreement with the non-parametric test ($F_{[5,325]} = 5.93$, $p < 0.001$) and a Duncan's multiple range test for pair-wise comparisons indicated that pod size during the period of March 2–16 was significantly larger than during all other periods except March 17–31.

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 indicates that, in many cases, escorts are males. All multiple-escort pods observed in 1981 exhibited aggression that centered around the escorts' competition for physical proximity to the cow. Lone escorts were typically seen behind and a little below the cow–calf pair. If another animal affiliated with 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. 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 our observations of noncalf 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 noncalf 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. Several of the accompanying or trailing whales in the noncalf 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 display. Here the lead escort simply moved horizontally or diagonally across the path of the intruder. Unfortunately, this level of threat usually occurred 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 head lunge was the most commonly observed aggressive behavior and appears to be indicative of a broad intermediate level of aggression. As shown in Fig. 2, 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 the species 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 head lunge. In the head lunge, 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 (Fig. 9). The lesser degree of engorgement seen during aggressive encounters may represent an attempt to increase apparent size without sacrificing hydrodynamic efficiency.

The head lunge also differed from the less frequently observed "head rise" or "spy-hop." In the head rise there was no engorgement of the ventral pleats and the rostrum was raised vertically out of the water in an almost languid fashion (see Figure 3.6 in Madsen and Herman 1980).

If the intruding whale was not initially discouraged, the frequency and strenuousness of the head lunges 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 Fig. 2 with Fig. 10. Often the head lunges of the lead escort were directly in front of the trailing animal which appeared, as a result, to be physically displaced to the rear. In some instances (see observation VI) forceful contact was evidenced by raw areas on the escorts' dorsal fins and rostrums. We have also observed scarring and abrasions on the back and sides of escorts (Figs. 2B and 3). 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.

Although we have observed displacement occurring underwater (described in observation VI), there may be an advantage to keeping the conflict near the surface, if the surface is used as a wall or barrier to constrain the movement of an opponent.

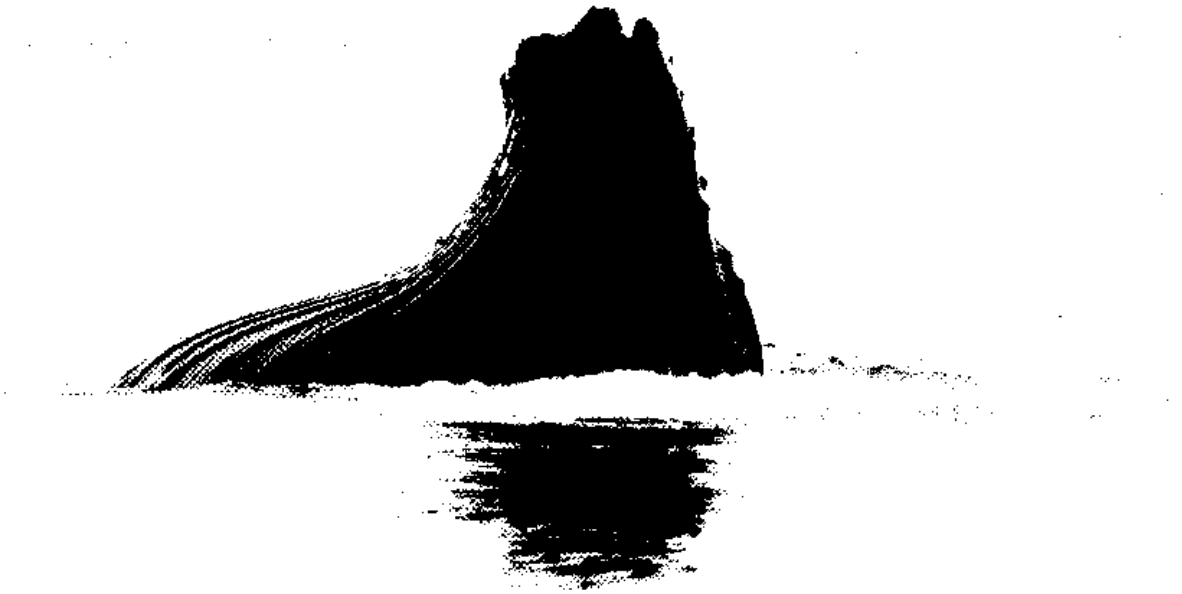

FIG. 9. Vertical lunge feeding by a humpback whale. During lunge feeding the throat is greatly enlarged and the ventral pleats are unfolded. Photograph by Thomas Kieckhefer, Kewalo Basin Marine Mammal Laboratory.

A similar strategy has been reported for feeding humpback whales (Jurasz and Jurasz 1979), which use the surface as a barrier to corral or concentrate schooling prey. On the wintering grounds, it appeared at times that the whale being displaced to the rear of the pod was 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 head lunging may act to the advantage of both contestants; the lead animal maintains his proximity to the female but must suffer vulnerability to suffocation.

The underwater release of air, referred to as "bubbling," was commonly observed in association with head lunging and characteristically took one of three forms: bubble trails, underwater blows, and, more rarely, the release of air from the mouth. As with the head lunge, the feeding behavior of the humpback whale may have preadapted it for these displays. Jurasz and Jurasz (1979), corroborating earlier observations by Ingebrigtsen (1929), described "bubble-net" feeding by humpback whales in southeast Alaska. During bubble-net feeding, a whale forms a spiral-shaped curtain of bubbles, apparently to concentrate the krill or small fish that are its prey. 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. However, like the bubble net, which in theory disorients the schooling prey, 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 metre or less. 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 our 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 head lunge, 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 we 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 head lunging and bubbling. In a few cases, however, the violence of the contest escalated beyond the level of displacement to the level of charge-strikes. We 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 Fig. 5. 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, we observed butting whales rise up out of the water in a near-vertical posture. Two examples of this are shown in Fig. 11. The position of the two whales in Fig. 11B 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.

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.

The third type of charge-strike was the most violent and was discussed in observation II and illustrated in Fig. 4. In this figure, the lead escort turned and headed directly toward the approaching whale to deliver a forceful strike with its caudal peduncle. As in Fig. 5, the whale on the receiving end turned and rolled to one side.

FIG. 10. Head-lunging 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.

In our 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 h 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 flipper slapping, fluke slapping, inverted fluke slapping, and breaching. Fluke slapping 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

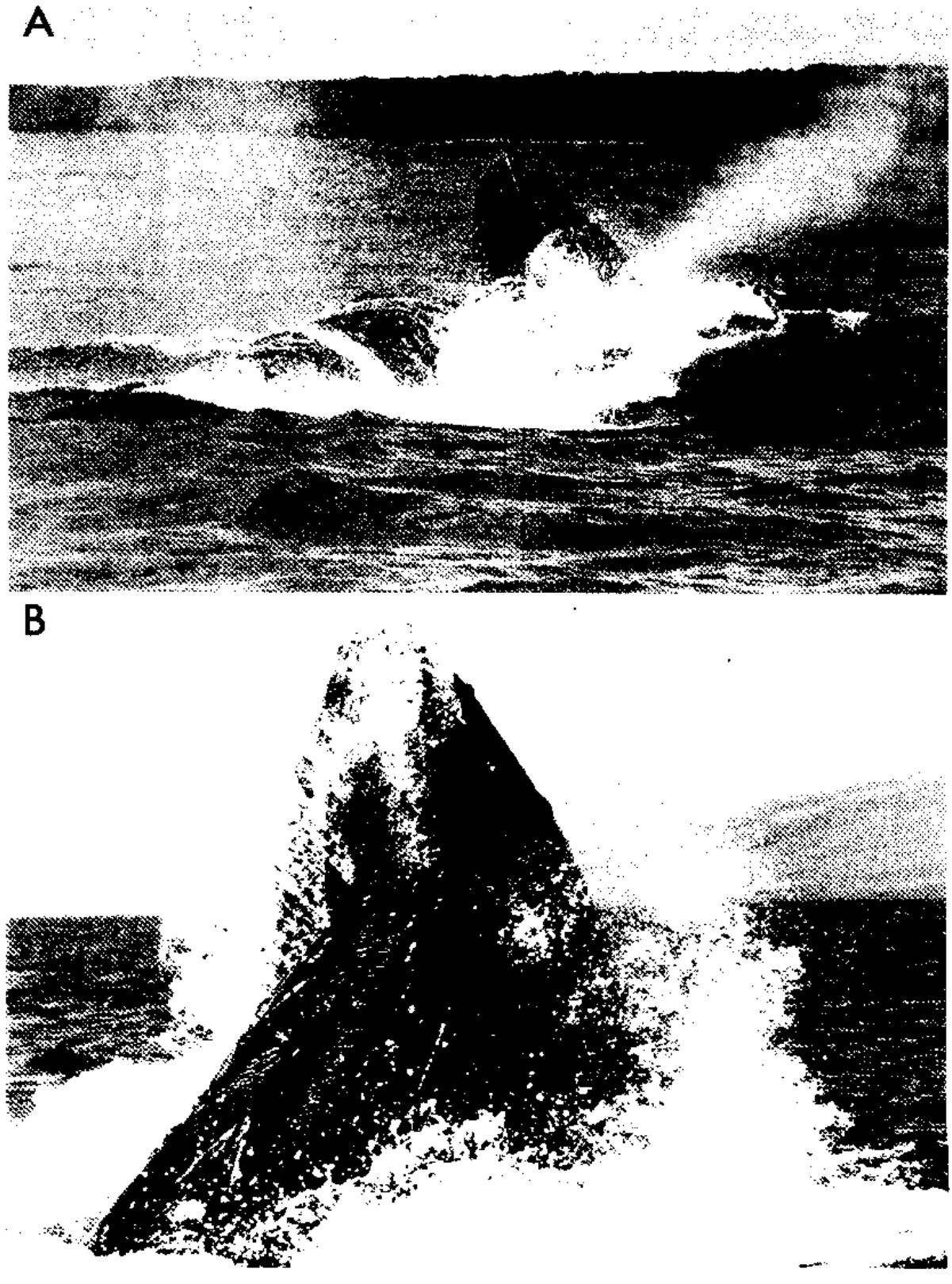

FIG. 11. Vertical posture of butting humpback whales. (A) One whale rises vertically out of the water as it butts a second whale. (B) Two whales butting and rising vertically out of the water in a ventral to dorsal position. Photographs by William Stifel and Thomas Kieckhefer, Kewalo Basin Marine Mammal Laboratory.

whale may fluke slap 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.

Based on his observations of the southern right whale, Don-

nelly (1967) first proposed a similarity between the reproductive behavior of mysticetes and ungulates. Many of the observations reported here 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 preestrus 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 we have described, aggression in humpback whales follows a progression from simple interception and broadside displays, to displacement and head lunging, to charge-strikes. Many unhorned ungulates follow a similar progression from broadside threats, to parallel threats of neck wrestling, to butting, biting, and kicking (Klingel 1974).

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. For example, No. 49 was seen four times over 5 years, always as an escort. Whale No. 13 was observed 10 times over 4 years and was an escort in all but one observation. Both Nos. 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 generally give birth every other year following sexual maturity (Chittleborough 1965). Consequently, an adult whale seen over several years without a calf is likely to be a male. Whale Nos. 22 and 48, not directly sexed, have resighting histories spanning 4 or 5 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 Nos. 49 and 13. Thus, it is likely that Nos. 22 and 48 are also males, and that escorting behavior is generally sex-specific.

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 Fig. 6. With but one exception, no two adults were seen together for more than a few hours over the 6 years and 33 sightings. Only Nos. 73 and 71, the latter a cow accompanied by her calf of the previous year, were seen together across a 2-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, like the tending male ungulate, a courting male humpback may accompany a female for as long as a few days. This is somewhat longer than the 3.5-h maximum period of affiliation reported by Mobley and Herman (1981). However, the overall pattern of social fluidity shown in Fig. 6 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 polygamous 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. The interchangeability 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 our observations documented whales singing and escorting simultaneously. In these cases it seemed that the vocalizations functioned, at least in part, as a threat display between escorts. In observation IV, one of the escorts was singing as it attempted to displace another escort. Whale Nos. 13, 22, and 83 were each singing while escorting cow–calf pairs away from underwater observers. In observation V, the escort, No. 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 by the authors that singing whales are at times accompanied by other whales (reported in 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.

Population dynamics

At least two factors could have contributed to the seasonal peak in the occurrence of aggression, shown in Fig. 7. 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 2-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. In our behavioral observations of humpback whales in southeast Alaska (Baker et al. 1982; Baker et al. 1983), we have found that aggressive behavior is rare during the summer feeding season, even though the local density of whales often exceeds that found in Hawaii. We have observed the behavior of 47 individuals photographically identified both in Hawaii during the winter and in Alaska during the summer. At least three of these individuals, Nos. 22, 512, and 564, were observed singing or escorting in Hawaii; some of the aggressive behaviors of Nos. 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 sexes and age-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 Fig. 8, 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 occurring as much as 3 weeks apart across a 3-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 2 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 initiating the departure of humpback whales from the summer feeding grounds are unknown (Dawbin 1966; Nishiwaki 1962; Baker and Herman 1981). 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 synchronize the gonadal activity of male and females despite the year-to-year shifts in migratory timing. We 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 and feeding is not observed (Herman 1979).

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).

We are 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, our attempts to determine the specific communicative function of singing, through playback studies, were inconclusive, as were similar attempts by Tyack (1983). Given the large investments of both sexes in the winter breeding season, synchronizing or inducing ovulation seem of paramount importance and may be a driving force for this complex and prolonged acoustic display by males.

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