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Review of the biology and exploitation of striped dolphins in Japan

TOSHIO KASUYA

Faculty of Bioresources, Mie University, Tsu, Mie, 514-8507 Japan
E-mail: Kasuya@bio.mie-u.ac.jp

ABSTRACT

The biology, distribution, abundance and exploitation of striped dolphins off Japan are reviewed in an attempt to collate the available information required for a better understanding of the status of populations exploited by Japanese fisheries. Striped dolphins are found in summer in three geographical aggregations in the Pacific waters off Japan, between 20° and 42°N. Occurrence is seasonal in the northern part of the range. They are uncommon in the Sea of Japan, East China Sea and Ryukyuan waters. School structure is believed to be fluid. Weaned juveniles usually leave their natal schools to aggregate with individuals of similar age. Adults move between schools depending on sex and reproductive status. They have been harvested along the Japanese coast since at least the 19th century. An annual catch of up to 21,000 continued from the end of World War II to the end of 1950s. This has been followed by a gradual decline in catches despite demand for dolphin meat. Changes in life history parameters such as female age at sexual maturity and perhaps in female reproductive cycles have occurred over time. Japanese multispecies dolphin fisheries now receive an annual quota of 725 striped dolphins. Fragmented information on morphology, life history, pollutant levels and genetics suggests that the striped dolphins taken by Japanese fisheries are from more than one population, with varying proportions among fisheries and perhaps over time. Further study is needed to clarify population structure, immigration among populations, site fidelity and the function of dolphin 'schools'.

KEYWORDS: STRIPED DOLPHIN; FISHERIES; DIRECT CAPTURE; POPULATION PARAMETERS; GROWTH; PACIFIC OCEAN; STOCK IDENTITY; MOVEMENTS; POLLUTANTS; SOCIAL BEHAVIOUR; REGULATIONS; REPRODUCTION; TRENDS.

INTRODUCTION

Striped dolphins, *Stenella coeruleoalba* (Meyen, 1833), have been commercially hunted in Japan by either drive or hand-harpoon fisheries since at least the 19th century. Statistics are incomplete for the period before World War II. Since then, the catch has declined from over 21,000 dolphins to less than 1,000 after 1980. It is continuing in three regions (Fig. 1 shows all places referred to in the text): Taiji and adjacent areas of the Wakayama Prefecture; Futo on the Izu Peninsula of Shizuoka Prefecture; and Choshi in Chiba Prefecture (Kishiro and Kasuya, 1993). In 1993, the Japanese government established catch limits for all the dolphin fisheries and dolphin species (Kasuya and Kishiro, 1995).

The large harvest of striped dolphins has prompted numerous studies on both biology and management (e.g. Nishiwaki and Yagi, 1953; Kasuya, 1972; 1985; Miyazaki and Nishiwaki, 1978; O'Shea *et al.*, 1980; Honda *et al.*, 1982; Itano *et al.*, 1984a; b; Miyazaki, 1984). Conservation concerns led to a number of studies of distribution and abundance in the western North Pacific (e.g. Kasuya, 1976a; Kasuya and Miyashita, 1989; Miyashita, 1993).

The Scientific Committee of the International Whaling Commission (IWC) has been greatly concerned about the status of the population, and reviewed the topic several times since 1976 (IWC, 1977). The most recent review was in 1992 (IWC, 1993). They noted the decline in catches over about 30 years, changes in reproductive parameters in a manner consistent with a density-dependent response, and depletion of a possible coastal stock by the fishery. This concern was reiterated the following year (IWC, 1994).

This review summarises existing knowledge on the biology, population, exploitation and management of striped dolphins off Japan, and presents an interpretation of the results of these studies in the hope of assisting the scientific consideration of the current status of population(s) involved in the fishery.

DISTRIBUTION

An analysis by Kasuya (1982) indicated that striped dolphins inhabit warm offshore waters above 18°C in surface temperature; this was based on data collected in the western North Pacific mainly from spring to autumn. Off Japan, water of this temperature moves seasonally by latitude; i.e. between 42°N off Hokkaido and 33°N off Shikoku and Kyushu in the Pacific, and between 44°N at the Soya Strait and 32°N off western Kyushu in the Sea of Japan/East China Sea Area (Fig. 1). However, the distribution of the striped dolphin is probably influenced by more factors than surface water temperature, and its apparent temperature preference may change seasonally, as observed for the short-finned pilot whale (Kasuya *et al.*, 1988). This would explain why striped dolphins are found in all seasons of the year off Taiji (34°N), where the winter temperature is lower than the range given above.

Miyashita (1993) studied the distribution of striped dolphins in the western North Pacific in August and September, when the sea surface temperature was highest and the northerly movement had probably reached its peak. The northern limit of distribution was around 42°N in offshore waters east of 145°E. It is unlikely that animals would be found further north in coastal waters west of 145°E, where the cold Oyashio Current approaches from the north, but a limited number of sightings in relation to effort has prevented confirmation.

In winter, survey data have shown striped dolphins to be found from 10°-35°N and 120°-145°E (Miyashita *et al.*, 1996), including waters from the Kii Peninsula/Shikoku area to the eastern offshore waters of the southern Ryukyu Islands at around 23°N. However, these winter surveys have not covered the main fishing grounds of the current striped-dolphin fisheries, which operate in the winter season.

A 104-day sighting survey in the Sea of Japan and East China Sea in July and August made no striped dolphin

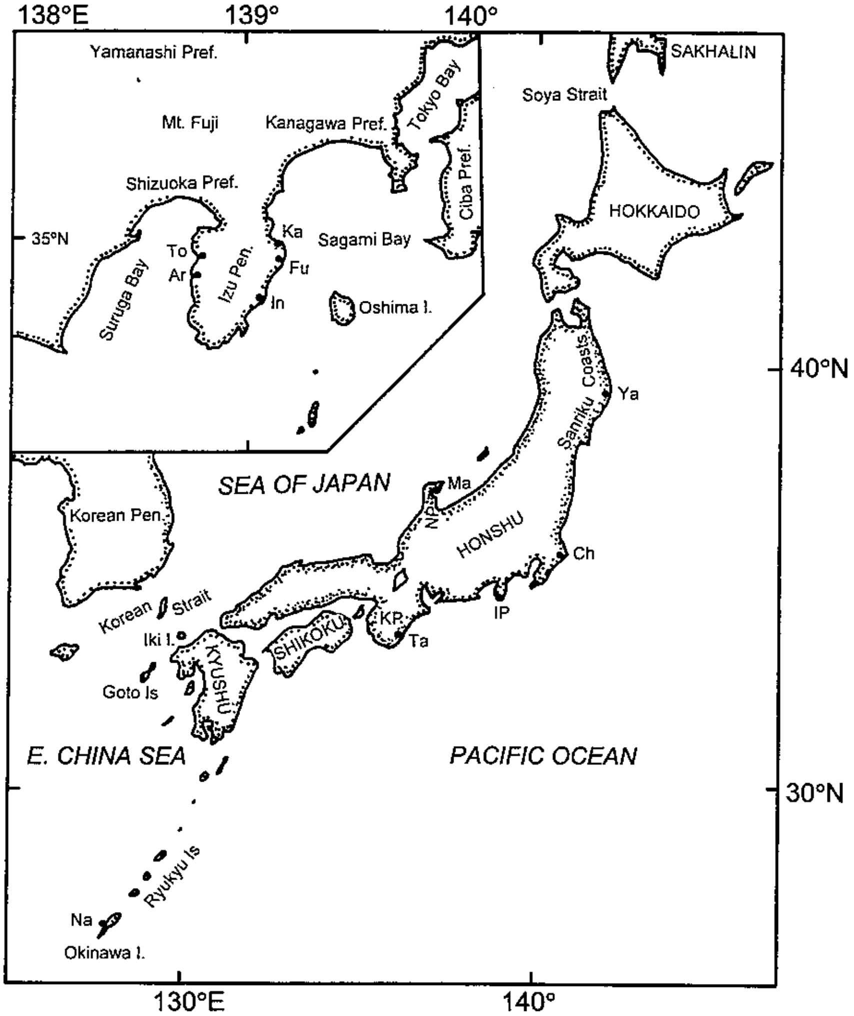

Fig. 1. Geography of area covered by the present review. Details of Izu area is shown in the inset map. Ar: Arari; Ch: Choshi; Fu: Futo; In: Inatori; IP: Izu Peninsula; Ka: Kawana; KP: Kii Peninsula; Ma: Mawaki; Na: Nago; NP: Noto Peninsula; Ta: Taiji; To: Toi; Ya: Yamada.

sightings (Iwasaki *et al.*, 1995). A similar survey from July to September in the Yellow Sea and East China Sea also resulted in no sightings (Miyashita *et al.*, 1995) as had several summer cruises in the Sea of Japan in earlier years (Kasuya, unpublished). Striped dolphins are also absent from the strandings records along the coasts of the Sea of Japan (Yamada, 1993) except for one mass stranding in May 1998 near Shimonoseki City, at the western end of Honshu (Anon., 1998).

This information suggests that striped dolphins are rare in the Sea of Japan. Winter occurrence is unlikely given the cold environment. It also concurs with their absence in the opportunistic driving operations in the Goto Islands or surveys made in the East China Sea in connection with the dolphin/fishery conflict in the Iki Island area (Anon., 1968).

There have been no confirmed striped dolphin sightings off Okinawa Island in the southern Ryukyu Islands (Uchida, 1985). They were similarly absent in the area in summer in more recent surveys (Iwasaki *et al.*, 1995) and only one sighting was made in winter in the northern part of the Ryukyu Islands (Miyashita *et al.*, 1996).

In China Taiwan there are only two records of striped dolphins, one was a landed animal at Suao north-eastern Taiwan (Yang, 1976) and the other was a skull found in a collection at National Taiwan Ocean University (Mizue, 1988 cited in Zhou *et al.*, 1995). Striped dolphins are apparently uncommon there (Yang, 1976). No confirmed striped dolphin specimens were found in 41 stranding incidents representing 15 cetacean species off Taiwan from 1990-1995 (Chou *et al.*, 1995), although they are apparently more common off Hong Kong (Parsons *et al.*, 1995).

In summary, striped dolphins are common along the Pacific coast of Japan south of 42°N, but they are uncommon or absent in the Sea of Japan, East China Sea and waters around the Ryukyu Islands (Fig. 2).

PAST DOLPHIN FISHERIES

Striped dolphins have been hunted in hand-harpoon and drive fisheries in Japan. The hand-harpoon, with a detachable head, has been known since the Jomon era (10,000-300BC) and has been used in the hunting of several marine species of suitable size, including dolphins and porpoises (Yamaura, 1996). The hunting of delphinoids using this technique was placed under the licensing systems of prefecture governments in 1989 (Kasuya, 1992).

Drive fisheries are effective for gregarious species; off Japan these are the tropical and temperate delphinids, including the striped dolphin. At least 52 Japanese villages have operated dolphin drive fisheries since the late 14th century; 6 on the Sea of Japan coast, 23 on the coast of the Korean Strait and the East China Sea, 1 at Okinawa Island and 22 on the Pacific coast (see Kishiro and Kasuya, 1993; Kasuya, 1994). They are all south of Yamada Town (39°28'N) on the Pacific coast or of Mawaki (37°20'N) on the Sea of Japan coast (Fig. 1). Except for three villages, Futo and Kawana on the Izu Peninsula and Taiji on the Kii

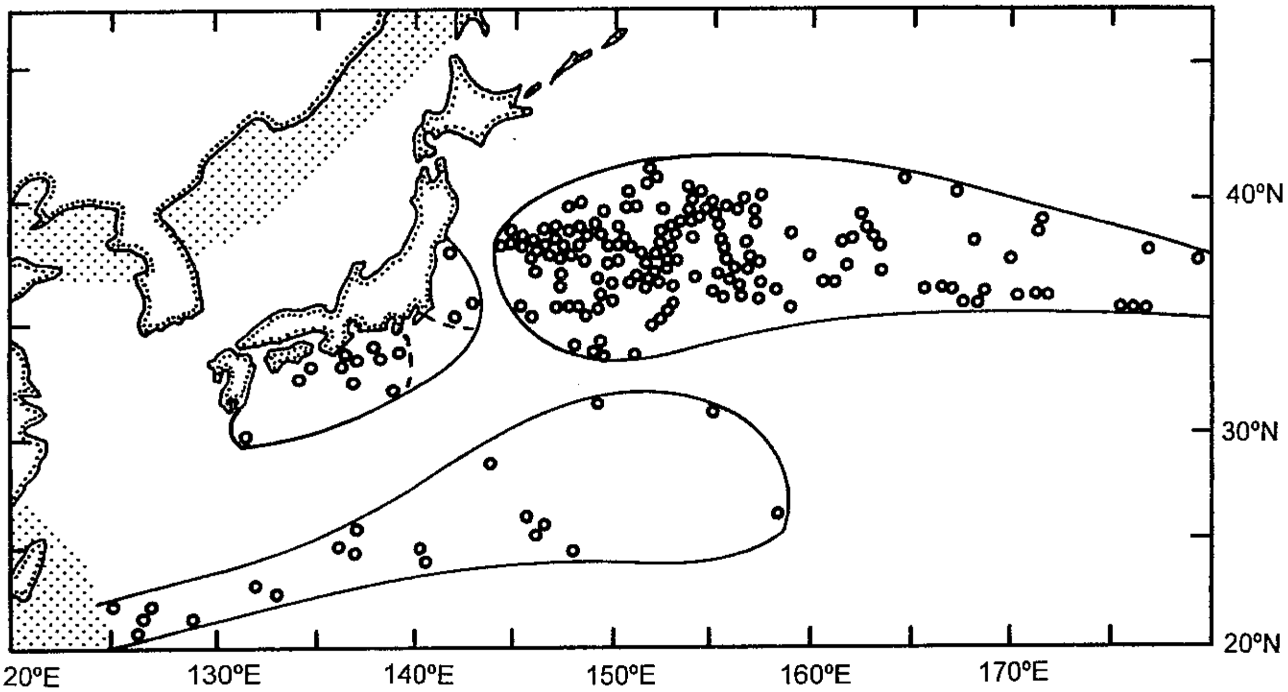

Fig. 2. Distribution of striped dolphins in the western North Pacific in July-September. Each circle represents a striped dolphin school in Miyashita (1993). Solid lines indicate my interpretation of three concentrations of striped dolphins in the western North Pacific, dotted lines sub-areas within the inshore concentration, and shaded area waters of insufficient data. Density of sighting effort is higher in coastal waters at 35°-43°N and west of 145°E, where sighting of striped dolphins are scarcer. Reproduced from figs 2-4 of Miyashita (1993) with permission.

Peninsula, most ceased operation before 1982, when the government placed drive fisheries under prefecture licensing systems.

The species taken by the earlier drive fisheries are unknown and no striped dolphin catch statistics exist. However, striped dolphins are unlikely to have been the major target of the fisheries in the Sea of Japan and East China Sea (including Okinawa), if the delphinid fauna has remained similar. This is partially supported by the absence of striped dolphin remains at the Mawaki archaeological site of dolphin hunting in the Jomon era, where many remains of common (*Delphinus delphis*), Pacific white-sided (*Lagenorhynchus obliquidens*) and bottlenose dolphins (*Tursiops truncatus*) and pilot whales (*Globicephala* sp.) were found (Hiraguchi, 1993). The exploitation of striped dolphins in villages around Taiji in central Japan is recorded in old scrolls (Yuboku, *ca.* 1660).

EXISTING FISHERIES FOR STRIPED DOLPHINS

Current Japanese fisheries for striped dolphins are limited to drive fisheries on the Izu Peninsula and in Wakayama Prefecture and hand-harpoon fisheries in Chiba and Wakayama Prefectures. Opportunistic driving at Nago, Okinawa and a subsequent crossbow fishery have reported no catches of striped dolphins (Fig. 1).

Drive fisheries on the Izu coast, Shizuoka Prefecture

(1) Operating bodies

The Izu Peninsula (Fig. 1) is surrounded by rugged shorelines. It is 55km in length and has a maximum width of 35km. It projects southward from the Pacific coast of central Japan at 35°N, 139°E and separates Sagami Bay to the east and Suruga Bay to the west. Ohsumi (1972) described the method of dolphin driving on each side of the Peninsula.

Such fisheries on the Izu coasts have been known since 1619 (Shibusawa, 1982). In the late 19th century, Kawashima (1894) recorded over 20 villages operating opportunistic dolphin drive fisheries. After World War II, scientists confirmed that the catches were almost exclusively striped dolphins which were called *mairuka* ('true' or 'common' dolphin) by the local fishermen. A species of the same vernacular name was the major target of the drive fishery that operated in the late 19th century on the Izu coast (Kawashima, 1894). The target species was described as weighing 90-200kg and was found in schools of over 1,000 individuals. The drives were carried out mainly in winter. All this leads to the conclusion that *mairuka* is likely to have referred to the striped dolphin since at least the late 19th century.

Following Kawashima's summary (1894), the Bureau of Fisheries (1911) reviewed the dolphin harvest. They recorded drive fisheries at eight villages on the Izu Peninsula but it is not clear if this was an exhaustive list or merely selected examples. A decline in the number of operating groups occurred during the early 20th century (see below), but little is known of the pre-War operations.

During World War II and the post-war period, the Izu fishery underwent expansion both in the number of operating groups and the number of dolphins taken (Shizuoka Board of Education, 1986; 1987; Nakamura, 1988), as a response to the difficulty of offshore fishing during the war and to the food shortage after the war. Postwar operations took place at the five villages of Arari, Futo, Inatori, Kawana and Toi (Nakamura, 1988). Of these, only Futo had not been recorded by Kawashima (1894).

Inatori resumed the fishery in 1947, after 50 years' cessation and Toi in 1946/47, after a cessation of unknown length (Nakamura, 1988). Both villages again ceased operations, sometime before 1961, when the fishery was investigated by M. Nishiwaki and S. Ohsumi (Kasuya, 1985).

Arari, which was very dependent on the dolphin drive fishery during the war, made its last significant catch in 1961 (Miyazaki, 1983; Kasuya, 1985) and was reported to have dissolved its driving team in 1973 (Shizuoka Board of

Education, 1987). However, it acquired an operating license in 1982 when the fishery came under the licensing system of the prefecture (Kishiro and Kasuya, 1993).

Kawana began a drive fishery for dolphins (presumably striped dolphins) in December 1882. Its last drive was made in 1983. It is unknown when the Futo drive fishery began. The first record is of a confrontation between driving vessels from Futo and Kawana in 1903 (Nakamura, 1988). Both teams considered the other as a competitor when I started examining their catches in 1961. However, they combined operations in autumn 1968 and this co-operation lasted until autumn 1983. Futo is now the only village operating a regular dolphin drive on the Izu coast (Shizuoka Board of Education, 1986; 1987).

(2) Change in the technology

The equipment used in the Izu drive fishery has changed over time (Kasuya and Miyazaki, 1982; Kasuya, 1985; Shizuoka Board of Education, 1986; 1987; Nakamura, 1988). In the early days, sail assisted rowing boats operated within several n.miles from the coast (Kawashima, 1894; Kasuya and Miyazaki, 1982). The use of motor driven vessels began in the 1920s and resulted in an expansion of the searching range to 20 n.miles from the port or the entire Sagami Bay area (Kasuya, 1985). The Shizuoka Bureau of Education (1987) reported that motor driven vessels were introduced to Kawana in 1900 and that the number increased slowly until 1925 when it underwent a nearly four-fold increase within a single year. A similar improvement probably occurred around the same time in the other Izu villages. Although no records are available, it seems likely that improvements to the efficiency of these vessels continued after their introduction in the 1920s.

Three high-speed motor vessels were introduced to Kawana in 1962, and occasionally searching expanded outside Sagami Bay, reaching up to 50 n.miles from port (Kasuya and Miyazaki, 1982). When first introduced, the maximum speed was 13 knots. This had increased to 40 knots by the time of the last operation in 1983 (Shizuoka Board of Education, 1987). Futo soon followed Kawana in the use of such high-speed boats.

In 1968, when Kawana and Futo began cooperative operations, four high-speed boats, two from each village were used, and this continued until these operations ceased in 1983. The last Izu drive fishery at Futo used two high speed boats from 1984-86 and has used one since then (Miyazaki, 1983; Kishiro and Kasuya, 1993). In addition, the fishery often utilises reports of dolphin sightings by other fishing vessels. In recent years, Kawana fishermen have sent information on sightings of striped dolphins to Futo fishermen and received 3% of the profit obtained from their drives (Shizuoka Board of Education, 1987).

(3) Regulations

Kishiro and Kasuya (1993) summarised regulations and the operation of the fishery. In 1951, Shizuoka Prefecture introduced a license system for all nominal drive fisheries in the prefecture (actual drives were known only for dolphins), and banned the establishment of new driving teams. In 1959, the fishing season was limited to the September-March period for the three license holders of the prefecture. The first effective catch limit was established in 1991, when a limit of 657 dolphins (species not specified) proposed by the Fisheries Agency for the entire Shizuoka Prefecture was accepted by the prefecture for the Futo fishermen. Quotas by species were first established in 1993. The fishery currently operates (Kasuya, 1997) with a quota of 600 dolphins comprising 70 striped dolphins, 75 bottlenose dolphins and 455 pantropical spotted dolphins (*Stenella attenuata*).

Although the fishing season extends from September to March, the Futo fishery actually ends in December.

Drive fishery off Taiji, Wakayama Prefecture

(1) Operating groups

Exploitation of various cetacean species at Taiji and the nearby area has continued since at least the early 17th century. The right to drive dolphins had already been authorised in the 19th century (S. Matsui, pers. comm.) and an opportunistic dolphin drive was recorded in 1933 (Hamanaka, 1979; Kasuya and Marsh, 1984; Kishiro and Kasuya, 1993). The current dolphin drive team was started in 1969 (for short-finned pilot whales) by a group of fishermen using eight vessels and a method learned from the Izu fishermen. Striped dolphins were included in 1973. Another drive team of seven vessels started in 1979. The two competing teams merged in 1982 and operated using a total of 15 vessels. The number of vessels decreased to 14 in the 1984/85 season (Kishiro and Kasuya, 1993).

(2) Method of operation

No significant changes in recent driving technology have been documented for the Taiji fishery, and the size of vessels has remained unchanged (Kishiro and Kasuya, 1993). However, the same authors reported increase in daily searching effort in recent years. Daily searching activity used only half (6-7 vessels) of the total vessels (15 vessels) until at least the 1984/85 season. Use of the full fleet started in 1990/91 or earlier.

Another factor affecting the searching effort of the team is cooperation with other fisheries vessels. Initially the drive team used to receive news of dolphin sightings in exchange for gratuities, but it started to pay for the information around 1988, when small-type whaling returned to Taiji and began to compete with the driving team for short-finned pilot whales (*Globicephala macrorhynchus*) and Risso's dolphins (*Grampus griseus*). Whaling vessels may also buy such information from particular fishing or whale-watching vessels. This will clearly increase the searching efficiency of the drive fishery, but quantifying this is difficult.

(3) Regulations

Wakayama Prefecture placed the Taiji drive fishery under its license system in 1982. The fishing season was limited to October-April and voluntary catch limits of 500 short-finned pilot whales and 5,000 other delphinids (without specification of species) were set. These became obligatory in 1986. The number of licensed vessels decreased from 15 to 14 in the 1986/87 season in concurrence with the actual decline that occurred in 1984/85.

In 1991, the catch limit was reduced to 2,900 delphinids including a maximum of 500 short-finned pilot whales. This was further reduced in 1992 to a total of 2,500 delphinids including a maximum of 1,000 striped dolphins and 300 short-finned pilot whales. This was the first catch limit set for striped dolphins in Japan.

In 1993, the Government set catch limits for six species of delphinids (Risso's, pantropical spotted, striped and bottlenose dolphins, false killer whales, *Pseudorca crassidens* and short-finned pilot whales) and the Dall's porpoise, *Phocoenoides dalli*, for the drive and hand-harpoon fisheries. The take of other small cetaceans by these fisheries is prohibited. The current drive fishery at Taiji operates with a total limit of 2,380 dolphins and a season of October to February, with an extension for short-finned pilot whales until the end of April. The quota comprises 450 striped dolphins, 890 bottlenose dolphins, 400 pantropical spotted dolphins, 300 Risso's dolphins, 40 false killer whales and 300 short-finned pilot whales (Kasuya, 1997).

Hand-harpoon fishery at Choshi, Chiba Prefecture

Ohsumi (1972) reported annual landings of 200-3,000 dolphins in Chiba Prefecture during 1957-1970. Kasuya and Miyazaki (1982) reported on a hand-harpoon fishery off Choshi, Chiba Prefecture (Fig. 1), for various dolphin species (including striped dolphins) and estimated the mean annual catch at 1,500 striped dolphins.

This hand-harpoon fishery now operates from November-April, using 14 vessels, with a catch limit of 80 striped dolphins.

Hand-harpoon fishery in Wakayama Prefecture

The fishermen of Taiji used to harpoon striped dolphins and other delphinids for local consumption. Their annual catches of striped dolphins ranged from a few hundreds to 2,000 individuals from 1963-1973 (Kasuya, 1985). When the drive team expanded operations to striped dolphins in 1973, the hand-harpoon fishery became unprofitable; and only about 15 vessels obtained licenses in 1989 when the hand-harpoon fishery for dolphins came under control of the Regional Fishery Adjustment Commission.

However, about 147 vessels from the Wakayama Prefecture, including some from Taiji, started harpooning dolphins in 1991 off the coast of Wakayama Prefecture. This became a political issue, and all the vessels finally obtained licenses. The fishery now operates from February to August with a total quota of 520 dolphins, comprising 100 striped dolphins, 100 bottlenose dolphins, 70 pantropical spotted dolphins, and 250 Risso's dolphins.

CATCH STATISTICS

Table 1 presents statistics of dolphins taken at Futo provided to me in the late 1970s by the coastal division of the Fisheries Agency. Table 2 (overleaf) reports all the catch statistics of striped dolphins available in published reports. Further details of the statistics are described below.

Izu coasts

Tobayama (1969) examined the species composition of dolphins taken in drive fisheries on the Izu coast for selected seasons. Kasuya and Miyazaki (1982) estimated that about 96.7% of the catch was composed of striped dolphins. They reported the mean annual catch (and the range) for the Izu coast between 1942-53 as Arari, 7,394 (277-20,131) and Kawana, 2,003 (0-5,311).

Catches by other villages on Izu coasts (e.g. Futo, Inatori and Toi) are not available for that period; it is known that Futo was relatively inactive.

Ohsumi (1972) presented catch statistics for 'dolphins' by prefecture in 1957 to 1970. The annual catch for Shizuoka Prefecture (almost exclusively along the Izu coast) fluctuated between 3,601 and 21,432. Kasuya and Miyazaki (1982) used correction factors derived from Tobayama (1969) to analyse Ohsumi's (1972) data by species: the estimated average annual catch of striped dolphins off Japan in the late 1950s to early 1960s was: Izu, 11,000; Chiba, 1,500; Taiji, 630; other areas, 1,000; Total, 14,000.

Miyazaki *et al.* (1974) were the first to report statistics for striped dolphins at Arari (1950-1970), Kawana and Futo (1949-1973) and Taiji (1963-1972). Kasuya (1976b) presented earlier catches missing in Miyazaki *et al.* (1974), i.e. for Arari (1942-1956) and Kawana (1942-1953).

Table 1

Japanese catch of striped dolphins by prefecture. •: no data; +: negatively biased due to incomplete coverage; -: positively biased due to inclusion of species other than striped dolphins.

Year	Chiba[1]	Shizuoka[2]	Wakayama[3]	Total
1942	•	21,591+	+	21,591
1943	•	7,763+	+	7,763
1944	•	7,660+	+	7,660
1945	•	7,319+	+	7,319
1946	•	8,180+	+	8,180
1947	•	95+	+	95
1948	•	5,892+	+	5,892
1949	•	13,441+	+	13,441
1950	•	15,186+	+	15,186
1951	•	11,899+	+	11,899
1952	•	8,152+	+	8,152
1953	•	4,059+	+	4,059
1954	•	298+	+	298
1955	•	2,669+	+	2,669
1956	•	8,991+	+	8,991
1957	•	3,172	+	3,172
1958	•	3,681	+	3,681
1959	•	21,953	+	21,953
1960	•	4,418	+	4,418
1961	•	10,569	+	10,569
1962	•	8,554	+	8,554
1963	•	8,509	331-	8,840
1964	•	6,428	934-	7,362
1965	•	9,696	642-	10,338
1966	•	8,371	422-	8,793
1967	•	3,664	819-	4,483
1968	•	9,250	400-	9,650
1969	•	3,130	499-	3,629
1970	•	5,348	997-	6,345
1971	•	3,315	1,717-	5,032
1972	•	7,235	700-	7,935
1973	•	6,799	727-	7,526
1974	•	11,715	967-	12,682
1975	•	5,996	759-	6,755
1976	•	5,175	1,053-	6,228
1977	•	4,020	562-	4,582
1978	•	2,028	1,644-	3,672
1979	•	1,300	893	2,193
1980	•	5,220	11,017	16,237
1981	•	73	4,710	4,783
1982	•	246	1,758	2,004
1983	•	40	2,179	2,219
1984	•	925	2,812	3,737
1985	•	578	2,639	3,217
1986	10	0	2,760	2,770
1987	20	0	369	389
1988	38	356	1,767	2,161
1989	48	102	1,000	1,150
1990	67	0	796	863
1991	14	32	971	1,017
1992	0	0	1,045	1,045
1993	6	0	538	544
1994	7	0	528	535
1995	6	0	533	539
1996	0	0	303	300
1997	0	0	702	702

[1] Hand harpoon fishery off Choshi from Japanese Progress Reports to IWC (no data for operation before 1986).

[2] Drive fishery off the Izu coast from Kishiro and Kasuya (1993) before 1992, and Japanese Progress Reports to IWC (1992-1996 fishing seasons).

[3] All fisheries taking striped dolphins, from Kishiro and Kasuya (1993) before 1992, and Japanese Progress Report to IWC (1992-1994 fishing seasons).

Table 2

Catch of all 'dolphins' at Futo, Izu coast, during the early stage of post World War II operations. Provided by Coastal Division, Fisheries Agency.

Year	Dolphins	Year	Dolphins
1950	0*	1961	8,606
1951	0*	1962	4,132
1952	120*	1963	4,599
1953	31*	1964	3,795
1954	0*	1965	8,757
1955	117*	1966	7,154
1956	484*	1967	1,250
1957	421*	1968	3,382
1958	1,060	1969	1,775
1959	2,848	1970	2,867
1960	3,172	1971	3,131

*: These figures are not included in Miyazaki *et al.* (1974) and Kishiro and Kasuya (1993), but are included in Table 2 of this study.

Miyazaki (1983) and Kishiro and Kasuya (1993) updated these statistics using data collected by the Fisheries Agency. Thus the striped dolphin statistics for the Izu fishery cover the following seasons: Arari, 1942-1970 (last significant drive in 1961); Kawana, 1942-1983 (last drive in 1983); Futo, 1949-1991 (missing years in 1950s); Inatori, missing (no operation since the 1960s).

Arari recorded a large catch of 20,131 individuals in 1942, the first year for which statistics are available, suggesting that it had started operations considerably earlier. Annual catches at Futo were small at 0-500 in 1950-1957 before increasing to 1,200-8,700 in the 1960s (Table 2). This suggests that the Futo team resumed post-war operations in the late 1940s or early 1950s. The currently available statistics for the drive fisheries off the Izu coast are complete from 1958 as summarised by Kishiro and Kasuya (1993). Some fragmentary 19th century statistics are available in Kawashima (1894). Other villages on the Izu coast may have operated driving dolphins for some pre-World War II period, but no statistics are available.

Taiji, Wakayama Prefecture

Miyazaki (1980) compiled statistics of striped dolphins landed at the Taiji wholesale market for 1963-1979. He used the numbers of dolphin viscera sold at the market as an indicator of the number of dolphins landed. However, because viscera were not separable between striped and pantropical spotted dolphins in the records, his striped dolphin statistics could have included small numbers of the latter species.

The Fisheries Agency started to collect statistics by species for each prefecture in 1979, and these data were used in Miyazaki (1983). Kishiro and Kasuya (1993) further extended the time range of the statistics using Fisheries Agency statistics.

Earlier statistics for Taiji could include striped dolphins taken by the hand-harpoon fishery and in small-type whaling. However, only drive and hand-harpoon fisheries now take the species there.

LIFE HISTORY STUDIES

Age determination

Most of the studies of life history of striped dolphins off Japan used carcasses from the drive fishery at Kawana and Futo on the Izu coast. Nishiwaki and Yagi (1953) made the first attempt to determine the rate of deposition of dentine layers by injecting lead acetate as a marker. However, the short survival time of the dolphins meant that no conclusions could be drawn. Using samples obtained from October to January, Kasuya (1972) examined the innermost dentine in the pulp cavity and found that alternation from opaque to translucent dentine occurred during November-December ($n = 275$ for November-January). A similar conclusion (December-January) was reached by Miyazaki (1977a; $n = 209$ for November-January). Their conclusion of annual dentine deposition of dentinal layers (one opaque and one translucent layer = one Growth Layer Group – GLG – see IWC, 1980) assumed that dentine will alternate from translucent to opaque layers sometime in early summer.

Kasuya (1976a) found cessation of dentine deposition at various ages over 10 GLGs after which age the use of cementum layers is necessary for unbiased age estimation. Some of the earlier studies based only on dentine layers (e.g. Kasuya, 1972; Miyazaki, 1977a; b; Miyazaki and Nishiwaki, 1978) are thus questionable for individuals over 10 GLGs.

Neonatal length

A simple comparison of the largest foetus and the smallest neonate found from samples collected from the Izu fishery gave a range of 90-110cm for neonatal length but the number of foetuses (73) was much greater than neonates (17) which might lead to a biased estimate (Kasuya, 1972). Kasuya (1972) corrected for this and estimated the mean neonatal length at 99.8cm. A similar analysis by Miyazaki (1977a) using different samples but again from the Izu fishery (68 foetuses at 95-108cm and 20 neonates at 98-115cm) resulted in almost the same estimate (100.5cm).

Body length frequency and mean growth curve

Kasuya (1972) reported the maximum body length of 567 females examined on the Izu coast from 1967-1970 as 243-247cm and the modal length as 223-227cm; corresponding values for males ($n = 391$) were 258-262cm and 238-242cm. The maximum body lengths from 47 animals killed for research purposes in the northern offshore concentration in 1992 (Fig. 2) were 251cm (females) and 257cm (males) (Iwasaki and Kasuya, 1993), similar to those from off the Izu coast (Kasuya, 1972).

Iwasaki and Goto (1997), using samples collected at Taiji for the 1991/92-1994/95 seasons, reported the maximum body length and modal length of females at 238cm and 210-219cm ($n = 412$) and of males at 249cm and 220-229cm ($n = 301$). They believed that the striped dolphins taken off Taiji were smaller than those studied by Kasuya (1972) on the Izu coast. The body length difference is about 10cm in females and 15cm in males and appears to be significant (see *Stock Identity*).

The mean asymptotic length of striped dolphins has been estimated from an age/length relationship for the Izu sample representing six schools in 1971-1975 (Kasuya, 1976a). The mean growth curve was determined visually to reach a plateau at age 21 years or at 236cm ($n = 41$, SD = 6.1) for males and 17 years or at 225.3cm ($n = 89$, SD = 15.3) for females. However, Miyazaki (1984), combining an Izu sample (28 schools in 1970-1973) and about 10% of the sample from Taiji (2 schools by driving plus catches by the hand-harpoon fishery in 1973, 1979 and 1980; see Fig. 8 for samples), estimated the corresponding figures as 17 years and 238.9cm for males and 11 years and 225.7cm for females. As the two studies agreed on the asymptotic body lengths but not the ages, this suggests disagreement in age reading or interpretation of growth curves. Little if any growth occurred after 11 years (females) or 17 years (males) in Kasuya (1976a) and the disagreement may be insignificant. A similar analysis by Miyazaki (1977a) is not considered here because it is based on ageing by dentinal layers.

Subsequently, Miyazaki (1984) constructed mean growth curves using larger sample sizes ($n = 3{,}362$) from the Izu fishery in 1970-1973 plus the additional samples from Taiji referred to above (Fig. 3). Individuals aged around 40 years in his sample would have been born between 1930-1940, and those around 17 years between 1953-1963. If the mean asymptotic length had significantly increased between the above two time periods in response to a decline in density then one might expect some increase in the mean body lengths for animals > 17 years on the mean growth curve. No such change is evident in the growth curves of Miyazaki (1984) (Fig. 3) or of Kasuya (1976a). This does not exclude the possibility, however, that density dependent growth changes either only occurred before physical maturity or that changes in asymptotic body lengths occurred for individuals born after 1953-1963 or before 1930.

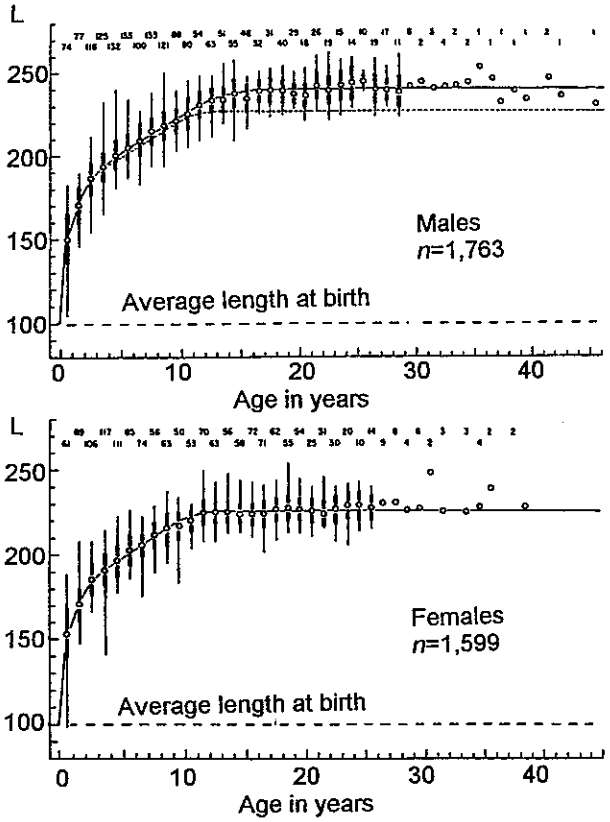

Fig. 3. Mean growth curve of striped dolphins constructed using samples obtained at Izu and Taiji in 1970-1980. Open circles indicate mean, vertical line range and black box two standard deviations. L = body length in cm. Numbers are sample sizes. Reproduced from figs 4 and 5 of Miyazakai (1984) with permission.

Similar analyses have been made in an attempt to look at density-dependent responses, usually with inconclusive results, for southern minke whales (Kato, 1987), North Pacific sperm whales (Kasuya, 1991), long-finned pilot whales (Bloch *et al.*, 1993) and Baird's beaked whales (Kasuya *et al.*, 1997). It has also been suggested that density-dependent improvements as a result of growth changes may be reflected in the age at sexual maturity rather than the lengths at sexual maturity or physical maturity (e.g. Read and Gaskin, 1990). Kasuya (1985) identified possible density-dependent changes in the age at sexual maturity for female striped dolphins born between the late 1950s and early 1970s (see *Sexual maturation of females*).

Sexual maturation of males

(1) Definition and age at maturation

Male sexual maturity was studied by Miyazaki (1977a) using ages based on dentine GLGs and by Miyazaki (1984) using cementum. Both studies used a similar sample set obtained from the Izu coast, with some additional samples from Taiji (see Fig. 8).

Classification of testicular maturity by Miyazaki (1977a; 1984) was in two steps. First he examined an unspecified number of tubules at the testicular centre and classified the testes into three categories: 'immature' without spermatogenetic tubules; 'puberty' with spermatocytes and without spermatozoa; and 'mature' with at least one spermatozoon. He further classified 'mature' testes, by examining 20 tubules, into: 'MI' having spermatozoa in one tubule; 'MII' spermatozoa in 2-19 tubules; and 'MIII' spermatozoa in all tubules examined. His maturity stages against testicular weight and age are shown in Table 3.

Table 3

Comparison of maturity, testis weight (g) and age (year) of male striped dolphins between authors.

Miyazaki (1977; 1984)			Iwasaki and Goto (1997)	
Stages	Weight	Age	Stages	Weight
Immature	<10	<15	Immature	<10
Puberty	4-40	2-14	Early maturing	5-37
MI	7-90	6-30	Late maturing	15-64
MII	15-200	6-30	Mature	12-229
MIII	40-225	7-46		

Testicular weight increased rapidly between 6-16 years, after which the correlation was weak (Kasuya, 1976a; Miyazaki, 1984). Spermatogenesis started between 2-10 years, and half of the males had reached his mature stage at age 8.8 years (Miyazaki, 1984).

The weights of testes at the M1, MII and MIII stages did not change greatly with age, but Miyazaki (1984) found that the proportion of MIII animals increased with age. At 16.5 years, half of the males were at the MIII stage and for most males at the MIII stage, the weight of single testis was > 80g. He also observed that males driven with females near oestrous tended to contain more males > 16.5 years than those taken with mature females at other reproductive stages. From this he concluded that MIII coincided with the attainment of social maturity.

In any analysis of male maturity, it is important to try to disentangle the effects of the male maturation process, seasonal cycles in males and male behaviour relative to the female cycle (also see *Seasonality in reproduction*).

Komyo (1983) studied the diameter of seminiferous tubules and the density of spermatozoa in the epididymal fluid using samples from the Izu coast. He confirmed histologically that the maturity stage did not vary among positions in an individual testis. The mean tubule diameter increased in three phases: (1) a rapid growth phase at testis weight < 40g; (2) slower growth at 40-110g; and (3) a plateau (about 200μm) at testis weight > 110g. The smallest testis with spermatozoa in the epididymis was 7.2g and the largest testis without spermatozoa was 57.2g. The highest sperm density (135×10^6/ml) was found at a testes weight of 50-60g. The density of epididymal sperms increased rapidly at a testis weight of 40-60g. By 100g it had reached a plateau of about 55×10^6/m although with wide individual variation of 25-100 ($\times 10^6$/ml). Komyo (1983) believed that males with epididymal sperm density $\geq 25 \times 10^6$/ml could be reproductively successful. Such densities could be found at testis weights >34.5g; all males with testes >86.2g had such densities. These testicular weights roughly agree with the social maturity classification of Miyazaki (1984). Age was not analysed by Komyo (1983).

Iwasaki and Goto (1997) determined four maturity stages of males taken off Taiji in winter 1993/94 and 1994/95 based on proportion of spermatogenetic tubules in the testicular centre (Kasuya and Marsh, 1984): (1) 'immature', no spermatogenetic tubules; (2) 'early maturing', $>0\%$ and $<50\%$; (3) 'late maturing', $>50\%$ and $<100\%$; and (4) 'mature', 100%. From this they concluded that half of the males were 'mature' when the mean weight of the two testes reached 40g. Ages were not estimated in this study.

There are difficulties in comparing these two approaches to assigning maturity stages. The use of a particular phase in the spermatogenetic cycle to classify maturation stages requires caution; the spermatogenetic cycle last only weeks and the phase varies between positions in a tubule, whilst the process of testicular maturation lasts for years. Further questions arise in the context of sample size; sampling of fewer tubules may result in a greater instability in classification.

No analyses trying to relate changes in age at the attainment of male sexual maturity with population density changes over time have been undertaken.

(2) Body length at maturation

Iwasaki and Goto (1997) found in the Taiji sample that spermatogenesis started at body lengths of 190-229cm. The smallest 'mature' male was 200-209cm and the largest male in the earlier stages 230-239cm; 50% of males were 'mature' at 224.4cm. It should be remembered that estimates of average body length at sexual maturity will be influenced by the age composition of the sample, e.g. a sample with a high proportion of juveniles (see *Segregation of juveniles*) may result in a greater estimated body length at sexual maturity.

Miyazaki (1984) found that 50% of his sample had spermatozoa in the testis (i.e. his MI to MIII stages) by age 8.8 years and obtained mean body length of 219cm by fitting this age to the mean growth curve. However, this body length is not necessarily equal to the length at which 50% of individuals are in the MI-MIII stages, because growth decreases after sexual maturity, and there is great individual variation in body length.

The two body-length estimates are not directly comparable due to differences in the definition of maturity chosen and the methods employed.

Again no attempts to examine this parameter in the context of a density-dependent response have been made.

Sexual maturation of females

Sexual maturity has been determined by the presence of at least one corpus luteum or albicans in the ovaries representing ovulation. About 70% of females having one corpus luteum or albicans were either pregnant or lactating (Miyazaki, 1984). This suggests that at least 70% of females conceived at their first ovulation; many of the remaining 30% will experience a second ovulation in the same season and have a high probability of conception. Since gestation time is believed to be about one year (see *Female reproductive cycle*), the age at first reproduction is close to one year after the first ovulation.

(1) Geographical variation

Using a sample from the Izu fishery in 1968-1971 ($n = 26$ for 8-10 layers) and ageing by dentine layers, Kasuya (1972) concluded that sexual maturity occurred at 8-10 years, with an average of 8.8 years. A similar study by Miyazaki (1977a) gave the age range of 4-12 and an average age of 8.8 years using a larger sample from the Izu fishery ($n = 363$ for 4-12 layers). These results were similar to those of a later study by Kasuya (1976a) who used cementum layers (mature at 5-12 years with an average of 8.5 years, $n = 110$ for the age range).

The smallest sexually mature female taken in the Izu fishery was 188-192cm long and the largest immature female was 218-222cm long ($n = 567$ for all postnatals), with 212cm as a rough estimation of body length at 50% maturity (Kasuya, 1972). Miyazaki's (1977a) estimate of 8.8 years, corresponded to 216cm on his mean female growth curve.

Using samples from Taiji for the 1991/91-1994/95 seasons, Iwasaki and Goto (1997) reported that the smallest mature females were around 190-199cm and the largest immatures around 220-229cm ($n = 259$). The reason for the differences in these ranges from the Izu sample (Kasuya, 1972) is difficult to ascertain given the differences in length groupings. They calculated mean length at sexual maturation at 199.8cm, about 12cm smaller than the corresponding figure for the Izu sample in 1968-1971.

(2) Density-dependent changes

Kasuya (1985), using samples from the Izu coast, examined historical changes in female age at sexual maturity. He compared the average age at sexual maturity (determined as the age at which 50% of individuals are mature) and variation between year classes in age at maturation. The average maturation age declined from about 9.4 years in 1956-58 cohorts to about 7.5 years in 1968-70 cohorts. The age of the youngest mature female also declined: females matured at >8 years for the 1956-62 cohorts, 7-9 years for the 1963-67 cohorts and 5-9 years for the 1968-71 cohorts. He interpreted these changes to reflect improvement in growth due to increased *per capita* food availability resulting from depletion of striped dolphin stocks off the Izu coast.

There are a number of potential confounding factors that may affect interpretation of the apparent density dependent response of striped dolphins. For example, the observed acceleration of growth occurred while the fishery moved offshore. A lowered proportion of a 'coastal stock' in the catch could either mask or enhance real changes in the coastal population if growth-parameter differences exist between the populations. One proposed mechanism for density-dependent responses is that *per capita* food supply increases as abundance decreases. However, if an unexploited dolphin population competed with the coastal striped dolphins for resources, then this might suppress acceleration of growth in the striped dolphin stock. The drive fishery for pantropical spotted dolphins started in 1959, possibly due to a decline in the availability of striped dolphins, and continued at a low level (Miyazaki *et al.*, 1974; Kasuya, 1985). The absolute effect of this harvest is unknown, but it may have enhanced the density-dependent response of striped dolphins if they competed for resources. In addition, possible changes in food availability for striped dolphins due to fishing activities needs further investigation.

At least one species of squid in the diet of striped dolphins is also known to be harvested by Japanese coastal fisheries (see *Food habits*).

No attempts to relate changes in body length at the attainment of sexual maturity over time with population abundance have been made.

Female reproductive cycle

(1) Gestation period

The short fishing season (October to December) and apparently extended breeding season means that it is not possible to reliably estimate the foetal growth curve of striped dolphins off Japan based on monthly samples of foetal body lengths. The need to disentangle seasonal growth of foetuses, school specific foetal length compositions and the effect of foetal size on the timing of migration to fishing grounds also confound efforts to determine the female reproductive cycle and foetal growth (see *Seasonality in reproduction*).

Kasuya (1972) observed that foetal body lengths in October-December samples from the Izu coast were continuous from <5cm to >100cm with three modes at <10cm, 40-60cm and 70-105cm. He concluded that their breeding was diffusely seasonal and that the gestation period was about 12 months. The 40-60cm mode of foetal lengths would represent conception in the early summer. Miyazaki (1984) plotted monthly foetal modes from an October-January sample plus a May sample from Nishiwaki and Yagi (1953) from Arari (see Fig. 5 on p. 91). A linear regression of the five means he believed to represent growth of foetuses conceived in February and March was used to obtain a gestation time of 13.4 months.

There appears to be a general positive correlation between neonatal body length and gestation period in toothed whales (e.g. Kasuya, 1985). The mean neonatal length and observed gestation period of the finless porpoise, *Neophocaena phocaenoides*, were about 78cm and about 11 months, respectively; those of Commerson's dolphins, *Cephalorhynchus commersonii*, about 100cm and 11.3 month; and those of bottlenose dolphins 117-128cm and 12.2 months (see Kasuya, 1995). This suggests that the gestation time of striped dolphins will be about 11-12 months.

(2) Age-dependent changes in female reproductive cycle

Kasuya (1985) examined age-dependent changes in the female reproductive cycle off the Izu coast using proportions of various reproductive classes in a sample from 1960-1980. Three parameters (mean length of lactation, resting period and calving interval) increased with age and the regression coefficient was significantly different from zero. However, the magnitude of the change in the calving interval (which showed the most distinct change) was so small that the 2-year cycle detected at age <15 years did not increase to 3 years until age >40 (uncorrected for sample bias, see below). Thus any age-dependent decline in reproductive activity of females seems inconsequential.

The oldest pregnant female was 48 years, and the oldest lactating and simultaneously pregnant female 42 years (Kasuya, 1985). There were only three females >48 years, of which two were resting (57 and 49 years) and one lactating (49 years). These data suggest that striped dolphins off the Izu coast in 1960-1980 had no significant post-reproductive survival (Marsh and Kasuya, 1986).

(3) Length of calving cycle

The average calving cycle was analysed by Kasuya (1972; 1976a and 1985) and by Miyazaki (1984). The first two and the last studies were similar in that they used the crude proportion of females in each reproductive stage and a mean gestation time of 1 year (Kasuya, 1972 and Kasuya, 1976a) or 1.1 years (Miyazaki, 1984). Kasuya (1985) however, attempted to correct the imbalance of the ratio of neonates and foetuses (see below). These results are shown in Table 4.

The estimate of calving interval by Kasuya (1972) was speculative in that it was based on only three drives by the Izu fishery. Although Kasuya (1976a) increased the sample to 165 females from the Izu fishery, it was still too small. Miyazaki's (1984) analysis used a greater sample (699 adult females) from the Izu coast combined with about 10% of sample from Taiji (see below).

Kasuya (1985) reanalysed data from 14 drives from the Izu coast during the period 1967-1980. These included the samples used in his earlier studies. He compared the number of pregnant females (412) with the number of calves aged <1 (262) in the same sample. If mortality is ignored, then these two values should be similar; however, calves represented only about 63% of foetuses. Incidentally, this imbalance was reversed in the case of pantropical spotted dolphins (Kasuya, 1985).

These imbalances might result from: (1) the timing of sampling and parturition; (2) geographical segregation of females by reproductive class; or (3) errors due to small sample sizes. Neonatal mortality or loss of neonates during the drive could not explain the opposing imbalances for striped and spotted dolphins. In the absence of conclusive evidence, Kasuya (1985) assumed that for striped dolphins either lactating females were under sampled or pregnant females were over sampled.

Results of his analysis were similar to those of Miyazaki (1984) who had used a greater sample size and no correction (Table 4). This suggested that the imbalance was largely due to small sample sizes. Thus it appears that the mean calving interval of striped dolphins off the Izu coast from the late 1960s to the early 1980s was about 3 years.

(4) Density dependent change in female cycle

Kasuya (1985) examined historical changes in the female reproductive cycle and found that the mean estimated calving interval of striped dolphins off the Izu coast had declined by about 1.24 years from 1955 to 1977. The regression coefficient was not statistically different from zero ($0.05 < p < 0.1$). Although the estimated resting period

Table 4

Estimates of the reproductive cycle of female striped dolphins off Japan (in years).

Author	Preg.	PL	Lactation	Resting	Total
Kasuya (1972)	← 1 →		1.5	0.3-0.5	c.3
Kasuya (1976a)	0.86	0.14	0.33	0.08	1.41
Miyazaski (1984)	← 1.1 →		1.36	0.69	3.17
Kasuya (1985)	0.82-0.88	0.18-0.12	1.48-1.36	0.33-0.22	2.81-2.58

and mean lactation period also showed apparent declines, the regression coefficients were not significantly different from zero ($0.1 < p < 0.2$). The only statistically significant change observed was an increase in proportion of females that were pregnant and simultaneously lactating. Thus, although one might have expected a historical increase in female reproductive activity off the Izu coast, the available data do not confirm this perhaps due to the small sample size.

The Izu fishing season has tended to start earlier in later years (see *Fishing season and migration*) and foetal lengths tended to be smaller in the early part of the fishing season whilst testis weight was greater (see *Seasonality in reproduction*). Possible effects of these factors on the analysis of historical changes in the female reproductive cycle (Kasuya, 1985) remain to be investigated.

The annual ovulation rates estimated from an age-corpora relationship were 0.414 (5-25 years, Kasuya, 1976a) and 0.4944 (7-28 years, Miyazaki, 1984), thereby giving an upper bound for the potential annual pregnancy rate.

Seasonality in reproduction

(1) Parturition peaks

The calving season was estimated by fitting foetal lengths of multiple years to a mean foetal growth curve, which was constructed from an assumption of a gestation period of about 1 year and average neonatal length of 100cm. Parturition thus estimated occurred in all months of the year, with two distinct peaks in May-July and October-January (Kasuya, 1982: Izu sample in October-December), in December-April and July-September (Miyazaki, 1977a: Izu sample and a few Taiji specimens in December-February and June), or January-April and June-November (Iwasaki and Goto, 1997: Taiji sample in October-January). This disagreement is most probably due to inter-annual variation in breeding season and different timing of migration into the fishing area by gestation stage.

The estimated calving season using neonate data resulted in indistinct modes from May-August and November-December (Miyazaki, 1977a), probably due to uncertainty in the estimation of postnatal growth, low sample sizes and greater individual variation. Miyazaki's (1977a) conclusion of three mating peaks (February-May, July-September and December) was based on the accumulation of information from foetuses and juveniles below the age of 2 years and should be considered with caution.

In summary, the calving pattern is not well understood at present. For a better understanding, foetal length data for a wider geographical range, more months of the year and a greater number of years are required to resolve problems surrounding annual and school specific variations in mating, timing of migration and the possibility of the inclusion of more than one population in the fishery (see below).

(2) Apparent school specific pattern in the season

The presence of school-specific foetal length compositions was identified by Kasuya (1972) and further supported by Miyazaki and Nishiwaki (1978) based on 26 striped dolphin schools from off the Izu coast (Fig. 4). All of the pregnant females in 11 schools were in early pregnancy, most of the pregnant females in seven schools were in late pregnancy, whilst there were two, almost equal, foetal modes in the remaining eight schools. The apparent pregnancy rates in these last schools tended to be lower for schools of the other two types. Thus, length frequencies of foetuses are school specific, and this character is most distinct in schools of high apparent pregnancy rate. Kasuya (1972) interpreted this as suggesting that oestrus may be one of the key factors in establishing a new association of females (Kasuya, 1972).

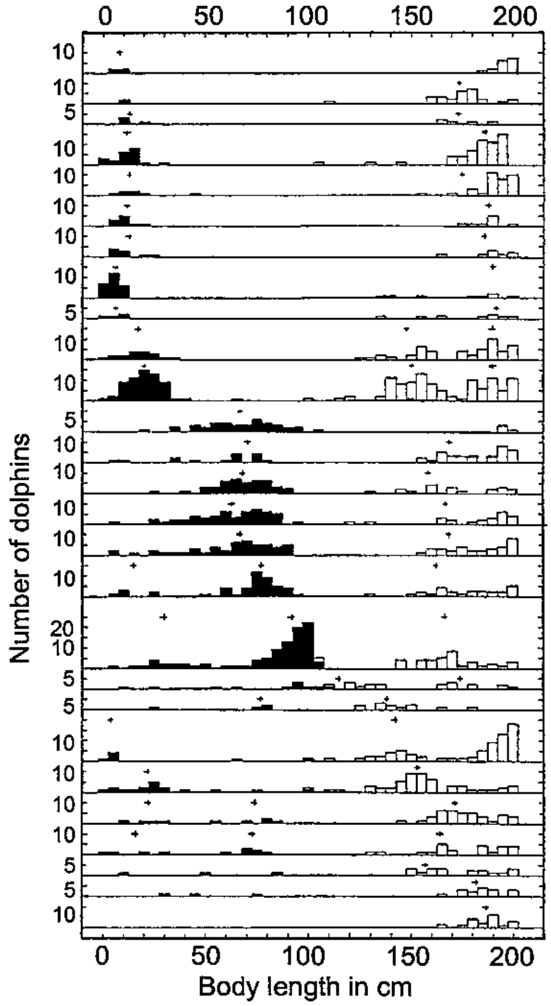

Fig. 4. Body length composition of foetuses (black squares) and juveniles (white squares) of striped dolphins for each school from the Izu coasts in October-December, 1968-1973. Larger postnatals over 2m in body length are not indicated. Reproduced from fig. 21 of Miyazaki and Nishiwaki (1978) with permission.

Miyazaki's (1977a) six years of foetal records revealed apparent annual variation in the timing of parturition, i.e. samples from certain years showed a single peak while other samples showed double peaks of similar strength. This was also evident in Iwasaki and Goto's (1997) Taiji sample, where 1994/95 samples suggested a calving season from April-October (peak in August), whilst the equivalent period from the 1993/94 samples was from October-July (peak in February). Such a situation could occur even in the absence of variation in the calving season, if the timing of migration is related to reproductive class (see below), or if more than one population (with different breeding seasons) migrate to the fishing ground.

An interesting feature of Miyazaki's (1984) data is the between-month variation in foetal length frequencies. While the October samples had more foetuses in the 0-40cm class than the 50-100cm, the reverse was true for December whilst the November sample was intermediate (Fig. 5). This suggests that females in early pregnancy tend to migrate into the fishing grounds early in the season while those with near-term foetuses arrive later in the season.

Using a sample from the Izu coast, Miyazaki (1977a) analysed 'mature' (> 15yrs) males by season and found that those taken in October had the greatest average testis weight (*ca* 140g). This value decreased to *ca* 80g in November and *ca* 30g in December (Fig. 6). This suggests a degree of correlation between male reproductive activity and the stage in the oestrus cycle of females they were caught with. This may reflect seasonality in male reproduction or a pattern of male-female association determined by reproductive cycle (also see *Sexual maturation of males*).

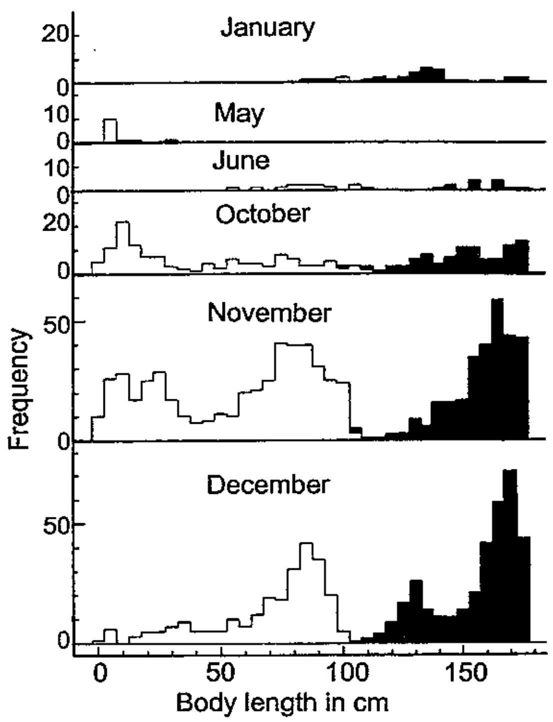

Fig. 5. Monthly body length composition of foetuses and juveniles of striped dolphins from the Izu coast (May and October-January) and Taiji (January and June). The May sample is from Arari cited from Nishiwaki and Yagi (1953). Reproduced from fig. 2 of Miyazaki (1984) with permission.

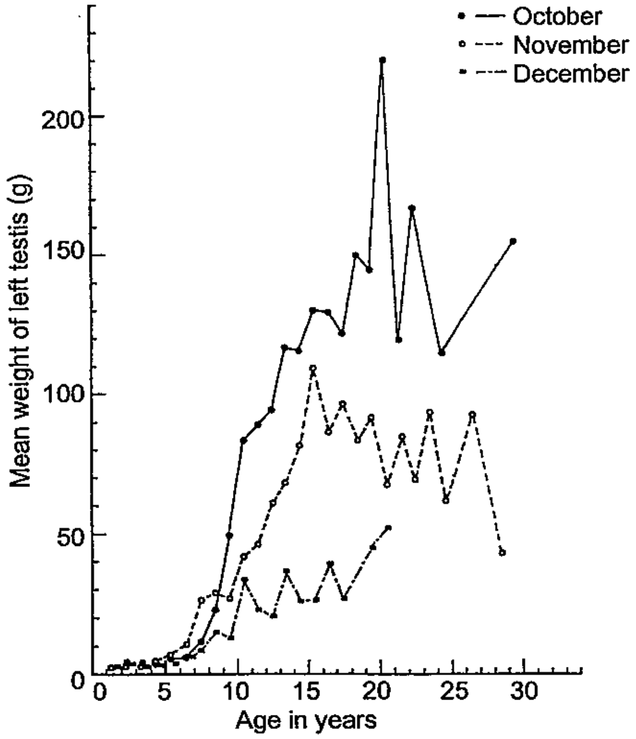

Fig. 6. Comparison of mean weight of left testis of striped dolphins on age. Samples were taken off the Izu coast by drive fishery (October-December, 1968-1973). Ages were determined from dentinal growth layers. Reproduced from fig. 8 of Miyazakai (1997a) with permission.

The Taiji samples of Miyazaki (1984) had only near term foetuses (taken in January and June) while his Arari sample (from Nishiwaki and Yagi, 1953) had small foetuses (May). The 1994/95 Taiji sample of Iwasaki and Goto (1997) had a distinct peak at 20-45cm (3 drives in November-January), and their 1991/92 and 1993/94 samples had a peak at 80-100cm (10 drives in October-January). That these Taiji samples do not show any clear season-dependent foetal size composition may reflect the small sample size rather than any lack of pattern. Further work is needed to clarify this.

Weaning

Miyazaki (1977a) examined the stomachs of 45 juveniles to determine the presence of milk in the stomach. The smallest individual with solid food remains was 133cm, and the largest individual with milk was 176cm. There were 23 individuals in this length range of which five had only milk in their stomachs (142-176cm), four had both milk and solid food remains (133-159cm) and 12 with solid food remains only (135-174cm).

The youngest individual with solid food was 0.25 years old and the oldest individual with milk was 1.25 years old (Miyazaki, 1977a). Of the 12 animals in this age range, three had only milk (0.25-0.75 year), two both milk and solid food remains (0.5-1.25 years) and seven only solid food remains (0.25-1.25 years).

These data suggest that calves start taking solid food at age 0.25-0.5 years and may continue to take both milk and solid food to age 0.75-1.25 years. However, this method can bias weaning age downward, as acknowledged by Miyazaki (1977a), because milk mixed with solid food is hard to identify.

Miyazaki's (1977a) also estimated weaning age by comparing the numbers of lactating females and juveniles driven together; this gives an upper bound of the age at completion of weaning. If calves are lost during the drive, or if a calf nurses from multiple females (not confirmed for the species), this method is likely to overestimate age at weaning. The age thus calculated was 1-2.5 years (17 schools), and the lower bound showed fair agreement with the first estimate. It can thus be concluded that suckling continues to at least close to 1 year but may often last to almost 2 years in the population studied.

In an analysis of school structure, Miyazaki and Nishiwaki (1978) showed that weaned juveniles started to live with other immatures at between 1 and 2 years and that the number of such individuals increased rapidly to 3-4 years of age, i.e. with the formation of juvenile schools (see *Segregation of juveniles*). Although there is no estimate of the length of time between the completion of weaning and the departure of calves from the mothers' school, it does not appear to be very great.

SCHOOL STRUCTURE

The structure of striped dolphin schools was first examined by Kasuya (1972). Subsequently, Miyazaki (1977b) and Miyazaki and Nishiwaki (1978) elaborated on this using a larger sample size from the Izu fishery. One potential confounding factor was that the drive fishermen may have combined some schools for driving or, in rare cases, only part of a larger aggregation might have been driven; such information is not usually available. Thus the school size and the size of a drive were not distinguished by the above studies; each drive was usually described as a 'school'.

Sex ratio

The estimated foetal sex ratio (male:female) was 58:57 (Kasuya, 1972), 152:163 (Kasuya, 1985), or 269:247 (Miyazaki, 1977a and Miyazaki, 1984); none differ statistically from parity ($p > 0.05$).

The overall postnatal sex ratio was also close to parity: 1,774:1,681 (Miyazaki, 1984). The apparently low proportion of males from ages 3-10 years (Miyazaki and Nishiwaki, 1978; Kasuya, 1985) reflects the tendency of males to leave adult schools after weaning to form juvenile schools, which had a lower probability of being driven than adult schools.

Both Miyazaki (1984) and Kasuya (1976a; 1985) identified a slight decrease in the proportion of males after age 35 years. Although this could be a reflection of a slightly higher natural mortality rate in males, there is no significant difference in the maximum age between sexes, i.e. 57 years for both sexes. There were five males and females aged between 45 and 57 years (Kasuya, 1985).

In conclusion, there appears to be little, if any, difference in natural mortality rates by sex among striped dolphins off Japan. This is in contrast to the result for pantropical spotted dolphins aged by the same author, where the oldest observed ages were 42 years in males and 45 years in females and the proportion of females increased steadily from 45% in foetuses to close to 100% at age 35-45 years (Kasuya, 1985).

School size

The number of individuals found in a single 'drive' ranged between 25 and 2,327 and the mean school size was 415; about 86% of the drives contained less than 500 individuals (Miyazaki, 1977b) (Fig. 7). The question of changes in school size over years has not been examined.

Miyazaki (1977b) analysed schools taken by the drive fishery on the Izu coast by month and area. In winter (November-January), the fishery operated on both the east and west coasts, but it operated only on the west coast in spring (April-May) and only before 1960. The average number of dolphins per drive in winter (*ca* 300) did not differ between the coasts, but the school size (*ca* 150) in spring operations on the west coast was significantly smaller than in the winter operation in the same area.

Schools found in the early morning were often large, suggesting merging of schools during feeding at night and splitting of schools in daytime (Miyazaki and Nishiwaki, 1978). By contrast, the diurnal pattern in school size observed for pantropical spotted, spinner and short-beaked common dolphins in the eastern Pacific was for larger school sizes late afternoon and smaller in the early morning (Scott and Cattanach, 1998).

Segregation of juveniles

Many of the striped dolphin schools taken off the Izu coast contained a large proportion of adults of both sexes as well as immature individuals, particularly of suckling age (these are termed 'adult schools' (see below)), but showed a deficiency in post-weaning juveniles. Other schools were composed mostly of immatures of both sexes between 2 and 12 years of age (usually with excess males) (Fig. 8). The proportion of immatures was discontinuous between the two types of schools (Miyazaki and Nishiwaki, 1978). This suggests that calves leave their natal school after weaning to associate with other immature individuals and thus form 'juvenile schools'. The proportion of mature females in these schools was usually negligible, although there were some males of later growth stages. Therefore, it appears that females join the adult schools at the onset of puberty, not pregnancy or parturition.

In juvenile schools, males exceeded females of the same age. This high proportion of males (*ca* 75% on average) implies a stronger tendency of males to leave the natal school combined with their higher age at maturation. Peak ages in these 'immature schools' are variable between schools, suggesting that formation of such schools is at least partly a function of age. The maximum size of juvenile schools was close to 1,000, but many were less than 100 individuals.

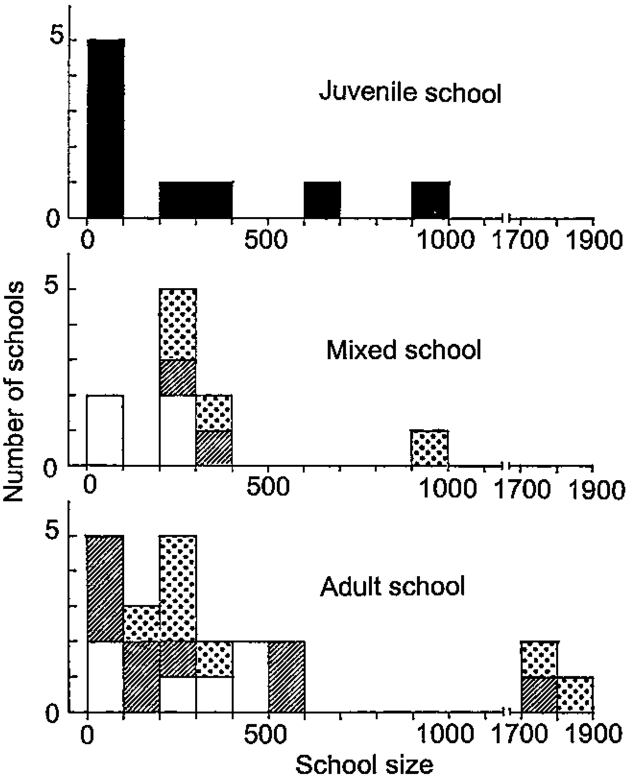

Fig. 7. School size frequencies of striped dolphins for juvenile (top), mixed (middle) and adult schools (bottom). The last two school types are further divided into mating (hatched), non-mating (dotted) and unclassified (white) schools (Miyazaki and Nishiwaki, 1978). Data are from drive fishery off the Izu coast in October-December, 1963-1973. Reproduced from fig. 10 of Miyazaki and Nishiwaki (1978) with permission.

Adult schools

'Adult schools' contained sexually mature males and females at various reproductive stages and their dependent calves. Although there was a deficiency of individuals aged 2-11, there were always some animals in this age range. Most ($n = 19$) adult schools contained less than 600 individuals, but some ($n = 3$) over 1,700 individuals (Fig. 7).

The composition of adult schools was variable and parametric values continuous among schools. Thus attempts by Miyazaki and Nishiwaki (1978) to draw a clear picture of the formation of adult schools or the movement of adults between them was unsuccessful.

Ten of the 41 schools examined by Miyazaki and Nishiwaki (1978) had characteristics of both juvenile and adult schools. This suggests the merging of several schools either as a natural process or by the fishery in an effort to combine several nearby schools for a drive.

Age composition and mortality

If dolphins mixed freely within a population and the fishery was not selective, then the age composition of the catch would reflect both the total mortality rate and yearly changes in recruitment. An alternative 'extreme' situation might be the situation if a drive fishery took place on resident killer whales (*Orcinus orca*) studied off the Vancouver Island area, which form matrilineal pods and where the offspring are believed to remain in their natal pods for life (e.g. Bigg *et al.*, 1990). Fishing mortality caused by a drive fishery on such pods would not directly alter the age composition of other pods, except through changes in recruitment and in natural mortality rate responding to decreased density.

The situation for striped dolphins off Japan is somewhat intermediate between the above two extremes. They have been exploited partially by hand-harpoon fisheries which are strongly selective for weaned juveniles (ages 2-7 years) (see Fig. 8 of this study and fig. 25 of Kasuya, 1978) and largely by drive fisheries which are the least selective (see fig. 25 of Kasuya, 1978). As noted earlier, the drive fishery may combine some small schools before the drive or may drive only part of a large aggregation. The social structure of Japanese striped dolphins is considerably more fluid than for resident killer whales. There appears to be considerable movement of individuals between schools by age and reproductive status (see *School structure*). The age composition of samples < 10 years is strongly affected by the probability of encountering juvenile schools and can not be reliably analysed at present.

Fig. 9 presents the age composition of striped dolphins taken by drive fisheries off the Izu coast from 1971-1977 (8 schools). Kasuya (1985) stated that the slope of the age composition changed from medium (10-22 years), low (20-34 years) and high (> 32 years), and suggested that the first two segments possibly reflected changes in total mortality rate and/or in recruitment caused by fishing operations after World War II, whilst the last portion reflected an increase in age-dependent natural mortality rate. The 'apparent annual mortality rates' calculated from the catch composition using method of Robson and Chapman (1961) are 0.1074 (11-22 years), 0.0622 (20-34 years) and 0.1408 (> 32 years) for females and 0.1486 (11-22 years), 0.0534 (20-34 years) and 0.1419 (> 32 years) for males (Kasuya, 1985). The catch curve of pantropical spotted dolphins in the same study (Kasuya, 1985) showed two phases for the adult ages; lower apparent mortality rates of

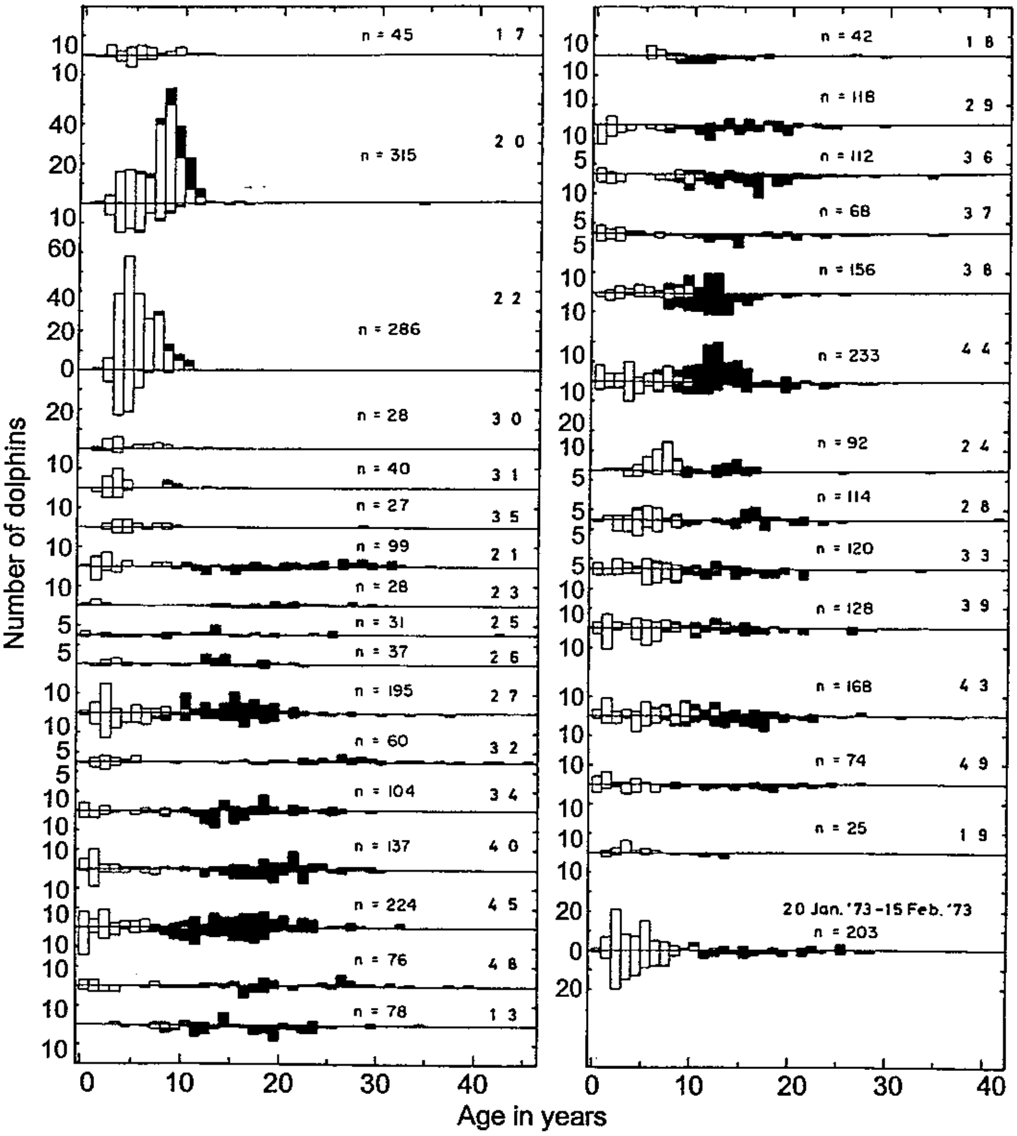

Fig. 8. Age composition of striped dolphin schools taken by drive fishery off the Izu coast in 1971-1977. School nos 13-45 are from the Izu coast (October-December, 1970-1973), nos 46-49 are from Taiji (January, June and December, 1975-1980). Catch of hand-harpoon fishery off Taiji is shown in the right bottom. Reproduced from fig. 1 of Miyazaki (1984) with permission.

0.0563 (females at 11-26 years) and 0.0590 (males at 7-22 years) for intermediate ages, and 0.1348 (females >24 years) and 0.1618 (males >20 years) for higher ages.

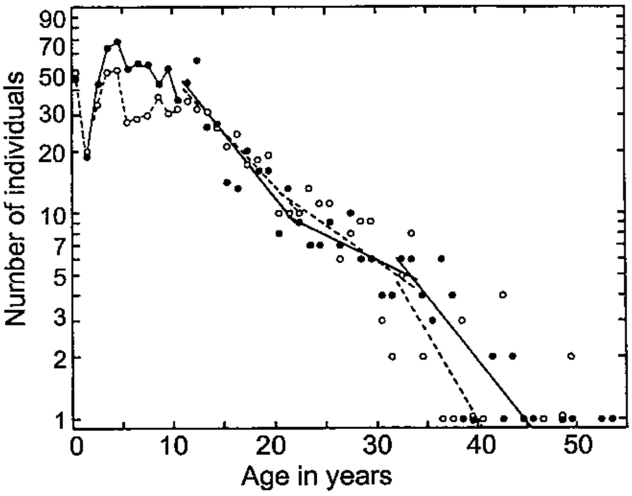

Fig. 9. Age composition of striped dolphins taken by drive fisheries off the Izu coast in November-December, 1971-1977. Eight schools are combined. Reproduced from fig. 10 of Kasuya (1985) with permission.

A qualitative comparison of apparent mortality rates for the two species, bearing in mind greater longevity of striped dolphins, suggests the following: (1) the greater apparent mortality rates in older individuals of both species is a reflection of higher natural mortality rates among old individuals; and (2) the apparent mortality rates of striped dolphins at intermediate ages (11-34 years) compared with corresponding figures of pantropical spotted dolphins probably reflects higher fishery related mortality rate and/or increased recruitment.

Feeding

There has been relatively little work carried out on the feeding of striped dolphins in Japanese waters. Miyazaki *et al.* (1973) studied the stomach contents of 27 striped dolphins from two schools taken off the Izu coast in December 1970. Nineteen dolphins had half-digested squid remains representing 35 individuals of two species, *Tadarodes pacificus* in both schools and *Symplectoteuthis luminosa* (c.f. *Eucleoteuthis luminosa*) in one school. Squid beaks (1,805 in total) were present in all the stomachs.

All 27 stomachs contained half-digested shrimps representing a total of 1,971 shrimps of four genera and three families. Of these *Bentheogennema borealis* was the most dominant (85.6% by number).

Only eight stomachs contained half-digested fish remains; these represented 30 individuals. In addition to these, fish otoliths (5,410 in total) and urohyals (1,448 in total) were found in the stomachs. Miyazaki *et al.* (1973) identified fish species using urohyals and partially digested food remains. Myctophidae (64.0%) was the most dominant in the urohyals, which was followed by Nemichthyidae (13.1%), Emmelichthyidae (8.1%) and Chauliodontidae (7.5%).

The authors concluded that the striped dolphins feed mainly on fish. It would be desirable, however, to consider the difference of digestion time among urohyals, squid beaks and shrimps and effect on their numbers found in the stomachs. The quantity, not the number, of these food items also needs to be considered.

Of the food species identified by Miyazaki *et al.* (1973) only one squid species, *Tadarodes pacifica*, is commercially exploited off Japan.

POLLUTANTS

Honda *et al.* (1982) studied the distribution of various heavy metals in the body tissues (muscle, liver, blubber and bone) of striped dolphins. Iron, manganese, copper, nickel and cadmium were highest in the liver, and zinc and lead were highest in bone.

Mercury and selenium in striped dolphins were first studied by Arima and Nagakura (1979) using samples collected in 1973 on the Izu coast. Mercury content in the skeletal muscle increased with age linearly from about 0.95ppm wet weight at 0 year to 9.43ppm at 30 years of age; selenium (0.22-0.48ppm) also increased linearly with mercury. A positive correlation between these metals was confirmed in tissues other than skeletal muscle (Itano *et al.*, 1984b) and by other studies of skeletal muscle (Itano *et al.*, 1984a).

Itano *et al.* (1984a) reported the mercury and selenium content in skeletal muscle of 55 striped dolphins collected in 1977-1979 off Japan (Fig. 10). They found that an increase in methylmercury ceased at around age 10 years while that of total mercury continued to increase further. From this they postulated that the species might have a demethylation mechanism. Levels of total mercury and selenium were low in neonates (mercury:1-2ppm; selenium: 0.5-1ppm) and increased almost linearly until age around 20 years, when the increase levelled off. The levels were not different between sexes and did not vary with the reproductive status of individuals in the same sample set. However, levels of selenium and mercury showed a large variation between schools. Dolphins taken in 1977 (Izu) and 1980 (Taiji) had muscle levels of 18-30ppm (total mercury) and 3.5-7.5ppm (selenium) at ages over 15 years, which were discontinuously higher than the corresponding figures (total mercury: 9-16ppm; selenium: 0.5-2.5ppm) for dolphins taken in 1978 (Taiji) and 1979 (Taiji). The tendency was the same for ages below 15 years if compared between individuals of same age. The number of sampled schools is not given in their publication (also see *Stock identity*).

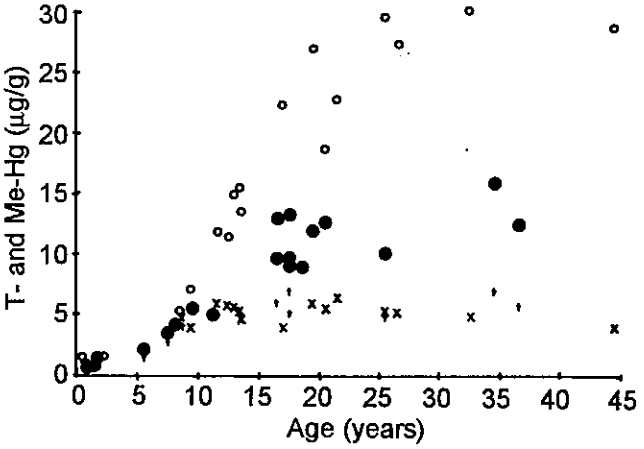

Fig. 10. Age dependent change in mercury levels in skeletal muscles of striped dolphins. Circles represent total mercury and × and † methylmercury. White circles and Xs represent samples from Kawana in October 1977 and Taiji in December 1980, and black circles and †s those from Taiji in December 1978 and 1979. Reproduced from fig. 1 of Itano *et al.* (1984a) with permission.

Tanabe *et al.* (1981b) studied the anatomical distribution of chlorinated hydrocarbons in postnatal striped dolphins and concluded that over 90% of the total burdens were deposited in the blubber, which comprised 17% of body weight. O'Shea *et al.* (1980) first studied organochlorine pollutants in the blubber of striped dolphins off Japan using samples from the Izu coast in 1968-1975. The levels of PCBs and total DDT were 1.2-4.8ppm and 1.26-18.04ppm, respectively, in wet blubber weight. Later, Tanabe *et al.* (1981a), Tanabe *et al.* (1982) and Tanabe (1985) studied the transfer of PCBs and DDTs from mother to offspring through the placenta and milk. The organochlorine content in female blubber sharply declined after age of 8-10 years, while that of males remained almost constant.

Loganathan *et al.* (1990) studied historical changes in organochlorine levels using two sets of adult male samples (aged 15-37 years) from off Taiji in 1978-1979 and 1986-1996. Ranges for the latter sample were (ppm in wet weight, mean in parentheses); PCB: 17-37 (28), DDTs: 23-51 (37), HCHs: 130-460 (270), HCB: 90-290 (150). These mean levels of PCBs and DDTs were the same as the earlier levels (PCBs: 29ppm; DDTs: 38ppm), but the levels of HCHs and HCB were considerably lower than the mean levels 10 years previously, 410ppm (HCHs) and 240ppm (HCB).

MIGRATION AND STOCK IDENTITY

Fishing season and migration

Ohsumi (1972) was the first to consider migration and stock identity in striped dolphins taken by the drive fisheries off the Izu coast and the hand-harpoon fishery off Taiji. He hypothesised that these fisheries exploited a single population of striped dolphins.

Miyazaki *et al.* (1974) analysed catch statistics to examine seasonality in striped dolphin fisheries off Japan. Taiji exhibited a peak in October-February, the west coast of Izu in December-February and April-June and the east coast of Izu in October-December. They concurred with the hypothesis that the Taiji and Izu fisheries exploited a single population. However, it should be recognised that the absence of catches in the summer in these regions does not necessarily mean the absence of striped dolphins. Even before the establishment of current fishing season regulations, the Taiji fishermen used to switch to more profitable trolling or net fisheries in the spring and summer months. The demand for dolphin meat was lower in spring and summer in the Kanagawa, Shizuoka and Yamanashi Prefectures on which the Izu fishery depended.

Miyazaki *et al.* (1974) also found that the annual catch of striped dolphins off the Izu coast was negatively correlated with the offshore distance of the Kuroshio Front. From this and from the results of sightings cruises made at *ca* 35°N and 141°E in September-October, they concluded that the fishery hunted striped dolphins that inhabited the northern front area of the Kuroshio Current; thus the advance of that current to the coast should increase the availability of dolphins to the fishery. However, Miyazaki's (1983) study, using a longer series of data, somewhat confounded this interpretation: the correlation was negative from 1961-66, positive after 1974, whilst no correlation was observed for the period 1967-73. The reasons for this are unknown.

Miyazaki (1983) identified two catch peaks (September/October and November/December), in terms of both number of individuals and number of schools, driven on the east coast of the Izu Peninsula. Although not referred to by the author, his data reveal a gradual advancement in the fishing season: the season started in December during 1950-52 at Kawana and Futo (east coast), but it began in November (1953), October (1956-77), and finally September in 1977-81 (no data for 1954-55). There has been no operation in January since 1969. A similar pattern can be seen for Arari (west coast), i.e. the proportion of the March-July catch decreased since 1942 whilst that for December-January increased. It is unknown whether this was due to a response of the fisheries to the market (higher prices for earlier catches) or to a change in the availability of dolphins to the fishery.

Using sightings data, Kasuya and Miyashita (1989) and Miyashita (1993) identified three geographic concentrations of striped dolphins in the western North Pacific in August-September: a northern offshore concentration; an inshore concentration; and a less distinct southern offshore concentration. The density of striped dolphins was apparently low between the concentrations and in northern inshore waters (west of 144°E and 35°-41°N) where striped dolphins from the Izu ground might be thought to summer.

Fig. 2 represents distribution of striped dolphin sightings in July through September based on data from Miyashita (1993) with my own interpretation of the concentrations (solid lines). The inshore concentration is limited to within about 200 n.miles from the Pacific coast, and apparently separated into two portions, north of 35°N and south of 33°20'N (dotted lines in Fig. 2). The southern portion of the inshore concentration showed no clear seasonal movements (Miyashita, 1997). Its range does not seem to cover the Izu fishery, but probably covered the Taiji fishery. Striped dolphins that summer in the northern part of the inshore concentration will enter the Izu area in the autumn/winter season.

Miyashita (1997) examined the monthly range of these concentrations from June to March. From spring to summer, the southern boundary of the northern offshore concentration moved from south to north: 32°N (June), 33°N (July), 34°N (August), and 36°N (September), whilst the western boundary of the concentration remained at 145°E. In October, the southwestern limit moved to the southwest, to 33°N and 141°E, i.e. approaching the recent operating area of the Izu fishery (34-35°N, 139°-140°E). It therefore is possible that the northern offshore concentration approaches the current Izu fishing grounds in autumn and is harvested by the fishery. However, this does not necessarily mean that the Izu fishery exploits only individuals from the northern offshore concentration.

Stock identity

The question of what comprises a 'stock' or 'population' is complex and no general accepted definition exists. Donovan (1991) emphasised that the nature of the definition was to some extent a function of the use to which it is being put (c.f. 'biological' and 'management' stocks). The situation for cetaceans is rarely simple and the structure of population(s) or stock(s) of striped dolphins off Japan remains unresolved. Previous discussions of stock identity for this region have not defined what is meant by either a 'stock' or 'population'. For example, it is possible to assume that several local populations of incomplete isolation constitute a metapopulation of wider geographical range (Hanski and Simberloff, 1997). These local populations, which may or may not be under different selection pressure, may have some limited degree of genetic exchange and may experience extinction due to natural or human related causes, followed possibly by recolonisation from other areas. The concept of a 'management stock(s)' for this fishery is complicated by a lack of understanding as to how the unit of harvest in the Japanese drive fishery often called 'school', functions within the 'population(s)' of striped dolphins. Consideration of these fundamental concepts is outside the scope of this review. The terms 'population' or 'stock' are used in the rather general sense that has been used in previous studies.

As noted in Donovan (1991), consideration of stock identity requires consideration of information for a suite of techniques. Information relating to stock identity of striped dolphins is summarised below. For geographical names see Fig. 1.

(1) Distribution

Kasuya and Miyashita (1989) considered that the three summer concentrations of striped dolphins off Japan might represent separate populations. They recognised the large abundance of the northern offshore concentration (see *Abundance*) and suggested that if these individuals were involved in the Izu fishery the fishery would not have experienced such a drastic decline. They proposed that for safe management, the northern offshore concentration should be assumed to be a different stock from that harvested and depleted by the Izu fishery.

(2) Osteology and growth

Amano *et al.* (1997) analysed geographical and temporal differences in skull morphology of striped dolphins in the western North Pacific based on:

(1) an early Taiji/Izu sample (45 individuals from Taiji and Izu in 1958-1979);
(2) a recent Taiji sample (24 from Taiji in 1992); and
(3) a recent northern offshore sample (21 from research takes in the northern offshore concentration in August 1992, see Iwasaki and Kasuya, 1993).

They identified significant sexual dimorphism in the early Taiji/Izu sample as described by Ito and Miyazaki (1990), but did not find this in the recent Taiji and northern offshore samples. Males of the three sample sets were distinguishable from each other by canonical variate analysis, but females were different only between the recent Taiji sample and other two samples combined.

Amano *et al.* (1997) found it difficult to reach any firm conclusions, particularly given the small samples and the greater uncertainty for females. However, they considered that the difference between the early Taiji/Izu sample and recent Taiji sample was real, and that the recent northern offshore sample also differed from the two coastal sample sets. The small sample sizes precluded comparison between early samples from Taiji and Izu. The degree of sexual dimorphism differs between populations of striped dolphins, and this can provide useful stock identity information (Archer, 1996). It is quite possible to find interpopulation differences only in males.

Iwasaki and Goto (1997) compared the body lengths of three striped dolphin samples: (1) a recent Taiji sample from 1991/92 and 1994/95; (2) a recent northern offshore sample from 1992 (Iwasaki and Kasuya, 1993); and (3) an early Izu sample (Kasuya, 1972). Lengths in the recent Taiji sample were smaller than those in the early Izu sample or the recent northern offshore sample (see Body length frequency and mean growth curve). Whilst growth may change in response to density, length differences between the two recent samples are also of relevance to stock identity.

(3) Genetics

Wada (1983) studied isozymes of 10 enzymes encoded by 15 genetic loci of 40 striped dolphins using samples collected from a single school driven on the Izu coast in 1980. Two loci (13.3%) were polymorphic and average heterozygosity for all 15 loci was 0.021. He thought that this low heterozygosity might reflect interbreeding. Because the tissues were collected from livers that had already been removed from the carcasses, it was not possible to examine the data in terms of growth and reproductive status. Subsequently, Shimura and Numachi (1987) examined 19 genetic loci encoding 12 enzymes of 370 striped dolphins taken on the Izu coast, which presumably represented multiple schools but this information was not given in the paper. The proportion of polymorphic loci (26.3%) and the average heterozygosity (0.089) were much greater than the values reported by Wada (1983) and were similar to values found for pantropical spotted dolphins from the same fishery and intermediate between values for bottlenose dolphins and Dall's porpoises (Shimura and Numachi, 1987).

Yoshida and Iwasaki (1997) analysed the control region of mitochondrial DNA of 43 striped dolphins from the northern offshore concentration in August 1992 and 34 animals from the Taiji area in September/November 1992. They identified 61 haplotypes, 36 of which were represented by 36 offshore specimens, 21 by 27 inshore specimens, and the remaining four (7%) shared by four offshore and 6 inshore individuals (13.7% of the total sample). The authors found no statistically significant genetic differences between the two sample sets, but felt that the very high haplotype diversity could have masked any true differences and they identified the need for further analyses that took into account social structure.

(4) Pollutants

Itano *et al.* (1984a) found distinct yearly variations in total mercury and selenium contents in the skeletal muscle of adult striped dolphins (see *Pollutants*): high in Izu (1977) and Taiji (1980) samples and low in Taiji (1978 and 1979) samples. Although the details of the sampled schools are not available, the number of schools is probably small and the differences might be school specific. It seems likely that the between-school differences in heavy metal levels probably reflect differences in prey species or major feeding grounds in the last 15-20 years. In view of the fluid school structure of the species (see *School structure*), then it is not an unreasonable hypothesis that these differences are indicative of different stock structure. However, as indicated in Reijnders *et al.* (1999), the age and sex structure of the sampled animals must be considered when examining differences in pollutant levels. Having said that, these results are not incompatible with the hypotheses that more than one population was involved in the Taiji fishery in the late 1970s and that the composition of populations was at least partially different between the Izu and Taiji fisheries.

(5) Synthesis

This section summarises the available information on stock structure in terms of reasonable hypotheses and supporting evidence (in parentheses). The term 'past' or 'early' denotes any period during 1959-1980 and 'recent' or 'current' that after 1990.

(1) Striped dolphins in the present northern offshore concentration may be different from those taken by the current Taiji fishery (osteology, growth and DNA) and also from those taken by the past Taiji fishery (osteology).
(2) Part of the current harvest at Taiji may be from a population that was not exploited by the past Izu fishery (osteology).

(3) The past Taiji fishery may have exploited at least two populations, one of which could also have been taken by the Izu fishery of the time (mercury level).
(4) The northern offshore concentration has not constituted a major portion of the catch of the Izu fishery (catch trend, distribution and osteology), although some degree of involvement cannot be excluded (seasonal distribution).

The above four hypotheses do not conflict with each other. One possible scenario for population structure exploited by the Japanese striped dolphin fisheries is that at least two coastal populations were involved in the fishery. The Taiji fishery exploited both of them, while the Izu fishery exploited at least one; the involvement of the northern offshore population with the fishery was small, if any. This would explain the observation that the Taiji fishery made a large catch in the earlier days of the operation, when the Izu fishery had already declined, and subsequently experienced major decline. There is accumulating evidence for local populations on the small and large scale for many small cetaceans (e.g. Perrin *et al.*, 1991; 1994; Perryman and Westlake, 1998). Further study is needed to understand stock structure of striped dolphins off Japan.

ABUNDANCE AND CATCH TREND

Kasuya (1976a) and Kasuya and Miyazaki (1982) concluded that the population of striped dolphins off Japan had been declining and could not sustain the catch levels of the early 1970s. Although their conclusion has been supported by a later decline in the fishery on the Izu coast, there are identified problems with the estimation methods they used at that time. For example, their model assumed that maximum productivity is achieved at 50% of carrying capacity (although there was little evidence to support or refute this; there are cases suggesting otherwise - Fowler, 1994). In addition, the use of fishing mortality rates derived from catch curves has been shown to be unreliable in most fishery situations.

Kasuya (1985) analysed historical changes in life history parameters and catch statistics of the Izu fishery. He concluded that the catch off the Izu coast had shown a major decline from about 10,000 in the early 1960s to less than 1,000 in the early 1980s, when the fishery was operated at Kawana and Futo using the same number of searching vessels (Kishiro and Kasuya, 1993), but with increasing speed (Shizuoka Board of Education, 1987). He believed that this decline was compatible with changes in reproductive parameters that one might expect as a result of a density dependent response. Kishiro and Kasuya (1993) concurred with this interpretation and estimated that the Japanese drive fishery had depleted the coastal stocks of striped dolphins to less than 10% of their post-World War II level.

Kasuya and Kishiro (1995) examined the catch statistics of the Taiji dolphin fisheries in the context of possible environmental factors. They found no correlation between variation in catches and variation in the Kuroshio Current or squid landings off the Wakayama Prefecture. However, they did find a statistically significant decline in the catch of striped dolphins (1979-1991) and short-finned pilot whales (1979-1994). The decline could not be explained by the fishing regulations; pilot whale catches rarely, if ever, achieved the catch limits, while no limits were set for striped dolphins during the period. The catch of striped dolphins decreased from over 12,000 in 1979 to below 1,000 since 1990. Thus, there is clear evidence that the availability of striped dolphins to the Taiji fishery has declined.

Miyashita (1993) estimated the abundance of striped dolphins for the three geographical concentrations in the western North Pacific (Fig. 2) using sighting data obtained during August and September from 1982-1996. The estimates were 497,725 (CV = 0.179) individuals for the northern offshore concentration (32°-42°N, 145°E-180°), 52,682 (CV = 0.952) for the southern offshore concentration (23°-30°N, 127°E-180), and 19,631 (CV = 0.696) for the inshore area (coastal waters north of 30°N and west of 145°E). The boundary for the estimation was placed for calculation purposes at the middle of the density hiatus, and the inshore area included vacant coastal waters north of the Izu ground; the author left open the question as to whether the population exploited by the Izu fishery was included in this estimate. It can be seen that the confidence intervals for the inshore and southern offshore areas are very large.

The above estimates were made during the peak of the summer migration of striped dolphins: this was not unreasonable because surveys were undertaken in favourable weather conditions and bias associated with seasonal movements was minimised. However, it left an important question unanswered. Where is the summering ground of the individuals that migrate to the fishing grounds during the winter season?

DISCUSSION

Trends in catch and striped dolphin availability

The dolphin fishery on the Izu coast has existed since at least the 17th century and appears to have exploited striped dolphins since at least the late 19th century. In addition to the observed decline in catches over time, two other historical trends can be seen. One is the decrease in the number of operating fisheries (the expansion of fisheries during and after the World War II was followed by rapid decline) and the other is the expansion of the operating area from the coast to outside the Sagami Bay.

A greater than 10-fold decline in the catch off the Izu coast occurred from 1961-1983, and the fishery almost collapsed. The trend did not change even for the 1968-1983 period when two drive teams co-operated, using four searching vessels that were continuously improved in speed. It is clear that the availability of striped dolphins to the fishery must have declined to $<10\%$ of original during the period.

In terms of explanations for this decline in availability, changes in the migration pattern of striped dolphins due to oceanographic changes or declines in food availability appear unlikely, because: (1) there have been no identified oceanographic changes extending for 30 years (Miyazaki, 1983; Kasuya and Miyashita, 1988); (2) striped dolphins off the Izu coast appear to be generalist feeders that do not appear to consume prey of high economic value (see *Feeding*); and (3) the age at sexual maturity has changed in a way one might expect of a population with improved nutrition (see *Sexual maturation of females*).

The importation of Dall's porpoises products from northern Japan to Kanagawa, Shizuoka, and Yamanashi Prefectures, where striped dolphins from Izu fishery were consumed, occurred in the 1970s (Kasuya and Miyashita, 1989). The total Japanese catch of Dall's porpoises and striped dolphins ranged between 10,000 and 15,000 during the early 1970s (Kasuya, 1982), near the level of the striped dolphin catch in the 1960s. It appears that the importation of Dall's porpoise products did not saturate the market for the

Izu fishery. However, this does not preclude the possibility that if Dall's porpoises had not been supplied to consumers, the price of striped dolphins might have been higher, leading to higher catches in the Izu fishery with more severe consequences for the striped dolphin population(s) exploited there.

The first dolphin drive team in Taiji began to take striped dolphins in 1973; a second team began in 1979. The maximum catch (> 12,000) occurred in 1980. The two drive teams merged in 1982, retaining the same fleet of 15 vessels (later it decreased to 14). The catch of striped dolphins showed a significant decline between 1980 and 1991 (from *ca* 12,000 to < 1,000) before a quota was set for the fishery (Kasuya and Kishiro, 1995). This decline occurred while the actual number of vessels used for daily searching almost doubled. Therefore, the availability of striped dolphins to the Taiji fishery as well as the Izu fishery must have declined after 1980.

Indices of abundance

Following suggestions by the IWC Scientific Committee (IWC, 1993), the Government of Japan collected daily operation records for the drive fisheries at Taiji and Izu, i.e. the number of searching vessels, searching hours, number of dolphin schools and individuals sighted, and dolphins actually taken (Kishiro and Kasuya, 1993). The low sighting rate makes analysis of the data from the Izu fishery difficult. Two difficulties with the use of such data for the Taiji fishery can be identified as discussed below.

The first reason lies in the nature of sighting rates. The number of dolphin schools/individuals sighted per unit of effort of search is only useful as an index of abundance in the fishing ground if the fishing mode remains constant over the period. However, in the early period of the fishery, almost every sighting was driven and all the individuals killed. This changed after the establishment of catch limits by species in 1993 as some schools were not driven because the animals present were small. In addition, large individuals within a driven school could be selectively killed and remaining individuals released. Finally, some striped dolphin schools might not be driven because the catch limit had been reached, although searching was continuing for other species. Thus, there is a possibility that recent sighting rates might be biassed upwards. In any event, simple comparison of abundance indices before and after 1993 is problematic.

A second problem is the need to quantify the effect of informer vessels that sell sightings information to the drive team. After Kawana ceased operations in 1984, Futo fishermen paid 3% of the profit to Kawana fishermen for sighting information that led to a successful drive (Nakamura, 1988). In Taiji, the drive team buys sighting information from other fishing vessels. The price seems to have been high since 1988, when competition with small-type whaling vessels resumed. Although this practice has probably occurred throughout the period of drive fisheries, the difficulty lies in quantifying its changing role over time.

Catch limits and inspection system

The current Japanese catch limit for the drive fishery is expressed as the maximum number of individuals to be killed by the fishery, and the catches are sold by weight. In addition, for Taiji the prefectural permit requests that 'whales' below 2m are released, although there is some confusion as to whether the striped dolphin is classified as a 'whale'. Irrespective of this, there are good economic reasons for the fishermen to select large individuals now that catch limits are in force. Unlike previous practice, it is now common for a greater number of striped dolphins to be driven than are to be landed; larger animals are killed and smaller ones released. If, as the author has observed, juveniles die in the enclosure 'naturally' they are discarded and not considered as part of the catch. Even if released alive, it seems likely that their probability of survival will decrease to an unknown degree.

This is suggested by *inter alia* the fact that the striped dolphin is known to be a difficult species to maintain in captivity. Attempts by aquariums to keep animals alive after transporting them from drives have all failed, although this method did not significantly affect survival of bottlenose dolphins. This explains the absence of striped dolphins in Japanese aquaria (Kasuya *et al.*, 1984). Similarly, of 11 striped dolphins (mostly adults) obtained from drives for radio tracking experiments, three had dummy radio-tags attached. Despite the attendance of aquarium personnel, all died in pens within 15 days of the drive, although some of them had started to feed. Subsequent necropsy revealed symptoms of stress, but it was not possible to determine if irreversible physiological changes had begun during the drive (Dr. T. Kotani and F. Hashimoto, September 1997, pers. comm.).

Given the possible mortality of released animals identified above and the unknown effects of social disruption caused by the selective removal of large animals from schools and the concerns about the status of the stock (e.g. IWC, 1993), it is clear that the manner in which catch limits are set should be reviewed as a matter of some urgency.

Further aspects of catch limits/inspection that warrant further consideration concerns the hand-harpoon fishery for striped dolphins. A total of nearly 150 vessels in Chiba and Wakayama Prefectures are licensed for this fishery even though the catch limit is only 180 animals. Catches can be processed at the sea and are not examined by scientists or inspectors prior to flensing. The potential for unreliable reporting and quota overruns is thus not insignificant.

Stock identity and dolphin movement

Although little is known about the population structure of the striped dolphins exploited in the western North Pacific, there is evidence to suggest that more than one population may be exploited in Japan. Irrespective of genetic mixing levels, the possibility of some degree of site fidelity, particularly at the extremes of the geographical range of a population, can make determination of sustainable catch limits difficult with the possibility of local 'extinction'. Some of the coastal population 'units' involved in the Japanese coastal fisheries may have been hunted to extremely low levels or even local 'extinction'; thus the composition of the population(s) in the fishing grounds may have changed during the long history (> 100yrs) of the fisheries. Northern coastal waters west of 145°E, which are now known to be almost vacant of striped dolphins, may have once been summering grounds for coastal population units depleted by the Izu fishery. The Taiji ground lies to the southwest of the Izu grounds, and the fishery operated mostly from autumn to spring seasons. The available information supports some partial overlap of exploited populations with the Izu fishery.

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