

# Humpback whales *Megaptera novaeangliae* in the Arabian Sea

Yuri A. Mikhalev\*

South Ukrainian Pedagogical University, Staroportofrankovskaya 26, Odessa 270020, Ukraine

**ABSTRACT:** The population identity of humpback whales *Megaptera novaeangliae* in the Arabian Sea has long been a matter of dispute. New information is presented from this region, based upon whaling and observations conducted by the Soviet Union, primarily in November 1966. In that month, a total of 238 humpbacks were killed off the coasts of Oman, Pakistan and northwestern India; 4 others were killed in 1965. Biological examination of these whales showed that they differed significantly from Antarctic humpbacks in terms of size, coloration, body scars and pathology. In addition, analysis of the length distribution of 38 fetuses indicates that the reproductive cycle of the Arabian Sea whales was unequivocally that of a northern hemisphere population. Mean lengths were 12.8 m for males (range: 9.5 to 14.9 m, n = 126) and 13.3 m for females (range: 9.5 to 15.2 m, n = 112). All whales 12.5 m or more in length were sexually mature. Among 97 females examined, 12 (12.4%) were immature. Of the 85 mature females, 39 (45.9%) were pregnant, 3 (3.5%) were lactating, and 43 (50.6%) were resting. A more plausible pregnancy rate, adjusted for underrepresentation of lactating females, was estimated at 39%. A majority of stomachs examined contained food, including euphausiids and fish. Overall, the data presented here argue strongly that Arabian Sea humpbacks constitute a discrete population which remains in tropical waters year-round, a situation which is unique for this species.

**KEY WORDS:** Humpback whale · Arabian Sea · Indian Ocean · Population biology · Reproduction

## INTRODUCTION

The humpback whales *Megaptera novaeangliae* of the Arabian Sea have long represented an enigma to cetologists. Elsewhere, humpbacks undertake well-documented seasonal migrations from summer feeding areas in high latitudes to winter mating and calving grounds in tropical waters, where they typically fast (Chittleborough 1965, Dawbin 1966, Katona & Beard 1990, Perry et al. 1990). However, the northern Indian Ocean has no polar component; thus, the humpbacks that are found there must either remain within tropical waters year-round or migrate great distances to feeding grounds in other oceans.

Little is known of this population, in large part because of the lack of observer effort in this region and

the scattered nature of historical sighting reports. Van Beneden (1887) mentioned humpbacks off the coasts of Oman and Pakistan, and Gervais (1888) described a humpback (*Megaptera indica*) from Basra Bay in the Persian Gulf. The maps compiled by Townsend (1935) from catch logs of 19th century whalers show no humpbacks north of Madagascar, despite the fact that there were whaling operations off the coast of the Arabian Peninsula, where sperm whales were taken (Wray & Martin 1983). Tomilin (1967, p 303) concluded, probably based upon these sources, that 'a small (seemingly insignificant) number of humpbacks passing north of Madagascar reach the coast of Arabia and Baluchistan, and even enter the Persian Gulf'.

Slijper et al. (1964) reported humpbacks at the entrance to the Gulf of Aden, near Oman, in the Persian Gulf and off Ceylon (present-day Sri Lanka). Yukhov (1969) summarized reports from survey vessels and noted sightings of small groups of humpbacks east of Cape Fartak, Oman, in October and November

\*Address for correspondence: c/o R. L. Brownell Jr, NMFS, Southwest Fisheries Science Center, PO Box 271, La Jolla, California 92038, USA. E-mail: brownell@caliban.ucsd.edu

of 1964–65. The northern part of the Indian Ocean is included on a map of humpback whale habitat presented by Borisov in Yablokov et al. (1972, Fig. 189, p 329), but no source is given for this information. Other sightings and strandings of humpback whales in the northern Indian Ocean are summarized by Reeves et al. (1991) and Papastavrou & Salm (1991).

Explanations of the origin and seasonal movements of humpbacks in this region have been varied. Tomilin (1967) and Brown (1957) expressed a common view that Arabian Sea humpbacks migrated from Antarctic feeding grounds, while Slijper et al. (1964) speculated that they came from the North Pacific. Whitehead (1985) recorded humpback whale songs off Oman in January, and determined that the structure of these songs was different from those recorded in the North Pacific and North Atlantic; he therefore hypothesized that the population was isolated and that it remained in local waters year-round. Reeves et al. (1991) summarized data from the northern Indian Ocean and noted that the species appeared to be present in the Arabian Sea region throughout the year. While agreeing with Whitehead that this supported the idea of a resident population, they cautioned that none of the proposed hypotheses could be ruled out: existing data were too sparse, and there was virtually no biological information on the animals of this region.

It was recently reported that the Soviet Union conducted large-scale illegal whaling operations, including for protected species (see Yablokov 1994, Zemsky et al. 1995). Although the majority of this activity occurred in the Antarctic, extensive illegal catches were also made in the northern hemisphere. Here, I present formerly secret data from catches of humpback whales taken in the Arabian Sea, primarily in the autumn of 1966. Analysis of these data provides strong evidence for the existence of a discrete population of this species that both feeds and breeds in the tropical waters of the northwestern Indian Ocean.

## DATA AND OBSERVATIONS

With the exception of 4 animals killed in 1965, the data summarized here come from catches of humpback whales made in November of 1966. These catches were never reported to the Bureau of International Whaling Statistics in Norway or to the International Whaling Commission; they are included in the overall totals appearing in the new catch report on Soviet whaling operations provided by Zemsky et al. (1995).

Prior to consideration of the results, it will be useful to provide a brief narrative of the development of Soviet whaling in the Arabian Sea. In the autumn of

1963, the Soviet floating factory 'Slava' and her associated catcher vessels steamed through the Red Sea for the first time en route to the whaling grounds of the Antarctic. During this voyage, a scout vessel noted 20 to 30 humpback whales in the Gulf of Aden. The first humpback whale was killed off the northeastern coast of Madagascar at 21° 48' S, 50° 42' E. During the following whaling season (that of 1964–65), the factory ships 'Slava' and 'Sovetskaya Ukraina' travelled together through the Suez Canal. Whaling subsequently began in the Gulf of Aden, and then moved across the tropical zone to the southern tip of India and Ceylon. No humpback whales were observed, probably because (as is related later) at that time of year they appear to occupy more northerly regions of the Arabian Sea.

On the 1965–66 season voyage, the fleets again began whaling in the Gulf of Aden. In addition to other species, 'Slava' killed a 13.8 m male humpback on 12 November (14° 21' N, 52° 34' E), as well as a 14.1 m male and an animal of unrecorded length and sex on 18 November (15° 53' N, 52° 22' E). 'Sovetskaya Ukraina' also took 1 humpback (details not recorded). After whaling in the Gulf of Aden, 'Slava' steamed south to the region of the Seychelles, while 'Sovetskaya Ukraina' proceeded towards Ceylon as on previous voyages, only later turning south. No other humpback whales were observed until the vessels reached Antarctic waters.

During the 1966–67 season, 'Slava' did not operate, but 'Sovetskaya Ukraina' began whaling in the Gulf of Aden after transiting the Suez Canal. It appears that the fleet commanders took into consideration the previous catches of humpbacks in more northerly areas, as well as a message from the shrimp trawler 'Van Gogh', commanded by a well-known former whaling captain named Solyanik. Solyanik reported seeing 2 aggregations of humpback whales off the coast of Pakistan in March (at 25° 04' N, 65° 21' E, and 24° 56' N, 61° 41' E). In addition, the rumor that Kuwait was proposing to begin whaling in the Persian Gulf area reinforced the fleet commanders' belief that the northerly region must represent an important habitat for whales. Thus, in early November 1966, 'Sovetskaya Ukraina' proceeded north along the coast of Oman and across the Arabian Sea to the coasts of Pakistan and northwestern India.

## RESULTS

### Total catch, sex ratio and length of whales

During a 10 d period between 5 and 15 November 1966, the 'Sovetskaya Ukraina' fleet killed a total of

238 humpback whales. Of these, 62 were taken in 3 d (5–7 November) off Oman, in 2 regions: 30 in the vicinity of the Kuria Maria Islands, and 32 off the island of Masirah. Of the others, 164 were killed in the Gulf of Kutch off Pakistan on 8–14 November, while 12 others were taken on 15 November off India, west of Bombay. These catches are plotted in Fig 1. A scout vessel recorded sightings of an additional 34 humpbacks; of these, 20 were in the approximate position 18°N, 57°E (northeast of the Kuria Maria Islands), and the remainder in various locations off the coast of Pakistan.

Of the 238 humpbacks killed, 126 (52.9%) were male and 112 (47.1%) female, a sex ratio which does not deviate significantly from parity ( $\chi^2 = 0.412$ ,  $\alpha = 0.05$ ,  $df = 1$ ). The lengths of these animals are presented by sex in Fig. 2. Among males, lengths ranged from 9.5 to 14.9 m (mean = 12.8 m, SE = 0.937). Females ranged in size from 9.5 to 15.2 m (mean = 13.3 m, SE = 1.270). The overall mean length for both sexes was 13.1 m.

**Reproductive biology of females**

A total of 97 female humpbacks were examined to determine their reproductive condition; the resulting data are given by length in Table 1. All females of 11.5 m or more in length were found to be sexually mature, as determined from the presence of corpora

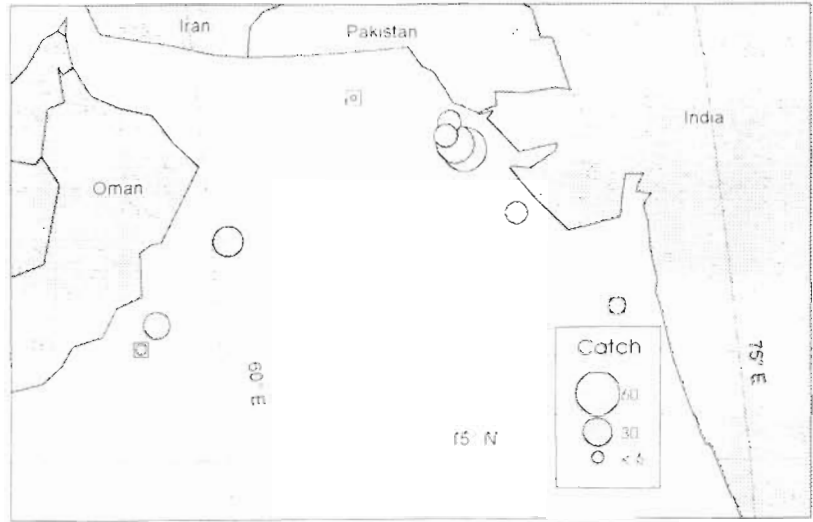


Fig. 1. Soviet catches of humpback whales *Megaptera novaeangliae* in the Arabian Sea, November 1966. Symbols in boxes indicate catches of 2 (Pakistan) and 5 (Oman) whales

bodies or from the condition of the endometrium (see Chittleborough 1958). Twelve (12.4%) of the 97 females were immature, having no evidence of past or present ovulation. Of the 85 mature females, 39 (45.9%) were pregnant, 3 (3.5%) were lactating, and 43 (50.6%) were resting (neither pregnant nor lactating).

The apparent pregnancy rate of 45.9% is misleading, since lactating (and therefore mature) females are underrepresented in the catch. A more accurate rate can be calculated using a method employed by Chittleborough (1965), who made the reasonable assumption that a humpback whale population will contain an approximately equal number of pregnant and lactating fe-

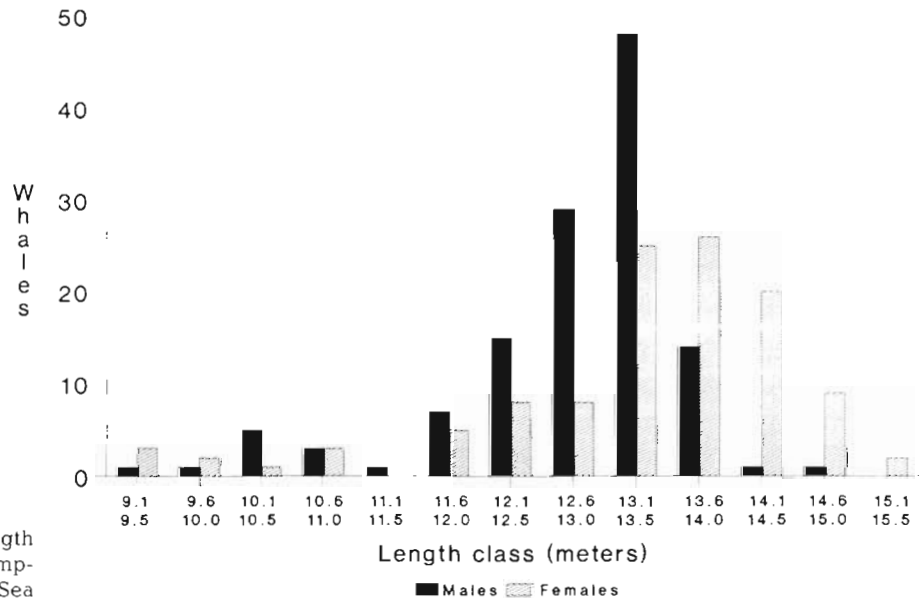


Fig. 2. *Megaptera novaeangliae*. Length frequencies of male and female humpback whales killed in the Arabian Sea

Table 1. *Megaptera novaeangliae*. Reproductive condition of female humpback whales caught in the Arabian Sea

Length (m)	Total	Pregnant		Lactating		Resting		Immature	
		n	%	n	%	n	%	n	%
9.1–11.5	9							9	100.0
11.6–12.0	4			1	25.0	1	25.0	2	50.0
12.1–12.5	7			1	4.3	5	71.4	1	14.3
12.6–13.0	8	2	25.0	1	12.5	5	62.5		
13.1–13.5	23	15	65.2	1	4.4	7	30.4		
13.6–14.0	20	7	35.0			13	65.0		
14.1–14.5	15	9	60.0	1	6.7	5	33.3		
14.6–15.0	9	2	22.2			7	77.8		
15.1–15.5	2	2	100.0						
Total	97	39	40.1	3	3.1	43	44.4	12	12.4

Table 2. *Megaptera novaeangliae*. Lengths of female and male foetuses, and of the mature females carrying them. The mean foetal length is 232 cm (SE = 37.63, n = 38). Note the one case of twins

Female foetuses		Male foetuses	
Length of mother (m)	Length of foetus (cm)	Length of mother (m)	Length of foetus (cm)
13.0	140	13.2	64
14.1	142	12.8	140
14.5	160	14.3	161
11.9	170	14.2	164
13.7	180	14.0	170
14.2	182	13.2	198
13.1	183	13.1	200
14.6	190, 210	12.1	213
13.2	200	13.8	230
13.7	230	13.3	275
13.4	250	14.3	340
13.1	250	14.3	375
14.3	260		
13.7	260		
13.3	269		
13.3	270		
12.7	280		
14.4	280		
13.4	280		
13.1	295		
15.2	300		
13.6	310		
13.3	310		
15.2	330		
13.3	353		

males. In the current case, figures of 39 pregnant, 39 lactating and 43 resting females would be used. However, one must also account for the fact that a minority of the lactating females will be pregnant. Chittleborough (1965), who did not attempt to compensate for this, gave an estimate of 8.5% for simultaneously pregnant and nursing animals. Since the data from which this figure was drawn are known to be biased, this esti-

mate is very likely to be too low. If we substitute a figure of 10%, then the adjusted pregnancy rate for the Arabian Sea humpbacks becomes 0.39 (39% of all mature females, which would comprise 43 pregnant, 35 lactating and not pregnant, and 43 resting).

The low percentage of lactating females in the catch was not an artifact of sampling, which was largely indiscriminate: the scarcity of mother/calf pairs was confirmed by a scout vessel, which recorded only one other such pair in the region.

Foetuses were examined from 37 of the 39 pregnant females. One 14.6 m female was carrying twin female foetuses, which were 190 and 210 cm in length. Lengths of the pregnant females and of their respective foetuses are summarized in Table 2. Female foetuses (26, or 68.4% of the 38 examined, including the twins) predominate in the sample, but the overall sex ratio is not significantly different from parity ( $\chi^2 = 2.602$ ,  $\alpha = 0.05$ ,  $df = 1$ ). Overall, the range of sizes among all the foetuses is relatively small: if one disregards the single 64 cm embryo, all the foetal lengths lie between 140 and 375 cm, with a mean of 232 cm (SE = 37.63).

### Stomach contents

The stomachs of 190 animals were examined. Of these, 19 (10.0%) had full stomachs. Among the remaining stomachs, 77 (40.5%) were approximately half full, 65 (34.2%) contained a small amount of food, and 29 (15.3%) were empty. In the majority of cases, stomach contents consisted of small (1 to 2 cm length) euphausiids of undetermined species. However, remains of fish were also found, including *Scomber* spp. and *Sardinella* spp. (in one animal, nearly a ton of sardines was discovered). During the period 5–7 November, off the coast of Oman, feeding on only fish was observed. Some mixed feeding on euphausiids and fish was noted in the northeastern Arabian Sea.

### Pathology

Many humpback whales in the Arabian Sea were found to have hepatic changes. Of 38 animals examined, pathology of the liver was reported in 26 (68.5%) cases. Degeneration of adjoining tissue in peripheral sections of the liver was also observed. Cone-shaped growths, sometimes up to 20 cm in diameter, were apparent, and bile ducts were blocked by a dense,

dirty gray paste. The observed pathology was similar to that caused by infection with trematode parasites, but none were found in the affected areas. Atherosclerosis of liver blood vessels was also noted in some cases, as well as hardening and thickening of arterial walls in the rectal area.

### External appearance

The external surface of the skin of the Arabian Sea humpbacks had relatively few barnacles, and those examined were quite small. Their species was not determined, although all belonged to the genus *Coronula* (the most common barnacle type found on humpback whales). Because white oval scars are commonly found on the skin of Antarctic humpback whales (Matthews 1937; author's unpubl. data), 30 of the Arabian Sea whales were examined specifically for this feature. No such scars were found.

The body coloration of 65 humpbacks was recorded for comparison to that of other populations. A subjective classification was used, in which ventral coloration was divided into 3 categories similar to those employed by Matthews (1937) and Omura (1953). These are predominantly black (type I), mixed/marbled (type II), and predominantly white (type III). Ventral coloration of whales in the second category is not dominated by either black or white, and these animals have white patches of varying size in the throat and genital regions. Of the 65 whales examined, 30 (46.2%) were of type I, 17 (26.2%) of type II, and 18 (27.6%) of type III.

## DISCUSSION

### Population identity

The data presented here argue strongly that the humpback whales found in the Arabian Sea constitute a discrete population that remains in the region year-round, both feeding and breeding in tropical waters. Evidence for this can be found in all aspects of the Soviet data, including the temporal occurrence of the whales, as well as their reproductive cycle, length, appearance and parasitology. These topics are discussed separately below.

### Occurrence

The occurrence of humpback whales off Pakistan in March, as reported by the shrimp trawler 'Van Gogh', is not necessarily inconsistent with the belief of Brown

(1957) and Tomilin (1967) that these whales originate in the southern hemisphere. However, this is not the case with the Soviet catches reported here, which were of feeding humpback whales in the month of November. Numerous sources, including Townsend (1935), Chittleborough (1953, 1965) and Dawbin (1966), clearly indicate that by the month of November or December all southern hemisphere populations of humpback whales are to be found on their austral summer feeding grounds south of latitude 35–40° S. Extensive distributional information derived from illegal Soviet catches of thousands of southern hemisphere humpback whales reinforces this (author's unpubl. data). Furthermore, neither scientific research vessels, nor whaling vessels in the 'Slava' and 'Sovetskaya Ukraina' fleets, sighted any humpbacks between 10° N and 20° S on their passages to and from the Antarctic during the months of October to December or April to May. It is also noteworthy that observers on scout and catcher boats off the coasts of Oman, Pakistan and India in November and early December reported seeing a general northerly or northeasterly movement of humpbacks in this region.

In short, the occurrence of feeding humpbacks in the Arabian Sea at a time of year when southern hemisphere populations are thousands of miles to the south, and the absence of sightings in intermediate areas, strongly supports the hypothesis that these animals are not part of the same population. Slijper et al.'s (1964) suggestion that Arabian Sea humpbacks come from the North Pacific was largely speculative, and there is little reason to suppose that animals from the latter population would undertake such a large longitudinal migration. That humpback whale songs from Oman are different from those of the North Pacific (Whitehead 1985) is significant in this regard, since differences in song structure appear to be a reliable indicator of population segregation (Payne & Guinee 1983)

### Reproduction

The data on the reproductive cycle of the Arabian Sea animals provide the most compelling evidence for their separation from austral populations of humpback whales. Although uncertainties exist regarding the precise rate and pattern of foetal growth in this species, even a broad range of estimated conception dates for the foetuses examined shows that the reproductive cycle is unequivocally that of a humpback population from the northern, not southern, hemisphere. If one assumes that the pattern of prenatal growth in the humpback whale is monoparabolic (Ohsumi et al. 1958, Laws 1959, Mikhalev 1980), the foetal length data reported here imply a 3 to 4 mo mating season



lasting from early January to late May, with a peak in early March. With a gestation period of 11 or 11½ mo (Chittleborough 1958), calving should begin in December, with a peak in February. This is entirely consistent with the data: the largest foetuses in the November catch were already 340 to 375 cm in length, close to the approximate average length at birth of 427 cm or 14 feet (Chittleborough 1958, Nishiwaki 1959). The single exception, a foetus of 64 cm, is certainly of interest; given that a foetus of such length would be approximately 4 mo of age, and thus conceived in July, this could be interpreted as a southern hemisphere whale. However, aseasonal conceptions in other humpback populations, while rare, are not unknown (Matthews 1937, Chittleborough 1958).

Overall, the relatively narrow range of foetal lengths recorded indicates a population with a single well-defined breeding season during the boreal winter. This conclusion is further supported by recordings of humpback whale songs in the Arabian Sea in January (Whitehead 1985); songs are sung solely by males, and are probably primarily a breeding display (see review in Clapham 1996). The timing of this season, from December to April/May, is synchronous with the mating and calving of other northern hemisphere populations, specifically those in the North Atlantic (Whitehead & Moore 1982, Katona & Beard 1990) and North Pacific (Nishiwaki 1966, Tomilin 1967, Perry et al. 1990).

The adjusted pregnancy rate given here (0.39) is within the range of reproductive rates reported from other whaling data and from long-term studies of identified individual humpbacks. Among whaling studies, these include 0.37 (western Australia, Chittleborough 1965), 0.39 (Aleutian Islands; value calculated by Chittleborough 1965 from data in Nishiwaki 1959), and 0.46 (California, Clapham et al. 1997; although if adjusted for lactating females in the manner described earlier, this rate would be 0.40). From long-term studies of living whales, calculated reproductive rates have commonly been expressed as 'calves per mature female per year'. Examples include 0.37 (southeastern Alaska, Baker et al. 1987), and 0.41 (the Gulf of Maine, Clapham & Mayo 1990).

The single instance of twins (in 1 of 37 females, or 2.7%) is somewhat higher (but probably not significantly so) than the frequency with which multiple foetuses have been reported elsewhere (0.39%, Slijper 1962; 0.28%, Chittleborough 1965).

The paucity of mother/calf pairs in the region (in both the catch and the observational data) is curious. Unlike in some other balaenopterids, strict segregation by reproductive condition is not known in humpback whales, although it has been suggested that during the winter females seek sheltered waters in which to give

birth (Whitehead & Moore 1982). Clapham & Mayo (1987) presented data from the Gulf of Maine to suggest that female humpbacks preferentially visit certain areas in years when they have a calf. It is thus possible that many of the lactating females in the Arabian Sea population were concentrated elsewhere at the time of the whaling operations. Certainly the high pregnancy rate indicates that the population was healthy and reproducing well, although we of course have no data on calf mortality. A final possibility, that most calves had been weaned by November, seems unlikely in light of extensive data on weaning in other populations (Clapham & Mayo 1990, Baraff & Weinrich 1993).

#### Pathology, length and external appearance

Other evidence points to the discreteness of this population. The pathologies of the liver and vascular systems observed in the majority of examined whales from the Arabian Sea contrast with a lack of such abnormalities among whales caught south of latitude 35°S (despite the fact that the Soviet hemotologist Skryabin initiated specific studies of this nature during the 1963–64 and 1965–66 seasons). In addition, the Arabian Sea population, as sampled in the Soviet catches, was significantly different in coloration from that of Antarctic Area III, where humpbacks from the southern Indian Ocean feed (for an illustration of Antarctic whaling management areas, see Mackintosh 1942, Fig. 2, p 239). In the latter population, more than 80% of the whales are of type I, with predominantly black ventral coloration (Ivashin 1958), compared to only 46.2% from the Arabian Sea.

Antarctic humpbacks frequently have white oval scars on their bodies (Matthews 1937, author's unpubl. data). The lack of such scars among the Arabian Sea whales provides further support for the idea that this population does not originate in the Antarctic, and further that it does not migrate across equatorial latitudes. Yablokov (1966) explained the principle behind the use of variation in scarification of the skin in population studies, and the recording of such scars has been a standard part of biological examinations of whales taken commercially. White oval scars are believed to result primarily from attacks by cookie-cutter sharks (*Isistius brasiliensis*; Shevchenko 1970, 1977, Jones 1971). Lillie (1915), and later Mackintosh & Wheeler (1929), considered these scars to be evidence of the regularity of whale migrations from warm to cold waters; this was based on the assumption that the scarring events occur in warm water, and that their quantity increases with the age (and subsequent migrations) of a given whale. Differences in scarring have been used to discriminate populations of sei whales

*Balaenoptera borealis* (Omura 1950) and blue whales *B. musculus* and *B. musculus breviceauda* (Ichihara 1966).

Regrettably, numerous body measurements and age-distribution data from the Arabian Sea catches have not survived, making it impossible to compare the meristics and age structure of these humpbacks to those of other populations. However, we can compare the length data collected during the November 1966 catches. The mean length of the whales from the Arabian Sea (13.1 m) is greater than that of southern hemisphere humpbacks taken by the 'Sovetskaya Ukraina' later in the same season (December, 12.6 m; January, 12.5 m; February, 12.4 m; and March, 12.1 m). A more standardized comparison can be made by examining the lengths within a single class, pregnant females. In the Arabian Sea these averaged 13.6 m, compared to 12.9 m for the Antarctic catch during the same whaling season. Furthermore, despite the fact that almost 53% of the Arabian Sea catch were males, which are the smaller of the 2 sexes (Matthews 1937), the mean length of the Arabian Sea animals was greater than those taken in all other months. It was also greater than the value of 12.5 m reported for southern hemisphere pelagic humpback catches during an earlier period of exploitation between 1933 and 1945 (Tomilin 1967). However, the absence of standard errors from the Antarctic sample makes inter-population comparisons difficult, and the data are reported with this caveat.

The apparently greater size of the Arabian Sea whales, the relatively high pregnancy rate among mature females, the low percentage of immature whales, and the even sex ratio all suggest a pristine population that had been previously untouched by whaling. The size difference relative to the Antarctic is all the more suggestive given that southern hemisphere humpbacks are normally somewhat larger on average than their boreal counterparts. The apparently healthy nature of this stock contrasts sharply with that of the Antarctic, which by this time had been nearly wiped out by intensive commercial whaling.

In conclusion, several lines of evidence argue strongly for the discrete and boreal nature of the Arabian Sea humpback whale population. The extent of this population's range cannot be determined on the basis of present data, and we do not know whether the Arabian Sea animals undertake predictable seasonal movements within the northwestern Indian Ocean region. However, in November, their habitat appears to be defined by the coastal waters of the Arabian Peninsula to the west, the northwestern coast of the Indian Subcontinent to the east, and the Persian Gulf and Gulf of Oman to the north.

Ultimately, the question of this population's identity and migratory behavior will be answered with molecu-

lar studies, which elsewhere have proved to be a valuable tool for assessing relationships and gene flow among and within populations of this species (Baker et al. 1993, Palsbøll et al. 1995, Larsen et al. 1996). In particular, it will be interesting to see whether the Arabian Sea population has its origin in an ancient influx of whales from the southern hemisphere, a phenomenon which is evident in certain portions of the North Atlantic humpback population (Palsbøll et al. 1995).

## Ecology

The abundance of prey found in the stomachs of many of the whales reflects the productivity of the region. This is known to be unusually high for a tropical system, and derives from a combination of monsoon-related currents and strong upwellings between May and September (Smith 1968, Currie et al. 1973). As noted by Reeves et al. (1991), productivity off Oman is sufficient to support a sardine fishery as well as marine organisms normally characteristic of temperate latitudes. Consequently, it is not surprising that a humpback whale population could be supported in this habitat. The data indicate that the diet of the Arabian Sea humpbacks comprises a variety of prey items, including euphausiids and a variety of small schooling fish. This is typical of humpback whales elsewhere (Matthews 1937, Whitehead 1983, Payne et al. 1986, Perry et al. 1990).

The Arabian Sea humpback whale population's apparent year-round residence in the tropics represents a unique situation for this species, which in other oceans makes predictable seasonal migrations between high- and low-latitude waters. One question that should be addressed with further research is whether the behavior of the Arabian Sea animals differs from that of migratory conspecifics in other oceans. Elsewhere, the migration of balaenopterids appears to be a response to the need to exploit seasonal pulses of productivity in high latitudes while fasting in warm water during winter to conserve energy (Brodie 1975). In the humpback, this distinct geographical division of the year is paralleled by a strong seasonal segregation of behavior: whales feed and do not breed in summer, then mate and calve but do not eat in winter (Dawbin 1966). Thus, it is possible that removal of migratory constraints would have an impact on the social ecology of the species. This has apparently occurred with the so-called 'inshore' stock of Bryde's whales *Balaenoptera edeni*, which feeds year-round in the tropics and which (presumably as a result) is the only baleen whale that breeds throughout the year (Best 1977). The fact that the Arabian Sea humpback's breeding season appears to be tightly defined in winter suggests that

these whales are similar to conspecifics in other oceans. The key factor may be the abundance of prey, which appears to be a seasonal phenomenon in the Arabian Sea.

### Status

The historic and present abundance of humpbacks in the Arabian Sea is unknown. That the whalers were able to locate and kill so many animals in a 10 d period suggests that the population was not small, although the tendency of humpbacks to aggregate might well have facilitated the capture of a significant portion of the population. Scientists on board the search vessel 'Bditelnyi-24' subjectively estimated that, during the November 1966 hunt, the animals that were killed represented approximately 60% of those sighted. Since it is very unlikely that the entire stock was observed during this short period, it is possible that, some 30 yr later, the population is now substantial in size. However, despite an increase in both local interest and sighting reports off Oman in recent years (Papastavrou & Salm 1991, Reeves et al. 1991), we currently know too little to assess the size and conservation status of this unique tropical stock of humpback whales, and further research is required.

*Acknowledgements.* I am very grateful to Bob Brownell and Phil Clapham for all of their help in the writing of this paper, and to Andy Dizon for help with graphics. I also thank Vladimir Mikhalev and Ted Sweeney for translation assistance, as well as Per Palsbøll and 2 anonymous referees for their helpful comments.

### LITERATURE CITED

- Baker CS, Perry A, Bannister JL, Weinrich MT, Abernethy RB, Calambokidis J, Lien J, Lambertsen RH, Urbán Ramirez J, Vásquez O, Clapham PJ, Alling A, O'Brien SJ, Palumbi SR (1993) Abundant mitochondrial DNA variation and worldwide population structure in humpback whales. *Proc Natl Acad Sci USA* 90:8239–8243
- Baker CS, Perry A, Herman LM (1987) Reproductive histories of female humpback whales *Megaptera novaeangliae* in the North Pacific. *Mar Ecol Prog Ser* 41:103–114
- Baraff LS, Weinrich MT (1993) Separation of humpback whale mothers and calves on a feeding ground in early autumn. *Mar Mammal Sci* 7:49–54
- Best PB (1977) Two allopatric forms of Bryde's whales off South Africa. *Rep Int Whal Commn (Spec Iss 1)*:10–38
- Brodie PF (1975) Cetacean energetics: an overview of intra-specific size variation. *Ecology* 56:152–161
- Brown SG (1957) Whales observed in the Indian Ocean. Notes on their distribution. *Mar Obs* 27:157–165
- Chittleborough RG (1953) Aerial observations on the humpback whale, *Megaptera nodosa* (Bonnaterre), with notes on other species. *Aust J Mar Freshwat Res* 4: 219–226
- Chittleborough RG (1958) The breeding cycle of the female humpback whale, *Megaptera nodosa* (Bonnaterre). *Aust J Mar Freshwat Res* 9:1–18
- Chittleborough RG (1965) Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust J Mar Freshwat Res* 16:33–128
- Clapham PJ (1996) The social and reproductive biology of humpback whales: an ecological perspective. *Mammal Rev* 26:27–49
- Clapham PJ, Leatherwood S, Szczepaniak I, Brownell RL Jr (1997) Catches of humpback and other whales from shore stations at Moss Landing and Trinidad, California, 1919–1926. *Mar Mammal Sci* 13 (in press)
- Clapham PJ, Mayo CA (1987) Reproduction and recruitment of individually identified humpback whales, *Megaptera novaeangliae*, observed in Massachusetts Bay, 1979–1985. *Can J Zool* 65:2853–2863
- Clapham PJ, Mayo CA (1990) Reproduction of humpback whales, *Megaptera novaeangliae*, observed in the Gulf of Maine. *Rep Int Whal Commn (Spec Iss 12)*:171–175
- Currie RI, Fisher AE, Hargreaves PM (1973) Arabian Sea upwelling. The biology of the Indian Ocean. *Ecol Stud* 3: 475–486
- Dawbin WH (1966) The seasonal migratory cycle of humpback whales. In: KS Norris (ed) Whales, dolphins and porpoises. University of California Press, Berkeley, p 145–170
- Gervais P (1888) Sur une nouvelle espèce de Megaptera (*Megaptera indica*) provenant du golfe Persique. Nouvelle archives du Museum d'Histoire Naturelle, Paris, p 199–218
- Ichihara T (1966) The pygmy blue whale, *Balaenoptera musculus brevicauda*, a new subspecies from the Antarctic. In: Norris KS (ed) Whales, dolphins and porpoises. University of California Press, Berkeley, p 79–113
- Ivashin MV (1958) The color type of the humpback whale body (*Megaptera nodosa* Bonnaterre) of the southern part of the Indian Ocean. *Informatsionnyj Sbornik VNIRO* 2: 61–65 (in Russian)
- Jones EC (1971). *Isistius brasiliensis*, a squaloid shark, the probable cause of crater wounds on fishes and cetaceans. *Fish Bull US* 69:791–798
- Katona SK, Beard JA (1990) Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Rep Int Whal Commn (Spec Iss 12)*:295–305
- Larsen AH, Sigurjónsson J, Øien N, Vikingsson G, Palsbøll PJ (1996) Population genetic analysis of mitochondrial and nuclear genetic loci in skin biopsies collected from central and northeastern North Atlantic humpback whales (*Megaptera novaeangliae*): population identity and migratory destinations. *Proc R Soc Lond B* 263:1611–1618
- Laws RM (1959) The foetal growth rates of whales with special reference to the fin whale, *Balaenoptera physalus*, Linn. *Discovery Rep* 29:281–308
- Lillie DG (1915) Cetacea. British Antarctic ('Terra Nova') expedition, 1910. *Nat Hist Rep, Zool I, No. 3*:85–124
- Mackintosh NA (1942) The southern stocks of whalebone whales. *Discovery Rep* 22:197–300
- Mackintosh NA, Wheeler JFG (1929) Southern blue and fin whales. *Discovery Rep* 1:257–540
- Matthews LH (1937) The humpback whale, *Megaptera nodosa*. *Discovery Rep* 17:7–92
- Mikhalev YA (1980) General regularities in prenatal growth in whales and some aspects of their reproductive biology. *Rep Int Whal Commn* 30:249–254
- Nishiwaki M (1959) Humpback whales in Ryukyuan waters. *Sci Rep Whales Res Inst, Tokyo* 14:49–87
- Nishiwaki M (1966) Distribution and migration of the larger cetaceans in the North Pacific as shown by Japanese



- whaling results. In: Norris KS (ed) Whales, dolphins and porpoises. University of California Press, Berkeley, p 171–191
- Ohsumi SK, Nishiwaki M, Hibiya T (1958) Growth of fin whale in the northern Pacific. Sci Rep Whales Res Inst, Tokyo 13:97–133
- Omura H (1950) Whales in the adjacent waters of Japan. Sci Rep Whales Res Inst, Tokyo 4:27–113
- Omura H (1953) Biological study on the humpback whales in the Antarctic whaling areas IV and V. Sci Rep Whales Res Inst, Tokyo 8:81–101
- Palsbøll PJ, Clapham PJ, Mattila DK, Larsen F, Sears R, Siegismund HR, Sigurjónsson J, Vasquez O, Arctander P (1995) Distribution of mtDNA haplotypes in North Atlantic humpback whales: the influence of behaviour on population structure. Mar Ecol Prog Ser 116:1–10
- Papastavrou V, Salm RV (1991) A note on recent sightings and strandings of cetaceans in Oman: Ra's Sawadi to Rakhyut. UNEP Marine Mammal Tech Rep 3:211–217
- Payne PM, Nicolas JR, O'Brien L, Powers KD (1986) Distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus*. Fish Bull US 84:271–277
- Payne RS, Guinee LN (1983) Humpback whale, *Megaptera novaeangliae*, songs as an indicator of 'stocks' In: Payne R (ed) Communication and behavior of whales. AAAS Selected Symposia Series 76:333–358
- Perry A, Baker CS, Herman LM (1990) Population characteristics of individually identified humpback whales in the central and eastern North Pacific: a summary and critique. Rep Int Whal Commn (Spec Iss 12):307–317
- Reeves RR, Leatherwood S, Papastavrou V (1991) Possible stock affinities of humpback whales in the northern Indian Ocean. UNEP Mar Mammal Tech Rep 3:259–269
- Shevchenko VI (1970) Puzzling white scars on a whale body. Priroda 6:72–73 (in Russian)
- Shevchenko VI (1977) Application of white scars to the study of the location and migrations of sei whale populations in Area III of the Antarctic. Rep Int Whal Commn (Spec Iss 1): 130–134
- Slijper EJ (1962) Whales. Cornell University Press, New York
- Slijper EJ, van Utrecht WL, Naaktgeboren C (1964) Remarks on the distribution and migration of whales, based on observations from Netherlands ships. Bijdr Dierkd 34: 3–93
- Smith RL (1968) Upwelling. Oceanogr Mar Biol Annu Rev 6: 11–46
- Tomilin AG (1967) Mammals of the USSR and adjacent countries, Vol IX, Cetacea. Izd Akad Nauk SSSR, Moskva. Israeli Program for Scientific Translations, Jerusalem
- Townsend CH (1935) The distribution of certain whales as shown by logbook records of American whalships. Zoologica (NY) 19:1–50
- Van Beneden PJ (1887) Histoire naturelle de la baleine à bosse (*Megaptera boops*). Mem Couronnés Acad R Belg 40:1–42
- Whitehead H (1983) Structure and stability of humpback whale groups off Newfoundland. Can J Zool 61:1391–1397
- Whitehead H (1985) Humpback whale songs from the North Indian Ocean. Invest Cetacea 17:157–162
- Whitehead H, Moore MJ (1982) Distribution and movements of West Indian humpback whales in winter. Can J Zool 60: 2203–2211
- Wray P, Martin KR (1983) Historical whaling records from the western Indian Ocean. Rep Int Whal Commn (Spec Iss 5): 218–242
- Yablokov AV (1966) Changeability of mammals. Nauka Zhizn 1–363 (in Russian)
- Yablokov AV (1994) Validity of whaling data. Nature 367:108
- Yablokov AV, Belkovich VM, Borisov VI (1972) Whales and dolphins. Academy of Sciences, Moscow (in Russian)
- Yukhov VL (1969) Observations of cetaceans in the Gulf of Aden and the northwestern part of the Arabian Sea. In: Arsenev VA, Zenkovich BA, Chapskii KK (eds) Marine mammals. Akad Nauka, Moscow, p 327–328 (in Russian; English translation available from National Marine Mammal Laboratory, Seattle, WA)
- Zemsky VA, Berzin AA, Mikhalev YA, Tormosov DD (1995) Soviet Antarctic pelagic whaling after WWII: review of actual catch data. Rep Int Whal Commn 46: Annex E, Appendix 3

This article was submitted to the editor

Manuscript first received: September 4, 1996

Revised version accepted: January 29, 1997