MASS STRANDINGS OF TOOTHED WHALES (ODONTOCETI) AS A POPULATION PHENOMENON

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ABSTRACT

From a study of *Globicephala melaena* and *Lagenorhynchus acutus* in the northwest Atlantic, and *Physeter catodon* at North Island, New Zealand, it is shown that mass strandings of Odontoceti occur at high population densities. Moreover, within the range of a single species, mass strandings occur within the " core " of the range but not at its periphery. They occur at high frequency among species of the subfamily Orcininae. In *Globicephala* spp. and *Pseudorca crassidens* the stranded herds include all sizes of animals of both sexes, and these species are therefore highly social. Amongst most Delphininae, mass strandings occur at lower frequency. Herds consist of reproductively mature animals and calves, or of immatures, or solitary immatures may strand. These species are therefore less social and, in captivity, an adult male *Tursiops truncatus* is aggressive towards immature animals. The social Orcininae nevertheless show greater sexual dimorphism than the Delphininae, a more delayed sexual maturity and a lower frequency of males, features usually associated with polygyny. The sperm whale *Physeter catodon* shows frequent mass strandings of harem herds and occasional mass strandings of adolescent males in warm seas, singleton strandings of solitary males in cool seas.

Age-specific mortality rates of Odontoceti and Mysticeti were studied from length-frequencies of stranded as compared with randomly-captured animals. Two Mysticetes (minke, humpback) showed a high mortality of newly-weaned animals, and minke—a high mortality at greatest lengths, among strandings. A weakly social Odontocete (*Phocoena phocoena*) showed the first feature. Three Delphinid species showed evidence of more even mortality through all ages. This feature is related to their sociality, including long parental care. Nevertheless there is evidence for enhanced mortality of immatures of both sexes in species showing aggression by adults. There is also evidence for density-dependent reproduction in several species of Odontoceti, though not so far in the most highly social Orcininae. Since most mortality in these latter species is mass mortality, mass mortality must regulate their populations. Psychological mechanisms leading to mass strandings remain to be investigated, but could include stress. The animals about to strand are regarded as being in a passive, moribund state, drifted to the coastline by currents.

INTRODUCTION

The Cetacea are divided into two suborders which differ in many ways, not least in size. The baleen whales or Mysticeti are all large (6 to 30 m adult body length) and feed by engulfing organisms much smaller than themselves which they trap and strain with their baleen plates. The toothed whales or Odontoceti are smaller (2 to 15 m) and feed on fish or squids not so much smaller than themselves. Very often, active cooperation aids capture of their prey, a habit which may have resulted in their commonly found and highly-developed social behaviour. Only among the Odontocetes, especially in the most highly social families, do we find the very curious tendency to come ashore and die in groups; the phenomenon of mass strandings. Mysticetes are found stranded en masse in only one circumstance, when pressed by pack ice on to the shore, a phenomenon found also in Odontocetes that live in cold seas (Taylor 1957; Sergeant, Mansfield and Beck 1970). This seems to be an accidental phenomenon, which does not necessarily imply social behaviour, other than that individual whales may be feeding or travelling together.

Mass-stranded animals are not obviously diseased or in an abnormal body state, and the phenomenon has so far defied explanation (Geraci 1978). Observers who have sought the cause at the level of the specific site and set of circumstances have so far produced no convincing explanations. While the stranding animals must be exhibiting abnormal behaviour, since it is almost always lethal, I have found it useful to look first at the phenomenon at the level of the population. Opportunity to do this came from the lucky chance that 30 years' data existed, from 1950 to date of writing (1981), on the abundant north Atlantic pilot whale *Globicephala melaena* at Newfoundland. I also found some less complete data on another delphinid, the white-sided dolphin *Lagenorhynchus acutus* in the northwest Atlantic, and on the sperm whale *Physeter catodon* at New Zealand. I have also been fortunate in that networks of published strandings have increasingly developed in recent years, notably in France and the United States.

THREE CASE HISTORIES

a. *North Atlantic pilot whale Globicephala melaena in the northwest Atlantic.*

Northern pilot whales have long been known to mass-strand in cool waters of the North Atlantic, from Cape Cod to Newfoundland, in Greenland, and from France to Iceland (Figure 1). In several regions of their abundance, especially at the Faeroes and at Newfoundland, inshore fishermen have taken advantage of this tendency to drive the animals ashore (Mitchell 1975a).

Catching in Newfoundland was intensive, with an organised industry, from 1947 to 1971 (Fig. 2). In the later years of this drive-fishery, annual catches became very low. It appeared that a population, of ill-defined extent, but probably inhabiting the area east of Newfoundland, had been decimated; the total catch had been approximately 54,000 animals (Mercer 1975). Figure 2 shows that high catches at the outset, peaking in 1956, were steadily reduced, lesser fluctuations being associated with variable abundance of the main food, the squid *Illex illecebrosus*, from year to year. There was, however, no overall decline of squid over the period of decline of pilot whales.

Fig. 1. Part of a herd of 58 pilot whales *Globicephala melaena* stranded at Port Maitland, Nova Scotia (44°01′N, 66°10′W) August 1–2, 1960. Photo by Ken Oxner, Yarmouth, N.S.

The area inhabited by *G. melaena* throughout the year is over deep water, extending in to the Continental Slope, where the species is generally abundant (Fig. 3). In late summer water temperatures become warm enough to allow the squid and pursuing pilot whales to concentrate over the continental shelf and inshore.

During the period of the drive fishery, there were no natural strandings in eastern Newfoundland. This is scarcely surprising since fishermen actively drove pilot whales ashore in much of the area (Conception, Trinity, Bonavista and Notre Dame bays). However, there was one stranding in 1957 in western Newfoundland (Sergeant, Mansfield and Beck 1970) where no driving took place (Table 1).

While pilot whales appeared to be scarce east of Newfoundland in the late

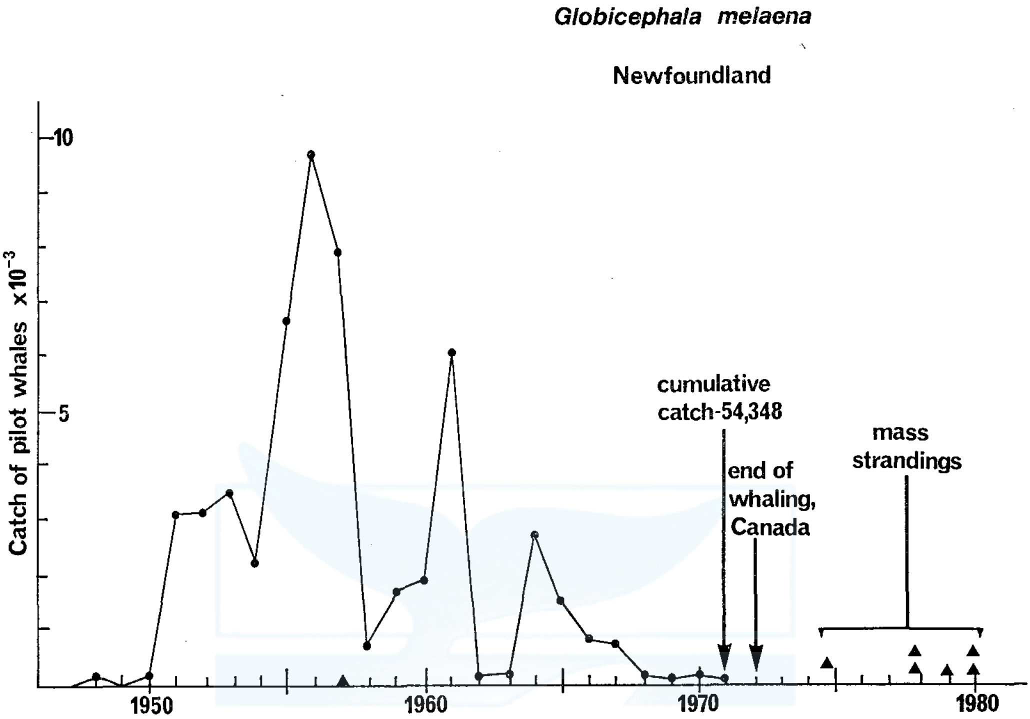

Fig. 2. *Globicephala melaena.* Catches and strandings at Newfoundland, 1948 to 1980.

1950's to early 1970's, they were still common off Nova Scotia (Fig. 3), and natural mass strandings took place both on the mainland and at offshore Sable Island (Table 1). This adjacent population must have contributed to the rather rapid recovery that took place when hunting stopped at Newfoundland, where by 1980 pilot whales were again abundant off the eastern coast (K. Hay, unpublished MS 1981).

In 1972 all whale hunting in Canada, with the exception of aboriginal hunting in the arctic, was prohibited. In 1975, natural strandings of pilot whales began to occur at Newfoundland (Mitchell 1977, Geraci and St. Aubin MS 1975; Table 1). Such had been the change in the world climate of opinion about Cetacea that fishermen were employed to save the animals by towing them to sea. In 1978 two mass strandings occurred at Miquelon Island off Newfoundland's south coast, and one in Notre Dame Bay on the east coast. In 1979 one large stranding occurred on the Burin Peninsula on the south coast. In 1980 strandings occurred on the south and northeast coasts of Newfoundland, and one at Prince Edward Island (Table 1). In 1981 there were two mass strandings in Newfoundland, one at the Magdalen Islands, Quebec, four in Nova Scotia and Cape Breton Island, and one at Cape Cod, Massachusetts. In 1980 K. Hay (unpublished MS 1981) estimated from aerial survey at least 14,000 pilot whales in Newfoundland's eastern waters up to 150 km offshore, and animals were seen to enter inshore waters in large numbers

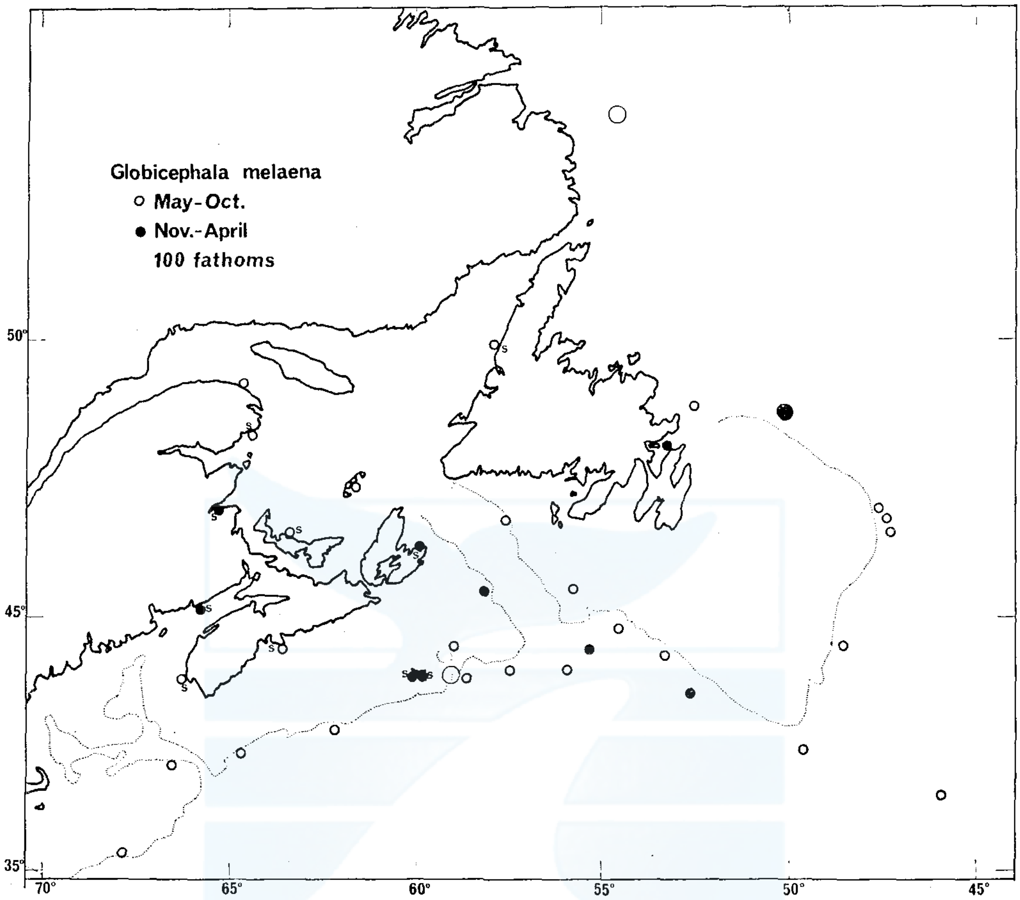

Fig. 3. Sightings and strandings (s) of *G. melaena* in the northwest Atlantic, 1957 to 1972 (from Sergeant 1979).

in early September (M. Moore, pers. comm.). In 1981 large numbers again entered inshore waters in late summer.

Mass strandings had therefore begun, coming from a population which had increased again and resumed its habit of moving inshore in late summer. A rough assessment of mortality due to mass strandings of *G. melaena* at Newfoundland in 1975 to 1980 can be made from the mean number stranded (Table 1), which is not less than 150 out of the population estimate of at least 14,000, or about 1%; this assumes that all animals were vulnerable to this kind of death, and excludes animals further than 150 km offshore. This is not a large proportion, but from the 1980 and 1981 data, mass strandings seem to be increasing in frequency and in area affected, if not in total number of animals dying.

b. White sided dolphin Lagenorhynchus acutus in the northwest Atlantic.

Lagenorhynchus acutus was observed at Newfoundland (Sergeant and Fisher

TABLE 1. MASS STRANDINGS OF PILOT WHALES IN EASTERN CANADA, 1957–1980
Sources: Sergeant, Mansfield and Beck (1970); Geraci and St. Aubin (1975, 1977), Mitchell (1977, 1980, 1981, MS 1981).

Date	Lat.	Long.	Locality	Province/State	Number
4 VIII 1957	49°51′	57°48′	Cow Head	Newfoundland	12 or more
2 X 1959	43°58′	59°48′	Sable I.	Nova Scotia	18
1 VIII 1960	44°	66°10′	Yarmouth	Nova Scotia	58
24 XII 1967	46°13′	59°57′	Glace Bay, Cape Breton I.	Nova Scotia	15
28 IX 1975	48°35′	53°30′	Charleston, Bonavista Bay	Newfoundland	300
26 XII 1976	43°58′	59°48′	Sable I.	Nova Scotia	130 or more
19 IX 1978	47°	56°15′	Miquelon-Langlande	(France; S. of Nfld.)	93+63
3 X 1978	49°28′	53°56′	Musgrave Hbr., Notre Dame Bay	Newfoundland	70
16 VII 1979	46°54′	55°33′	Pt. au Gaul, Burin Peninsula	Newfoundland	135
18 X 1980	49°09′	55°20′	Pt. Leamington, Notre Dame Bay	Newfoundland	75
25 X 1980	47°15′	55°30′	Grand Beach, Burin Peninsula	Newfoundland	18
9–18 XI 1980	46°23′	63°48′	Bedeque Bay	Prince Edward Island	52

1957) and at New England (Schevill 1956) in the early 1950's and its noteworthiness, as well as the infrequency of previous reports, suggests that it was not a particularly abundant species in the northwest Atlantic at this time. The same was true in the 1960's when Mercer (1973) recorded it in southern Newfoundland and far to the east of the island over deep water, and Sergeant, Mansfield and Beck (1970) recorded it stranded on Sable Island. During the 1970's, however, it has very often been reported in the waters off New England and Nova Scotia, and in summer in the Gulf of St. Lawrence (Katona, Testaverde and Barr 1978; Sergeant, St. Aubin and Geraci 1980; Testaverde and Mead 1980). While some of this increase must be due to an increase in observers, it seems certain that a real increase of population has occurred. The aerial surveys carried out by the University of Rhode Island's Cetacean and Turtle Assessment Program (CETAP; see Hain, Edel, Hays, Katona and Roanowicz 1981) found *Lagenorhynchus acutus in* 1979 to be the most numerous cetacean along the northeastern seaboard of the U.S.A., exceeding 10,000 individuals observed. The species occurred throughout the Gulf of Maine, especially in the vicinity of Cape Cod and over Georges Bank, and south to waters off Chesapeake Bay.

During the 1970's there were two mass strandings of *L. acutus*: at Cape Cod in May 1973 and in the northern Gulf of Maine in September 1974. There was a third multiple stranding at almost the same site in the Gulf of Maine in September 1981 and also a small multiple stranding at Prince Edward Island in the Gulf of St. Lawrence in November 1979 (Mitchell 1981). There have been numerous single strandings in New England, Nova Scotia and the Gulf of St. Lawrence throughout the 1970's. In September and October 1981, the species several times entered the waters of Bedford Basin, Halifax Harbour, Nova Scotia. Thus irregular mass strandings, and frequent single strandings, have been a feature of the biology of *L. acutus* during the period of its population abundance in the northwest Atlantic.

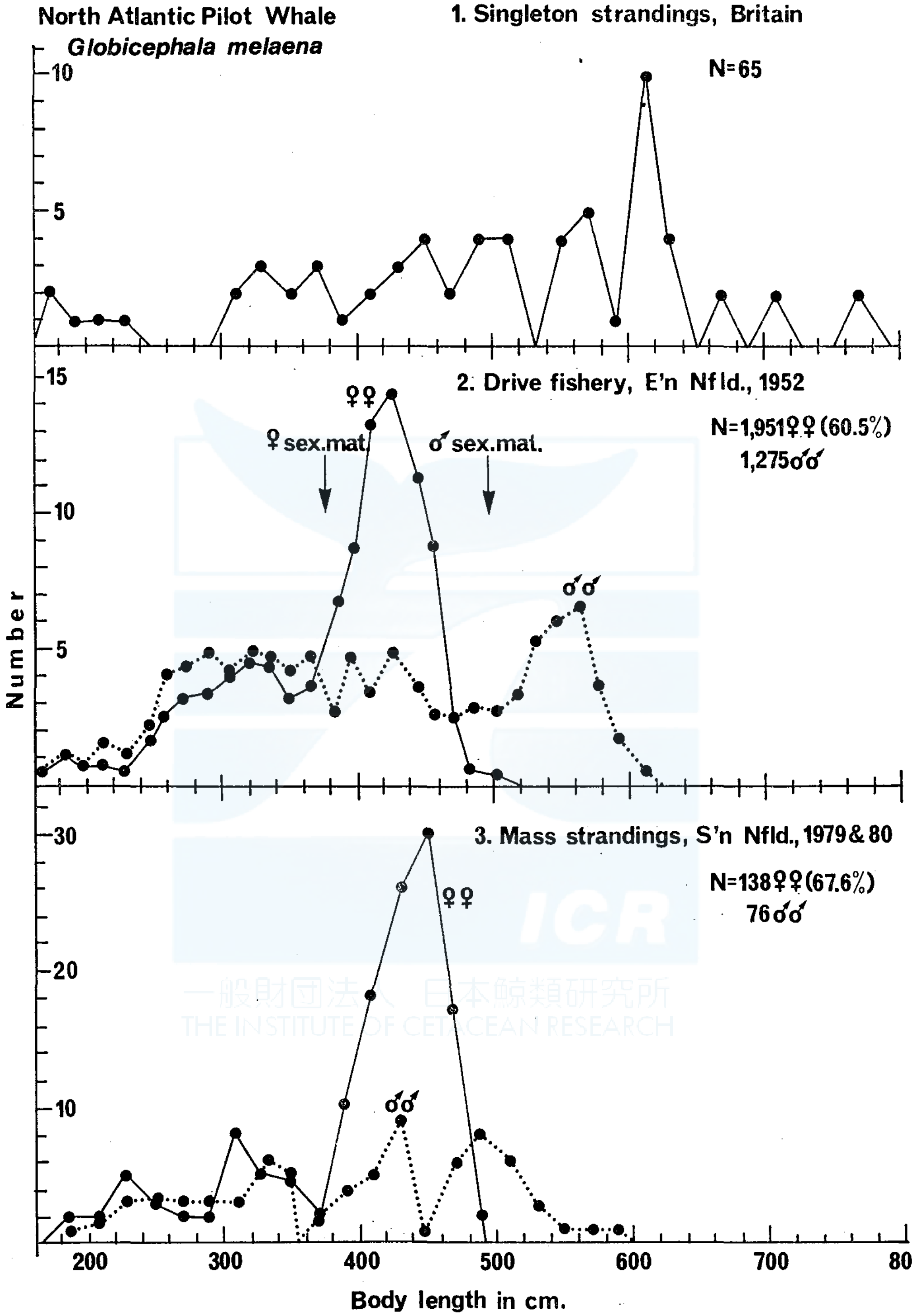

Fig. 4. Length frequencies of *G. melaena*, stranded naturally and driven shore.

c. *Sperm whale Physeter catodon at New Zealand*

At North Island, New Zealand, multiple strandings of harem herds of sperm whales have repeatedly occurred up to at least 1972 (Gaskin 1968; Robson and Van Bree 1971; Stephenson 1975). Best (1974, Figs.–1 and 11–2) shows that the surrounding area of sea has one of the highest known densities of sperm whales, and the highest known density of female sperm whales, in the southern hemisphere.

d. *Conclusions*

From the preceding review of three commonly-stranding species one may conclude that mass strandings come from a dense population and not from a reduced one. In ecological parlance, they are either density- or resource-dependent (DeMaster 1981). As to the condition of naturally-stranded *G. melaena*, I am indebted to K. A. Hay (*in litt.* 1979) and J. Lien and staff (*in litt.* 1981) for measurements and sexings of animals in three herds stranded at Newfoundland in 1979 and 1980. The distribution of lengths (Fig. 4) differs little from length frequencies which were obtained from large samples of driven animals in the 1950's (Sergeant 1962). The sex ratio is more variable, being low for males in the two 1980 samples, and high for a stranding at Sable Island in 1976 described by Geraci and St. Aubin (1977), but with little difference if the samples are summed (Table 2). The length-specific blubber thickness is comparable (Table 3). There is therefore no obvious difference between the state of animals driven ashore by man and those naturally stranded. Both sets of beachings result from the dense herds which form up in the coastal waters when the population is abundant.

TABLE 2. SEX RATIOS OF NORTHWEST ATLANTIC PILOT WHALES, DRIVEN AND STRANDED. Date from Sergeant (1962) Geraci and St. Aubin (1977), Hay (pers. comm.), and Lien (pers. comm.).

Sample	Date	Males	Females	Male ratio
Driven	1952—1957	1,825	2,778	.395
Stranded	1977—1980	141	173	.450

TABLE 3. MID-LATERAL BLUBBER THICKNESS OF FEMALE PILOT WHALES AT NEWFOUNDLAND, DRIVEN AND STRANDED
Data from Sergeant (1962, Table IV) and Hay (pers. comm.).

Sample	Date	N	Range of body lengths (cm)	Blubber thickness (cm)	
				Range	Mean
Driven	August 1952	40	185—470	2.1—3.2	2.7
Stranded	July 1979	74	206—470	2.3—4.0	3.3

DISTRIBUTION OF MASS STRANDINGS AMONG THE ODONTOCETI

a. *Definition*

I define a mass- or multiple-stranding as one consisting of two or more animals, other than the simultaneous stranding of a female and her calf.

b. *Offshore and onshore mortality*

Although I have assumed up to now that all dead cetaceans arrive on the coastline, this cannot be true. Skulls of pilot whales *G. melaena* are dredged by trawlers from Georges Bank off New England (Lord and Chandler 1969). This bank is separated by channels from the land, showing that animals which die at sea may sink there. Mass strandings, by definition, occur on the coast and it is difficult to imagine mass, almost simultaneous deaths occurring at sea among a herd of Cetacea. If they do occur, no concentrations of carcasses have been reported at sea, to my knowledge, nor of a sequence of carcasses drifting ashore. Mass strandings are of live animals, though singleton animals can arrive on the beach dead or alive. That some dead singletons do not reach the shore could bias upward the percent of animals recorded dead en masse. Other sources of bias work in the same direction.

c. *Reporting bias*

For most past reporting, it is likely that multiple strandings are over-reported as compared with single animals because they are the more conspicuous phenomenon.

It is extremely hard to quantify this statement, but it seems likely that the more intensive the stranding network, the more this bias is removed. I have identified three relatively intensive stranding networks: that of Great Britain from 1913 to 1966, of France from 1971 to the present, and of the United States from 1976 to the present. Since none of these is complete or perfect, not all bias has been removed. For France I compared reports of strandings of pilot whales in the period 1961–1960 (Duguy and Baudouin-Bodin 1965, Budker 1968 and Le Tallec 1968) to those in 1971–1980 (Duguy and Budker 1972, Duguy 1973, 1974, 1975, 1976, 1977, 1978, 1979, 1980, 1981). In the earlier decade, there were reports of 310 individual *G. melaena* of which 303 (97.7%) were mass-stranded. In the later decade there were only 5 out 80 (6.25%) *G. melaena* mass-stranded. Clearly the change cannot be due solely to a change in sighting intensity since the absolute frequency of mass strandings of pilot whales decreased. This could be due, in part, to chance: mass-strandings are rare events and more than a decade may be necessary to obtain an index of their frequency. Unfortunately, the density of the population involved may change during a decade (see section 4 d (ii), so that solution of the problem seems impossible There seems little left to do except to use the most complete data available, and to use the much more evenly distributed singleton strandings, together with the mass strandings, as an index of natural mortality rate, and therefore of abundance.

The classification of the Odontoceti as usually divided (Rice 1977, Fraser and Purves 1960) is shown in Table 4.

d. *British strandings*

Systematic observations of stranded Cetacea around the British coasts were begun in 1913 and I have drawn freely on this long-continued record (Harmer

TABLE 4. SYSTEMATIC ORDER OF ODONTOCETI ACCORDING TO RICE (1977)
Genera including species known to mass-strand shown with an asterisk.

Ziphiidae			*Tasmacetus*
		*	*Mesoplodon*
		*	*Ziphius*
		*	*Hyperoodon*
			Berardius
Physeteridae		*	*Physeter*
			Kogia
Platanistidae			
Stenidae			*Sotalia*
			Sousa
		*	*Steno*
Phocaenidae		*	*Phocoena*
			Phocaenoides
Delphinidae			
	Delphininae	*	*Delphinus*
		*	*Grampus*
		*	*Lagenorhynchus*
			Lagenodelphis
		*	*Stenella*
		*	*Tursiops*
	Cephalorhynchinae		*Cephalorhynchus*
	Lissodelphinae	*	*Lissodelphis*
	Orcininae	?	*Feresa*
		*	*Globicephala*
			Orcaella
		*	*Orcinus*
		*	*Peponocephala*
		*	*Pseudorca*

1929; Fraser 1934, 1946, 1953, 1974.) While it is impossible to define its completeness, the existence of a reporting network, together with a responsible central museum over a long period of time, makes it a good starting point.

(i) Frequency of mass strandings:

As stated at the outset, there are no mass strandings of Mysticeti. The British records give the number of individual Odontoceti in each mass stranding and also the number of singleton strandings of each species. Table 5 summarises these data. There are rare species, such as the arctic white whale *Delphinapterus leucas* and narwhal *Monodon monoceros*, and the more southerly blue-white or euphrosyne dolphin *Stenella coeruleoalba*, that give few records. The others can be divided into a group of mainly mass-stranders, comprising pilot whale *G. melaena*, false killer whale *Pseudorca crassidens* and white-sided dolphin *Lagenorhynchus acutus* and a group of species stranding mainly as individuals, comprising killer whale *Orcinus orca*, several other dolphin species (*Lagenorhynchus albirostris*, *Grampus griseus*, *Delphinus delphis*, *Tursiops truncatus*), bottlenose whale *Hyperoodon ampullatus* and common porpoise *Phocoena phocoena*. All sperm whales *Physeter catodon* stranded singly, although

TABLE 5. FREQUENCY OF MASS-STRANDED TO TOTAL STRANDED INDIVIDUAL ODONTOCETI BY SPECIES IN BRITAIN, 1913 TO 1966
Data from Harmer (1927) and Fraser (1934 to 1974).

Species	Number of animals			Percent multiple
	single	multiple	total	
Delphinapterus leucas	1	—	1	(—)
Delphinus delphis	121	14	135	10.4
Globicephala melaena	66	429	495	86.7
Grampus griseus	63	4	67	5.9
Hyperoodon ampullatus	61	11	72	15.3
Lagenorhynchus acutus	24	67	91	78.2
Lagenorhynchus albirostris	78	9	87	10.3
Monodon monoceros	2	—	2	(—)
Orcinus orca	36	6	42	14.2
Phocoena phocoena	596	35	631	5.5
Physeter catodon	13	—	13	0.0
Pseudorca crassidens	5	227	232	97.8
Stenella caeruleoalba	3	—	3	(—)
Tursiops truncatus	175	14	189	7.4

the species is known to mass-strand elsewhere and has done so in western Europe (Boschma 1938). However, mainly solitary males reach northern seas, and singleton strandings are the rule also in Norway (Haug and Gulliksen 1981) and in Newfoundland (J. Lien MSS 1980, 1981).

(ii) Consistency of mass strandings through time:

Because of the uniquely long (53 year) period of the British strandings, it is instructive to examine the consistency through time of mass-strandings of a species. In Table 6 I have done this for 6 species, retaining the unequal time periods into which Harmer and Fraser divided their reports. [To use decades, as S. G. Brown (1975) did, would not materially alter results.] The analysis shows that one species, *Pseudorca crassidens*, stranded at high frequency during its short occurrence in seas around Britain. Three species, *Grampus griseus*, *Lagenorhynchus albirostris*, and *Tursiops truncatus*, mass-stranded at low frequency throughout the 5 episodes of time. Two species remain. *Lagenorhynchus acutus* decreased markedly after 1932, whereas *Globicephala melaena* increased markedly after 1937. Not unexpectedly, both species

TABLE 6. MULTIPLE STRANDINGS PER TIME PERIOD IN BRITAIN
Number of individuals stranded in multiple strandings and in total.

Years Species	1913–1926 (14)	1927–1932 (6)	1933–1937 (5)	1938–1947 (10)	1948–1966 (19)
G. melaena	2/10	0/6	2/6	20/26	405/447
G. griseus	2/10	0/9	0/10	2/19	0/19
L. acutus	32/40	35/39	0/3	0/3	0/6
L. albirostris	2/30	0/8	2/14	0/7	5/28
P. crassidens	—	150/150	77/82	—	—
T. truncatus	4/27	2/27	4/23	2/35	2/77

TABLE 7. FREQUENCY OF SINGLE (S), MULTIPLE (M) AND TOTAL (T) STRANDED INDIVIDUAL ODONTOCETI IN NEW ZEALAND (Gaskin 1968, Fraser 1955), Tasmania (Guiler 1978) and South Australia (Aitken 1971)

Species	New Zealand				Tasmania				S. Australia				Overall			
	S	M	T	%M	S	M	T	%M	S	M	T	%M	S	M	T	%M
Berardius arnouxi	17	0	17	0.0	1	—	—	0	1	—	—	0	19	0	19	0.0
Cephalorhynchus commersoni	16	0	16	0									16	0	16	0
Delphinus delphis	15	0	15	0	6	114	120	95.0	7	—	7	0	28	114	142	80.2
Globicephala melaena	3	856	859	99.7	9	908	917	99.0	—	5	5	(high)	12	1,769	1,781	99.3
Grampus griseus	1	0	1	—									1	—	1	(0)
Hyperoodon planifrons	2	0	2	(0)					1	—	1	0	3	—	3	(0)
Kogia breviceps	21	1	22	4.5	1	—	1	0	10	—	10	0.0	32	1	33	3.0
Lagenorhynchus obscurus	17	3	20	15.0									17	3	20	15.0
Lissodelphis peroni	—	3	3	(100)									—	3	3	(100)
Mesoplodon bowdoini	6	—	6	0	1	—	1	0					7	—	7	0.0
M. densirostris	—	—	—	—	1	—	1	0					1	—	1	(0)
M. grayi	24	25	49	51.0	3	—	3	0	0	—	3	0	30	25	55	45.5
M. hectori	—		—	—	1	—	1	0					1	—	1	(0)
M. layardi	19	0	19	0	3	—	3	0					22	—	22	0.0
Orcinus orca	4	20	24	83.3	1	—	1	0	1	—	1	0	6	20	27	76.9
Physeter catodon	16	65	81	80.2	13	129	142	90.8	3	—	3	32	32	194	226	85.8
Pseudorca crassidens	4	148	152	97.4	6	243	249	97.5	(a few)	250	( )	(high)	10	391	401	97.5
Tasmacetus	6	0	6	0									6	—	6	(0)
Tursiops truncatus	8	2	10	(20.0)	6	15	21	71.4	12	—	12	0.0	26	17	43	39.5
Ziphius cavirostris	19	0	19	0.0	8	—	8	0.0	1	—	1	—	28	—	28	0.0

show high mass stranding rates with high overall stranding rates. None of these data support the idea that mass-stranding rates vary with time, in contrast to the French data discussed earlier (section 4-c). The data do, however, support the concept that populations of Odontocetes may change in abundance with time.

e. *Strandings in the southern hemisphere*

In amplification of the British stranding records, there is an excellent set of tabulated data on strandings on New Zealand coasts, chiefly due to Gaskin (1968). To these I have appended details given for Tasmania by Guiler (1978) and for south Australia by Aitken (1971), since all are cool-water coasts with much the same fauna (Table 7).

In these seas *Globicephala melaena* and *Pseudorca crassidens* retain a very high percentage of individuals mass-stranded (97.5–99.3%). Nearly as high are *Physeter catodon* with 85.8% of individuals mass-stranded, *Delphinus delphis* with 80.2% and *Orcinus orca* with 76.9%. High values are also found for *Mesoplodon grayi* (45.5%), *Tursiops truncatus* (39.5%) and *Lagenorhynchus obscurus* (15.0%). Other Ziphiidae (*Berardius arnouxi*, *Ziphius cavirostris* and other *Mesoplodon* spp.) had no multiple strandings, nor did the pigmy sperm whale *Kogia breviceps*.

f. *Strandings in Florida*

Table 8 shows strandings from a well-documented sub-tropical region, that of Florida with its extensive sandy coasts.

High multiple stranding frequencies are again shown by pilot whales, this time the tropical short-finned species *Globicephala macrorhyncha*, and by false killer whales *Pseudorca crassidens*, which are here within their normal range of distribution at sea in the sub-tropical North Atlantic (Morzer-Bruyns 1969), Gulf of Mexico (Bullis and Moore 1956; Brown, Caldwell and Caldwell 1966) and Caribbean Sea (Caldwell, Caldwell, Rathjen and Sullivan 1971). *Stenella longirostris* shows a high mass-stranding rate (92.7%) with two mass strandings, and *Steno bredanesis* with but a single one. Both *Tursiops truncatus* and *Kogia breviceps* show singleton strand-

TABLE 8. STRANDINGS IN FLORIDA

Sources: [1]Moore, 1953; [2]Layne, 1965; [3]Caldwell, Caldwell and Walker, 1970; [4]Mead, Odell, Wells and Scott, 1980; [1]Odell, Asper, Baucom and Cornell, 1980.

	Single	Multiple	Total	%M
Globicephala macrorhyncha[1]	1	323	324	99.7
Globicephala macrorhyncha[2]	6	212	218	97.2
Kogia breviceps[1,2]	12	—	12	0.0
Mesoplodon europaeus[1]	1	—	1	—
Physeter catodon[1,2]	5	—	5	0.0
Pseudorca crassidens[1,3,5]	3	241	242	99.6
Stenella longirostris[4]	5	64	69	92.7
Steno bredanensis[2]	—	16	16	(100.0)
Tursiops truncatus[1,2]	13	—	13	0.0
Ziphius cavirostris[1]	3	—	—	(0)

ings only; for other species data are scarce.

g. *United States Eastern Seaboard*

Six years' intensive observations, from 1976 to 1981, were available to me for this region from the monthly reports of strandings given in SEAN (Smithsonian Scientific Event Network).

The resulting summary of data (Table 9) refers to 32 species, such a large fauna being the result of the wide geographical extent of the coast from a cold to a warm sea. Some cold-water species, e.g. *Hyperoodon ampullatus*, were absent, others, e.g. *Orcinus orca*, were rare.

TABLE 9. UNITED STATES EASTERN SEABOARD. STRANDINGS, 1976–1981 (Source—SEAN monthly reports).

Species	1977–1981		Multiple Frequency
	Total	Multiple	
Balaenoptera acutorostrata	27	—	—
B. borealis	—	—	—
B. edeni	3	—	—
B. musculus	—	—	—
B. physalus	22	—	—
Delphinapterus leucas	1	—	—
Delphinus delphis	29	4	.138
Eubalaena glacialis	3	—	—
Feresa intermedia	4	—	—
Globicephala macrorhyncha	43	28	.651
G. melaena	42	18	.429
Grampus griseus	21	5	.238
Hyperoodon ampullatus	—	—	—
Kogia breviceps	105	—	—
K. simus	30	2	.066
Lagenorhynchus acutus	78	19	.245
L. albirostris	1	—	—
Megaptera novaeangliae	10	—	—
Mesoplodon bidens	—	—	—
M. densirostris	3	—	—
M. europaeus	14	—	—
M. mirus	3	—	—
Orcinus orca	3	—	—
Phocoena phocoena	177	(12)	(.062)
Physeter catodon	30	11	.366
Pseudorca crassidens	30	30	1.000
Stenella caeruleoalba	45	6	.133
S. longirostris	32	29	.906
S. plagiodon/attenuata	32	—	—
Steno rostratus	23	21	(.913)
Tursiops truncatus	543	(7)*	(.013)
Ziphius cavirostris	6	—	—

* Strandings of several animals close in space and time were reported but it could not be determined if these were in fact multiple strandings.

The data allowed comparison with older data (Table 8) from parts of the same seaboard. Thus, multiple strandings of *Globicephala macrorhyncha* fell from 99.7–97.2% for earlier data from Florida to 65.1% for the whole coast. At first, I thought this was the result of more thorough examination of beaches for singletons. However, examination of SEAN records by state showed a geographical trend. A high multiple stranding rate was still recorded for Florida but northward this decreased to zero. I therefore analysed data for *G. macrorhyncha* and *G. melaena* by latitude in order to quantify such geographical changes (section h).

The strandings from the east coast of the United States show a similar sequence of frequency of mass-strandings to that found in other regions. Ten species show multiple stranding frequencies exceeding 10%, in order of descending rank:

Species	Frequency	Number of	
		animals	mass events
Pseudorca crassidens	1.000	30	1
Steno rostratus	.913	23	2
Stenella longirostris	.906	32	1
Globicephala macrorhyncha	.651	43	4
G. melaena	.429	42	1
Physeter catodon	.366	30	1
Lagenorhynchus acutus	.245	78	4
Grampus griseus	.236	21	2
Delphinus delphis	.138	29	1
Stenella caeruleoalba	.133	45	2

The three commonest species to strand: *Tursiops truncatus*, *Phocoena phocoena* and *Kogia breviceps*, all showed extremely low rates of multiple strandings, as noted earlier by Mead (1979). Indeed, for *P. phocoena* and *T. truncatus*, there was doubt whether animals that stranded at the same time and place were, in fact, from the same group. These data agree with those from Britain (Table 5), although mass strandings of *Tursiops truncatus* were noted from the southern hemisphere (Table 7), where perhaps a different species or stock with different social behavior is involved.

h. *Geographical variation in mass stranding rate within a species.*

This problem is sufficiently common to require resolution. In order to study it I selected the east coast of North America where the excellent data from the U.S.A. (from SEAN and from earlier faunal studies) could be supplemented by less complete data from Canada. I selected the two pilot whale species *G. melaena* and *G. macrorhyncha* because of their high mass stranding frequency, and listed all strandings known to me by geographical position, and whether single or multiple, then analysed these by half-degrees of latitude (Table 10).

The table shows that the cold-water species *G. melaena* mass-strands mainly in the northern part of its range north of 46°N. Sable Island, located at 44°N, accounts for most mass strandings south of this latitude. There are in modern times few mass strandings at Cape Cod, at ca 41°30′N Lat., although the species was

TABLE 10. STRANDINGS OF THE PILOT WHALES *GLOBICEPHALA MELAENA* AND *G. MACRORHYNCHA* ALONG THE EASTERN SEABOARD OF CANADA AND THE UNITED STATES

The records are summed by half degrees of latitude, and separated into single and multiple strandings. Sources: Various, from varied starting dates up to end 1981 in SEAN.

G. melaena			*G. macrorhyncha*		
Latitude Zone	(1)	(2)	Latitude Zone	(1)	(2)
51°31′—52°	1		39°00′—39½°	3	
—51½°					
—51°			35°31′—36°	4	
—50½°			—35½°	3	
—50°		12	—35°	1	
—49½°	1	129	—34½°	1	5
—49°		125	—34°	1	19
—48½°			—33½°		
—48°	3		—33°		13+
—47½°	4	18	—32½°		26
—47°	3	291	—32°		3
—46½°		15	—31½°	1	30
—46°			—31°		
—45½°	1		—30½°		150
—45°	1		—30°		72
—44½°	3		—29½°	2	57+
—44°	2	203	—29°		63
—43½	1		—28½°		
—43°	1		—28°	1	64
—42½°			—27½°	1	
—42°	5		—27°	2	51
—41½°	4	18	—26½°		
—41°	3		—26°		
—40½°	1		—25½°		70+
—40°	1		—25°	2	12
—39½°	3		24°00′—24½°	1	50
—39°	(1)*				
—38½°	1				
—38°					
—37½°					
—37°					
—36½°					
35°31′—36°	1				

(1) Number of animals stranded singly.
(2) Number of animals in multiple strandings.
* Species uncertain.

driven here in the past and herds are sometimes seen (*e.g.* by Starrett and Starrett 1955). Singleton strandings occur further south as far as about 36°N.

The warm-water *G. macrorhyncha* has its highest frequency of mass-strandings in the southern part of its range. Mass strandings occur along the U.S. east coast from the Florida Keys at 24°30′N to about 34°30′N. Northward only singleton strandings occur, as far as 39°N. Thus, both species show a " core " area where mass-strandings occur, and a peripheral area where they do not. I would deduce from this that mass-strandings occur where the population of the species is high. Mass strandings of *G. macrorhyncha* continue through the West Indies southward to at least Isla Margarita, Venezuela, at 12°N Lat. (Casinos and Bou, 1980). Thus in *G. melaena* there seems to be no northern limit to the mass strandings (in relation to the population as a whole), in *G. macrorhyncha* no southern limit, suggesting that it is inter-specific competition between the species that determines density of both.

I know no other pair of contiguous species where such an analysis is possible, but note other cold-water species that show mass strandings towards the north of their range, *e.g. Orcinus orca* in Norway but not in Britain, see footnote this p.; other warm-water species that show mass strandings mainly in the south of their range, *e.g. Delphinus delphis* in west Africa but not in Europe, see pp. 37 and 11 respectively.

i. *Individual species considered.*

The false killer whale *Pseudorca crassidens* is unusual in that virtually all of its mortality on the coasts of Britain, New Zealand, Tasmania, South Australia, South Africa (Smithers 1938) and Florida, occurs as mass strandings. It is a warm-water species (Bullis and Moore 1956, Morzer-Bruyns 1969), that does not normally occur round the British coasts; thus the mass strandings that occurred there in 1927, 1935 and 1936 were in the nature of immigrations followed by mass mortality. However, its mass strandings in Florida occur within the species' normal range. As its diet consists of large fish and squids, including tuna which it frequently takes off long-line hooks (Moore 1953, Brown, Caldwell and Caldwell 1966, Mitchell 1975), we have the impression of a top carnivore exerting pressure on its food supply.

In tropical seas, the short-headed electra dolphin *Peponocephala electra* has mass-stranded in eastern Australia (Dawbin, Noble and Fraser 1970), the New Hebrides (Rancurel 1974) and Japan (T. Kasuya, pers. comm.). Analysis of some of these records by Perrin (1975) gives a very high frequency (about 95%) of individuals mass-stranded. The genus is placed within the Orcininae as is another tropical genus *Feresa*, of which we know little. We now have three genera from among this subfamily: *Globicephala*, *Pseudorca* and *Peponocephala*, which show high frequencies of multiple strandings. The killer whale *Orcinus orca* has shown a low incidence of mass strandings in Britain[1], but a high incidence in New Zealand. Killer whales mass-stranded in British Columbia before live captures for aquaria started in 1964 (Ford and Ford 1981). Carl (1946) and Pike and MacAskie (1969) together record 39 animals stranded in the period 1941–1967, of which 36 or 92.3% represented multiple strandings.

Among the typical dolphins (Delphininae) many species have been recorded

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[1] None were recorded by Harmer or by Fraser from 1913 to 1966, but Turner (1871) described a drive-hunt of 18 *Orcinus orca* at Bressay Sound, Shetland in February 1871, which makes it seem likely that mass strandings might occur to the north of Britain. A pod of 14 animals indeed stranded at Lofoten, Norway in June 1981 (Haug and Sandnes, 1982).

with a high frequency of strandings, yet there is considerable variability in this feature; *e.g. Delphinus delphis* and *Tursiops truncatus* may show a low incidence in one region and a high incidence in another. There is also a high incidence of strandings in the pelagic long-snouted dolphin *Stenella longirostris* in Florida. The species *Stenella coeruleoalba* and *S. attenuata* are driven ashore in large groups by fishermen in Japan, which makes one believe that they would mass-strand there naturally, if not being hunted.

Among the porpoises Phocoenidae, the harbour porpoise *Phocoena phocoena* normally strands singly or in groups of 2–4 animals. It is known to be weakly gregarious, with schools of 9 animals or less observed by Gaskin, Arnold and Blair (1974).

There are about 20 known mass strandings of *Physeter catodon* in the world in the last 300 years and more than half of these have come from New Zealand (Anon 1979). I have also heard of two unpublished mass strandings (in the Seychelles and Falkland Is.) since beginning this study. Most mass strandings are of harem herds (Robson and van Bree 1971, Stephenson 1975). Considering that the main mass of harem herds of sperm whales live in the tropical oceans, which are grossly under-reported for Cetacea (consider the late discovery of tropical genera such as *Feresa, Peponocephala* and *Lagenodelphis*), the scarcity of reported mass strandings of *Physeter* is not surprising. At high latitudes most strandings of sperm whales are of single adult or subadult males. The pigmy sperm whale *Kogia breviceps* seems always to strand singly or in numbers not exceeding three, suggesting a group size no larger than a family.

Mass strandings are also known among several genera of the Ziphiidae: *e.g.* a herd of 25 *Mesoplodon grayi* at the Chatham Is., New Zealand (Gaskin 1968); a herd of 4 *Ziphius cavirostris* at the Netherlands Antilles; and records of *Hyperoodon ampullatus* in Britain (van Bree and Kristensen, 1974). There are no known mass strandings from among the freshwater Platanistidae, nor from among the small group Cephalorhynchinae, but we have noted one of three animals from among the Lissodelphinae (*Lissodelphis peroni* at New Zealand, Fraser 1955).

Considering the high incidence of mass strandings among members of the Orcininae it is worth looking at the biological characteristics of the subfamily, as compared with those of members of the typical dolphin subfamily Delphininae. There are now sufficient studies of life histories of a number of genera to make such a comparison possible. The social structure of the sperm whale *Physeter* is also well known.

SOCIAL STRUCTURES COMPARED

a. *Orcininae*

As Norris and Dohl (1980) have previously observed, mass strandings occur especially in the group Orcininae of the Delphinidae, which contains the genera *Pseudorca, Orcinus, Orcaella, Globicephala, Feresa,* and *Peponocephala.* Of these only *Globicephala* is well known bionomically, *Orcinus* is beginning to be so (Bigg 1981), and knowledge on *Pseudorca* must be assembled from the few data of various authors.

I studied the social structure of *G. melaena* from a drive fishery in Newfoundland in the 1950's (Sergeant 1962), having a large number of animals available to examine. Main features relevant were: (1) a marked sexual dimorphism, males reaching 20 ft (6 m) in length compared with 16 ft (5 m) for females; (2) an extremely delayed sexual maturity for males—16 ft (5 m) length and 12 years of age compared with 12 ft (4 m) and 6 years of age for females; (3) a higher male mortality rate throughout life. The last two features resulted in a low ratio of adult males to adult females. Most importantly (4), the composition of 91/92 schools was homogeneous, consisting of all sizes of both sexes of animals. The only atypical herd was a group of adult males with a few very large females. I deduced that the species was exceptionally social, with no signs of aggressiveness, there being no segregation of size groups associated with aggression.

McCann (1974) found tooth scars or scratches on the body of almost all Odontocete genera studied which he attributed to various behaviour patterns, including play between younger animals and aggression by adult males. In driven *G. melaena* I found fresh scratches on all animals, which I attributed to the panic of the drive, since I could find no old scars. Norris and Prescott (1961) found tooth scratches on young male *G. scammoni* and not on adult males, leading Norris

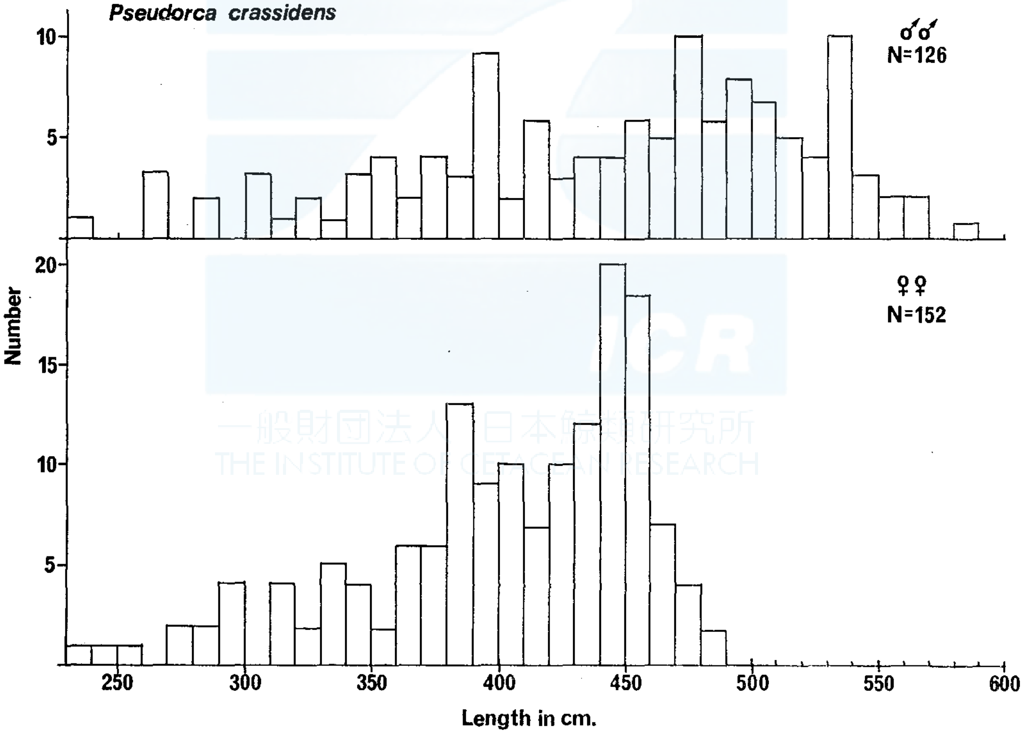

Fig. 5. Length frequencies of naturally stranded male and female *Pseudorca crassidens*.

(1967) to deduce that these were produced by schoolmates in play. Thus I suppose that tooth scratches are not necessarily an index of aggression. McCann noted that Ziphiids have deeper scars than most Delphinidae and he believed that such less social species show more aggression.

Information on *Pseudorca crassidens* comes from samples examined by Hinton (1928), Fraser (1936), Peacock, Comrie and Greenshields (1936), and Yamada (1956) from animals stranded in Britain; by Smithers (1938) from strandings in South Africa; by Scott and Green (1975) from strandings in Tasmania; and by Odell, Asper, Baucom and Cornell (1980) from strandings in Florida. Comrie and Adam (1938) examined reproductive tracts collected by Peacock *et al.* (1936). Figure 5 shows length frequencies which indicate clearly that the species is sexually dimorphic. Extreme recorded lengths in all these strandings are males 589 cm and females 489 cm, or a ratio of about 1.2: 1, which compares with 1.3: 1 in extreme and peak lengths for large samples of *G. melaena* (Sergeant 1962). If one omits the length frequencies of Scott and Green (1975), who examined part of the same set of females twice, the sex ratio is about 53.5% females for a sample size of 198. Lengths at first maturity of female *Pseudorca* were well-studied by several authors, as follows:

	Body length (cm)	
	largest immature	smallest mature
Hinton 1928	—	427 (pregnant)
Fraser 1936	418	429 (several corpora albicantia)
Comrie and Adam 1938	284	425 (9 corpora albicantia)
Harrison, Brownell and Boice 1972	293	414 (large corpus luteum plus corpora albicantia)
Scott and Green 1975	337	360 (pregnant)
Odell *et al.* 1980	358	440 (8 corpora albicantia)
Highest/lowest	418	360

This analysis gives a range of 360 to 420 cm for length at first pregnancy, a wide spread. One wonders if all workers measured length in the same way, or whether the populations differed in size. For males, we know only that a large male 520 cm in length was mature, with testis in active spermatogenesis weighing 8.2 kg (Odell et al. 1980), and that a male 366 cm was immature, while males 511, 530 and 534 cm in length were mature with testis volumes 50×16×8 cm or larger (Fraser 1936). Thus, we can only say that male *Pseudorca crassidens* mature at body lengths of 511 cm or less. Since the animal measured by Fraser as 511 cm in length had a testis significantly smaller in volume (50×16×8 cm) than those of 530 and 544 cm in length (60×20×16 cm and 62×22×11 cm) it is possible that it was just mature; this compares with a 520 cm male *P. crassidens* measured by Odell *et al.* (1980), the testis of which weighed 8.2 kg (see also Sergeant 1962, Fig. 19 for a curve relating testis length to body weight in *G. melaena*). If *P. crassidens* males mature at about 500 cm body length, as compared with about 400 cm for females, then the ratio of numbers of mature females to mature males from the data of Fig. 5 is about 90/34 or 2.65: 1, a ratio comparable with that

TABLE 11. RATIO OF ADULT LENGTHS OF ODONTOCETES (cm)

Species	Region of Study	Sample size	Peak M	Peak F	Extreme M	Extreme F	Ratio M/F	Authors
Delphininae								
Delphinus delphis	Black Sea	4,217	170	170	205	200	1.02	Sleptsov 1941
Stenella attenuata	E. Tropical Pacific	3,504	—	—	200	190	1.05	Perrin, Coe & Zweifel 1976
Tursiops truncatus	Florida	46			270	250	1.08	Sergeant, Caldwell & Caldwell 1973
Tursiops truncatus	N. W. Atlantic	120			250	250	1.00	Hohn 1980
Tursiops aduncus	S. Africa	16			254	252	1.01	Ross 1977
Lagenorhynchus acutus	N. W. Atlantic				260	245	1.06	Sergeant, St. Aubin & Geraci 1920
Orcininae								
Orcinus orca		567	655	609	944	822	1.15	Nishiwaki & Handa 1950
			890	780	—	—	1.15	Bigg 1981
Globicephala melaena					610	503	1.21	Sergeant 1962
Pseudorca crassidens					590	490	1.20	(see p. 21)
Physeter catodon			15.8				1.44	Lockyer 1976

TABLE 12. ATTAINMENT OF SEXUAL MATURITY OF ODONTOCETES

Species	Length (cm) M	Length (cm) F	Age (yr) M	Age (yr) F	Ratio lengths	Authors
Delphininae						
Delphinus delphis	170	158			1.08	Sleptsov 1941
Stenella attenuata	195	181	12	9	1.08	Perrin, Coe & Zweifel 1976
Tursiops truncatus	245	235	13	12	1.05	Sergeant, Caldwell & Caldwell 1973
Lagenorhynchus acutus	230	210	(10)	(9)	(1.11)	Sergeant, St. Aubin & Geraci 1980
Orcininae						
Orcinus orca	579	488	12	8	1.18	Bigg 1981 and in litt.
Globicephala melaena	487	366	12	6–8	1.33	Sergeant 1962
Physeter catodon	12 m	8.5 m	19	9	2.1	Best 1974

TABLE 13. SEX RATIO OF ODONTOCETES

Species	Overall No. of males	Overall No. of females	Overall Male ratio	Mature No. of males	Mature No. of females	Mature Male ratio	Authors
Delphininae							
Delphinus delphis	2,079	2,138	0.493	890	1,179	0.435	Sleptsov 1941
Stenella attenuata			0.449			0.43	Perrin, Coe & Zweifel 1976
Orcininae							
Orcinus orca	247	320	0.436	60*	72*	0.455	Nishiwaki & Handa 1958; Bigg 1981
Globicephala melaena			0.396	418	1,364	0.234	Sergeant 1962
Pseudorca crassidens	92	106	0.465	90	34	0.265	(See discussion)

* excluding juveniles and calves.

found in *G. melaena.* Unfortunately the variance of estimate of this ratio is high as between samples: using Scott and Green's (1965) mean female maturity length of 348 cm it would be 128/34 or 3.8: 1, using Fraser's (1936) value of 423 cm it would be 68/34 or 2: 1 (Fig. 5).

For *Orcinus orca*, Nishiwaki and Handa (1958) and Bigg (1981 and *in litt.*) provide good data on body lengths of adult males and females, allowing calculation

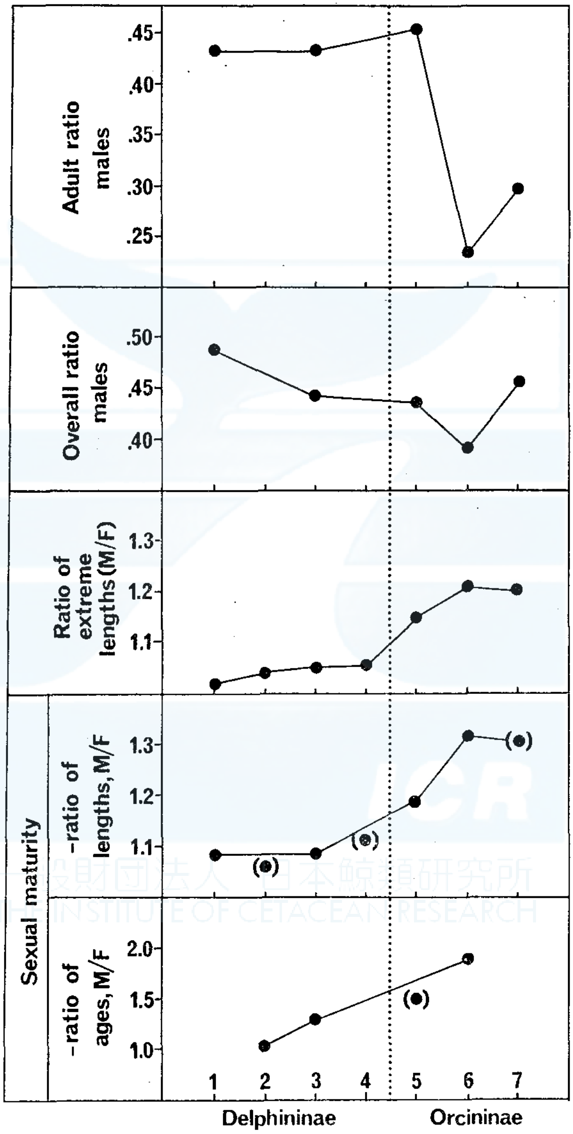

Fig. 6. Summary of information on sexual dimorphism within the Delphinidae. 1. *Delphinus delphis*, 2. *Tursiops truncatus*, 3. *Stenella attenuata*, 4. *Lagenorhynchus acutus*, 5. *Orcinus orca*, 6. *Globicephala melaena*, 7. *Pseudorca crassidens*. (The ordering of species within each subfamily was random.)

of the degree of sexual dimorphism, which seems to be somewhat less than in *Globicephala* and *Pseudorca*. There is less good information on lengths and ages at sexual maturity. Data are summarised in Tables 11 to 13 and Figure 6. One gains the impression that *Orcinus* in some ways is an intermediate between the strongly sexually dimorphic Orcininae and the weakly dimorphic Delphininae (see below).

For *Peponocephala electra*, data are as yet too few to assess the degree of sexual dimorphism in length and at sexual maturity with any accuracy (see Bryden, Harrison and Lear 1977).

b. *Delphininae*

Good information on the bionomics exists for several genera. Sleptsov (1941) studied large numbers of *Delphinus delphis* in the Black Sea, this species proving to show very little sexual dimorphism in either body size or length at sexual maturity. Perrin, Coe and Zweifel (1976) studied equally large numbers of *Stenella attenuata* in the eastern tropical Pacific with rather similar results. There is some information for the species *Tursiops truncatus* (Sergeant, Caldwell and Caldwell 1973, Hohn (1980); and *T. aduncus* (Ross, 1977), summarised in Tables 11 and 12.

In *Lagenorhynchus acutus* (Sergeant, St. Aubin and Geraci, 1980) mass stranded herds were found to be composed of adults, mostly females, together with young calves. Singly-stranded animals by contrast were found to be made up chiefly of adolescents. This kind of heterogeneity could account for much of the variability which we have found in the frequency of mass strandings in various members of the Delphininae, as discussed in section 4 above.

In both *Stenella attenuata* and *S. coeruleoalba* driven ashore in Japan, abundant data show the existence of juvenile schools and adult schools, with the juveniles rejoining the adult, mating schools at puberty (Kasuya, Miyazaki and Dawbin 1974; Miyazaki and Nishiwaki 1978).

A valuable study on living animals, which indicates the behaviour that may be involved in such segregation, comes from the work of Tavolga and Essapian (1957) and Tavolga (1966) on the former captive colony of *Tursiops truncatus* at Marineland, St. Augustine, Florida. This colony in the 1950's was not subjected to heavy pressure to perform in public; it was large (13 animals) and composed of variably sized animals. Its behaviour was thus probably close to that of a wild herd. In this colony a dominant male drove off three immature males and maintained a harem structure of females and calves. There was also a dominance hierarchy of adult females, although other pubertal and older females took much care of the calves. Another study, from the USSR, gave similar findings. Shurepova (1973) states that a large male in a group of 11 captive animals "had the dominating position in the school: it grabbed fish from the others during feeding, chased young females which shied away from its mating advances, chased young males, bit them, beat them vigorously with its tail and snout and so on."

Aggressiveness and dominance hierarchies could give rise to the segregation of immature animals seen among the Delphininae, and we have seen, at least in

Lagenorhynchus acutus, that it is often these immature animals which strand singly. Indeed such animals may attach themselves to a group of one of the social species, such as *Globicephala melaena* (Sergeant and Fisher 1957) or *Orcinus orca* (Sergeant, St. Aubin and Geraci 1980 *fide* R. D. Elliot). Hence, probably, arises the lower frequency of mass strandings among the Delphininae. But of course in all species sick and injured animals can strand singly.

In summary the Orcininae are more sexually dimorphic than the Delphininae, males having a greater excess of asymptotic body length over females. There is also a greater delay in attainment of male sexual maturity, and with this delay comes a greater male mortality, resulting in a lower overall male sex ratio than in the Delphininae.

All these features are usually associated with polygyny and male aggression in sea mammals (*e.g.* in elephant seals, fur seals and the sperm whale). Yet, paradoxically, the polygynous Orcininae are the more highly social of the Delphinidae, with a more homogeneous herd composition and with a higher mass stranding rate. Thus polygyny is not necessarily associated with male aggression.

c. *Phocaenidae*:

Phocoena phocoena shows a larger size of females than males (Mohl-Hansen 1954). It seems likely that this is due to the need to produce a neonate which is large enough to be viable in cold water (Kanwisher and Sundnes 1965). In support of this, a larger member of the family Phocoenidae, *Phocoenoides dalli*, has a male asymptotic length about 1.05 times that of the female (207 and 198 cm, Kasuya 1978), as typical for Delphininae. I have noted previously (Sergeant 1969) that *Phocoena phocoena* has a high metabolic rate throughout life, as determined from its food consumption and heart weight/body weight ratio, and that the same is true for *Phocoenoides dalli*. The high activity appears to be an adaptation to life in cold water with a thin blubber layer.

d. *Sperm whale*

The sperm whale *Physeter catodon* is a well-researched species because of its commercial importance. Because of the migrations of males to high latitudes we already know that its sociality is not total. A number of mass-strandings have been well-documented (*e.g.* by Robson and van Bree (1971) and by Stephenson (1975) in New Zealand), and these are usually harem herds. It seems likely from the records of Gilmore (1957, 1959) and Bryant (1979) in the Gulf of California that herds of adolescent males may also strand. This distribution of strandings would accord with the types of sperm whale schools classified by Gaskin (1970) and Best (1979), which include bachelor schools of young males. As the males mature, they become less and less social and some become the harem bulls, loosely attached to the schools of females and calves, others the northern wanderers. Sexual maturity in male *Physeter* is much delayed as compared with the female (Best 1969, 1974), sexual dimorphism is marked and harem-masters are intolerant of other adult males. The social structure of the sperm whale therefore comes closer to that of the Delphininae than of the highly social Orcininae, which fits the sperm whale's lower frequency of mass-strandings to total strandings.

HERD SIZE

Herd size is extremely difficult to define. As Norris and Dohl (1979) and others have shown, there is a whole range of groupings within a species (pod, herd, school) from the family up to large schools with varying cohesion and varying stability. The basic subgroup does not vary very much and is thus not a useful measure of sociality. Thus for *Pseudorca crassidens*, which we would judge from its stranding behaviour to be a species travelling in large aggregations, Morzer-Bruyns (1969) has this to say from observations of animals feeding at sea:

" The normal school of *Pseudorca crassidens* contains 20 to 30 animals divided into " family " groups of four to six animals, covering an area of about 0.5 mile in diameter."

About the only generalisation possible is that inshore species *e.g. Sousa plumbea* have only small school sizes, while in offshore species, *e.g. Delphinus delphis*, *Stenella coeruleoalba*, large aggregations can occur (Saayman, Bower and Tayler 1972, Saayman and Tayler, 1979); but the basic unit remains small, a family of females and calves with loosely attached males of all ages older than calves in *Stenella longirostris* (Pryor and Kang 1980), much as in *Tursiops truncatus* (Tavolga 1966). In both these species in the wild groupings may have a very temporary, changing existence (Norris and Dohl 1979, Wursig and Wursig 1979).

There seem to be two features which must be separated in considering the relation of mass strandings to school size: 1. Species such as *Phocoena phocoena*, *Kogia breviceps* and perhaps also some of the Ziphiidae (Morzer-Bruyns 1968) have small herd size; that is, one scarcely or never finds large aggregations. These show mass strandings rarely because they are rarely in groups; 2. Social species may have aggressive adult males, which split the herd into harem (or reproducing) herds and the rest, chiefly immature (occasionally adult) males, and immature females. Harem herds tend to mass-strand, presumably because females and calves are closely associated and females are rarely aggressive (Tavolga 1966 for *Tursipos truncatus*). The rest tend to strand singly because they are weakly associated, so mass stranding frequency is reduced.

For *Globicephala melaena* I noted (Sergeant 1962) that the mean number of animals in groups driven ashore was about 85, the same as in natural mass-strandings reported around the world; however the mean number for animals observed far to sea was about 20. This could be due to aggregation of herds as they increase in density in inshore waters. For *Orcinus orca* stranded herd sizes recorded are: in British Columbia 20, 11 and 5 (Carl 1946); 10 for an ice-stranded herd in Newfoundland (Dearden 1958); 19 for a herd stranded in Norway (Haug and Sandnes 1982), for an overall mean of 14. This compares with means of 10.5 and 11.4 for observed pod sizes in the southern and northern components of the killer whale population observed in the sounds of British Columbia and

Washington by Bigg, MacAskie and Ellis (MS, 1976).

AGE-SPECIFIC MORTALITY IN CETACEA

a. *General*

It is rather generally assumed that age-specific patterns of mortality in Cetacea are similar; that Odontocetes can be lumped together with Mysticetes, in spite of their very different social structure. I shall here show that this is not the case, and the evidence I shall use is again from strandings.

b. *Mysticetes*

British strandings again prove useful and the source is a compilation by Fraser (1953) of strandings of the minke whale *Balaenoptera acutorostrata* on British coasts, reproduced here as Figure 7. Fraser showed a peak stranding length of 16 ft (5 m) and one again at the greatest lengths attained. The latter peak, one must assume, contains a good many estimated lengths. However the peak at 16 ft must be measured or estimated accurately and I believe it is significant that this is the length at which weaning occurs (Jonsgaard 1951). In other words, minke whales strand (die) especially at the length of first independence, and again in old age.

These peaks do not represent the normal occurrence of these length-classes in the North Sea, as can be seen from data (1951) on length-frequencies of catches from different areas around Norway given by Jonsgaard (1951). For areas such as Lofoten, immature whales were commonly hunted, but in Jonsgaard's area 1 (Skagerrak and the eastern North Sea), catches consisted mainly of adults (Fig. 7). Thus the evidence suggests that newly weaned animals strand selectively.

For a long time I was unable to obtain information on mortality patterns of other Mysticetes owing to the paucity of stranding information. However, recently there became available information on the length frequency of humpback whales *Megaptera novaeangliae* caught in nets at Newfoundland (Perkins and Beamish 1979, Lien MS 1981), and further information on some natural deaths and several accidental deaths from gill-netting and a ship collision on the U.S. east coast (Mead

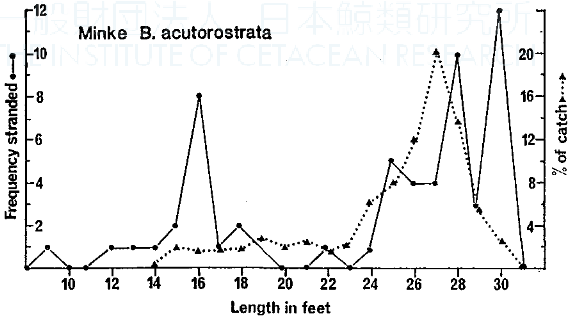

Fig. 7. Solid line: mortality by length for minke whales *B. acutorostrata* stranded on British coasts. Dotted line: catches by length in the North Sea.

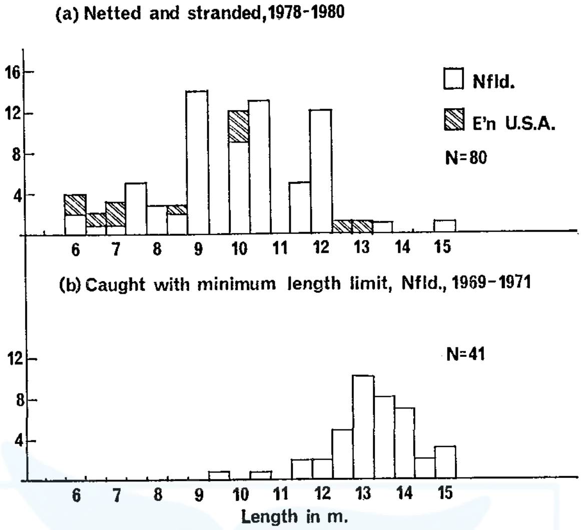

Fig. 8. Lengths of humpback whales *M. novaeangliae* caught in nets (a) and harpooned at sea with a lower length limit (b).

1980). Both sets of data come from the same population, which migrates between the Caribbean in winter and the Gulf of Maine and eastern Newfoundland in summer (Kellogg 1929).

Analysis of these data (Fig. 8) shows that the dead humpbacks, many of which were imperfectly measured because of their entrapment in floating nets, were largely immature animals, 6 to 12 m in length. Weaned immatures, about 9–10 m in length, greatly exceeded younger calves and older animals, though sometimes an adult female entrapped itself with its calf. The lower frequency distribution in the Figure essentially shows the length of adults, upwards of 12 m, from this population; it is derived from a selective and specially licensed catch taken in 1969–1971 off eastern Newfoundland (Mitchell 1973). Thus, mainly immature humpbacks die in nets, owing to their inexperience. I infer that immature humpbacks probably have a higher death rate than adults to other forms of hazard which might be considered more " natural " than nets. Putting minke whales and humpbacks together, I would expect that Mysticetes as a whole show similar patterns of mortality. Allen (1980) can throw little light on the subject, doubtless because of the imposition of a lower size limit on whaling for all species except the minke whale.

c. *Odontocetes*

Natural mortality rates of Odontocetes are profitably examined from strandings, owing to the large numbers of animals involved and to some precision of size estimation. For several genera (*Phcooena*, *Delphinus*, *Tursiops*, *Globicephala*) some comparison is possible between length frequencies of stranded animals and non-selective length-frequencies coming from fisheries made by mass-netting or driving.

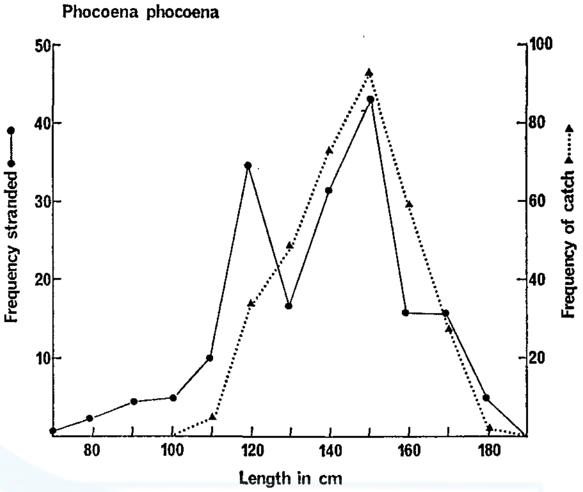

Fig. 9. Common porpoise *P. phocoena*. Length frequencies of animals stranded in Britain (solid line) and taken by driving in Denmark (dotted line).

Phocoena phocoena (Fig. 9). Size frequency of strandings in the U.K. (from Fraser 1934 to 1974) is compared with a revived drive-fishery in Denmark during the second world war (from Mohl-Hansen 1954). The size range of the animals is the same, as might be expected from the nearness of the two samples. The main difference is a peak of stranded animals at 4 ft (120 cm) which seems to be real, in spite of rounding of estimates of size in strandings. This size corresponds to animals aged about 1 year, which is also the age at weaning (Fisher and Harrison 1970). Thus it is possible that *Phocoena phocoena* endures a somewhat higher mortality rate at weaning than at younger or older ages, just as do minke whales. The distribution of older deaths seems to be proportional to the abundance of animals.

Delphinus delphis (Fig. 10). The distribution of stranded animals comes from British strandings (Fraser, *op. cit.*); that of unselected hunted animals from Soviet fihseries in the Black Sea (Sleptsov 1941). Black Sea *D. delphis* constitute a dwarf race (Kleinenberg 1956), although exceedingly abundant. Thus, the peak of adult lengths is very different. However there is no sign of a peak of juvenile deaths in either graph.

Tursiops truncatus (Fig. 11). The sample of stranded animals again comes from Britain. The very small sample of driven animals comes from Cape Hatteras, North Carolina, as described by True (1890). From what is known about relative sizes of *T. truncatus* from Europe and North America (Hohn 1980), adults from the second area should be considerably smaller. There seems to be no difference in the distribution of deaths.

Globicephala melaena. If one compares driven and naturally-stranded animals from Newfoundland, there are no differences in the size frequencies (Fig. 4). Owing to the high percentage of multiple strandings there are only small numbers

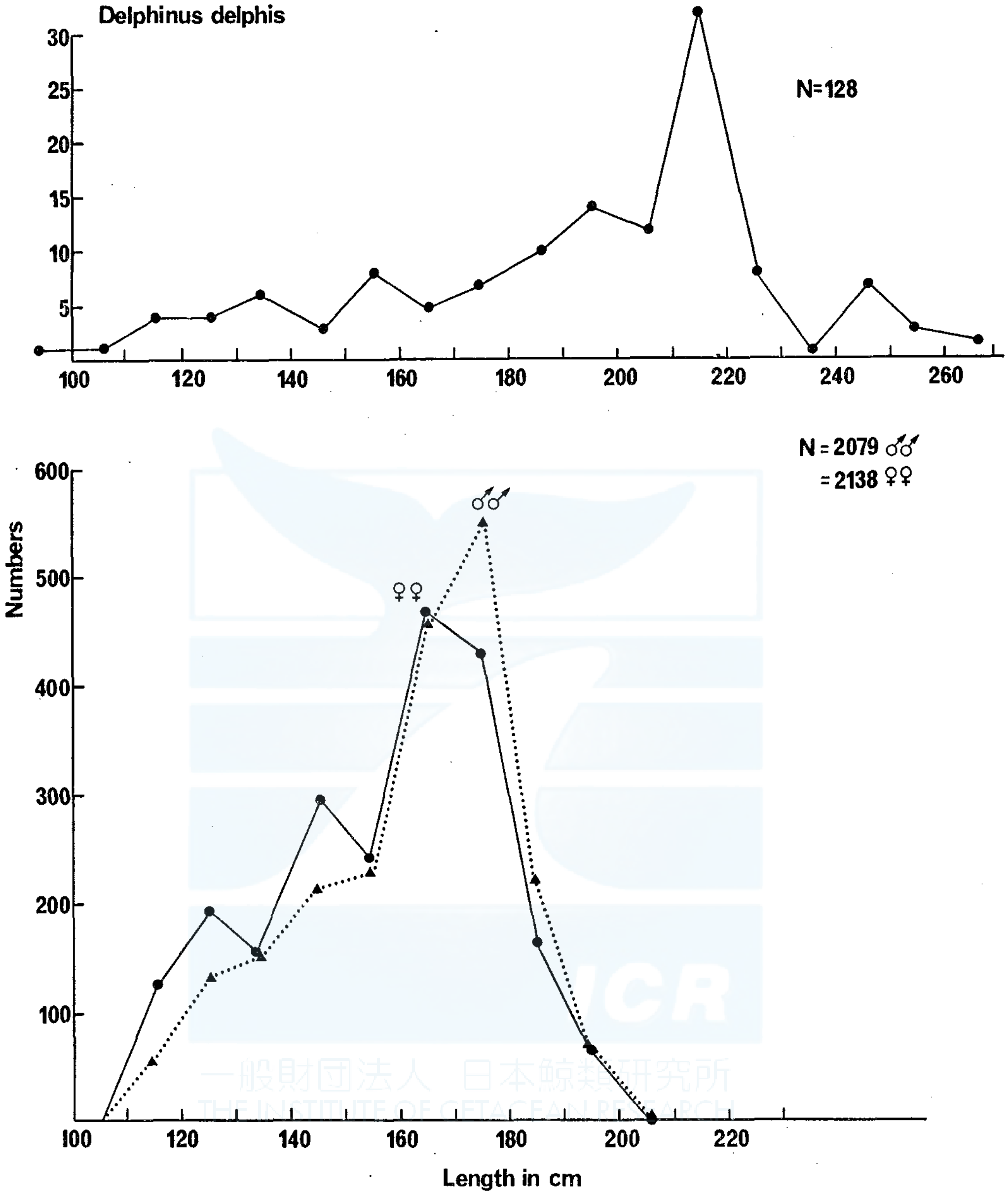

Fig. 10. Length frequencies of saddleback dolphin *D. delphis* stranded in Britain (above) and taken in net fisheries in the Black Sea (below).

of measured, singly-stranded animals from Britain. Thus, although there may be a tendency for neonates and old animals to die selectively in these strandings, the number of animals involved must be small.

In summary, the porpoise *Phocoena phocoena* may show raised juvenile mortality,

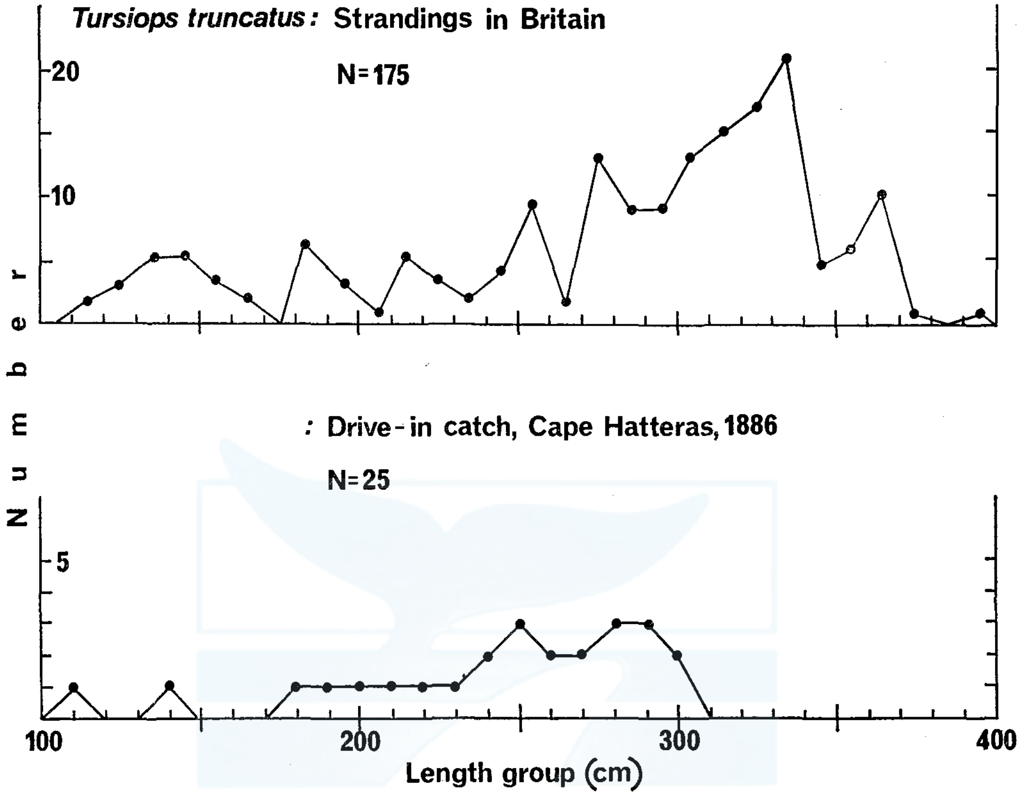

Fig. 11. Length frequencies of bottlenosed dolphin *T. truncatus* stranded in Britain (above) and taken in a drive fishery at Cape Hatteras (below).

but the three Delphinid genera examined show no sign of this phenomenon. Their natural mortality, as measured by their strandings, appears to occur in proportion to the abundance of animals of different sizes in the population. If this is so, then the Delphinidae (at least) must have evolved adaptations to reduce juvenile mortality. What these adaptations might be involve a comparison of Mysticete and Odontocete reproductive cycles (see next section).

However, many weaned, immature dolphins remain independent of the reproductive herds: in *Lagenorhynchus acutus* they may travel as singletons or in loose immature herds (Sergeant, St. Aubin and Geraci 1980); in *S. coeruleoalba* they may keep together in semi-permanent herds (Miyazaki and Nishiwaki 1978), and perhaps in *Stenella attenuata* also when not aggregated by purse-seining (Pryor and Kang 1980). Perrin and Powers (1980) found a higher incidence of skull lesions caused by the nematode *Crassicauda* sp. in juvenile than in older *Stenella attenuata*; highest rates were at 2–8 years, which are just those animals expected to be in separate schools. A higher mortality is implied because of the permanent scars left by the parasite on the skulls. Therefore in this species, there is evidence from a unique source for higher immature than adult mortality; there are not sufficient strandings of the same species to make a comparison by the method we have used for the more inshore species.

REPRODUCTIVE CYCLES IN MYSTICETES AND ODONTOCETES

As Laws (1959) made clear, the length of gestation in most Balaenopterid whales is one year. This feature involves an accelerated foetal growth rate in late pregnancy. Coupled with it is a short lactation period of 6–11 months (Gambell 1973). Since pairing occurs in winter, and a migration to high latitudes in summer, the two features appear to ensure that birth will occur in the winter, and independence in the following summer, so that the lactating female and young animal are loosed upon a rich food supply. The whole process of gestation and lactation is extremely rapid for such large animals.

The Odontocetes by contrast have gestation lengths which increase with the size of the animals, from 10–11 months in *Phocoena phocoena* (Fisher and Harrison 1970), 11–12 months in genera such as *Stenella* (Perrin, Coe and Zweifel 1976; Kasuya 1976) and *Delphinus* (Sleptsov 1941), to 16 months in large Delphinidae such as *Globicephala* (Sergeant 1962) and 14–15 months in the Monodontid genus *Delphinapterus* (Sergeant 1973). The sperm whale *Physeter catodon* also has a gestation of 16 months (Best 1968).

The lactation period also increases with body size, being 8 months (as short as in a Mysticete) in *Phocoena phocoena* (Fisher and Harrison 1970), ranging up to two years in *Tursiops*, *Globicephala*, *etc.* From *Tursiops truncatus* in captivity it is known that, though solid food may be taken at 6 months, lactation may continue intermittently to 2 years (Tavolga and Essapian 1957).

Care of juveniles continues during this period or beyond (Tavolga 1966), and adult females (" aunties ") other than the mother may share this task. Care-giving or succorant behaviour is well-known in many Delphinids, in sperm whales and in Ziphiids (Caldwell and Caldwell 1966; Best 1979; Benjaminsen and Christensen 1979). It is little wonder, then, that juvenile mortality is reduced among Odontocetes.

We may suppose, therefore, that one major direction of evolution in Odontocetes has been towards increasing the length of the reproductive cycle coupled with an increase in size. The resulting lowered reproductive rate is offset by a decrease in juvenile mortality. One may ask, therefore, if density-dependent control of reproductive rate still occurs in the Odontoceti.

Mysticeti (*Balaenoptera* sp.) exhibit a shorter period between pregnancies, and age at sexual maturity falls, when populations are reduced (Gambell 1973). Attempts to find the same phenomenon in Odontoceti have been more recent and have shown less clear-cut results. Let us start with the examination of a time series within one population which has been reduced by hunting—or the reverse, a population which has been allowed to increase by relaxation of hunting—and pass to comparisons of adjacent populations of the same species believed to exist at higher and lower population densities.

Density-dependence:

a. Time series within one population

In 1952 to 1954 and again in 1957 I measured the reproductive rate in unselected samples of *Globicephala melaena* in search of a change of reproductive rate (Sergeant 1962, Table XIX). I failed to find such a change (Table 14), there being a decrease rather than an increase of pregnancy rate and no change in lactation length. Yet we now know (Fig. 2) that 15% of the population had been removed at the mid-point of the first sample, 50% at the beginning of the second. At the time, I put the failure to find a change in reproductive rate to the short time period between samples and to a possible lag in the system, since female pilot whales take 6 years to reach sexual maturity. This still seems a reasonable explanation. However, had I returned to resample, it might not have been possible to obtain adequate further data owing to depletion of the population (Fig. 2).

Perrin, Coe and Zweifel (1976) studied the reproductive rate of a population of the spotted dolphin *Stenella attenuata* in the eastern tropical Pacific from 1968 to 1973. Perrin, Miller and Sloan (1977) continued these studies up to 1975. Reproductive rate was best calculated as the proportion of females in the population, times the proportion of females reproducing, times the annual pregnancy rate; this was 0.146 in 1968–73, 0.14∓0.008 in 1973, 0.135∓0.008 in 1974, 0.140∓0.007 in 1975 and 0.140∓0.004 in 1973–75, thus showing no significant change in 7 years. In 1974 this population was at or near its maximum productivity, with a kill of about 80,000 to 100,000 occurring annually in a purse-seine fishery for tuna (Perrin, Smith and Sakagawa 1975). Kills had been higher in 1971 to 1973 and the population was believed to have declined, though the amount was unknown.

Length of lactation period was 11.2 months in 1968–1973.

Henderson, Perrin and Miller (1980) calculated a reproductive rate of about 0.12 for northern *S. attenuata* from the eastern Pacific in 1974–1978. Length of lactation increased steadily from 8 to 36 months between 1973 and 1978. They noted a " dramatically decreased (porpoise) kill over the same period " in tuna purse-seines. These data would tend to suggest that length of lactation can be very sensitive to exploitation rate in *Stenella* spp., given a long enough time for study. Here it increased, making the reproductive rate fall, as the rate of exploitation slackened.

TABLE 14. REPRODUCTIVE RATES OF PILOT WHALES THROUGH TIME
Data from Sergeant (1962, Table XIX).

Females	1952–1954		1957	
	No.	%	No.	%
Mature	415	100	114	100
in active reproduction in oestrus	395	95.2	105	92.1
or ovulated	35	8.4	16	14.0
pregnant	140	33.7	29	25.4
lactating	220	53.0	60	52.6
Percent animals removed from population	15		50	

TABLE 15. INCIDENCE OF FEMALE SPERM WHALES IN EARLY AND LATE PREGNANCY FOR TWO TIME PERIODS
from Best (1980).

	1962–1967	1973–1975
No females examined	1,029	1,127
Percent in early pregnancy	17.1	20.7
Percent in late pregnancy	4.5	3.1
Percent with large corpus luteum but no foetus	2.2	6.2
Total	23.8	30.0

Kasuya (1976) studied *Stenella coeruleoalba* off eastern Japan. The population was depleted to about half its initial size between about 1945 and 1972–73. The mean calving interval became shorter, changing from 3.2 years in 1952 to 2.4 years in 1972–73, with a decrease in lactation period of from two years to less than one year. This is the same process in reverse as seen by Henderson et al. (1980) in *S. attenuata.*

Best (1980) studied female sperm whales off Natal, South Africa (Table 15). Sampling was done twice with an interval of 10 years, during which period the female population was believed to have been halved. The results are a little hard to interpret, because a category " females with large corpus luteum but no foetus " might have been either females with large foetuses lost in towing, or recently calved females. The total number of pregnant females, if this category is included, increased from 23.8% to 30.0%, if excluded, from 21.6% to 23.5%. Even though each sample exceeded 1000 animals, Best regarded them as barely adequate. It cannot be said that this example is clear-cut, but the conditions of sampling were not ideal.

Judging from the studies reported above, about a decade of studies is needed on a population subject to a changing exploitation pattern, probably because of the long time required to attain sexual maturity in the genera studied.

b. Comparisons of two populations of the same species

(1) by the same author

Perrin and Henderson (1979) compared reproductive rates in two populations of spinner dolphins *Stenella longirostris* which had been exploited at markedly different rates. There was no difference in gross reproductive rates (proportion of females times proportion mature times pregnancy rate) although there were differences in these individual components of reproduction.

(2) by different authors

These comparisons are listed separately since methodology cannot always be closely compared.

Perrin, Coe and Zweifel (1976) and Perrin, Miller and Sloan (1977) examined the reproductive rate of *Stenella attenuata* in the eastern tropical Pacific Ocean, a population which had sustained a heavy fishery. Kasuya, Miyazaki and Dawbin (1974) examined the reproductive rate of the same species off Japan, from a popu-

TABLE 16. WHITE WHALES: A COMPARISON OF LIFE HISTORY PARAMETERS IN TWO POPULATIONS
from Brodie 1971, Sergeant 1973.

Character	Western Hudson Bay	Cumberland Sound
Sample size:		
Hunted	257	17
Netted	293	107
Total	550	124
Maximum no. tooth layers	50	40
Maximum no. corpora albicantia	15	9
Mean age at sexual maturity (tooth layers):		
male	16–18	16
female	8–13 (10)	9–11 (10)
Gestation	14 months	14.5 months
Lactation	20 months	2 years
Frequency of calving	1 in 3 years	1 in 3 years

lation which had only been exploited for about 10 years at a low rate (6000 caught in 1963–1973), both fisheries exploiting populations of unknown size. Reproductive rate was calculated in a different way from Perrin *et al.*, but the data allow recalculation by Perrin *et al.*'s (1976) method: thus percent females (193/323)=0.60; percent reproductive females (124/193)=0.64; and annual pregnancy rate=0.256, including simultaneously pregnant and lactating females assigned half to each category. This gives a reproductive rate close to 0.100 as compared with Perrin *et al.*'s rate of 0.140 to 0.145. The difference appears to be due to a lower rate of ovulation prolonging lactation in the population from the Japanese seas.

Brodie (1971) examined the reproductive rate of a population of white whales *Delphinapterus leucas* as Cumberland Sound, Baffin I. This population has undoubtedly been under heavy exploitation for a long time (Brodie, Parsons and Sergeant 1981) and should show the maximum reproductive rate of which the species is capable. Sergeant (1973) examined a population of white whales in western Hudson Bay which he later believed (Sergeant 1981) to be in a balanced though not low state of exploitation. No differences are apparent (Table 16) in mean age at female sexual maturity, nor in frequency of calving. It is unfortunate that the western Hudson Bay population was not sampled for these features around 1950 at the outset of the industrial fishery at Churchill, Manitoba.

Thus the majority of the comparative population studies show a difference in reproductive rates between lightly and intensively exploited populations. Sergeant and Brodie's populations of white whales may have been exploited at similar rates, or the parameters may not have been measured sufficiently accurately. No change in mean age at first reproduction has yet been demonstrated in any of the within-population or between-population studies; the changes are all changes in length of lactation. Probably the mechanism is between a lactation anoestrus in females within a denser population, and ovulation during lactation in better-fed females within a heavily exploited population. There is therefore a density-dependent reproductive rate within an Odontocete population. It remains to be shown whether or not a calf suckled for only 8 months by its mother has a higher mortality rate than a calf suckled for 24 months. Probably, the length of lactation has little significance, since later lactation is intermittent (Tavolga and Essapian 1957; Tavolga 1966) in *Tursiops truncatus*; and the existence of " aunties " from among younger or anoestrous females safeguards an older calf when the mother has a new one. Therefore, a higher reproductive rate is probably not necessarily associated in Odontoceti with a higher calf mortality rate. It is only when the adolescents form herds on their own account that their mortality rate may rise, as demonstrated by the high singleton death rate of adolescent *Lagenorhynchus acutus*, and by Perrin and Powers (1980) in *Stenella attenuata* from infections with *Crassicauda* (p. 31). These mortalities might be density-dependent. However the existence of social mechanisms maintaining calves within the herds will continue to keep calf mortality low.

Thus in Odontocetes survival of juveniles is maximixed by a high degree of parental care and sociality. Old animals too may benefit from care-giving behaviour. The only mechanism remaining to increase mortality among adolescents is aggressiveness of older animals, and this mechanism disappears within the most social species.

A population however must expand slowly if it is to maintain itself. Eventually it will come up against an environmental barrier which will limit its continued growth. Such barriers must in some way involve either food or space. Mass strandings represent a high proportion of the total mortality of the social species and must therefore constitute the main mechanism by which populations of these species are limited.

It is just possible that the true Delphinidae can be divided into two groups: the Delphininae with about a year's gestation, and a normally long lactation period which can be shortened in the way described; and the Orcininae with a long pregnancy, and a long lactation not susceptible to being shortened. This dichotomy, if real, would fit with the subdivision into frequent mass-stranders and others. Unfortunately there are not yet enough data on pregnancy length or on density-dependence in lactation length to know if the suggested division is real. For instance, the lengths of pregnancy and of lactation of *Orcinus orca* seem to be unknown. The same is true for *Pseudorca crassidens* and *Peponocephala electra* though it should be only a matter of time before a sufficient number of animals are examined in mass strandings of these species.

PROXIMATE CAUSES OF STRANDINGS

Examination of mass-stranded Cetacea has shown no obvious bacteriological, helminthological or other pathological findings including those of neuropathology (Hall, Gilmartin and Mattson 1971, Hall and Schimpff 1979). Yet single-stranded animals are frequently highly infected either with trematodes in the liver and brain (Ridgway and Dailey 1972), or with nematodes in lung alveoli or head air sinuses (Delyamure 1955, Dailey and Perrin 1973, Dailey and Stroud 1978). Since many delphinds are known to have heavy infections of nematodes in air-sinuses or lungs, it is important to obtain quantitative information on numbers of parasites in normal and stranded animals. The only such data known to me are due to Delyamure (1955), who examined *D. delphis* from the Black Sea. Seven naturally-stranded animals had heavy infections of the nematode *Skjrabinalius cryptocephalus* in their tracheae and bronchi with pus blocking the small respiratory passages, together with hyperemia, and destruction of the bronchial mucosa. Examination of the lungs of 604 *D. delphis* caught in the fishery showed that 175 (28.9%) had *S. cryptocephalus* infections with from 3 to 227 nematodes present. Infections increased with age, though a few adults were self-cured with healed lesions. Evidence for acute bacterial infections tends to come more from captive animals where the water must have high concentration, *e.g.* of *Staphylococcus aureus* (Colgrove and Migaki 1976). In summary, nearly all singly-stranded animals are diseased or highly parasitised, but mass-stranded animals are not. Geraci and St. Aubin (1979) found that the adrenal cortex of mass-stranded adult female *Lagenorhynchus acutus* showed cysts characteristic of prolonged stress. This interesting observation needs to be followed up, and it is particularly important to examine the cortex from free-living controls to compare with those of the stranded animals.

Most authors (*e.g.* Dudok van Heel 1962) have placed emphasis on the immediate circumstances of mass-strandings, such as the configuration of the coastline, but I do not believe these features to be important. Certainly, many strandings occur on shoaling coasts. Thus Maigret (1979) notes a concentration of mass strandings of *Globicephala macrorhyncha*, *Delphinus delphis*, *Tursiops truncatus* and *Steno bredanensis* on the north side of the Cap-Vert peninsula, Senegal. Six of seven strandings occurred in May and June when there are trade winds from the northwest and a surface current setting from the northeast on to the shore. Another such region may be the neighbourhood of Wellfleet, Cape Cod, where, according to SEAN reports, *Lagenorhynchus acutus* strand repeatedly as well as other species such as *Globicephala melaena* occasionally. I believe that the animals can best be regarded as " drift bottles " which will inevitably tend to arrive on such sites. Passivity of the animals is stressed in many observations, e.g. the pilot whales *G. macrorhyncha* which stranded repeatedly along the west coast of Florida in August 1971 (Fehring and Wells, 1976); and the 30 *Pseudorca crassidens* which were filmed coming ashore at the Dry Tortugas, Florida in June 1976 (Porter, 1977). Moreover, as is well known, a herd once so stranded is likely, if taken out to sea, to strand again (Fehring and Wells, 1976). I therefore judge it more important to examine the internal causes of the observed passivity.

MASS STRANDINGS AS EMIGRATIONS

Considering the extralimital occurrences of mass-stranding *Pseudorca crassidens* at Britain and probably also in south temperate seas one would expect mass-strandings within an increasing population to be accompanied by some range expansion. This does not seem to have occurred as yet with *Lagenorhynchus acutus* which has merely increased within its known range in the northwest Atlantic, there being no evidence of a concomitant increase of the same species within the northeast Atlantic (Evans, 1980, 1981). Thus for this species, the scope of a population increase so far been has quite restricted. It will be worthwhile to continue to monitor it.

PRACTICAL APPLICATIONS

Sergeant (1977) used the frequency of singleton strandings of fin whales on the coasts of Britain over time, expressed as an order of rank within all Cetacean strandings, in order to determine changes of the population as a result of commercial whaling.

If frequency of mass and singleton strandings varies directly with the abundance of an Odontocete species, prone to mass strand, then occurrence of mass strandings could give additional evidence on the state of such a stock. This could be of practical value for a species such as the sperm whale.

In the *eastern North Atlantic,* Fairlie (1981) notes that there has been no decline in recent years in the (singleton) stranding rate of sperm whales in Ireland, though all Mysticetes have declined in their stranding rate at Britain, this correlating well with the reduction of their populations by hunting (Sergeant 1977, 1979). From the evidence given I would deduce that sperm whales have not declined in the eastern North Atlantic. Mitchell (1975b) demonstrated a cross-over from Nova Scotia to Spain from tagging, showing that eastern and western North atlantic sperm whales are not isolated from one another. Allen, Compton-Bishop and Gordon (1979) demonstrated a reduction in catch and increase in catch per unit effort of sperm whales at the Azores between the 1950's and 1970's, due to massive human emigration and reduction in number of whaling stations. Catches there in the 1950's were about 400 per annum; in the 1970's about 200 and falling. The main catch of sperm whales is now at Iceland (about 200 per annum) where only adult males are available. I conclude that the North Atlantic population of sperm whales is probably not reduced nor are present catches excessive. The main concern appears to be whether the falling mean size of males due to selective catching of them(Martin 1981) could affect reproductive success.

In the *eastern North Pacific* there have been 4 recent mass strandings: in the Gulf of California in 1953 and 1954 (Gilmore 1957, 1959) and in 1979 (Byrant 1979; SEAN Bull., January 1979), and on the coast of Oregon in June, 1979 (Anon, 1979, SEAN Bull. June 1979). The Mexican strandings were all or mainly of males; the Oregon stranding was of a harem herd. Pike and MacAskie (1979) show that harem herds normally extend as far north as off the coast of British Columbia between spring and autumn. Knowledge of stock identity of sperm whales in the North Pacific Ocean is still incomplete, but Bannister and Mitchell (1980), basing themselves partly on unpublished tagging recoveries due to D. W. Rice, and partly on discontinuous distributions of sperm whales at sea, accept the existence of an eastern North Pacific or American stock. Horwood and Garrod (1980), examining the state of this stock from catch per unit of effort and comparisons of pregancy rate over time, conclude it is in a healthy state.

At *New Zealand*, there were mass strandings of sperm whales in 1970 (Robson and Van Bree 1970), 1972 (Robson 1978) and 1974 (Stephenson 1975)with apparently none subsequently (*fide* SEAN Bulls. to December 1981). Best (1976), table 2) shows that stock reductions of sperm whales in the southern hemisphere generally and the New Zealand area in particular (Best's division VII) were severe for exploitable males, reducing them to about half initial stock size by 1972. However it had been computed that the stock of mature females was reduced only to ca 90% of initial sock. Clearly, the females are the main animals which appear in strandings of harem herds.

I conclude that analysis of mass and single strandings of sperm whales may throw light on the status of stocks additional to that which may be obtained by other methods, and that this finding makes important the widespread dcoumentation of their strandings.

SUMMARY

1. In eastern Newfoundland from 1950 to 1971 an abundant oceanic population of pilot whales *Globicephala melaena* was hunted down to low catch levels. Its cumulative catch gave an initital population estimate of 54,000. It was protected in 1972. The population was estimated in 1980 to number at least 14,000 animals. Recovery of the population was presumably accelerated by immigration from areas where the species had remained common. From 1975, mass-strandings began at Newfoundland and neighbouring areas and continue at the rate of between 100 and 200 animals a year.

In the area of the northwest Atlantic extending from the Gulf of Maine to the Gulf of St. Lawrence, white-sided dolphins *Lagenorhynchus acutus* have become very common since about 1970 with at least 10,000 individuals present in the U.S. sector of this range. During the 1970's there were two mass strandings and many singleton strandings of this species.

At North Island, New Zealand, harem herds of sperm whales have mass-stranded on many occasions, and this area contains one of the highest densities of sperm whales and especially females in the southern hemisphere.

From these examples, mass strandings can be associated with dense populations of Odontocetes.

2. From an examination of the literature, mass strandings are the main source of coastal mortality (perhaps exceeding 90% of deaths) in a group of species (*Globicephala* spp., *Pseudorca crassidens*, *Peponocephala electra*) belonging to the subfamily Orcininae of the family Delphinidae. Mass strandings represent a lower percentage of deaths in typical dolphins of the subfamily Delphininae.

3. The frequency of mass strandings can vary geographically, whatever the rate of overall incidence. A study of the incidence of mass strandings by latitude in the allopatric species *Globicephala melaena* and *G. macrorhyncha* along the eastern North American seaboard showed that each species has a wide " core " area where

both mass and singleton strandings occur, located to the northward in *G. melaena* and southward in *G. macrorhyncha*. At the edges of the respective ranges, where the two species are in contact, only singleton strandings occur in both species. This evidence is taken to mean that mass strandings occur in that part of the range where the species is abundant.

4. A comparison of life histories shows that *Globicephala melaena* among the Orcininae exhibits greater sociality, expressed by greater homogeneity of herds, than do *Tursiops truncatus* and *Lagenorhynchus acutus* among the Delphininae. Pilot whales also show absence of aggression by adult to immature animals. This greater sociality occurs among member species of the Orcininae in spite of a greater sexual dimorphism, delayed sexual maturity and higher male mortality rate, features typical of territorial marine mammals of other groups.

Physeter catodon exhibits mass mortality among harem herds, but solitary stranding mortality of subadult and adult males at high latitudes, consistent with the known aggressive behaviour of harem bulls.

5. No evidence exists for emigration among mass-stranding populations of Odontoceti, except for the examples of *Pseudorca crassidens* stranding in cool seas.

6. In Mysticetes, high mortality occurs among young animals just after weaning, and at extreme old ages. This pattern remains among Odontoceti in the weakly social *Phocoena phocoena*, but is not observed from length frequencies of stranded *Delphinus*, *Tursiops* and *Globicephala*. However high adolescent mortality remains due to aggression in *Lagenorhynchus acutus* and *Stenella attenuata* at least. It is argued that sociality reduces the mortality of juveniles of the social Odontoceti, probably through such features as the long lactation and other features of parental care such as succorant behaviour. Since length of lactation has been demonstrated to be density-dependent among members of the Delphininae and among sperm whales, social behaviour must be important in reducing calf mortality. When other sources of mortality are reduced, social mortality expressed in mass strandings becomes the major source.

7. The main purpose of the study has been to emphasise internal factors and especially population density as responsible for mass strandings and to discount immediate external factors such as coastal configuration. What the internal factors might be leading to morbidity of herds is unknown but it is suggested that studies of stress might be valuable, with the need to study controls from among normal animals at sea.

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REFERENCES

Aitken, P. F., 1971. Whales from the coast of South Australia. *Trans. Roy. Soc. S. Australia*, 95: 95–103.

Allen, K. R., 1980. *Conservation and management of whales*. Univ. of Washington Press, Seattle; Butterworths, London. 107 pp.

Allen, P., Q. Compton-Bishop, and J. Gordon., 1979. *Report of the Cambridge Azores Expedition 1979*. Dupl., 46 pp.

Anon., 1979. *Teeth of stranded sperm whales studied to determined age*. U.S. Dept. of Commerce, Nat. Mar. Fisheries Serv., Northwest and Alaska Fisheries Center Monthly Rept., July 1979. U.S. Nat. Mar. Mammal Lab., Seattle, Washington.

Bannister, J., and E. D. Mitchell., 1980. North Pacific sperm whale stock identity: Distributional evidence from Maury and Townsend charts. *Rep. int. Whal. Commn* (*Special Issue 2*): 219–230.

Benjaminsen, T., and I. Christensen., 1979. The natural history of the bottlenose whale *Hyperoodon ampullatus* (Forster). pp. 143–164. *In*: H. E. Winn, and B. L. Olla (eds.) *Behavior of marine animals, 3 Cetaceans*. Plenum Press, 438 pp.

Best, P. B., 1968. The sperm whale *Physeter catodon* of the west coast of South Africa. 2. Reproduction in the female. *Investl. Rep. Div. Sea Fish. S. Africa*, 66: 1–32.

Best, P. B., 1969. The sperm whale *Physeter catodon* of the west coast of South Africa. 3. Reproduction in the male. *Investl. Rep. Div. Sea Fish. S. Africa*, 72: 1–20.

Best, P. B., 1974. The biology of the sperm whale as it relates to stock management. pp. 257–293. *In*: W. E. Schevill, (ed.) *The whale problem. A status report*. Harvard Univ. Press, Cambridge, Mass., 419 pp.

Best, P. B., 1976. *Review of sperm whale stocks*. Food and Agr. Org. Un. Nations, Advis. Ctee. on Mar. Res. Research, Marine Mamm. Symp. EC 8, 35 p., Mimeo.

Best, P. B., 1979. Social organization in sperm whales. pp. 227–289. *In* H. E. Winn and B. L. Olla (eds.) *Behavior of marine animals, 3. Cetaceans*. Plenum Press, 438 pp.

Best, P. B., 1980. Pregnancy rates in sperm whales off Durban. *Rep. int. Whal. Commn* (*Special Issue 2*): 93–97.

Bigg, M. A., 1981. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. Int. Whal. Commn, Workshop on killer whales, Cambridge, U.K. 23–25 June 1981. Working Paper SC/JN81/KW4, 31 pp.

Bigg, M. A., I. B. MacAskie and G. Ellis., 1976. Abundance and movements of killer whales off eastern and southern Vancouver Island, with comments on management. Unpubl. MS, Arctic Biological Station, Ste. Anne de Bellevue, Que., 20 pp.

Boschma, H., 1938. On the teeth and some other particulars of the sperm whale (*Physeter macrocephalus L.*). Temminckia, Leyden III: 151–278, XIII plates.

Bree, P.J.H. van, and I. Cristensen., 1974. On the intriguing stranding of four Cuvier's beaked whales, *Ziphius cavirostris*, G. Cuvier 1823, on the Lesser Antillean Island of Bonaire. *Bijdr. Dierkd.*, 44: 235–238.

BRODIE, P. F. 1971. A reconsideration of aspects of growth, reproduction and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Island, population. *J. Fish. Res. Board Can.*, 28: 1309–1318.

BRODIE, P. F., J. L. PARSONS, and D. E. SERGEANT., 1981. Present status of the white whale (*Delphinapterus leucas*) in Cumberland Sound, Baffin Island. *Rep. int. Whal Commn*, 31: 579–582.

BROWN, D. H., D. K. CALDWELL, and M. C. CALDWELL., 1966. Observations on the behavior of wild and captive false killer whales, with notes on associated behavior of other genera of captive Delphinids. *Contr. Sci. Mus. Los Angeles County, 95*: 32.

BROWN, S. G., 1975. Relation between stranding mortality and population abundance of smaller Cetacea in the Northeast Atlantic Ocean. *J. Fish. Res. Board Can.*, 32: 1095–1099.

BRYANT, P., 1979. The Baja sperm whale mass-stranding. *Whalewatcher. J. Amer. Cetacean Soc.*, *13*(2): 10.

BRYDEN, M. M., T. J. HARRISON, and R. J. LEAR., 1977. Some aspects of the biology of *Peponocephala electra* (Cetacea, Delphinidae). Part I. General and reproductive biology. *Aust. J. Mar. Freshwater Res.*, 28: 703–716.

BUDKER, P., 1968. Stranding of pilot whales (*Globicephala melaena* (Traill)) on the coast of Normandy, France. *Norwegian Whaling Gazette* 1968(1): 17–19.

BULLIS, H. R., and J. C. MOORE., 1956. Two occurrences of false killer whales, and a summary of American records. *Amer. Mus. Novitates* 1756: 5.

CALDWELL, M. C., and D. K. CALDWELL., 1966. Epimeletic (care-giving) behavior in Cetacea. pp. 755–789. *In*: K. S. Norris (ed.) *Whales, dolphins and porpoises.* University of California Press, Berkeley and Los Angeles, 789 pp.

CALDWELL, D. K., M. C. CALDWELL, W. F. RATHJEN, and J. R. SULLIVAN., 1971. Cetaceans from the Lesser Antillean Island of St. Vincent. *Fishery Bull.*, *69*: 303–312.

CALDWELL, D. K., M. C. CALDWELL, and C. M. WALKER. 1970. Mass and individual strandings of false killer whales, *Pseudorca crassidens*, in Florida. *J. Mamm.* 51: 634–636.

CARL, G. C., 1946. A school of killer whales stranded at Estevan Point, Vancouver Island. *British Columbia, Prov. Mus. Nat. Hist. and Anthrop., Rep. 1945*: 321–328.

CASINOS, A., and J. BOU., 1980. On a massive stranding of short-finned pilot whale, *Globicephala macrorhynchus* Gray, 1846, on Margarita Island (Venezuela). *Sci. Rep. Whales Res. Inst.*, 32: 145–148.

COLGROVE, G. S., and G. MIGAKI., 1976. Cerebral abscess associated with stranding in a dolphin. *J. Wild. Dis.*, 12: 271–274.

COMRIE, L. C., and ANN B. ADAM., 1938. The female reproductive system and corpora lutea of the false killer whale *Pseudorca crassidens* Owen. *Trans. Roy. Soc. Edin.*, 59(2): 521–531.

DAILEY, M. D., and W. F. PERRIN., 1973. Helminth parasites of porpoises of the genus *Stenella* in the eastern tropical Pacific. *Fish. Bull.*, 71: 455–471.

DAILEY, H., and R. STROUD., 1978. Parasites and associated pathology observed in cetaceans stranded along the Oregon U.S.A.coast. *J. Wild. Dis.*, 14: 503–512.

DAWBIN, W. A., B. A. NOBLE, and F. C. FRASER., 1970. Observations on the electra dolphin, *Peponocephala electra*. *Bull. Brit. Mus. Nat. Hist.*, 20: 173–201.

DEARDEN, J. C., 1958. A stranding of killer whales in Newfoundland. *Can. Field-Nat.*, 72: 166–167.

DELYAMURE S. L., 1955 [1968]. *Helminthofauna of marine mammals* (Ecology and Phylogeny). Transl. from Russian. U.S. Dept. of the Interior, and Nat. Sci. Foundation, Washinton, D.C., 522 pp.

DE MASTER, D., 1981. Editorial. pp. 1–2. *In*: Marine Mammal Information June 1981. Oregon State Univ., Sea Grant College Program, Corvallis, Oregon. 23 pp.

DUDOK VAN HEEL, W. H., 1962. Sound and Cetacea. *Netherlands J. Sea Res.*, 1: 407–507.

DUGUY, R., 1973. Rapport annuel sur les Cetaces et les Pinnipedes trouves sur les cotes de France. II Annee 1972. *Mammalia*, 37: 669–677.

DUGUY, R., 1974. *Ibid.* III Annee 1973. *Mammalia*, 38: 545–555.

DUGUY, R., 1975. *Ibid.* IV Annee 1974. *Mammalia*, 39: 689–701.

DUGUY, R., 1976. *Ibid.* V Annee 1975. *Mammalia*, 40: 671–681.

DUGUY, R., 1977. *Ibid.* VI Annee 1976. *Ann. Soc. Sci. Nat. Charente-Maritime*, VI(4): 308–317.

Duguy, R., 1978. *Ibid.* VII Annee 1977. *Ann. Soc. Sci. Nat. Charente-Maritime*, VI(5): 333–344.

Duguy, R., 1979. *Ibid.* VIII Annee 1978. *Ann. Soc. Sci. Nat. Charente-Maritime*, 6(6): 463–474.

Duguy, R., 1980. *Ibid.* IX Annee 1979. *Ann. Soc. Sci. Nat. Charente-Maritime*, 6(7): 615–632.

Duguy, R., 1981. *Ibid.* X Annee 1980. *Ann. Soc. Sci. Nat. Charente-Maritime*, 6(8): 803–818.

Duguy, R. and J. Baudouin-Bodin., 1965. Rapport sur l'echouage d'une troupe de Globicephales *Globicephala melaena* (Traill, 1809) a l'Ile d'Yeu. *Mammalia*, 29: 61–64+Tables, Fig.

Duguy, R., and P. Budker., 1972. Rapport annuel sur les Cetaces et Pinnipedes trouves sur les Cotes de France. 1. Annee 1971. *Mammalia*, 36: 517–520.

Evans, P.G.H., 1980. Cetaceans in British waters. *Mammal Review*, 10: 1–52.

Evans, P.G.H., 1981. Cetacean expedition around western Britain July 15-Oct. 17, 1980. Marine Mammal Information, June 1981: 4–5.

Fairlie, J., 1981. *Irish whales and whaling.* Blackstaff Press, Belfast, 234 p.

Fehring, W. K., and R. S. Wells., 1976. A series of strandings by a single herd of pilot whales on the west coast of Florida. *J. Mamm.*, 57: 191–194.

Fisher, H. D., and R. J. Harrison., 1970. Reproduction in the common porpoise (*Phocoena phocoena*) of the North Atlantic. *J. Zool. Lond.*, 161: 471–486.

Ford, J., and D. Ford., 1981. The killer whales of B.C. *Waters, J. Vancouver Public Aquarium*, 5: 3–32, illus.

Fraser, F. C., 1934. *Report on Cetacea stranded on the British coasts from 1927 to 1932.* No. 11. Brit. Mus. (Nat. Hist.) 1–41, 6 maps.

Fraser, F. C., 1936. Recent strandings of the false killer whale, *Pseudorca crassidens*, with special reference to those found at Donna Nook, Lincolnshire. *Scottish Nat., July-Aug.*, '36: 105–114.

Fraser, F. C., 1946. *Report on Cetacea stranded on the British coasts from 1933 to 1937.* No. 12. Brit. Mus. (Nat. Hist.), 1–56, 7 maps.

Fraser, F. C., 1953. *Report on Cetacea stranded on the British coasts from 1938 to 1947.* No. 13. Brit. Mus. Hist.), 1–48, 9 maps.

Fraser, F. C., 1955. The southern right whale dolphin, *Lissodelphis peroni* (Lacepede). External characters and distribution. *Bull. Brit. Mus. (Nat. Hist.) Zool.*, 2: 341–346, 1 pl.

Fraser, F. C., 1974. *Report on Cetacea stranded on the British coasts from 1948 to 1966.* No. 14. Brit. Mus. (Nat. Hist.) 1–65, 9 maps.

Fraser, F. C. and P. E. Purves., 1960. Hearing in cetaceans. *Bull. Brit. Mus. (Nat. Hist.) Zool.*, 7: 1–140, 53 pls.

Gambell, R., 1973. Some effects of exploitation on reproduction in whales. *J. Reprod. Fert., Supple.*, 19: 533–553.

Gaskin, D. E., 1968. *The New Zealand Cetacea.* Fish. Res. Bull. No. 1 (N.S.), Fisheries Research Division, N.Z. Marine Dept. 92 pp.

Gaskin, D. E., 1970. Composition of schools of sperm whales *Physeter catodon* Linn. east of New Zealand. *N.Z. J. Mar. Freshw. Res.*, *4*: 456–471.

Gaskin, D. E., P. W. Arnold, and B. A. Blair., 1974. *Phocoena phocoena. Mammalian Species*, 42: 1–8.

Geraci, J. R., 1978. The enigma of marine mammal strandings. *Oceanus*, 21: 38–47.

Geraci, J. R., and D. J. St. Aubin., MS 1975. *A mass stranding of pilot whales in Bonavista Bay*, Newfoundland. U.S. Mar. Mammal Comm. Rep. Contract MMC-47.

Geraci, J. R., and D. J. St. Aubin., 1977. Mass stranding of the long finned pilot whale, *Globicephala melaena*, on Sable Island, Nova Scotia. *J. Fish. Res. Board Can.*, 34: 2196–2199.

Geraci, J. R., and D. J. St. Aubin., 1979. Stress and disease in the marine environment: Insights through strandings. pp. 223–233. *In*: J. R. Geraci, and D. J. St. Aubin (eds.) *Biology of Marine Mammals: Insights through strandings.* U.S. Dept. of Commerce, Nat. Tech. Info. Service, PB-293 890, 343 pp.

Gilmore, R. M., 1957. Whales aground in Cortes' Sea: Tragic strandings in the Gulf of California. *Pacific Discovery*, 10: 22–27.

Gilmore, R. M., 1959. On the mass strandings of sperm whales. *Pacific Naturalist*, 1: 9–16.

Guiler, E. R., 1978. Whale strandings in Tasmania since 1945 with notes on some seal reports. *Pap. Proc. Roy. Soc. Tasmania*, 112: 189–213.

HAIN, J.H.W., R. K. EDEL, H. E. HAYS, S. K. KATONA, and J. D. ROANOWICZ., 1981. General distribution of cetaceans in the Continental Shelf waters of the Northeastern United States. Section II, 277 pages. *In A characterization of marine mammals and turtles in the Mid and North Atlantic areas of the U.S. outer Continental Shelf.* Ann. Rept. for 1979 for the Cetacean and Turtle Assessment Program (CETAP). Univ. of Rhode Island, Kingston, R.I.

HALL, J. D., W. G. GILMARTIN, and J. L. MATTSSON., 1971. Investigation of a Pacific pilot whale stranding in San Clemente Island. *J. Wild. Dis.*, 7: 324–327.

HALL, N. R., and R. D. SCHIMPFF., 1979. Neuropathology in relation to strandings: mass stranded whales. pp. 236–214. *In:* J. R. Geraci, and D. J. St. Aubin (eds.) *Biology of Marine Mammals: Insights through strandings.* U.S. Dept. of Commerce, Nat. Tech. Info. Service PB-293 890, 343 pp.

HARMER, S. F., 1927. *Report on Cetacea stranded on the British coasts from 1913 to 1926.* No. 10. Brit. Mus. (Nat. Hist.) 1–91 7 maps.

HARRISON, R. J., R. L. BROWNELL, and R. C. BOICE, 1972. Reproduction and gonadal appearances in some Odontocetes. pp. 362–429. *In:* R. J. Harrison (ed.). *Functional Anatomy of Marine Mammals, Vol. I.* Academic Press, London and New York.

HAUG, T. and B. GULLIKSEN., 1981. Remarks concerning a sperm whale stranding in North Norway in December 1980. *Fauna,* 34: 68–76.

HAUG. T., and O. K. SANDNES., 1982. Mass stranding and successful rescue of killer whales *Orcinus orca* (L.) in Lofoten, North-Norway. *Fauna,* 35: 1–7.

HENDERSON, J. R., W. F. PERRIN, and R. B. MILLER., 1980. *Rate of gross annual production in dolphin populations (Stenella spp. and Delphinus delphis) in the eastern tropical Pacific, 1973–1978.* U.S. Dept. of Commerce, Nat. Mar. Fish. Serv., Southwest Fisheries Center Admin. Rept. JL-80-02. La Jolla, CA. 51 pp.

HINTON, M.A.C., 1928. Stranded whales at Dornoch Firth. *Nat. Hist. Mag.* 1: 131-000 (cited and quoted by Purves and Pilleri 1978) *Invest. on Cetacea IX*: 67-227, Berne.

HOHN, A. A., 1980. Age determination and age related factors in teeth of western North Atlantic bottlenose dolphins. *Sci. Rep. Whales Res. Inst.*, 32: 39–66.

HORWOOD, J. W. and D. J. GARROD., 1980. The status of the North Pacific Sperm Whale. *Rep. int. Whal. Commn,* 30: 187-192.

JONSGAARD, A., 1951. Studies on the little piked whale or minke whale. *Norwegian Whaling Gazette,* 1951(5): 55.

KANWISHER, J., and G. SUNDNES, 1965. Physiology of a small cetacean. *Hvalraadets Skrifter,* 48: 45–53.

KASUYA, T., 1976. Reconsideration of life history parameters of spotted and striped dolphins based on cemental layers. *Sci. Rep. Whales Res. Inst.*, 28: 73–106, 4 pls.

KASUYA, T., 1978. The life history of Dall's porpoise with special reference to the stock off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst.*, 30: 1–63.

KASUYA, T., N. MIYAZAKI, and W. H. DAWBIN., 1974. Growth and reproduction of *Stenella attenuata* on the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst.*, 26: 157–226.

KATONA, S. K., S. A. TESTAVERDE, and B. BARR., 1978. Observations on a white-sided dolphin, *Lagenorhynchus acutus,* probably killed in gill nets in the Gulf of Maine. *Fishery Bull. U.S.A.*, 76: 475–476.

KELLOGG, R., 1929. What is known of the migrations of some of the whalebone whales. *Ann. Rept. Smithsonian Inst.*, 1928: 467–494.

KLEINENBERG, S. E., 1956. *Mlekopitayuschie Chernogo i Azovskogo morei (Mammals of the Black and Azov Seas).* U.S.S.R. Academy of Sciences Press, Moscow, 287 pp. (Transl. 1978 by Dept. of Secretary of State of Canada, for Arctic Biological Station, Ste. Anne de Bellevue, Que.)

LAWS, R. M., 1959. The foetal growth rates of whales, with special reference to the fin whale, *Balaenoptera physalus* Linn. *Discovery Rep.*, 29: 281–308.

LAYNE, J. N., 1965. Observations on marine mammals in Florida waters. *Bull. Flo. State Mus., Biol. Sci.*, 9: 131–181.

LE TALLEC, J., 1969. Quelques notes sur les echouages en masse de Globicephales, *Globicephala melaena* (Traill, 1809) en Bretagne le 29 aout 1968. *Mammalia,* 33: 735–737.

LIEN, J. Ms, 1980. Baleen whale collisions with inshore fishing gear in Newfoundland. MS, Memorial Univ. of Newfoundland, 26 p. + tables.

LIEN, J. Ms, 1981. Humpback whale collisions with inshore fishing gear in Newfoundland. MS, Memorial Univ. of Newfoundland, 64 p.+figs., tables.

LORD, E. I., and R. A. CHANDLER., 1969. Whale skulls on Georges Bank. *Fisheries of Canada*, 11(1): 17–18.

MAIGRET, J., 1979. Les echouages massifs de cetaces dans la region du Cap-Vert (Senegal). Univ. de Daker—Inst. Fondamental d'Afrique Noire. *Publ. Trimestrielle*, Jan. 1979: (161) 23–28.

MARTIN, A. R., 1981. Further analysis of the post-war Icelandic sperm whale catch. *Rep. int. Whal. Commn*, 31: 765–768.

McCANN, C., 1974. Body scarring on Cetacea-Odontocetes. *Sci. Rep. Whales Res. Inst.*, 26: 145–155, 8 pls.

Mead, J. G., 1979. An analysis of Cetacean strandings along the eastern coast of the United States. pp. 54–68. *In*: J. R. Geraci and D. J. St. Aubin (eds.). *Biology of marine mammals: insights through strandings*. Mar. Mamm. Commn, Washington, D.C. N.T.I.S. PB-293890, 343 pp.

MEAD, J. G., 1980. Strandings (of humpback whales) along the Atlantic coast of the U.S. from 1970-Novermber 1980. Abstr. Proc. Workshop " Humpback whales of the western North Atlantic," 17-21 Nov. 1980, New England Aquarium, Boston, pages 13-14. *In* Mate, B. (ed.) *Marine Mammal Information, Dec. 1980* (Oregon State Univ., Corvallis, Oregon).

MEAD, J. G., D. K. ODELL, R. S. WELLS, and M. D. SCOTT., 1980. Observations on a mass stranding of spinner dolphin, *Stenella longirostris*, from the west coast of Florida. *Fish. Bull.*, 78(2): 353–360.

MERCER, M. C., 1973. Observations on distribution and intraspecific variation in pigmentation patterns of Odontocete Cetacea in the western North Atlantic. *J. Fish. Res. Board Can.*, 30: 1111–1130.

MERCER, M. C., 1975. Modified Leslie-DeLury population models of the long finned pilot whale (*Globicephala melaena*) and annual production of the short finned squid (*Illex illecebrosus*) based upon their interaction at Newfoundland. *J. Fish. Res. Board Can.*, 32: 1145–1154.

Mitchell, E. D., 1973. Draft report on humpback whales taken under special scientific permit by eastern Canadian land stations 1969–1971. *Rep. int. Whal. Commn*, 23 (App. B): 138–154.

MITCHELL, E. D., 1975a. Porpoise, dolphin and small whale fisheries of the world. Status and problems. *Int. Union Cons. Nat. Natural Res.*, Monograph No. 3, 129 pp.

MITCHELL, E. D., 1975b. Preliminary report on Nova Scotia fishery for sperm whales (*Physeter catodon*). *Rep. int. Whal. Commn*, 25: 226–235.

MITCHELL, E. D., 1977. Canadian progress report on whale research–June 1975 to May 1976. *Rep. int. Whal. Commn*, 27: 73–85.

MITCHELL, E. D., 1980. Canada Progress Report on Cetacean Research, June 1978 to May 1979. *Rep. int. Whal. Commn*, 30: 145–151.

MITCHELL, E. D. 1981. Ibid., June 1979 to May 1980. Ibid. 31: 174–175.

MITCHELL, E. D. 1981. Ibid., June 1980 to May 1981. Rep. Int. Whaling Commn, Doc. SC/33/Prog. Rep. Canada, 19 p.

MIYAZAKI, N., and M. NISHIWAKI., 1978. School structure of the striped dolphin off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst.*, 30: 65–115.

MOHL-HANSEN, U. 1954. Investigations on reproduction and growth of the porpoise (*Phocoena phocoena* (L.)) from the Baltic. *Vidensk. Medd. Dansk. naturh. Foren.*, 116: 368–396, 3 pls.

MOORE, J. C., 1953. Distribution of marine mammals to Florida waters. *Amer. Midl. Nat.*, 49: 117–158.

MORZER-BRUYNS, W.F.J., 1968. Sight records of Cetacea belonging to the genus *Mesoplodon* Gervais 1950. *Z. Saugetierk.*, 33: 106–107.

MORZER-BRUYNS, W.F.J., 1969. Sight reords and notes on the false killer whale, *Pseudorca crassidens* (Owen 1846). *Saugetierk. Mitteil.*, 17: 351–356.

NISHIWAKI, M., and C. HANDA., 1958. Killer whales caught in the coastal waters off Japan for recent 10 years. *Sci. Rep. Whales Res. Inst.*, 13: 85–96.

NORRIS, K. S., 1967. Aggressive behavior in Cetacea. pp. 225–241. *In*: C. D. Clemente and D. B. Lindsley (eds.) *Aggression and defence. Neural mechanisms and social patterns.* Berkeley, Univ. Calif. Press.

NORRIS, K. S. and T. P. DOHL., 1979. Behavior of the Hawaiian spinner dolphin *Stenella longirostris*. *Fishery Bull.*, 77 (4): 821–849.

NORRIS, K. S., and T. P. Dohl., 1980. The structure and functions of cetacean schools. pp. 211–261. *In*: L. M. Herman, (ed.) *Cetacean behavior: mechanisms and functions.* Wiley-Interscience, 463 pp.

Norris, K. S., and J. H. Prescott., 1961. Observations on Pacific cetaceans of Californian and Mexican waters. *Univ. Calif. Publ. Zool.*, 63: 291–462.

Odell, D. K., E. D. Asper, J. Baucom, and L. H. Cornell., 1980. A recurrent mass stranding of the false killer whale *Pseudorca crassidens*, in Florida. *Fish. Bull. U.S.A.*, 78(1): 171–176.

Peacock, A.D.L., L. Comrie, and F. Greenshields., 1936. The false killer whales stranded in the Tay estuary. *Scot. Nat.*, July-Aug. 1936: 93–104.

Perkins, J. S., and P. C. Beamish., 1979. Net entanglements of baleen whales in the inshore fishery of Newfoundland. *J. Fish. Res. Board Can.*, 36: 512–528.

Perrin, W. F., 1976. First record of the melon headed whale *Peponocephala electra* in the eastern North Pacific, with a summary of world distribution. *Fishery Bull. U.S.A.*, 74: 457–458.

Perrin, W. F., J. M. Coe, and J. R. Zweifek., 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. *Fishery Bull. U.S.A.*, 74: 229–268.

Perrin, W. F., and J. R. Henderson., 1979. *Growth and reproductive rates in two populations of spinner dolphins, Stenella longirostris, with different histories of exploitation.* U.S. Dept. of Commerce, Nat. Mar. Fish. Serv. Southwest Fish. Center, La Jolla. Admin. Rept. LJ-79-29, Aug. 1979, 13 pp.

Perrin, W. F., R. B. Miller, and P. A. Sloan., 1977. Reproductive parameters of the offshore spotted dolphin, a geographical form of *Stenella attenuata*, in the eastern tropical Pacific, 1973–75. *Fishery Bull. U.S.A.*, 75: 629–633.

Perrin, W. F., and J. E. Powers., 1980. Role of a nematode in natural mortality of spotted dolphins. *J. Wildl. Mgmt.*, 44: 959–963.

Perrin, W. F., T. D. Smith, and G. T. Sakagawa., 1975. Status of populations of spotted dolphin, *Stenella attenuata*, and spinner dolphin, *Stenella longirostris*, in the eastern tropical Pacific. Working document for meeting of ad hoc consultants on small cetaceans and sirenians. Food Agric. Org. United Nations, Advis. Ctee. Mar. Resources Res., Wkg. Party on Marine Mammals, Dec. 1974, 22 pp.

Pike, G. C., and I. B. MacAskie., 1969. Marine mammals of British Columbia. *Bull. Fish. Res. Board Can.*, 171: 1–54.

Porter, J. W., 1977. *Pseudorca* stranding. *Oceans*, 10(4): 8–15.

Pryor, K. and I. Kang., 1980. *Social behavior and school structure in pelagic porpoises (Stenella attenuata and S. longirostirs) during purse seining for tuna.* U.S. Dept. of Commerce, Nat. Mar. Fish. Serv., Southwest Fisheries Center. Admin. Rept. LJ-80-11C, 80 pp+Apps.

Rancurel, P., 1974. Echouage en masse du Cetace *Peponocephala electra* aux Nouvelles-Hebrides. *Biol. Cons.*, 6: 232–234.

Rice, E. W., 1977. A list of the marine mammals of the world. *U.S. Dept. of Commerce, Nat. Mar. Fish. Serv., Spec. Sci. Rept. Fish.* 711: 1–15.

Ridgway, S. H., and M. D. Dailey., 1972. Cerebral and cerebellar involvement of trematode parasites in dolphins and their possible role in stranding. *J. Wildl. Dis.*, 8: 33–43.

Robson, F. D., 1978. The way of the whales: Why they strand. *Whalewatcher. J. Am. Cetacean Soc.*, 12(4): 4–11.

Robson, F., and P.J.H. van Bree., 1971. Some remarks on a mass stranding of sperm whales (*Physeter macrocephalus* L. 1758) near Gisborne, New Zealand on March 18, 1970. *Z. f. Saugetierk.*, 36: 55–60.

Ross, G.J.B. 1977. The taxonomy of bottlenosed dolphins *Tursiops* species in South African waters, with notes on their biology. *Ann. Cape Prov. Mus. (Nat. Hist.)*, 11: 194 p.

Saayman, G. S., D. Bower, and C. K. Tayler., 1972. Observations on inshore and pelagic dolphins on the south-eastern Cape coast of South Africa. *Koedoe*, 15: 1–24.

Saayman, G. S., and C. K. Tayler., 1979. The socioecology of humpback dolphins (*Sousa* so.). pp. 165–226. *In*: H. E. Winn and B. L. Olla (eds.) *Behavior of marine animals. 3. Cetaceans.* Plenum Press, N.Y. and London, 438 pp.

Schevill, W. E., 1956. *Lagenorhynchus acutus* off Cape Cod. *J. Mamm.* 37: 128–129.

Scott, E.O.G., and R. H. Green., 1975. Recent whale strandings in northern Tasmania. *Pap. Proc. R. Soc. Tasmania*, 109: 91–96.

Sergeant, D. E., 1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfound-and waters. *Bull. Fish. Res. Board Can.*, 132: 84.

SERGEANT, D. E., 1969. Feeding rates of Cetacea. *Fisk. Dir. Skr. Ser. HavUnders.*, 15: 246–258.

SERGEANT, D. E., 1973. Biology of white whales (*Deplhinapterus leucas*) in western Hudson Bay. *J. Fish. Res. Board Can.*, 30: 1065–1090.

SERGEANT, D. E., 1977. Stocks of fin whales *Balaenoptera physalus* L. in the North Atlantic Ocean. *Rep. int. Whal. Commn*, 27: 460–473.

SERGEANT, D. E., 1979. Ecological aspects of cetacean strandings. pp. 94–113. *In*: J. R. Geraci and D. J. St. Aubin (eds.) *Biology of marine mammals: Insights through strandings*. Mar. Manmm. Comm, Washington, D.C. N.T.I.S. PB-293 890, 343 pp.

SERGEANT, D. E., 1981. On permissible exploitation rates of Monodontidae. *Rep. int. Whal. Comm, 31*: 583–588.

SERGEANT, D. E., D. K. CALDWELL, and M. C. CALDWELL., 1973. Age, growth and sexual maturity of bottlenosed dolphin (*Tursiops truncatus*) from Northeast Florida. *J. Fish. Res. Board Can.*, 30: 1009–1011.

SERGEANT, D. E., and H. D. Fisher., 1957. The smaller Cetacea of eastern Canadian waters. *J. Fish. Res. Board Can.*, 14: 83–115.

SERGEANT, D. E., A. W. MANSFIELD, and B. BECK., 1970. Inshore records of Cetacea for eastern Canada, 1949–1968. *J. Fish. Res. Board Can.*, 27: 1903–1915.

SERGEANT, D. E., D. J. ST. AUBIN, and J. R. GERACI., 1980. Life history and northwest Atlantic status of the Atlantic white-sided dolphin, *Lagenorhynchus acutus*. *Cetology*, 37: 1–12.

SHUREPOVA, G. A., 1973. Aggressive behaviour of captive *Tursiops truncatus* Barabasch. pp. 130–153. *In*: K. K. Chapskii and V. E. Sokolov (eds.) *Morphology and ecology of marine mammals: Seals, dolphins and porpoises*. Israeli Program for Scientific Translations. John Wiley and Sons, 232 pp.

SLEPTSOV, M. M., 1941. O Biologii Rasmnozheniya Chermonorskaya Del'fina (On the biology of reproduction of the Black Sea dolphin *Delphinus delphis*). *Zool. Zh.*, 20: 632–653. (Russian with English summary).

SMITHERS, R.H.N., 1938. Notes on the stranding of a school of *Pseudorca crassidens* at the Berg River mouth, December 27, 1936. *Trans. Roy. Soc. S. Africa*, 25: 403–411.

STARRETT, A., and P. STARRETT., 1955. Observations on young blackfish, *Globicephala*. *J. Mamm.*, 36: 424–429.

STEPHENSON, A. B., 1975. Sperm whales stranded at Muriwai Beach, New Zealand. *N.Z. J. Mar. Freshw. Res.*, 9: 299–304.

TAVOLGA, M. C. 1966. Behavior of the bottlenose dolphin (*Tursiops trucnatus*). Social interactions in a captive colony. pp. 718–730. *In*: K. Norris, (ed.) *Whales, dolphins and porpoises*. Univ. of Calif. Press.

TAVOLGA, M. C., and F. S. ESSAPIAN., 1957. The behavior of the bottle-nosed dolphin (*Tursiops truncatus*); Mating, pregnancy, parturition and mother-infant behavior. *Zoologica, N.Y.*, 42: 11–31, 3 pls.

TAYLOR, R.J.F., 1957. An unusual record of three species of whales being restricted to pools in Antarctic sea-ice. *Proc. Zool. Soc. London.*, 129: 325–331.

TESTAVERDE, S. A., and J. G. MEAD., 1980. Southern distribution of the Atlantic whitesided dolphin *Lagenorhynchus acutus* in the western North Atlantic. *Fish. Bull. U.S.A.*, 78(1): 167–169.

TRUE, F. W., 1890. Observations on the life history of the bottlenose porpoise. *Proc. U.S. Nat. Mus.*, 13: 197–203.

TURNER, W., 1871. On the gravid uterus and on the arrangement of the foetal membranes in the Cetacea. *Trans. Roy. Soc. Edinb., 26*: 467–504.

WURSIG, B., and M. WURSIG., 1979. Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus,* in the South Atlantic. *Fishery Bull.*, 77(2): 399–412.

YAMADA, M., 1956. An analysis in mass osteology of the false killer whale, *Pseudorca crassidens* (Owen). *Okajimas Folia Anat. Jap., 28*: 451–463.