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Life History and Multivariate Analyses of Habitat Selection Patterns Among Small Cetaceans in the Central North Pacific Ocean

by

Richard Carlo Ferrero

A dissertation submitted in partial fulfillment
of the requirements for the degree of

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1998

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Abstract

Life History and Multivariate Analyses of Habitat Selection Patterns Among Small Cetaceans in the Central North Pacific Ocean

by Richard Carlo Ferrero

Chairperson of the Supervisory Committee
Associate Professor Glenn R. Van Blaricom
Washington Cooperative Fish and Wildlife Research Unit

Habitat selection and life history patterns were compared among three species of small cetaceans in the central North Pacific Ocean: Dall's porpoise (*Phocoenoides dalli*), northern right whale dolphin (*Lissodelphis borealis*) and Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). Biological samples and fisheries data used for analysis of habitat preferences were obtained by observers monitoring Japanese high seas squid driftnet operations between 36°N and 46°N, and 152° E and 150°W during 1990 and 1991. Supplementary data used for analysis of Dall's porpoise life history were collected between 46°N and 53°N and 168°E and 175°E in the Japanese salmon mothership fishery from 1981 to 1987.

The main objective was to determine if habitat partitioning mechanisms could be detected among the three marine mammal species. Two approaches were taken. First, reproductive patterns were compared, with special attention to calving seasonality. The timing and location of calving activity were indicated as possible factors differentiating habitat use, operating: a) spatially between *P. dalli* and *L. borealis*, b) temporally between *L. borealis* and *L. obliquidens*, and c) both spatially and temporally between *L. obliquidens* and *P. dalli*.

Second, canonical correspondence analysis (CCA) was used: a) to compare species locations in ordination space along observed environmental gradients (i.e., habitat features), and b) to compare community association patterns among the three marine mammal species and other marine organisms caught in the same driftnets. Monthly records, from June to September were examined separately and compared. Sea surface temperature was the most influential habitat parameter examined, with *L. borealis* occupying the warmest waters, *P. dalli* the coolest, and *L. obliquidens* in between, but with greater preference overlap with *P. dalli*. Habitat partitioning was best expressed by mature female *L. borealis*, in July, during their calving period. Mature female *L. borealis* associated with a consistent assemblage of other marine organisms during July and August while associations among other species were more varied. Collectively, these findings suggest that habitat preference patterns for these three species may be specific to reproductively active females, while coincident habitat use among other species constituents is common.

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DEDICATION

To Jo and Kristian

INTRODUCTION

The vast pelagic environment of the North Pacific Ocean provides habitat for a variety of often seen but poorly studied small cetacean species. Anecdotal sighting records and dedicated research survey efforts have documented species occurrence and provided data for population estimation, but relatively little is known about the life history, community association, and habitat use patterns for most species. These circumstances apply to the three species most common to the central North Pacific: the Pacific white-sided dolphin (*Lagenorhynchus obliquidens* Gill), the northern right whale dolphin (*Lissodelphis borealis* Peale), and Dall's porpoise (*Phocoenoides dalli* True).

The Pacific white-sided dolphin is widely distributed in the temperate waters of the North Pacific Ocean. In the eastern North Pacific, they are reported from the continental shelf and slope waters extending from the southern reaches of the Gulf of California, Mexico (approx. 23°N), north along the coasts of California, Oregon, Washington, British Columbia, and Alaska (Scheffer and Slipp 1948, Brown and Norris 1956, Pike 1956, Norris and Prescott 1961, Brownell 1964, Fiscus and Niggol 1965, Leatherwood *et al.* 1984, Walker *et al.* 1986, Dahlheim and Towell 1994, Forney *et al.* 1994). In the western North Pacific Ocean this species occurs from the South China Sea northward along the coast of Japan to the Kurile and Commander Islands (Okada and Hanoaka 1939, Tomilin 1957, Sleptsov 1961, Nishiwaki 1967, Kasuya 1971, Miyashita and Berzin 1991, Wang 1993). They have also been observed infrequently in the southern Bering Sea (Leatherwood *et al.* 1984, Kajimura and Loughlin 1988). Recent sightings made during studies of the high seas driftnet fisheries indicate that the Pacific white-sided dolphin has a continuous distribution across the temperate waters of the North Pacific Ocean between 38°N and 47°N (Hobbs and Jones 1993, Miyashita 1993).

The northern right whale dolphin is endemic to the North Pacific Ocean. In the eastern North Pacific, its normal distribution is from 30° N to 50°N (Leatherwood and Walker 1979). Occasional sightings as far north as the Gulf of Alaska and near the southern Aleutian Islands in the central North Pacific have been reported (Kajimura and Loughlin 1988). The northern right whale dolphin has been reported as far south as 29°N off Baja California, Mexico, during periods of unseasonably cool water temperatures (Leatherwood and Walker 1979). Its distribution in the western North Pacific Ocean is from 35°N to 51°N (Sleptsov 1961, Nishiwaki 1967, Kasuya 1971).

Dall's porpoise occur across the North Pacific Ocean from the west coast of North America to the Sea of Japan and southern Okhotsk Sea (Okada and Hayashi 1951, Sleptsov 1961, Kasuya 1982). The species is found from approximately 62°N in the Bering Sea southward to 28°N along the coast of Baja California (Morejohn 1979) and 41°N in pelagic waters (Kasuya and Jones 1984).

All three species show considerable range overlap latitudinally in waters from the Aleutian Islands to about 40°N, and longitudinally from nearly the coast of Japan to the continental slope off the western United States. Such broad range overlap offers little information towards determination of each individual species habitat preferences. The Pacific white-sided dolphin and northern right whale dolphin show even less distinction in habitat selection since they are often sighted in the same areas, frequently traveling in mixed schools (Leatherwood and Walker 1979, Hobbs and Jones 1993). The reasons for the apparent close association are unknown, but may be related to similarities in prey selection. What little foraging data exist for Pacific white-sided dolphin and northern right whale dolphin in the central North Pacific Ocean suggest that both species feed mainly on cephalopods and Myctophid fishes (Walker and Jones 1993). Dall's porpoise likewise feed on a variety of Myctophids and cephalopods, although the data are from more northerly latitudes in the vicinity of the western Aleutian Islands (Crawford 1981).

Range overlap and limited differentiation of habitat selection patterns, particularly between Pacific white-sided dolphin and northern right whale dolphin, may suggest mutualistic behavior, if, for instance, both species benefitted from combined foraging effort. No data exist, however, to test this theory. Alternatively, the outward appearance of ecological similarity may suggest that one or more of the populations is below carrying capacity and that resource partitioning mechanisms are currently unnecessary (note that carrying capacity is unknown with reference to any of the three species). If so, then habitat selection patterns may change with population size or in response to disturbances, both natural and anthropogenic.

Likewise, any competitive advantage one species might have over another may shift over time in response to changing conditions such that their individual habitat preferences or niches may not be distinguishable in any particular Hutchinsonian dimension (Hutchinson 1957). In other words, complete competitive exclusion (Hardin 1960) among members of a community may never be maintained, if it could exist at all. The paradox of multiple species occupying the same habitats and apparently the same ecological niches was, in fact, described for phytoplankton by Hutchinson (1961). For the three species of marine mammals of interest in this study, correlations between observed species distributions and habitats, therefore, may also be confounded, for instance, by latent advantages offered by differing life history strategies in the face of changing environmental conditions.

Nonetheless, this study focuses on detecting measurable relationships between environmental features and species distributions that could define basic habitat preferences in a fundamental Hutchinsonian sense. Such information may indicate how a species is linked to its environment, and what factors set limits on its distribution and abundance. Furthermore, this research is a critical first step to take before the more complex processes can be explored. Limited speculation on the broader ecological significance of differing life history strategies relative to niche partitioning patterns is addressed in Chapter 5.

Despite the apparent similarities between the three cetacean species, some detectable resource partitioning patterns may be evident at levels not previously considered for small cetaceans. Such differences may occur with reference to seasonal use patterns, or may differ by sex or reproductive condition of individuals between or within populations. The degree of observed habitat similarity among the species may simply reflect the lack of data required to resolve these differences at the appropriate scale. For the most part, the requisite environmental and biological data needed to examine habitat use patterns either among or within these three species have been lacking. Only limited information on a few basic life history parameters appear in the scientific literature. These data are summarized in Chapters 1-3.

Investigation of the fundamental patterns of habitat selection among species occupying similar habitats such as Pacific white-sided dolphin, northern right whale dolphin, and Dall's porpoise is an important step toward comparing life history strategies and understanding population responses to either natural or human caused perturbations. The mid-basin pelagic habitats in the central North Pacific Ocean vary with time in response to large-scale atmospheric and oceanographic disturbances such as regime shifts; changes in zooplankton abundance and distribution provide a biological signature for such events (Venrick 1993, 1995). The recent disturbance history in the North Pacific Ocean, coupled with knowledge of habitat use by the three species of small cetaceans would provide an ecological basis for predicting shifts in habitat use under different conditions. The current environmental conditions favoring the observed dynamic may change as conditions favor one life history strategy over another.

Opportunities to explore these processes in the marine environment are rare, but highly valuable as a foundation for rational conservation and management decisions. These pelagic resources occur in international waters where long term management is complicated by the vagaries of disparate political, economic and social considerations. Natural resource consumption can be expected to continue at its current pace or to accelerate, with increasing attention to marine systems, concurrent to rapid global population growth. To consider that the vast resources of the North Pacific Ocean will be immune to future exploitation would be unrealistic if not naive.

While many of the most complex ecological questions concerning marine ecosystems simply cannot be addressed, with limited data and our rudimentary understanding of ecosystem scale dynamics, the more basic steps can and should be taken where data exist to do so. The primary objective of this study, therefore, is to take the an step to explore partitioning patterns between the three common small cetacean species coexisting in the central North Pacific Ocean using the biological and fisheries interactions data collected on the high seas. The underlying goals are, to answer the question whether niche partitioning mechanisms can be detected using existing data and, to the extent possible, to identify them.

This question is addressed both qualitatively, through analyses and comparison of each of the three small cetacean's life history strategies, and quantitatively, through multivariate analyses where the relationships between species distribution, habitat conditions and presence of other marine community constituents can be compared. These analyses have become possible through the collection of biological and environmental data as part of cooperative research efforts in high seas driftnet fisheries.

Driftnet Fisheries and their Relevance to the Study

Pelagic drift-gillnetting was one of the most widely practiced fishing techniques in the North Pacific Ocean as recently as 1991. The first large scale high seas gillnet fisheries were established by Japan prior to World War II to target salmonids. The fisheries subsequently experienced massive growth during the post war era; by 1959, at the peak of the Japanese high seas salmon mothership fishery, over 450 catcherboats were setting nearly 7,600 km of net each night over a 3 month season. During the late 1970's and 1980's, fishing effort in the Japanese salmon mothership fishery was substantially reduced although 172 catcherboats still set over 2,800 km of gillnet per night each June and July (Jones *et al.* 1987). The mothership fleets no longer operated after 1990, owing to a combination of adverse litigation and economic obsolescence.

As the Japanese high seas salmon mothership fishery was phasing out during the 1980's, Japan, the Republic of Korea and Taiwan each began developing new pelagic driftnet fisheries to target squid over vast areas of the central North Pacific Ocean. The majority of fishing operations occurred in June to November between 34°N and 46°N, and 171°E to 147°W. Although short-lived (having been terminated in 1991 by the United Nations ban on high seas driftnets), the scale of these fisheries was enormous, dwarfing even the salmon mothership fishery at it peak. In 1990, 457 Japanese squid vessels each set approximately 50 km of net per night for a total of 1.15 million km in 23,656 vessel days (Yatsu *et al.* 1993). Concurrently, 139 Korean vessels fished nearly 1.23 million km of similar gillnet gear (Gong *et al.* 1993) and 138 Taiwanese catcherboats set over 450,000 km of gillnet (Yeh and Tung 1993). Thus, peak fishing effort may have approached 35,000 km of squid gillnet set per night.

Such staggering amounts of gear set per vessel in the squid fisheries were necessitated by the low catch per unit effort (CPUE) of the target species, neon flying squid (*Ommastrephes bartrami*), which by 1990 averaged less than 10 kg per 50 m of net (Yatsu *et al.* 1993, Gong *et al.* 1993). While maximizing gear deployment maintained the squid fishery's economic viability, it also precipitated substantial levels of by-catch. Incidental catches in the three squid fisheries included over 65 species of finfish, 25 species of seabirds, and at least 12 species of marine mammals (International North Pacific Fisheries Com-mission 1992). Among the marine mammals involved, three species, Dall's porpoise, Pacific white-sided dolphin and northern right whale dolphin were taken in the greatest numbers. The estimated mortalities for the three species in 1990 were 3,821, 4,725, and 10,349 respectively (Hobbs and Jones 1993). In comparison, only one small cetacean species, Dall's porpoise, was commonly taken in the Japanese high seas salmon mothership fishery where total estimated mortality ranged from 1,456 (1986), to 4,187 (1982) (Jones *et al.* 1987).

Concerns over the potential impacts of large scale driftnet fisheries on non-target species, both in the case of the Japanese salmon mothership fishery in the late 1970's and the three squid fisheries in the late 1980's, prompted U.S. involvement in cooperative scientific monitoring programs. In 1978, under the auspices of the International North Pacific Fisheries Commission (INPFC), the Japan-United States joint Dall's porpoise research program was established to study the impact of incidental take by the salmon mothership fishery. In exchange for agreement by Japan to abstain from salmon fishing east of 175°E latitude (to reduce the interception of North American origin salmon), the fishery was allowed to operate inside the U.S.E.E.Z between June 10 and July 31 each year. In addition to the INPFC Protocol, the United States and Japan signed a Memorandum of Understanding which detailed elements of the joint marine mammal research program. A large component of the research was the collection of biological samples from Dall's porpoise mortalities for use in life history investigations.

The cooperative research programs in the squid fisheries began in 1989 as a result of negotiations between the U.S. State Department and the Japanese equivalent. The 1989 pilot program with Japan soon expanded in 1990 to three separate scientific observer programs between the United States and Japan, the Republic of Korea and Taiwan. Once again, the objectives were to assess fisheries impacts on a variety of marine organisms, including marine mammals, through the collection of fisheries data and biological specimens. Approximately 25 percent of the scientific observers were specifically trained to collect biological specimens from marine mammals.

In general, the cooperative research programs contributed valuable insights on the nature and extent of non-target/fisheries interactions. However, some aspects like the marine mammal sampling effort played little role in the formulation of management decisions. In the case of the Japanese high seas salmon mothership fishery, Dall's porpoise life history investigations were incomplete when, in 1987, the fishery failed to secure renewal of its U.S. Marine Mammal Protection Act Certificate of Inclusion to take marine mammals in U.S. waters. Although a take permit was initially granted to the fishery by NOAA Administrative Court decision, it was subsequently revoked as the legality of (infrequent) northern fur seal (*Callorhinus ursinus*) takes was challenged. The litigation, driven by social and political pressures, focused not on Dall's porpoise issues, but rather on the annual mortality of less than 50 northern fur seals. Nonetheless, the cooperative research program on Dall's porpoise was terminated along with the fishery. Similarly, the squid fisheries were abandoned well before life history studies were sufficiently complete to contribute results for management decisions. The demise of the squid fisheries came as a result of international social and political pressures which culminated in the passage of the United Nations ban on the use of pelagic driftnet gear (United Nations General Assembly, Burke *et al.* 1993).

Although no longer relevant to assessing the long term impacts of the now extinct pelagic squid and salmon driftnet fisheries, the biological specimen collection and associated fisheries data obtained in the cooperative research programs provides the sample necessary for examining and comparing life history strategies, community associations and habitat selection patterns.

Analytical Approach

The data derived from the driftnet observer programs were incorporated into four individual studies, comprising Chapters 1-4. In Chapters 1-3, the age, growth and reproductive patterns for each of the three small cetacean species were analyzed in detail to provide a fundamental understanding of their life history strategies and to provide a basis for subsequent analyses. Benchmark parameters including average age at sexual maturation (ASM), average length at sexual maturation (LSM), sex ratios, length at birth, and postnatal growth rates were also estimated. Likewise, seasonal and geographical distribution patterns associated with calving or population segregation were also examined.

The sources of life history data for Pacific white-sided dolphin and northern right whale dolphin were the squid fisheries, however, the sample of Dall's porpoise from these fisheries was insufficient for estimating most reproductive parameters. Instead, the Dall's porpoise growth and reproduction study was based on the large collection of specimens from the Japanese high seas fishery (1981 to 1987) which likely represented the same population occupying the squid fishing grounds. The fisheries or catch data from this fishery was not combined with squid fishery data in subsequent analyses due to temporal and spatial heterogeneity.

In Chapter 4, the age and length based criteria for determining sexual maturity identified for each species in Chapters 1-3, were used to stratify the small cetacean sample into four sexual maturity categories (i.e. mature and immature males and females) plus a neonatal component for each species. All small cetacean samples used in these analyses were collected in the squid driftnet fisheries during 1990 and 1991. The multivariate statistical technique canonical correspondence analysis (CCA) was used to explore relationships between the presence of each marine mammal species relative to other marine organisms and environmental features. The computer program CANOCO (ter Braak 1986) was used throughout. These analyses generally followed the techniques used for eastern tropical Pacific dolphin species habitat selection studies (Reilly and Fiedler 1993). However, where individual marine mammal sightings were previously used as the sample unit, in this study each individual gillnet operation where approximately the same amount of gear was set and soaked for a similar length of time is considered equivalent to one sample plot.

The canonical correspondence analyses were approached in two ways. First, the relative positions of species in ordination space and their locations along environmental gradients were used to explore differences in habitat preferences between and within species. Second, species positions in ordination space were compared to the presence of other marine organisms caught in the same gillnets. This step allowed identification and comparison of community association patterns. Each set of mutlivariate analyses included separate monthly runs to examine the effect of time and its covariant, latitude, (given northward movement of the fishing fleets across the summer months) on habitat and community association patterns.

Finally, the qualitative results from Chapters 1-3 and the quantitative results from Chapter 4 are summarized in Chapter 5.

CHAPTER 1

Growth and Reproduction of the of the Northern Right Whale Dolphin, *Lissodelphis borealis*

Little biological information on the northern right whale dolphin (*Lissodelphis borealis*) was available prior to the initiation of cooperative research programs in the Japanese high seas driftnet fisheries targeting neon flying squid (*Ommastrephes bartrami*) in 1990. Leatherwood and Walker (1979) summarized reproductive data for 20 animals (10 males and 10 females) from the coastal waters of California. Reproductive data on one additional specimen were presented by Sullivan and Houck (1979).

In the western Pacific Ocean, no biological data has been reported on *L. borealis*. Published accounts discuss only morphology, distribution, and seasonal movements (Ogawa 1937, Okada and Hanaoka 1940, Kasuya 1971, Ohsumi 1972). Studies on age or growth have not been conducted for either the eastern or western Pacific Ocean.

Iwasaki (1991) presented a preliminary analysis of age and reproductive data (25 males and 40 females) for *L. borealis* sampled by Japanese squid fishery observers during 1990. Ferrero *et al.* (1993) presented a preliminary analysis of similar data (40 males and 65 females) collected during the 1990 season using specimens collected by U.S. and Canadian squid fishery observers.

In 1978, the Japanese initiated a high-seas driftnet fishery for flying squid and by the early 1980s, the fishery had not only expanded greatly, but had become notorious for its high levels of non-target mortality, particularly marine mammals. *Lissodelphis borealis* was the most frequently killed small cetacean in this fishery (U.S. Department of Commerce 1989, Hobbs and Jones 1993). Beginning in 1990, and continuing through 1991, under an international cooperative agreement, biological samples were collected from marine mammals killed in this fishery. The combined 1990 and 1991 biological sample provided an unique opportunity to examine growth patterns and to estimate reproductive parameters for pelagic *L. borealis*. This chapter presents the results of those analyses.

METHODS

Specimen Collection

U.S. and Canadian scientific observers were trained to collect biological data and specimens from all cetaceans caught in Japanese squid driftnets. Within 2 hours after arrival on deck, each cetacean was identified, sexed, measured (total length to nearest 1.0 cm), photographed twice (left lateral and ventral) and given a unique specimen number.

When an animal was dissected, the left lower jaw was tagged and frozen intact. For males, the right testis and epididymis were collected whole, tagged, and preserved in 10% formalin. Females were checked for evidence of lactation by longitudinal incision through the left mammary gland. The ovaries and uteri for most females were collected intact. The left ovary was tagged and the entire tract preserved in 10% formalin. If the animal was pregnant with a large fetus or was recently postpartum, only the ovaries and a cross-section of the left uterine horn were collected. Fetuses were sexed, weighed to the nearest 1.0 g, and measured to the nearest 1.0 cm.

Frozen and preserved samples were shipped to the National Marine Mammal Laboratory in Seattle, Washington, for analysis.

Age Determination

Teeth were extracted from the center of the left lower jaw for age determination. Each tooth was decalcified and sectioned longitudinally on a freezing microtome (24 µm). Comparisons of tooth preparations from this sample with published accounts on other delphinid species indicated that *L. borealis* has a similar dentinal layering pattern to that reported for *Stenella* spp. in Myrick *et al.* 1983 and Myrick *et al.* 1984. As a result, tooth slide preparation and dentinal growth layer group (GLG) identification guidelines developed by Myrick *et al.* (1983) for *Stenella* spp. were used. Staining times were increased to up to 40 minutes in some cases to improve readability of dentinal layers. Six to eight sections from the center of each tooth were mounted on a glass slide and examined under a compound microscope at 40x and 100x magnification with transmitted light. Ages were determined by counting dentinal GLGs (terminology of Perrin and Myrick 1981). One GLG was assumed to represent

1 year of growth.

Each tooth was read independently by three readers. Ages were recorded to the nearest 0.5 layer when the innermost (most recent) layer was incomplete, otherwise ages were recorded to the nearest whole layer. Predetermined limits on reader variability were established as criteria to decide when teeth should be reread. Based upon the limits set for ageing *Lagenorhynchus obliquidens* in Walker *et al.* (1986), 0.5 layers difference was allowed between readings for estimated ages up to 5 years (measured from the median reading), one layer for estimates between 5 and 10 years, then one additional layer for every 5-year interval thereafter. When readings differed by more than these limits the tooth was reread.

Examination of Reproductive Organs

Males

The right testis with epididymis attached were weighed to the nearest 0.01 g and measured to nearest 0.1 cm. A 1 cm^3 block of tissue was removed from the center of each testis; a similar section of epididymis was removed at mid-length. Both samples were prepared histologically. Paraffin-embedded tissues were sectioned at 6 μm, stained with hematoxylin and eosin, and mounted on glass slides. Testes and epididymides were examined for evidence of spermatogenesis using a compound microscope at 100x with transmitted light.

Females

Ovaries were weighed to the nearest 0.01 g. Maximum diameter of the left uterine horn was measured to the nearest mm. Each ovary was sliced transversely into about 1-mm thick serial sections with a scalpel and examined for presence of corpora lutea and corpora albicantia. Two measurements of corpus diameter, taken at right angles, were recorded for well-regressed corpora; three diameters were recorded for larger corpora. Total corpus counts include both corpora albicantia and corpora lutea. Females were classified as sexually mature if at least one corpus was present on either ovary.

Corpora were examined externally for indications of regression, including color change (i.e., darkening) and reduced size and surface furrowing, and classified by type following Perrin *et al.* (1976).

RESULTS

The Sample

From May-October 1990 and 1991, a total of 229 *L. borealis* (99 males and 130 females) were dissected and sampled (see Fig. 1 for sampling locations). In addition, sex and length data were obtained from 460 (188 males and 272 females) additional specimens that were not dissected due to constraints posed by other observer duties. Although these data were not used to estimate growth or reproductive parameters, the length frequency distribution of the aggregate sample (n=689) was used to assess potential sampling bias and for comparison with sex ratio estimates obtained from the analyzed sample.

Male northern right whale dolphins ranged from 0 to 27 years in age; 7% were newborns, 13% were yearlings and the remainder were more than 1 year old. Female ages ranged from 0 to 41.6 years; 7% were newborns and 8% were yearlings.

On visual inspection, the number of samples for both sexes (Fig. 2) trended downward with age except in two cases: the neonatal component (0-0.5 years), which appears to be under-represented, and the number of juvenile males age 5-7 and females age 5, which is low relative to the sample size of animals in surrounding age groups.

Males ranged in length from 99 to 291 cm. Females ranged from 97 to 224 cm (Fig. 3).

Growth

Length at Birth

Mean length at birth was calculated three ways for comparison: 1) logistic regression following Hohn and Hammond (1985) 2) a modified DeMaster (1978) method, and 3) the mean size of neonates.

Logistic regression was used to estimate the mean length at birth as the length at which 50% of a combined sample of the fetuses collected (n=15) and the youngest neonates with no postnatal dentine layering (n=13) had reached parturition (Table 1). The model used is explained in detail under average age at sexual maturation (ASM).

DeMaster's method was modified to use length rather than age and applied to the same sample of fetuses and neonates, grouped into 4 cm intervals. Details are provided under average length at sexual maturation.

A third method, which gives an upper bound to the mean age at birth, is calculated as the mean of the lengths of 13 neonates showing no postnatal dentine layering (i.e., presumed recent births). Lengths of the 14 largest fetuses ranged from 87.6 to 104 cm; the 13 neonates ranged from 97 to 112 cm.

Using the logistic regression method, the average length at birth was determined to be 99.7 cm (95% C.I., 96.4-104.9 cm) (Fig. 4). Using DeMaster's method, the value was 100.6 cm (SE=0.3482). The mean length of the 13 neonates was 103.8 cm (SE=1.4315).

Gestation Period

Because this sample did not contain a sufficient size distribution of fetuses collected throughout the year, an empirical method such as that described by Hugget and Widdas (1951) or Laws (1959) could not be used. Instead, the gestation period was determined by comparison, using an apparent relationship between size at birth and gestation period among several species of delphinids as described by Perrin *et al.* (1977). The Perrin *et al.*

(1977) regression equation:

$$Logy = 0.1659 + 0.4586Logx,$$

was used, substituting x with the length at birth that we calculated for *L. borealis* which yielded y.

The *L. borealis* length at birth estimates of 99.7 cm and 103.8 cm were used to approximate the gestation period at 12.1 months and 12.3 months, respectively.

Postnatal Growth

Growth curves were fitted separately for males and females using a non-linear least-squares method. The Laird formula (Laird 1969) was used as a base model for both sexes:

$$L(t) = L_0 \exp\{a[1 - \exp(-\alpha t)]\},$$

where, $L(t)$ is the length at age t, L_0 is the length at birth, t is the age, a is the specific rate of exponential growth, and α is the rate of decay of exponential growth.

For both sexes we achieved the best growth model fits using two Laird curves intersected at the average ages of sexual maturation. In each case, the lower curve was fitted to sexually immature animals and the upper curve to sexually mature animals.

The female growth curve through age 2 is steep and nearly linear (Fig. 5); its slope decreases over the next three age groups before increasing slightly again. Asymptotic length is reached at about 210 cm.

The lower portion of the male growth curve mirrors the lower female curve. The upper segment is comparatively steeper and more pronounced, however, reaching an asymptotic length of 265 cm by age 15 (Fig. 6).

The mean length of females age 12 and older was 211.2 cm (n=54, SE=1.2242). Males at age 12 reached total lengths of at least 210 cm by age 12, with one animal measuring nearly 260 cm. The mean length of males age 12 and older was 237.9 cm (n=19, SE=5.1267), which was significantly greater than females (T-test, P<0.0005).

Reproduction

Sex Ratio

Sex ratios were estimated for animals less than 1 year old, for each 2-year age class from 1 to 17 years old, and for all animals 18 years or older using the empirical logistic transform method (Cox and Snell 1989) as

$$r = \frac{m + 0.5}{f + 0.5}$$

where r is the ratio of males to females, m is the number of males in the sample and f is the number of females in the sample. The natural logarithm of r is normally distributed with variance,

$$var[\ln(r)] = \frac{(n+1)(n+2)}{n(m+1)(f+1)}$$

where $n = m + f$. The confidence limits on r are then

$$(\frac{r}{k}, r\,k) \quad where \quad k = e^{1.96\sqrt{var[\ln(r)]}}$$

Using a linear regression model, the sex ratio was then compared by age (Fig. 7). The slope of the regression line was significant (R^2=0.75), although only the sex ratio of animals in the age 18+ interval differed significantly from 1.0 ($P<0.005$). This is probably due to higher mortality rates in males than in females.

Average Age at Sexual Maturation

The average age at sexual maturation (ASM) was calculated by the logistic regression and the DeMaster (1978) method. DeMaster's equation computes the mean age as

$$ASM = \sum_{a=j}^{k} a(f_a - f_{a-1}),$$

where, f_a is the fraction of mature animals in the sample aged a, f^a is the number of immature animals in the sample aged a, j is the age of the youngest mature animal in the sample, and k is the age of the oldest immature animal in the sample. The estimated variance is calculated as:

$$var(ASM) = \sum_{a=j}^{k} \frac{f_a(1-f_a)}{(N_a-1)},$$

where, N_a is the total number of animals aged a.

The logistic regression (Cox and Snell 1989) fits a logistic curve, ($\mu(a)$), the probability that a dolphin of age a is mature, to the distribution of mature and immature animals by age:

$$\mu\text{-} = \frac{e^{ab+c}}{1+e^{ab+c}},$$

where, a is the age of the dolphin (expressed in GLGs) and b and c are the slope and intercept of the regression. ASM is then estimated as the age where $\mu(a)=0.50$, so that ASM=$-c/b$.

The regression was done using a maximum likelihood and iteratively re-weighted least-squares algorithm (Chambers and Hastie 1992). The standard error for μ was obtained by transforming the standard error of the linear fit.

Males

For males the average age at onset of sexual maturity using the logistic curve method was estimated to be 9.9 years (95% C.I., 9.0-11.0 years) (Fig. 8). Based on this sample, 5% of males would reach sexual maturity at age 8.1 (95% C.I., 4.9-9.0 years) and 95% are mature at age 11.7 (95% C.I., 10.7-15.4 years). Using DeMaster's (1978) method, our estimate of average age at attainment of sexual maturity was 10.1 years (SE=0.4007).

There was a significant linear correlation between testis mass and age among the immature animals (R^2=0.73), but the overall increase in testes mass was small. The relationship between age and testis mass was roughly linear among mature animals also, but testes mass dramatically increased between ages 10 and 16 (Fig. 9). The sample contained 28 sexually mature and 71 sexually immature males. The youngest sexually mature male was 8.3 years (testis weight 117.4 g); the oldest immature was 10.5 years (testis weight 35.8 g). Weights of mature testes ranged from 117.4 to 1,300 g.

Females

Female average age at sexual maturation, estimated by the logistic method, was 9.7 years (95% C.I., 8.9-10.6 years) (Fig. 10) with five percent mature by age 6.9 (95% C.I., 4.3-8.0 years), and 95% mature by age 12.5 (95% C.I., 11.4-15.3 years). Using DeMaster's (1978) method, the estimated average age at sexual maturation was 10.4 years (SE=0.4541).

A total of 67 mature and 63 immature females was examined. The youngest sexually mature females (n=3) were 8 years old; one was pregnant (94 cm fetus). The oldest immature female was 12.0 years old (Fig. 11).

Of the mature females, 11 were pregnant with near-term fetuses, 2 were pregnant and lactating, 16 were not pregnant but lactating, 22 were postpartum and lactating, and 7 were resting. Nine females had stage-2 corpora (terminology of Perrin *et al.* 1976), 8 of which were not pregnant or lactating, nor did the uteri indicate postpartum conditions. These stage-2 corpora, therefore, may be corpora of ovulation only. The uterine condition of the remaining female indicated recent pregnancy and may have been the result of a recent abortion.

Average Length at Sexual Maturation

Logistic regression and the modified DeMaster (1978) method were also used to estimate mean length at onset of sexual maturity (LSM). The logistic regression formulas are the same as for the ASM calculation with length substituted for age.

$$LSM = \sum_{i=i_{min}}^{i_{max}} l_i(f_i - f_{i-1}),$$

DeMaster's method was modified to use length rather than age and applied to each sex, grouped into even intervals, where i_{min} is the index of the size class with the smallest mature animal, i_{max} is the index of the size class with the largest immature animal, l_i is the lower limit of the ith size class, and f_i is the fraction mature in the ith size class.

The variance estimate is modified from the formula of DeMaster (1978) to account for the interval width (*w*) so that

$$var(ASM) = w^2 \sum_{i=i_{\min}}^{i_{\max}} \frac{f_i(1-f_i)}{N_i-1},$$

where N_i is number of individuals in the ith size class and the interval width (*w*) was constant.

Males

Male average length at sexual maturation, using the logistic method, was 215.1 cm (95% C.I., 210.6-220.8 cm) (Fig. 12). Five percent were estimated to reach sexual maturity at 198.4 cm (95% C.I., 181.6-204.6 cm); 95% at 231.7 cm (95% C.I., 224.5-252.1 cm). Using the modified DeMaster (1978) method, the estimated average length of sexual maturation was 214.7 cm (SE=0.4851).

There was a significant linear correlation between length and individual testis weight among immature animals (R^2=0.80). Testes weights changed little with age up to the onset of sexual maturity when weights then increased dramatically (Fig. 13). The smallest sexually mature male was 203 cm long (testis weight 117.4 g); the largest immature animal was 223 cm (testis weight 15.9 g).

Females

Female average length at sexual maturation, using the logistic method, was 201.1 cm (95% C.I., 195.3-205.4 cm) (Fig. 14). Five percent were estimated to reach sexual maturity at 172.8 cm (95% C.I., 149.4-182.9 cm); 95% at 229.4 cm (95% C.I., 221.4-247.6 cm). Using DeMaster's (1978) method, the estimated average length at onset of sexual maturity was 199.8 cm (SE=0.6347).

The smallest sexually mature female measured 179 cm, had two corpora and was lactating. The largest immature female was 221 cm (Fig. 15).

Ovulation Rate

Calculation of ovulation rate followed methods used for *Stenella attenuata* in Perrin *et al.* (1976). All females with one or more corpus up to age 19 were grouped in 2-year intervals; females age 20 to 24 were pooled, as were all others 25 and older. These groupings were necessary in order to achieve an adequate sample size of mature females within a given interval. The average reproductive age(Ā) in interval *p* was calculated as

$$\overline{A_p} = \frac{(\sum_{i}^{p} a_i * b_i)}{c},$$

where, *a* is the percent maturing in the *i*th interval, *b* is the average reproductive age in interval *p* of females which matured in *i* and *c* is the percent mature in interval *p*.

This approach was modified for the last interval (age 25+) to better reflect the distribution of reproductive ages in the interval because it contained relatively few animals (n=9) but ranged to age 41. Here we calculated the mean age of females 25 and older, then added the difference between it and the mean age of the previous interval to the average reproductive age of the 20- to 24-year interval.

The average corpus count in each age interval was calculated by dividing the sum of corpora counted in interval *i* by the number of mature females in interval *i*. The average corpus count was then regressed on the average reproductive age.

Examination of *L. borealis* ovarian scars indicated that a range of 1 to 20 corpora was present among mature females. Curvilinear and linear model fits to the corpus count and average reproductive age data were similar; the correlation coefficient (r) of the former was 0.9750 compared to 0.9822 for the latter.

Seasonality

There appeared to be a seasonal reproductive pattern in *L. borealis*. Lactating females with large corpora were present in the sample from June to October, but with a higher frequency in August. Pregnant females with near or full-term fetuses (90-104 cm) were only collected from mid-July to mid-August (Table 2); no smaller fetuses were taken. Of the 13 newborns collected, 1 was taken in June, 6 in July and 6 in August. These observations suggest a summer calving season which peaks in July and August.

Lactating females with only fully regressed corpora were collected in June-August and in October, while no newly forming corpora were observed at any time during the sampling period. This lack of ovarian activity but obvious lactation suggests that these females had given birth at least 1 year previously, perhaps during the previous calving period, but the actual duration of nursing remains unknown. Although we cannot empirically estimate the calving interval, this pattern, coupled with the gestation period estimate of over 12 months suggests a minimum of 2 years between successful pregnancies. Examination of data for a newborn and four fetal specimens of *L. borealis* from sources other than the squid fishery (Table 3) reveals some inconsistency with the July-August calving period indicated by our 1990-91 data. Of these five specimens, two (JWS-002 and JWS-003) are of particular interest. Both specimens were collected in a salmon research gillnet on June 12, 1980 in the same general area as our squid fishery sample. The fetal lengths (40.9 cm and 33.9 cm) were less than half the length of the smallest (90 cm) fetus which we collected during July or August. It is unlikely that the 1980 fetuses would have been born in July or August; it is more likely that they would have been born in late fall or early winter.

DISCUSSION

The reason for the apparent difference in reproductive seasonality suggested by the small fetuses collected in 1980 is unknown, but may be related to changes in oceanographic conditions in the study area. The current systems associated with the North Pacific subarctic and transitional zones are complex and subject to dynamic seasonal changes as well as annual fluctuation in intensity (Favorite *et al.* 1976). The observed disparity in calving season may reflect the existence of more than one stock of *L. borealis* which may have been present in that part of the study area in 1980.

The *L. borealis* sample contained no animals between 120 and 160 cm. However, there was no comparable gap in the age groups. Following both the male and female growth curves, this size range corresponds to the interval between 0 and 1 year old and probably represents the average increase in size over the first year. The absence of animals in this size range also suggests that the timing of the previous year's births was similar to those observed and is further evidence of a consistent late-summer calving period.

Previous studies of small cetacean reproduction and growth caution that a number of potential biases have been recognized and may effect the utility of vital rate estimates. In the present study, the sample was carefully considered with particular reference to potential biases caused by a) the sampling method (i.e., incidental entanglement in gillnets), b) the limitation of the sampling period from May to October, c) reproductive seasonality, and d) segregation, both within schools and geographically.

Following the assumptions listed for each reproductive parameter in Perrin and Reilly (1984), the sample was unsuitable for calculation of pregnancy rates, calving interval, length of lactation, age of weaning, and length of resting period principally because evidence of strong seasonality in calving had been identified. Conversely, sampling from large-scale pelagic driftnets such as those used in the Japanese squid fishery probably did not introduce significant biases in the parameters that were estimated, and that *L. borealis* was essentially sampled in proportion to their availability in the study area. This conclusion was based on three points.

First, *L. borealis* mortalities were distributed randomly along the length of the gillnets and were found in low numbers per individual net (DOC 1989). Groups of entangled animals were never encountered in the same area of net as one might expect if whole schools or large portions of schools encountered the net. Instead, *L. borealis* appeared to become entangled individually. This observation suggests that potential bias introduced by spatial orientation of *L. borealis* within a school or age/sex composition of individual schools was minimal.

Second, the sampling effort was distributed over a large geographical area and was essentially continuous during the fishing season. Observer placement was randomly distributed throughout the fishery. If *L. borealis* are geographically segregated, then the broad distribution of sampling effort over a large portion of the species' known range should have dampened its effect.

Finally, the *L. borealis* age frequency distribution did not indicate a sampling bias readily explained by differences in susceptibility to entanglement. Although this finding is based on our sample of 229 fully sampled animals, the length frequency distribution of the aggregate sample of sexed and measured animals (n=689) also suggests that the sample is representative.

Two unusual features of the age distribution, however, do suggest potential biases that are probably not related to sampling from driftnets: a) under-representation of the newborns and b) fewer animals in the 5-7 year age groups compared to the size of the surrounding age groups.

Under-representation of the newborn component may be explained by the timing of the collections which bracketed the late summer calving period. Fewer newborns would be expected prior to the peak of calving as they simply have not reached parturition and, therefore, are unavailable for sampling. If the number of fetuses (all near term) collected is added to the number of newborns collected, the age distribution more closely resembles that of a reasonably stable population.

The low number of 5-7 year olds suggests either ageing error or population segregation. Error in ageing, however, is an unlikely factor because dentinal layers in the juvenile age class were typically distinct and very little discrepancy between readers was encountered in this portion of the ageing sample. Some degree of segregation in the study area is more likely. Under-representation of juveniles appears to be a recurring pattern in samples of delphinid cetaceans (Perrin and Reilly 1984). One possibility in our *L. borealis* sample is a tendency for juveniles in the 5-7 year groups to be more widely dispersed resulting in lower densities in the areas sampled.

Leatherwood and Walker (1979) reported that the largest male in their sample was 307 cm and that no females exceeding 230 cm were collected. They speculated that male *L. borealis* reach a larger overall size than females; this is in agreement with the findings in the present study.

In general, the growth patterns for both male and female *L. borealis* are similar to those reported for *Stenella attenuata* by Perrin *et al.* (1976). The growth curve fit using the double Laird model for females of both species was good. In males, however, the variability in adult length results in a poor fit. Perrin *et al.* (1976) suggested one explanation may be that growth in adult *S. attenuata* males is more complex than in adult females and that more complex growth models may be called for to describe these events.

The present treatment of the *L. borealis* data indicates a marked increase in secondary growth among some animals at the ages of 11-15 years with an asymptotic length of 265 cm. This secondary growth surge is also characterized by a precipitous increase in testis weight. This secondary growth phase around the mean age of sexual maturity and apparent correlation with greatly increased testicular activity was interpreted to be an event related to the attainment of full or social maturity in *L. borealis.*

Secondary increase in growth of males correlated with puberty has been reported for numerous other species of odontocete cetaceans including killer whale (*Orcinus orca*) (Christensen 1984); sperm whale (*Physeter macrocephalus*) (Best 1969, 1970, Best *et al.* 1984); pilot whales *Globicephala* spp. (Sergeant 1962, Kasuya and Marsh 1984); spotted dolphin (*Stenella attenuata*) (Perrin *et al.* 1976) and eastern spinner dolphin (*Stenella longirostris*) (Perrin *et al.* 1977). The disparity between age and/or length at puberty and social maturity based on testicular activity has also been reported for the striped dolphin (*Stenella coeruleoalba*) (Miyazaki 1984) and common dolphin (*Delphinus delphis*) (Collet and Saint Girons 1984).

Leatherwood and Walker (1979) reported that the largest sexually immature male of 10 examined was 212 cm and the smallest sexually mature was 219.5 cm. For females, their largest sexually immature of 10 examined was 200 cm and the smallest mature was 201 cm. On the basis of these data they speculated that males were larger at the onset of sexual maturity than females. Reproductive data from our sample support this observation.

Iwasaki (1991) reported on preliminary analyses of life history parameters for *L. borealis.* The estimates of length at birth (around 100 cm) and age and length at sexual maturity (i.e., males: 9-13 years, 210-230 cm; females 5-9 years, 180-210 cm) are sufficiently wide to bracket the estimates from the present study in each case except for female age at sexual maturity.

In the present study the point at which 50% of the females are mature was estimated to be 9.7 years, with only 5% mature at age 6.9. This suggests that Iwasaki's estimate may be low.

The estimates of length at birth combining lengths of both fetuses and neonates differ by only 0.9 cm, which is less than the precision of most field measurements; therefore, a length of 100 cm is a reasonable estimate of length at birth. The third estimate, 103.6 cm, is likely biased upward by inclusion of animals that were probably weeks rather than days old.

The estimated sex ratios for ages 0-1, 2-3 and 3-4 favored males but none were significantly different from a ratio of 1.0. The aggregate sample contained 28 males and 28 females less than 140 cm which corresponds to age 1 or less and suggests parity at birth.

A non-linear model has been suggested as preferred over linear models for estimation of ovulation rates (Perrin *et al.* 1976, Perrin *et al.* 1977, Perrin and Henderson 1984); however, little difference in fit between themwas found in the present study. *Lissodelphis borealis* appear to ovulate at a fairly constant rate of about 0.81 corpora per year through average reproductive age 11 (about total age 21) and only a slight drop thereafter. If the gestation period estimate of 12+ months and the presence of lactating, but not reproductively active, females in the sample is considered, then the ovulation rate appears high. This may suggest that some of the observed ovarian activity did not culminate in birth. Such cases may include abortions or corpora development in the absence of fertilization. These circumstances, leading to uncertainty in the interpretation of corpora counts, have been previously discussed relative to several other delphinid species (Perrin and Reilly 1984).

Table 1. Length, sex, location and date of collection for 15 *Lissodelphis borealis* fetuses collected in the Japanese high seas squid driftnet fishery during 1990/91.

Specimen	Length (cm)	Sex	Date	Position
EJW 004F	90.0	F	7/16/90	41°20'N 157°17'W
JHY 021F	104.0	M	7/18/90	41°45'N 163°44'W
EJW 005F	95.0	F	7/22/90	41°39'N 165°25'W
KLK 011F	97.0	F	7/24/90	42°24'N 158°42'W
EJW 007F	93.0	F	7/26/90	41°41'N 165°28'W
NWR 009F	91.0	M	8/03/90	44°35'N 179°34'W
NWR 010F	91.0	F	8/03/90	44°35'N 179°34'W
NWR 011F	100.0	F	8/07/90	44°44'N 178°39'W
EJW 014F	94.0	M	8/10/90	43°29'N 157°24'W
RCR 013F	100.2	F	8/22/90	44°51'N 178°09'W
CEH 012F	96.1	F	7/08/91	42°37'N 155°54'W
CEH 013F	96.0	M	7/08/91	42°37'N 155°54'W
CEH 016F	87.6	M	7/08/91	42°37'N 155°54'W
TTV 021F	100.0	F	7/15/91	42°48'N 159°04'W
PHB 016F	96.0	M	7/20/91	42°48'N 162°41'W

Table 2. Reproductive condition of mature *Lissodelphis borealis* females by month collected in the Japanese high seas squid fishery in 1990/91.

Month	Reproductive Condition			
	Pregnant	Pregnant and Lactating	Lactating with Large Corpora	Lactating without Large Corpora
May	1	0	0	0
June	0	0	0	3
July	8	1	8	9
August	3	1	6	4
September	0	0	5	0
October	0	0	0	1

Table 3. Four *Lissodelphis borealis* fetuses and one newborn collected from sources other than the Japanese squid driftnet fishery.

Specimen Number	Date	Length (cm)	Location
Fetuses:			
JWS - 002	06/12/80	40.9	38° 58.5'N 179° 55.5'W
JWS - 003	06/12/80	33.9	38° 58.5'N 179° 55.5'W
DWR 1969-80	03/09/69	26.0	32° 10.0'N 118° 33.0'W
SBMNH-81-26A	05/03/81	18.1	Avila Beach, Santa Barbara, CA
Newborn:			
CAL ACAD 3813	02/03/86	97.0	Monterey, CA

SBMNH = Santa Barbara Museum of Natural History
CAL ACAD = California Academy of Science

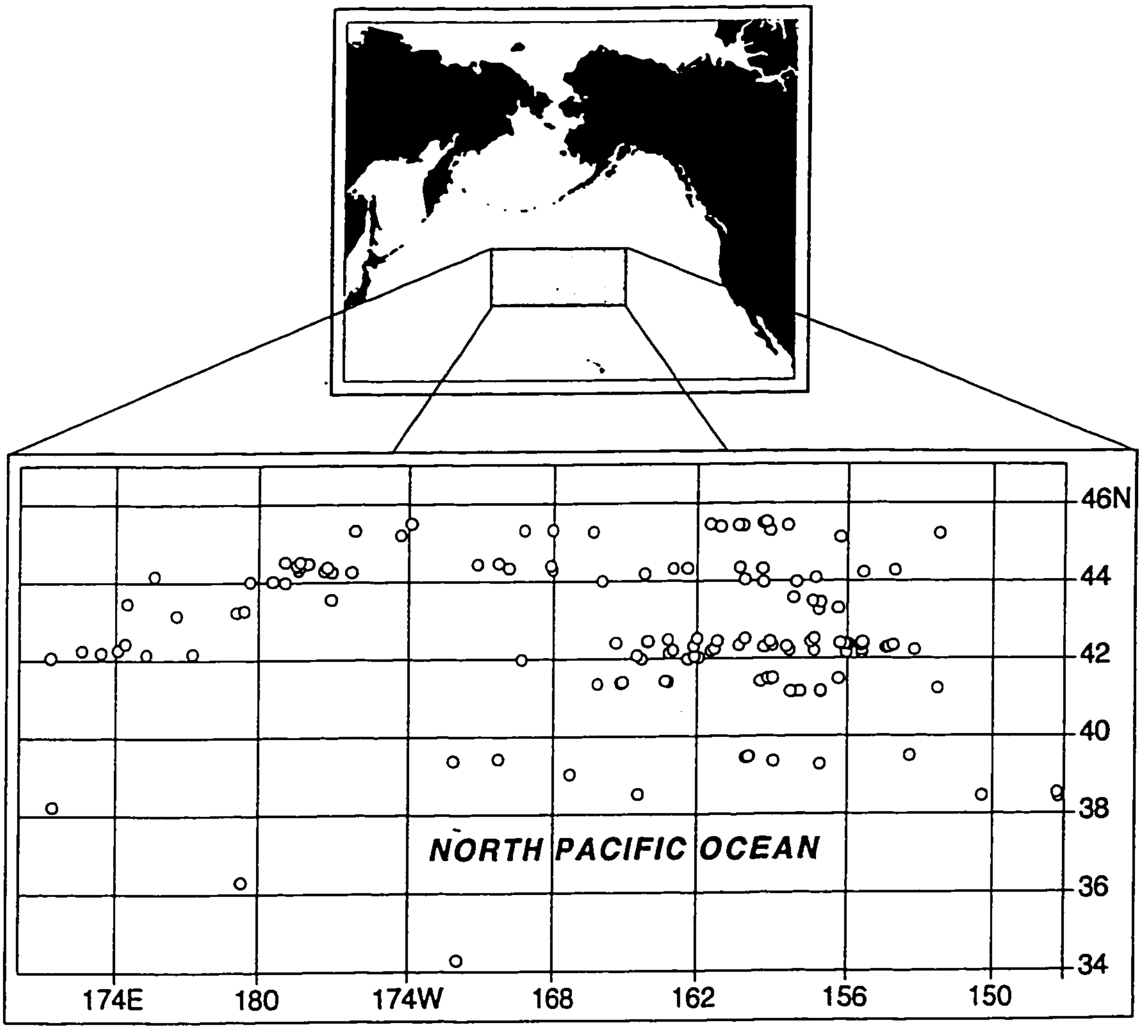


FIGURE 1: Sampling locations of 99 male and 130 female *Lissodelphis borealis* caught in Japanese high seas driftnets, May-October 1990 and 1991.

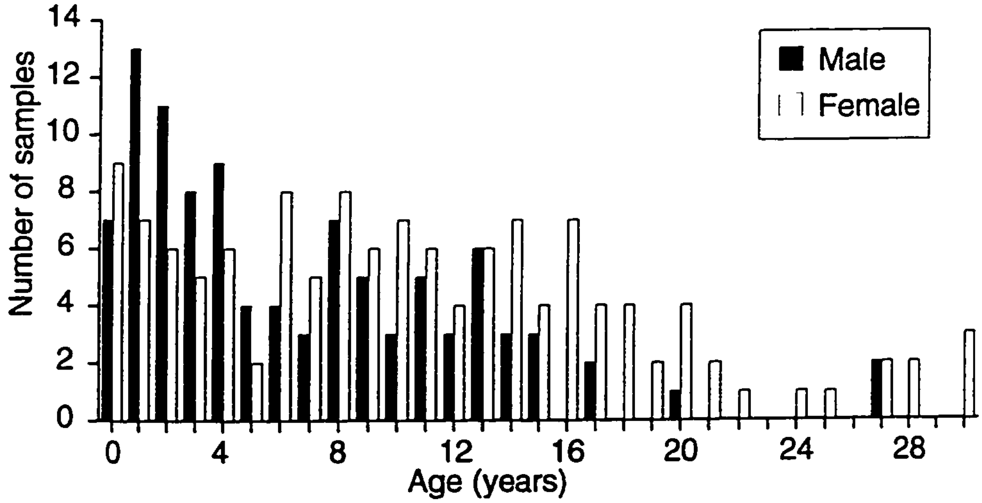


FIGURE 2: Age frequency distribution of 99 male and 130 female *Lissodelphis borealis.*

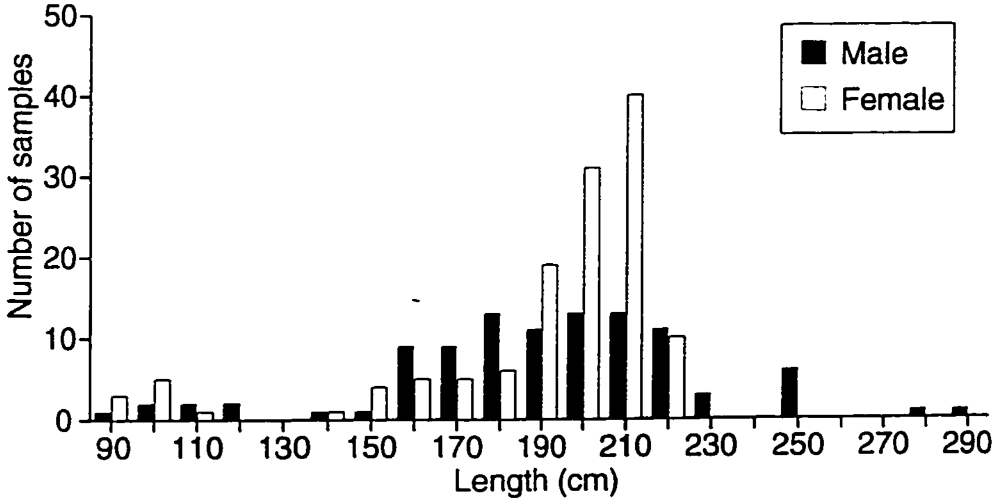


FIGURE 3: Length frequency distribution of 99 male and 130 female *Lissodelphis borealis*. The x-axis labels show the lower bound of the length interval.

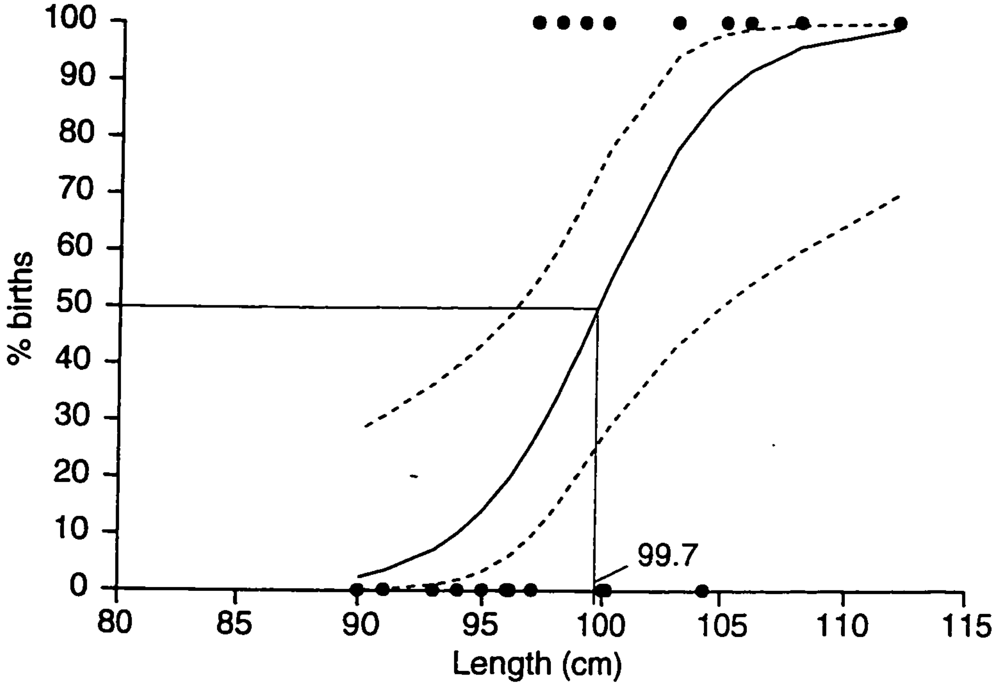


FIGURE 4: Logistic curve fitted to length and birth status. The dashed lines represent the 95% confidence limits on the fitted curve. The points represent individual samples.

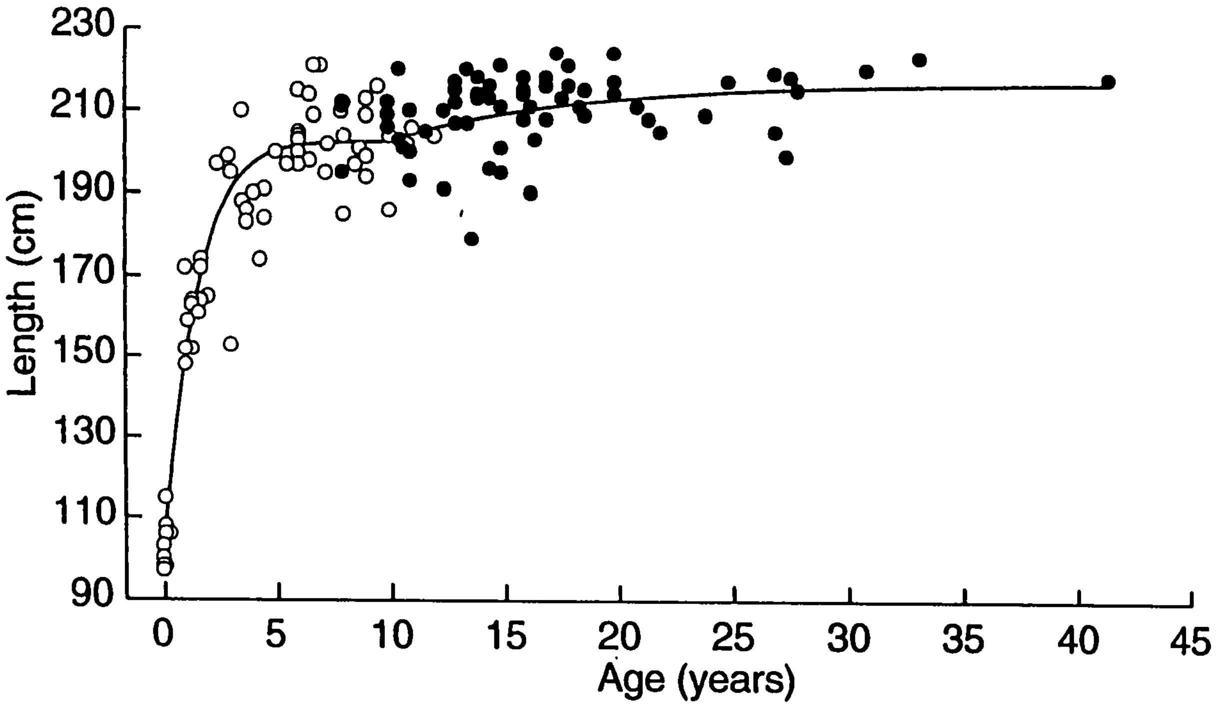


FIGURE 5: Age-at-length of female *Lissodelphis borealis* with fitted growth curves (2-stage Laird (1969) model). The open circles are immatures and the closed circles are matures.

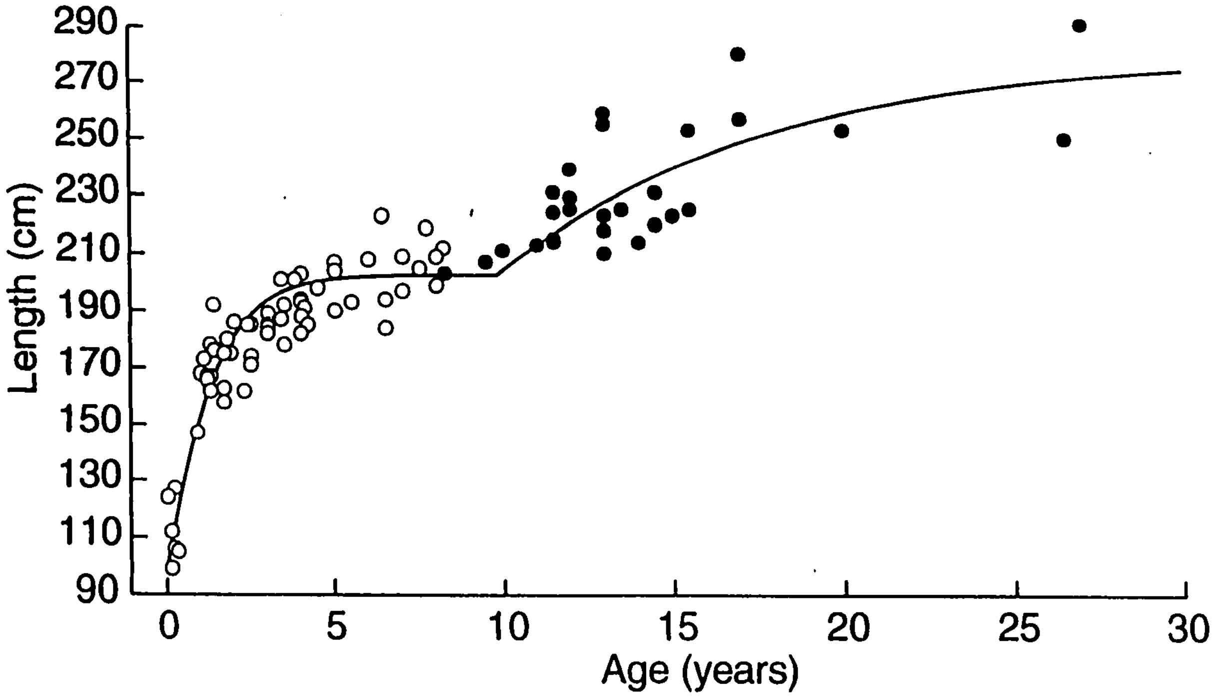


FIGURE 6: Age-at length of male *Lissodelphis borealis* with fitted growth curves (2-stage Laird (1969) model). The open circles are immatures and the closed circles are matures.

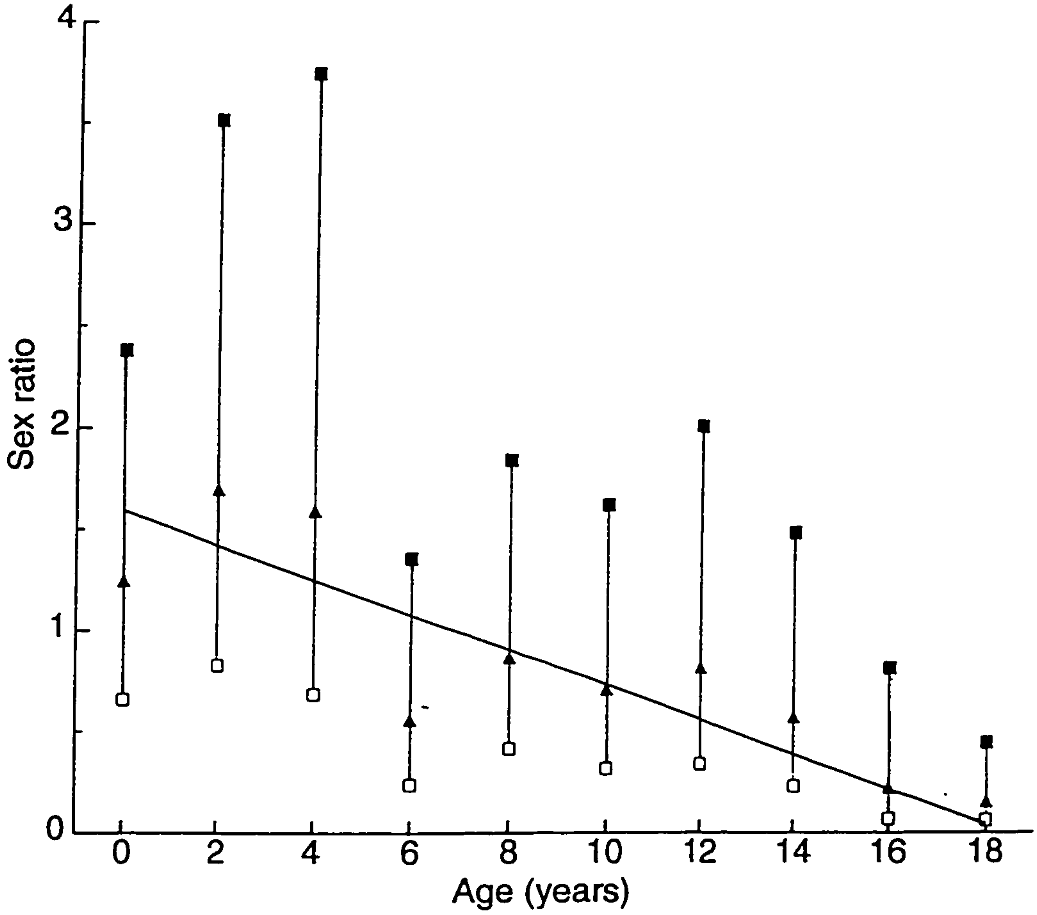


FIGURE 7: Estimated sex ratios for *Lissodelphis borealis* by two-year age intervals and all others aged 18 and older. The closed triangles are means and the vertical bars are the 95% confidence intervals about the mean. The regression line is y=0.7335-0.1143x.

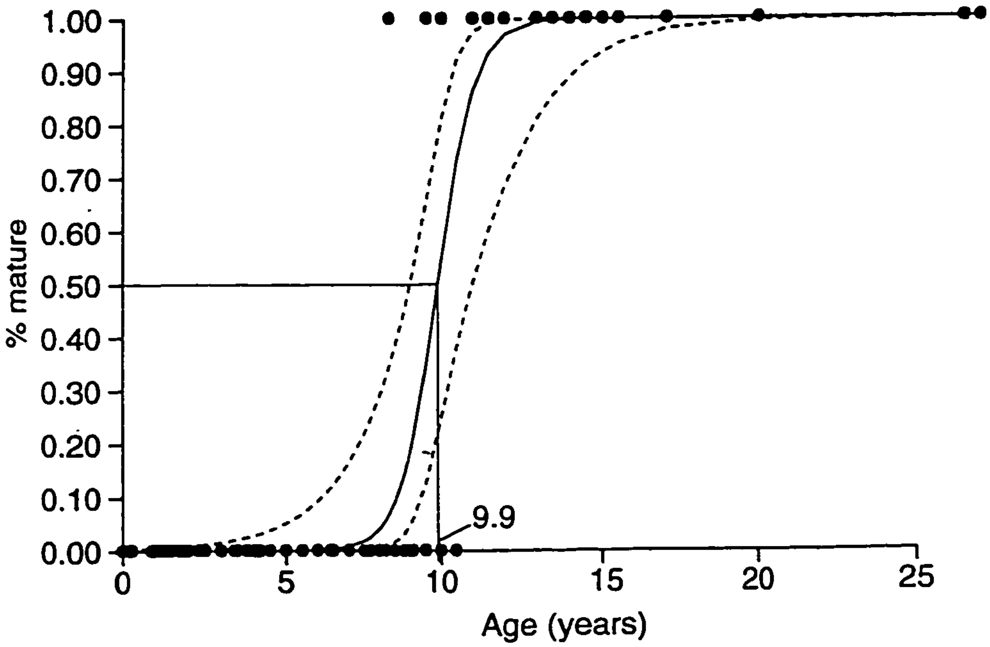


FIGURE 8: Logistic curve fitted to age and sexual maturity status of male *Lissodelphis borealis*. The dashed lines represent the 95% confidence limits on the fitted curve. The points are individual samples.

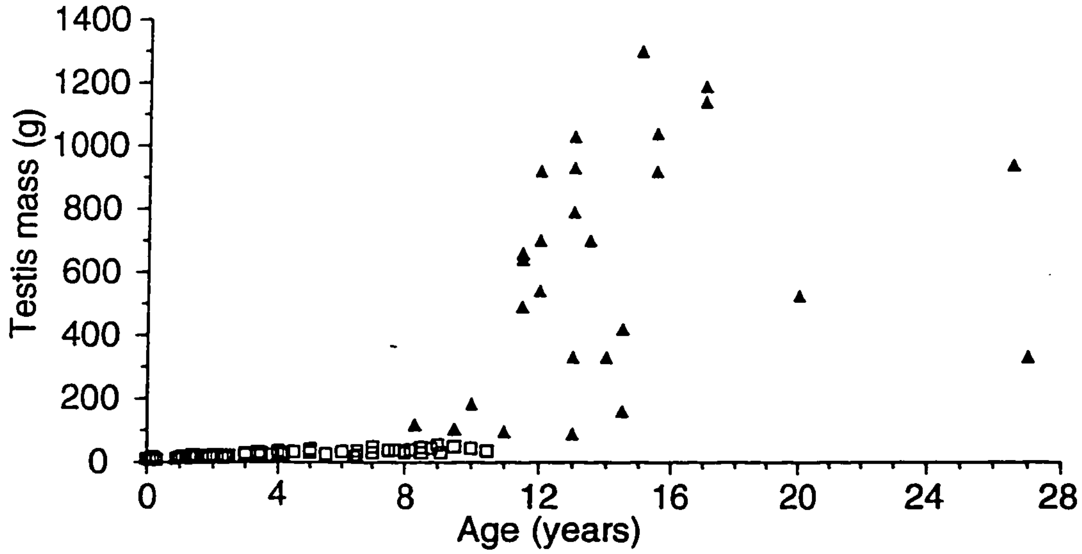


FIGURE 9: Scatterplot of age (years) and testis mass (g) for 99 *Lissodelphis borealis* males. The squares represent immature animals; the triangles represent mature animals.

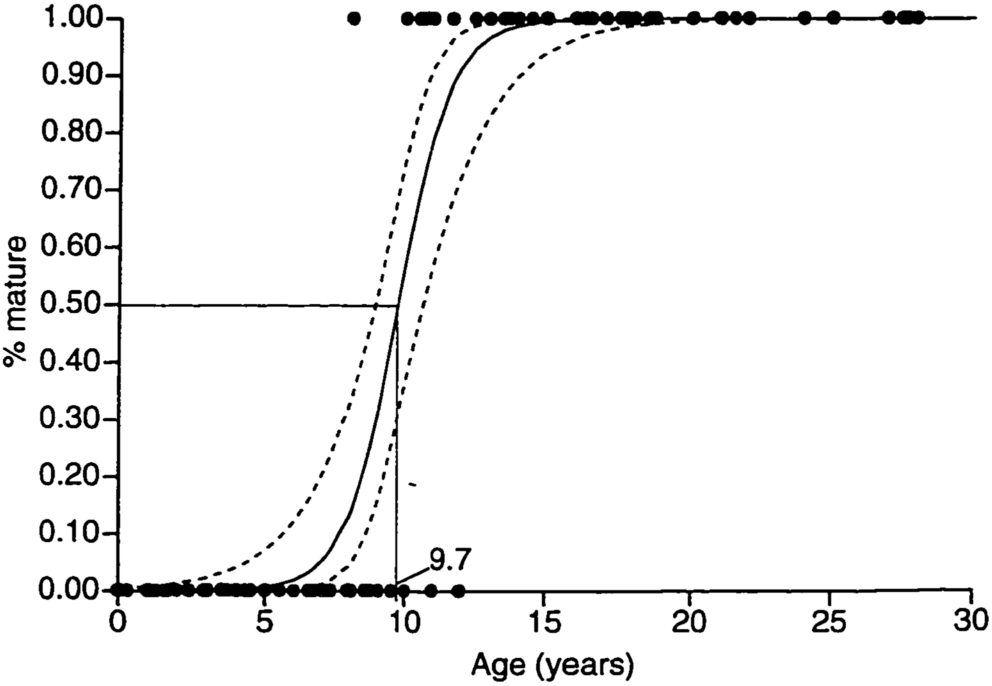


FIGURE 10: Logistic curve fitted to age and sexual maturity status of female *Lissodelphis borealis*. The dashed lines are the 95% confidence limits on the fitted curve. The points represent individual samples.

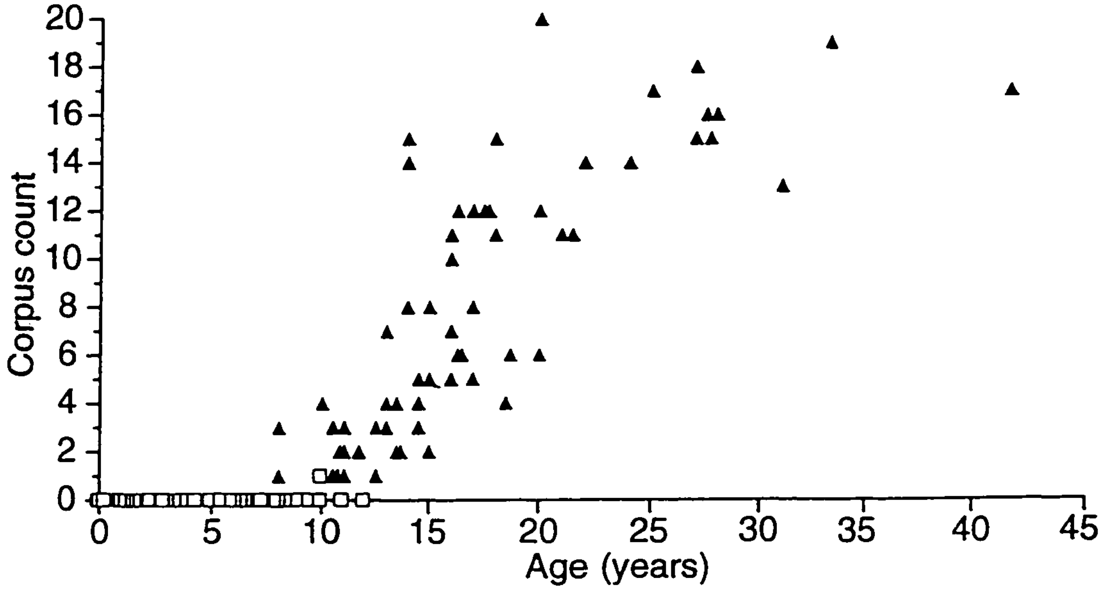


FIGURE 11: Scatterplot of age (years) and total corpus count for 63 immature and 67 mature *Lissodelphis borealis* females. The squares represent the immatures; the triangles represent the matures.

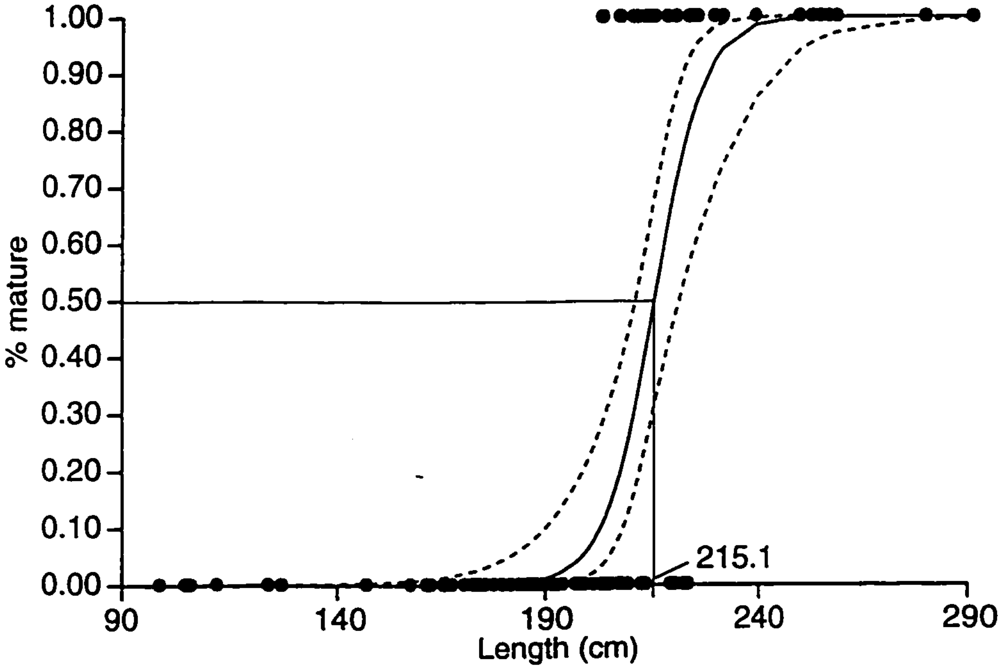


FIGURE 12: Logistic curve fitted to length and sexual maturity status of male *Lissodelphis borealis*. The dashed lines are the 95% confidence limits on the fitted curve. The points represent individual samples.

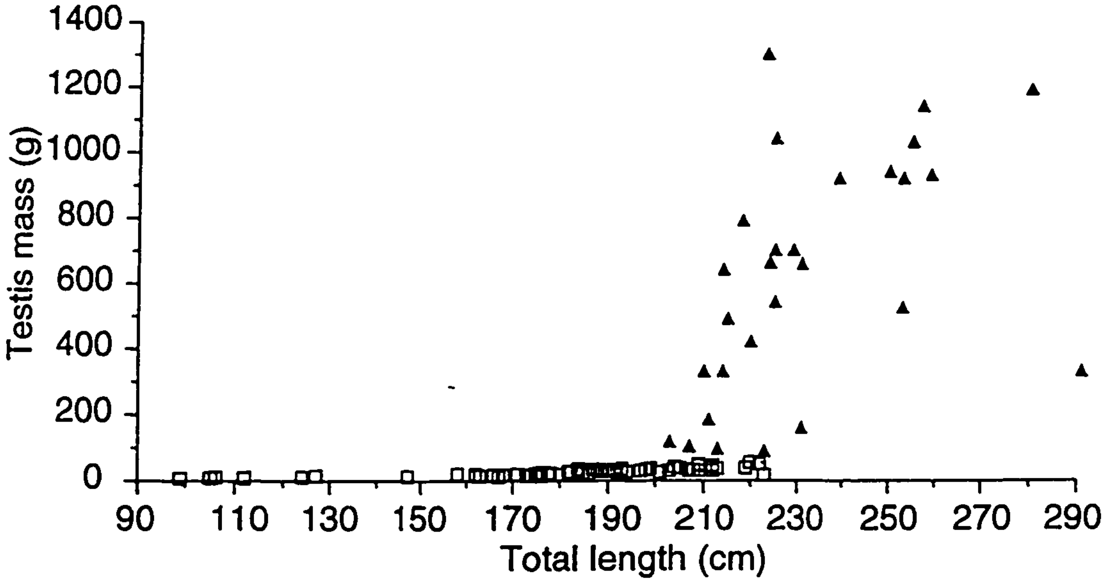


FIGURE 13: Scatterplot of length (cm) and testis mass (g) for 99 *Lissodelphis borealis* males. The squares represent immature animals; the triangles are mature animals.

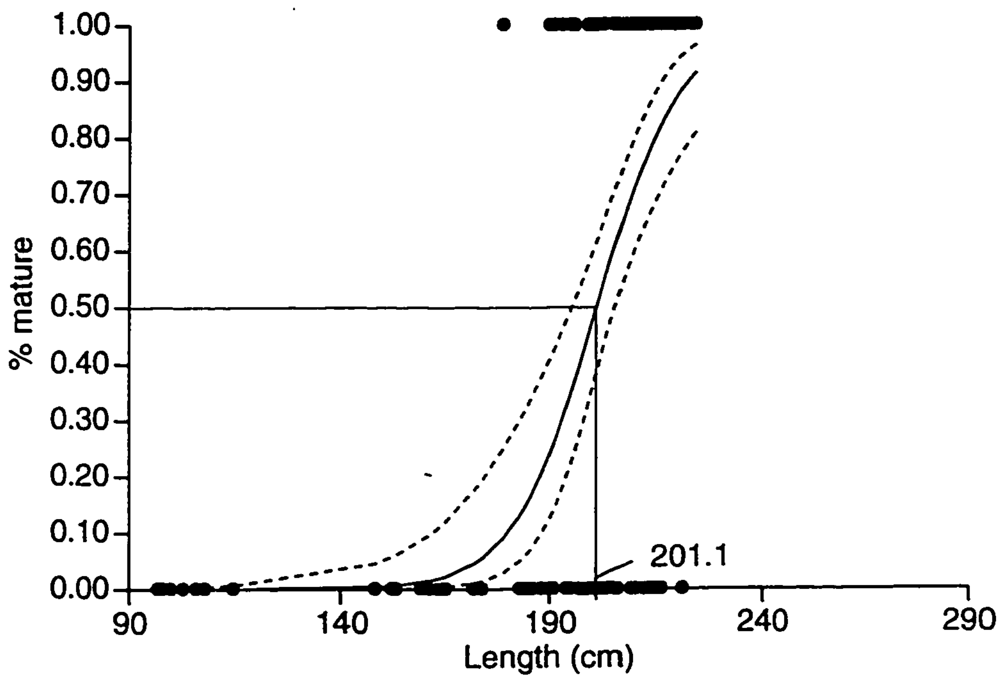


FIGURE 14: Logistic curve fitted to length and sexual maturity status of female *Lissodelphis borealis*. The dashed lines are the 95% confidence limits on the fitted curve. The points represent individual samples.

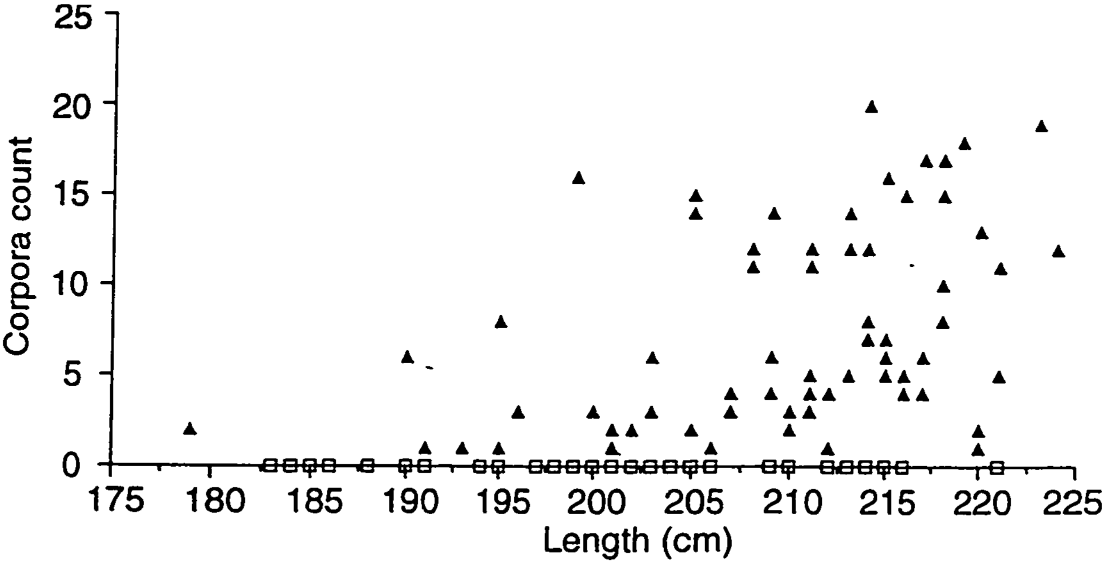


FIGURE 15: Scatterplot of length (cm) and total corpus count for 27 immature (>175 cm) and 67 mature *Lissodelphis borealis* females. The squares represent the immatures; the triangles represent the mature animals.

CHAPTER 2

Age, Growth and Reproductive Patterns of the Pacific White-Sided Dolphin (*Lagenorhynchus obliquidens*)

Biological information on Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in the coastal waters of the eastern North Pacific was summarized by Walker *et al.* (1984) and Walker *et al.* (1986). These accounts provide age and reproductive data on 142 animals collected primarily off the coasts of California and Mexico, but the sample likely contained a mixture of individuals from two populations and was not used to describe population parameters. For the western North Pacific Ocean, little biological information has been published on this species. Reproductive data have been reported for a small number of animals taken off the Pacific coast of northern Japan (Wilke *et al.* 1953). Miyazaki and Shikano (1989) used age-to-length relationships and osteology to identify two populations of *L. obliquidens* in the coastal waters of Japan.

Research on the Japanese high seas driftnet fishery has recently provided a large number of biological samples from *L. obliquidens* in the oceanic portion of its distribution. Based on samples and data from this region, Iwasaki (1991) presented preliminary analyses of age (75 males and 73 females) and reproductive parameters (25 males and 40 females) from animals taken incidentally in Japanese squid driftnets from 1988 to 1990. Ferrero *et al.* (1993) presented a preliminary analysis of similar data (38 males and 42 females) collected by U.S. and Canadian observers in the squid fishery during 1990.

During 1991, additional biological samples and data were collected by U.S. observers in the Japanese, Korean, and Taiwanese squid driftnet fisheries, and the Taiwanese large-mesh fishery. The combined 1990 and 1991 sample provided a unique opportunity to examine growth patterns and to estimate reproductive parameters for *L. obliquidens* in the mid-oceanic waters of the North Pacific Ocean. This chapter presents the results of these life history investigations.

METHODS

Specimen Collection

Scientific observers collected biological data from all cetaceans caught incidentally in Japanese driftnet operations monitored. Soon after arrival on deck, each cetacean was identified, sexed, measured (total length to nearest 1.0 cm), photographed twice (left lateral and ventral), and given a unique specimen number.

When an animal was dissected, the left lower jaw was tagged and frozen intact. Stomachs were collected whole, tagged and frozen. For males, the right testis and epididymis were collected whole, tagged, and preserved in 10% formalin. Females were checked for evidence of lactation by longitudinal incision through the left mammary gland. The ovaries and uteri for most females were collected intact. A tag was placed adjacent to the left ovary and the entire reproductive tract was preserved in 10% formalin. If the animal was pregnant with a large fetus or was recently postpartum, only the ovaries and a cross-section of the left uterine horn were collected. Fetuses were sexed and weighed to the nearest 1.0 g, and standard length was measured to the nearest 0.1 cm.

Examination of Reproductive Organs

Males

Right testes with epididymides were weighed to the nearest 0.01 g and measured to the nearest 0.1 cm. A 1-cm^3 block was removed from the center of each testis; a similar section of epididymis was removed at mid-length, and both were prepared histologically. Paraffin-embedded tissues were sectioned at 6 µm, stained with hematoxylin and eosin, and mounted on glass slides. Testes and epididymides were examined for evidence of spermatogenesis using a compound microscope at 100X with transmitted light. Males were considered mature if sperm were present in testes tubules.

Females

Ovaries were weighed to the nearest 0.01 g. Maximum diameter of the left uterine horn was measured to the nearest millimeter. Each ovary was sliced transversely into serial sections (≈1 mm thick) with a scalpel and examined for the presence of corpora lutea and corpora albicantia. Two measurements of corpus diameter, taken at right angles, were recorded for well-regressed corpora; three diameters were recorded for larger corpora. Total corpus counts included corpora albicantia and corpora lutea from both the right and left ovaries. Females were classified as sexually mature if at least one corpus was present on either ovary.

Corpora were examined externally for indications of regression, including color change (i.e., darkening), reduced size and surface furrowing, and classified by type following Perrin *et al.* (1976).

Stomach Contents

The food habits data presented in this paper were restricted to presence or absence of milk and solid food as indications of weaning. Each stomach chamber was opened and visually inspected for milk, then rinsed of all solid food remains.

Age Determination

Teeth were extracted from the center of the left lower jaw for age determination. Each tooth was decalcified and sectioned (24 µm) longitudinally on a freezing microtome. The teeth were oriented on the microtome stage so that each cut section was parallel to the plane encompassing the crown apex and the approximate center of the root canal. The crown apex was oriented horizontally. The tooth section preparation and dentinal growth layer group

(GLG) counting guidelines developed by Myrick *et al.* (1983) for *Stenella* spp. were adopted for this study. Eight to 10 stained sections from the center of each tooth were mounted on a glass slide and examined under a compound microscope at 40X and 100X magnification with either transmitted or polarized light. One GLG was assumed to represent 1 year of growth (Fig. 16).

Each tooth was read independently by two readers at least twice. Ages were estimated to the nearest 0.5 layer except for animals with less than one complete GLG. In these cases, the fractional portion of the incomplete layer was recorded as 0.1 GLG if only a trace could be identified, 0.3 GLG if greater than a trace, but less than 0.5, 0.5, and 0.7 if greater than half the layer was present. Predetermined limits on reader variability were established following those utilized for *L. obliquidens* in Walker *et al.* (1986), and for *Lissodelphis borealis* in Ferrero and Walker (1993). The procedure allowed for a 0.5-layer difference between readings for estimated ages 1 to 5 years (measured from the median reading), one layer for estimates between 5 and 10 years, then one additional layer for every 5-year interval thereafter. Within these limits, the two readers' estimates were averaged to obtain the final age. When readings differed by more than these limits the tooth was re-read. For animals with < 1 complete GLG, the independent readings were compared, and if different, both readers jointly re-read the tooth to arrive at a single best estimate.

The abundance of young animals in the sample, a corresponding interest in examining early postnatal growth, and the relative imprecision in ageing animals less than 1 year old by assessing presence of GLG components prompted us to measure postnatal dentine thickness as an index of age following descriptions in Perrin *et al.* (1977), Kasuya and Brownell (1979), Hohn (1980), and Myrick *et al.* (1983). This approach constituted an alternative method for estimating first-year growth rates.

Postnatal dentine thickness measurements were taken perpendicular to the longitudinal axis of the tooth, from inner border of the prenatal dentine to the adjacent wall of the pulp cavity, as close as possible to where the neonatal line approached the outside of the tooth (Fig. 16). To provide the best consistency between measurements, only tooth sections taken at the center of the tooth were examined. In addition, noting lateral asymmetry in the postnatal dentine deposition, the same side of the tooth (i.e., the convex side with respect to the crown) was always measured.

The measurements were obtained using digital imaging equipment. The system for recording and analyzing tooth section images included a Sony digital RGB video camera (model XC-77) mounted in the camera tube of a Nikon Labphot-2 compound microscope. The camera was linked to a 486-DX50 personal computer equipped with an Imaging Technology VISIONplus-AT Overlay Frame Grabber processing board, and Image-Pro Plus (version 1.2) image processing software. The images were viewed in black and white on a Sony Trinitron high-resolution color video monitor (model PVM-1344Q) in both real time (as an aid to two reader examinations) and after image capture. The

Image-Pro Plus linear measurement routines were used to calculate distances between endpoints that were identified on screen at 40X or 100X. The Image-Pro Plus linear measurement routines were calibrated, converting pixels to microns, for each microscope magnification based on captured images of a stage micrometer.

RESULTS

The Sample

A total of 341 *L. obliquidens* (171 males and 170 females) were examined from June to September 1990 and 1991. Sex, total length, collection date, and catch location (Fig. 17) were recorded for each specimen, while biological samples were collected from 149 of these dolphins (73 males and 76 females).

Postnatal growth, tooth ageing patterns, and the average age and average length at sexual maturation were examined using the sample of animals from which biological samples were collected, minus two males for which reproductive status could not be determined (i.e., leaving 71 males and 76 females). To assess potential sub-sampling biases, testes for differences in the length distributions of the total sample and the dissected sample for each sex were run; no significant differences were detected (Kolmogorov-Smirnov Test, males: D=0.0648, P>0.50, females: D=0.0999, P>0.50). The total sample (n=341) was used to examine sex ratios, gestation period and reproductive seasonality.

The latitudinal distribution of sampling locations indicated a northward shift from June to August (Fig. 18). This followed squid driftnet fisheries movements typical of the summer months when the northern boundary of the fishing grounds was relaxed. Longitudinally, the sampling area expanded both east and west as the fishing area broadened from June to August (Fig. 19). A slight contraction of the sampling area in September corresponded to tightened limits in the northern boundary imposed during the fall (Gong *et al.* 1993, Nagao *et al.* 1993, Yatsu *et al.* 1993, Yeh and Tung 1993).

Male *L. obliquidens* ranged from 0 to 36 years in age (n=73); 1% were newborns (n=2), 34% were calves <1 year old (n=25), 19% were yearlings (n=14) and the remainder were >2 years old. Female ages ranged from 0 to 40 years (n=76); 5% were newborns (n=4), 26% were calves <1 year old (n=20), and 12% were yearlings (n=9). The age distribution of non-neonates declined intrinsically for both sexes (Fig. 20).

In the total sample, males ranged in length from 89 to 237 cm. Females ranged from 90 to 210 cm. For both the total and dissected samples there was a complete bell-shaped frequency distribution of lengths below 130 cm (Figs. 21 and 22). This portion of the length frequency distribution, and a corresponding pattern in the frequency of calves <1 year old (Fig. 20), suggested that sampling had occurred after peak calving. In the following analyses, animals less than 130 cm were treated as the youngest cohort sampled each year.

Growth

Length at Birth and Gestation Period

No near full-term fetuses were collected; therefore, a length at birth estimate using rigorous methods described by Hohn and Hammond (1985) could not be generated. Instead, a preliminary estimate was derived by averaging the lengths of newborns (Perrin and Reilly 1984) which met the following criteria:

1. No neonatal line or postnatal dentine could be detected in prepared tooth sections, and
2. External features indicating recent birth were present (e.g., unhealed umbilical scars, pronounced evidence of fetal folds, and curling of the fluke margins (Tavolga and Essapian 1957, Kasuya *et al.* 1974).

Of the six animals collected with no evidence of a neonatal line or postnatal dentine, only four also met the second criterion. The mean length of these four newborns, ranging from 91 cm to 93 cm, was 91.8 cm (SE=0.4787). The reader is cautioned that this estimate should be regarded as tentative pending future treatment with a larger sample. Furthermore, it may be biased upward slightly owing to growth between birth and sampling.

Assuming, however, that this mean length estimate at least approximated the length at birth, and using the lengths of two early-term fetuses collected (13.0 cm and 19.2 cm), preliminary estimates of the gestation period were calculated in two ways: 1) using the relationship between fetal length and time described by Hugget and Widdas (1951), and 2) using the relationship between size at birth and gestation period described for several species of delphinids by Perrin *et al.* (1977).

Following Hugget and Widdas (1951), the lengths (y) of the two fetal specimens and the four newborns were regressed on time, indexed by day of the year of collection (x), to estimate the linear phase of growth (t_g-t_o), where t_g is the gestation period and t_o is the "nonlinear" phase of growth. The regression equation

$$y = 7.978 + 0.261\,x$$

was significant (r^2=0.996, P<0.001). The linear growth phase was estimated to be 10.7 months. The nonlinear phase was not calculated because fetal mass data necessary to use the formula derived by Calder (1982) were lacking.

The Perrin *et al.* (1977) regression equation:

$$Log(y) = 0.1659 + 0.4586\,Log(x)$$

was used, substituting x with our preliminary estimate of length at birth. The *L. obliquidens* length at birth estimate of 91.8 cm approximated the gestation period at 11.6 months.

Postnatal Growth

Male and female growth curves were each fitted using a nonlinear least-squares method. The Laird-Gompertz formula (Laird 1969) was used as a base model for both sexes:

$$L(t) = L_0 \exp\{a[1 - \exp(-\alpha t)]\}$$

where $L(t)$ is the length at age t, L_0 is the length at birth, t is the age, a is the specific rate of exponential growth, and α is the rate of decay of exponential growth.

Females

For females, a single Laird-Gompertz curve was fitted (Fig. 23) with L_0 fixed at 92 cm, the preliminary estimate of length at birth. The distribution and magnitude of the residuals in the upper portion of the curve indicated a satisfactory fit, however, the residual distribution in the lower portion of the curve was strongly positive. The predicted length at age 1 was 128.8 cm. Asymptotic length was predicted to be 177.1 cm. For comparison, the growth curve was shifted to optimize the fit in the lower region of the curve (ignoring the lack of fit above age 1) and a predicted length at age 1 of 149.9 cm was obtained.

Males

For males, two Laird-Gompertz curves were fitted, one for the sexually mature animals and the other for the sexually immatures, in order to minimize the number of positive residuals in the upper curve segment (Ferrero and Walker; 1993, 1995) (Fig. 24). For the lower curve, L_0 was fixed at 92 cm. Lacking samples around the age of sexual maturation, an iterative fit of the two curve segments could not be achieved to locate the intersection point. As in the case of females, a satisfactory fit the growth model to the data for animals over 1 year old could be achieved, predicting an asymptotic length of 183.8 cm, however, the residual distribution at ages less than 1 year were again strongly positive. The predicted length at age 1 was 133.4 cm. By shifting the growth curve to provide the best fit in the lower region (again, ignoring the lack of fit at ages above age 1), a predicted length at age 1 of 147.8 cm was obtained.

Alternative Approach to Predicting Length at Age One

First-year growth patterns were reexamined using length and postnatal dentine thickness in place of GLG estimates. This approach was considered less susceptible to potential ageing biases inherent in visual estimation of first GLG completeness. Measurements of postnatal dentine thickness were obtained from 47 teeth (25 males and 22 females) with incomplete first GLGs, and plotted against total length (Fig. 25).

Length and postnatal dentine thickness were regressed for females less than age 1 (n=22) and obtained the equation:

$$y = 98.4 + 0.1548x,$$

where x equaled postnatal dentine thickness and y equaled total body length. The slope was significant ($P<0.001$).

Similarly, length and postnatal dentine thickness were regressed for all males less than 1 year old (n=25) and obtained the equation:

$$y = 101.0 + 0.1419x,$$

where x equaled postnatal dentine thickness and y equaled total body length. The slope was significant ($P<0.001$).

To convert postnatal dentine accumulation to age and use it to predict length at age 1, 44 teeth (23 males and 21 females) from animals with one or more complete GLG showing clearly stained first GLG boundaries were measured. The mean thickness of the first complete GLG (males: $\bar{x}=308.0$ µm, SE=3.127, females: $\bar{x}=312.1$ µm, SE= 3.239) was measured; no significant difference was detected between the male and female means (Student's T test, t=0.9193, P>0.35), so samples were combined and a new mean calculated ($\bar{x}=309.9$ µm, SE=2.246).

Substituting the mean thickness of the first GLG (309.9µm) for $\underline{x}$ in the female GLG regression equation, a predicted length at age 1 of 146.4 cm was obtained for females. For males, the mean thickness of the first GLG (309.9 µm) was substituted for x in the corresponding GLG regression equation to obtain a predicted length at age 1 of 145.0 cm. For both sexes, the predicted values were slightly less than the predicted lengths at age 1 derived by simply adjusting the growth curve to optimize the fit for young animals (i.e., 149.9 cm for females and 147.8 cm for males).

For use in subsequent analyses, a monthly growth rate mean was calculated for each of the three methods. Using length and age (in GLGs), the length at birth estimate (92 cm) was subtracted from the predicted length at age 1, and divided the difference by 12. Then, using length and postnatal dentine thickness, 92 cm was subtracted from the predicted lengths at age 1 from the GLG regression equation for each sex, and those differences divided by 12 (Table 4).

Comparison of Predicted Asymptotic Lengths

The Laird-Gompertz growth model fits (Figs. 23 and 24) were used as the basis for comparing male and female asymptotic lengths. The mean length of males age 15 and older (i.e., the animals likely to have reached maximum size based on predicted length at age 15 falling on the asymptotic portion of the upper growth curve) was 184.3 cm (n=6, SE=1.89). The mean length of females age 15 and older was 178.1 cm (n=8, SE=1.20). The difference in mean lengths between sexes was significant (Student's T-test, two-tailed, P=0.02).

Reproduction

Age and Sexual Maturation

Average age at sexual maturation (ASM) could not be calculated for either sex using an empirical method such as described by DeMaster (1978) due to the insufficient number of indeterminant age classes represented in the sample. The range of ages bracketing the onset of sexual maturation was characterized, however, by the ages of the youngest mature and oldest immature animals sampled. For males, the range was 10 to 11 years. There was a significant linear correlation between testis mass and age among the immature animals (r^2=0.74, P<0.0001), but the overall increase in testis mass was small (<50 g over 10 years). A linear relationship between age and testis mass was not apparent among mature animals (r^2=0.002, P>0.90). Testis mass dramatically increased at about age 10 (Fig. 26).

The sample for which reproductive tissues were available contained 11 sexually mature and 60 sexually immature males. The testis masses of the two youngest sexually mature males (both age 10) were 290 g and 580 g; the testis mass of the oldest immature (6.2 years) was 50.1 g. Masses of mature testes ranged from 99.2 to 580 g.

For females, the oldest sexually immature animal was 8.3 years; the youngest sexually mature female was 11.0 years and had one corpus (Fig. 27). Of the 76 female reproductive tracts collected, 10 were from mature animals; 3 were pregnant and 7 were lactating (Table 5).

Length and Sexual Maturation

Calculation of average length at sexual maturation was accomplished using the DeMaster (1978) method, modified to estimate the average length instead of average age (Ferrero and Walker 1993). The modification of the DeMaster (1978) method used lengths grouped into even intervals as

$$LSM = \sum l_i(f_i - f_{i-1}),$$

where $i_{\min}$ is the index of the size class with the smallest mature animal, $i_{\max}$ is the index of the size class with the largest immature animal, l_i is the lower limit of the ith size class, and f_i is the fraction mature in the ith size class.

The variance estimate on female LSM was obtained by modifying the formula of DeMaster (1978) to account for the interval width (w) so

$$var(\,LSM\,) = w^2 \sum_{i=i}^{i_{\max}} \frac{f_i(1-f_i)}{N-1},$$

that where N_i is number of individuals in the ith size class and the interval width (w) was constant.

For males, the length at sexual maturation was estimated to be 173.7 cm (SE=0.8953). The smallest sexually mature male was 171 cm; the largest sexually immature was 179 cm. There was a significant linear correlation between length and individual testis mass among immature animals

(r^2=0.59, P<0.001). Testis masses changed little with length up to the onset of sexual maturity when masses increased greatly (Fig. 28). No correlation between length of mature animals and testis masses was detected (P>0.4).

For females, the average length at sexual maturation was estimated at 177.5 cm (SE=1.5). The smallest sexually mature female measured 173 cm; one corpus was present on the left ovary. The largest sexually immature female was 181 cm (Fig. 29).

Sex Ratio

Sex ratios were estimated for three subsets of the total sample of sexed and measured animals (n=341) representing first-year, adolescent, and "mature" life stages. The predicted lengths at age 10 from the postnatal growth models (Figs. 23 and 24) were used to approximate a separation between the two older subsets, assuming that most animals at age 10 (both sexes) were either sexually mature or close to it. Due to uncertainty in our predictions of length at age one as a suitable criteria for separating the two youngest subsets, 130 cm was used as the upper bound for the youngest subset which likely included only animals in the most recent cohort. The animals greater than 130 cm but less than 178 cm were included in the middle group. The empirical logistic transform method (Cox and Snell 1989) was used to estimate the sex ratio as

$$r = \frac{m + 0.5}{f + 0.5}$$

where r is the ratio of males to females, m is the number of males, and f is the number of females. The natural logarithm of r is normally distributed with variance

$$var[\ln(r)] = \frac{(n+1)(n+2)}{n(m+1)(f+1)}$$

where n is the total number of males and females, m is the number of males, and f is the number of females. The three sex ratios were 1.000 (SE=0.1990) for first year animals, 1.096 (SE=0.1513) for adolescents, and 0.813 (SE=0.2437) for "matures". None of the ratios was significantly different from 1.0 (Exact Binomial Test, P-values were all >0.30).

Seasonality

Four features of the sample suggested a pattern of reproductive seasonality characterized by a peak in calving prior to the start of the sampling season. First, as previously noted, the overall length frequency distribution contained a distinct mode separated from the rest of the distribution by a sparsity of animals between 130 and 140 cm. This gap was interpreted as the size range not yet reached by the youngest cohort as of late September when sampling terminated, but which the previous year's cohort had already grown through by the beginning of sampling in June. Very few neonates were collected during either year of sampling (n=6): four were collected in mid-June and two were collected in the first week of July. This period probably marked the latter tail of the calving period.

Second, the mean size of animals in the mode below 130 cm increased each month from June to September. The monthly means were: June, 99.4 cm (SE=1.5642); July, 108.0 cm (SE=1.2619); August, 115.4 (SE=1.7968); September, 123.57 cm (1.5408). The means were significantly different between adjacent months (ANOVA, F=24.22, P<0.0001).

The third indication of reproductive seasonality was the presence of lactating and pregnant females with small fetuses. All but one female, which was lactating and had fully regressed corpora (Type 3), suggested either recent calving or mating activity. Six of the seven lactating females collected had partially regressed (Type 2) corpora albicantia. The lengths of the two fetuses collected (Table 2) were less than 25% of the estimated size at birth and considered early term.

Fourth, the stomach contents analyses showed the first evidence of solid food only in those animals >120 cm, collected after mid-August. Four stomachs from animals between 120 and 123 cm collected in late August and September contained both milk and solid food remains. Only solid food remains were found in animals larger than 130 cm. It appeared that weaning began in late summer of the animal's first year.

Due to the timing of the collections, neither the duration nor the timing of peak calving could be determined directly. Instead, the birth dates for all neonates and calves were back-calculated in two ways. First the equation:

$$d_b=d_c-30\frac{(l_c-l_b)}{r},$$

was used, where d_b was the day of the year of the birth date, d_c was the day of the year of collection, l_c was the length at collection, l_b was the length at birth, and r was the growth rate in centimeters per month. The value 92 cm was used for l_b. The resulting distribution of birth dates suggested that calving may have begun as early as January, peaking in March, and ending in July (Table 6).

Second, a similar distribution of neonate and calf birth dates was back-calculated, based on the amount of postnatal dentine present, using the following equation:

$$d_b=d_c-365(\frac{t_d}{309.9}),$$

where d_b was the day of the year of the birth date, d_c was the day of the year of collection, and t_d was the postnatal dentine thickness (μm). The mean estimate of the first GLG thickness (309.9 μm) was constant. The resulting distribution of birth dates again ranged from January to July, but peaked in June (Table 6).

DISCUSSION

The Calving Season

The two birth date distributions back-calculated for the youngest cohort sampled were similar in duration, but different in the frequency of births at each tail of the distribution. The length-based distribution (Table 6, method A) was centered around an earlier date than the distribution based on postnatal dentine accumulation (Table 6, method B). Two factors, one affecting each distribution, were considered to explain the apparent differences.

The large number of birth dates in June indicated by the postnatal dentine-based analysis (Table 6, method B) probably stemmed from a lag in growth of postnatal dentine for some period after birth. Hohn and Hammond (1985) speculate that the neonatal line may not be deposited immediately after birth in *Tursiops truncatus*. In the present study, of the six *L. obliquidens* without a neonatal line, two showed external characteristics indicative of calves rather than neonates (i.e., healed umbilical scars, rigid flukes and only faint fetal folds). Animals with zero or trace amounts of postnatal dentine, therefore, may have been under-aged. Assuming there was a time lag in the formation of the neonatal line, and that the mean thickness of the first GLG does represent 1 year, then the underestimation bias impacted estimates for the youngest animals the most, but less so as age 1 was approached. The calving date distribution, therefore, if corrected for this bias would have shifted all dates out of July and most of the June births into May. The remainder of the distribution may also have shifted earlier in the year, depending on the extent of the lag period.

The early tail of the length-based distribution (Table 6, method A) was particularly sensitive to estimates of length at birth. If a value higher than the 92 cm preliminary estimate was used, the early tail of the length-based distribution shifted approximately 1 month later for each 4 or 5 cm increment increase, corresponding to the estimated monthly growth rate used.

Published data on *L. obliquidens* birth size are scant. Harrison *et al.* (1972) estimated length at birth at "about 95 cm" and Walker *et al.* (1986) reported one live birth in captivity of a 95 cm male. If the estimate were low, then an alternative value based on those earlier observations (e.g., 95 cm) would have shifted the early tail of the length-based distribution into February. Further predictions of the calving distribution were confounded because the variability in size at birth could not be adequately considered.

While both methods of back calculating the calving distribution are subject to biases, the likelihood that a large portion of the calving period spans at least March, April, and May remain high. The existence of neonates, but no fetuses in the June and July samples suggested that the sampling occurred after the end of the calving period, while the timing and extent of the earliest portion of the calving season remained uncertain.

Ratio of Calves to Sexually Mature Females

The high number of calves less than 1 year old encountered in this study was a consequence of sampling during a postcalving period. However, the ratio of calves and neonates to sexually mature females collected was also considered high, assuming one offspring born per female. Our ratio was 2.7 overall, with a high in June of 8.7, decreasing to 4.8 in July, 1.6 in August, and 0.7 in September. Several possible explanations were considered.

As in earlier studies on small cetacean life histories using high seas driftnets as a source of samples (Ferrero and Walker 1993, 1995), the possibility of sample bias resulting from the age/sex composition of individual schools or the spatial orientation of individuals within schools traveling in the vicinity of the nets was considered. *Lagenorhynchus obliquidens* entanglements (including calves), however, were scattered in low numbers throughout the nets with very few multiple entanglements observed in any particular net section (U.S. Department of Commerce 1989). The entanglements appeared to be individual rather than whole school events which would negate the impact of schooling characteristics.

The *L. obliquidens* sample contained an age class of calves 0.3 to 0.7 years old, which were not seen in the previous studies of small cetaceans collected in the high seas driftnets. Those earlier samples contained younger calves (i.e., <0.3 years old), neonates or yearlings. Where previously we found no indications of different entanglement rates among the population segments sampled, in the current study, we can not dismiss the possibility that calves aged 0.3 to 0.7 years may have been attracted to, or less able to avoid driftnets. The validity of calf behavior as a factor influencing their entanglement rate could not be assessed further in these analyses.

The effect of spatial segregation was also considered. Unusual patterns of relative abundance between age and sex strata observed for other species taken in the high seas driftnet fisheries (e.g., *Delphinus delphis*) were thought to be the result of areal shifts in fishery (and sampling) effort between regions inhabited by segregated elements of the population (Ferrero and Walker 1995). For those species, the segregation appeared based on sex or sexual maturity status. These segregation patterns were not apparent with the *L. obliquidens* sample nor we did not consider spatial segregation between calves and lactating females likely. The downward trend in the ratio across the summer months, however, indicated a different form of segregation. Fewer calves or more sexually mature but not lactating females appeared to inhabit the higher latitudes of the study area. This further indicated that calving grounds for *L. obliquidens* included the southern portion of the study area.

Aside from the possibility that calves could have a higher entanglement rate than sexually mature females, their comparatively high proportion in the sample could also be explained by the difference in the amount of time that calves and adult females spend at the surface. In comparison to adult females, calves are likely to have limited diving capabilities and be more restricted to the surface and shallow depths. Extensive foraging would be unnecessary for the calf until well into the weaning period. Conversely, 4 of the 71 stomachs that contained solid food remains were from lactating females and these revealed prey typical of adult foraging activity. Compared with the adult females, the calves' exposure time to the driftnets may then be greater, resulting in a higher probability of entanglement.

Two previous studies on small cetacean entanglements in high seas driftnets did not indicate a similarly high ratio of calves to sexually mature females even though both coincided with calving periods (Ferrero and Jones 1986, Ferrero and Walker 1993). The difference may stem from the timing of sampling, relative to the calving period. Both the northern right whale dolphin and Dall's porpoise studies were conducted during calving peaks while the *L. obliquidens* sample was collected several months after peak calving. Tavolga and Essapian (1957) reported that in captive *Tursiops truncatus* the cow/calf bond remains strong for about 6 weeks, after which the calf shows greater independence. The two previous studies may have ended before the bond relaxed enough for differences in times spent at the surface to become pronounced.

Monthly Growth Increments during the Sampling Season

In the calculations of mean size of calves during each of the 4 months sampled, the growth increment between adjacent means was high compared with estimates of the monthly growth rates predicted using length and age or length and postnatal dentine accumulation (Table 4). The highest growth rate estimates, corresponding to ages 6 months and less, were approximately 4.5 cm per month, while the differences in mean monthly sizes ranged from 7.4 cm to 8.6 cm. The apparent disparity in the growth rates suggested by the two approaches could have been caused by the relationship between the timing and location of calving and sampling.

The calving season began well ahead of the start of the fishing season, perhaps as early as February, in, or contiguous with, the southernmost latitudes sampled in June. The earliest biological samples thus contained both neonates and calves, and resulted in a mean size in June of about 99 cm. Assuming that cow/calf pairs eventually disperse from the calving areas, then the animals birthing earliest may also disperse earliest. Similarly, the first to disperse would also be larger than those born later in the season. If the dispersion pattern included areas north of the calving area, then the northward movement of the fishery during the summer months may have resulted in the collection of progressively older and larger calves. The apparently inflated change in mean size per month would then reflect both growth, and a sampling artifact caused by shift in effort from areas with more recently born calves, to areas with (larger) calves born earlier in the season.

Early Postnatal Growth

The *L. obliquidens* growth curves (Figs. 23 and 24) adequately reflected the growth rate of animals greater than 1 year old and provided useful asymptotic length estimates, but they appeared to understate growth in the observed portion of the first year. In the analyses of growth and attempts to fit the Laird-Gompertz model to the *L. obliquidens* length and age data, two possible causes for failure to achieve a satisfactory fit for all regions of the curve were considered.

For the first case, it was assumed that the age data for 1 year olds or less were not biased and that other unrecognized biases in older age classes were affecting the curve fit. The curve was shifted to fit the data below age 1 and its effect on the predicted length at age 1 was examined. The results (Table 4) were not consistent with the observed length frequency distributions (Figs. 21 and 22) and the timing of the calving period. If the animals had grown to nearly 150 cm by age 1, most should have moved through the 135 to 150 cm size range prior to the start of sampling in June, yet this length class was well represented in the sample.

With very few data for animals between 6 months and 1 year old, the fit was largely driven by the observed lengths and ages from animals 0 to 6 months old. It is possible, therefore, that this rapid growth period was followed by a period of slower growth.

In the second case, the possibility that the <1 GLG age estimates were biased was assumed, and that the lower region of the growth curve, despite the strongly positive residual distribution, actually reflected the growth rate. The GLG age parameter was replaced with the dentinal thickness measures. As with the first hypothesis, this approach did not provide an acceptable solution since the resulting predicted lengths at age 1 were only slightly lower than those obtained using the original age data. Again, the predicted length conflicted with the observed length frequency distribution.

One additional explanation for the lack of fit, related to the application of the growth model itself can also be considered. The two-phase Laird-Gompertz model has been used in previous small cetacean growth studies to improve the fit of age/length data over the fits achieved using single curves (Perrin *et al.* 1976, 1977; Ferrero and Walker 1993, 1995). The two-phase model can accommodate a significant change in growth rate, which is presumably linked to a biological event. To date, the two-phase curve has been used to describe a secondary increase in growth occurring at about the onset of sexual maturity.

The *L. obliquidens* sample indicated that a more complex growth model also may be necessary to adequately characterize changes in early postnatal growth. If the growth rate for *L. obliquidens* slows over the course of the first year, departing from a nearly linear form and becoming more curvelinear, then a separate phase of the growth model may be warranted.

The effect of weaning may be the biological event which triggers slower growth. The *L. obliquidens* stomach contents analyses were consistent with this hypothesis as they showed evidence of weaning during the latter half of the first year.

Parameter Comparisons

This study represented a significant expansion and update of the preliminary report of Ferrero *et al.* (1993). In addition to substantially increasing the sample size with data from the 1991 driftnet fisheries, we also modified our ageing techniques for animals less than 1 year old. The inclusion of photo-documented external features as criteria for judging recent births also provided a more conservative basis for estimating length at birth. The Ferrero *et al.* (1993) length at birth estimate of 98 cm included animals which were determined by that study to be calves rather than neonates.

Iwasaki (1991) presented findings on a comparable sample of *L. obliquidens* collected from the Japanese squid fishery at approximately the same time of year as our sample. Our calculated mean lengths at sexual maturity for males (174.9 cm) and females (177.2 cm) fall well within the length ranges for males (170 to 210 cm) and females (170 to 230 cm) in Iwasaki (1991). Due to the small number of animals aged 7 to 10 years, the mean age at onset of sexual maturation was not calculated in either study. Iwasaki (1991) presented a range of 7 to 9 years for both sexes. In the present study, the age range at sexual maturity in males was higher (10 to 11 years) while the female age range was more comparable (8.3 to 11 years). The difference in the Iwasaki (1991) 100 cm length at birth estimate and the current estimate (91.8 cm) was probably due to more rigorous discrimination between calves and newborns in our study.

Comparisons of the findings on age, length and reproductive parameters with data published for *L. obliquidens* in the coastal waters of the eastern North Pacific Ocean were problematic. In the latter region, considerable variability in length at onset of sexual maturation has been reported for both sexes (Harrison *et al.* 1972). In summarizing length, age, and reproductive data for *L. obliquidens* collected in the coastal waters of California and Mexico, Walker *et al.* (1986) suggested that two populations of this species, differing markedly in overall size, were actually represented in the sample. Methods for discriminating between the two populations were not determined, thus parameter estimates were not attempted.

Table 4. Monthly growth rates calculated for male and female *Lagenorhynchus obliquidens* using three methods: the Laird-Gompertz growth curve, the Laird-Gompertz growth curve with optimal fit to the animals less than one year old (i.e., "shifted" curve fit) and the linear regression of postnatal dentine thickness and length.

Parameter	Laird-Gompertz Curve Fit		"Shifted" Curve Fit		Dentinal Thickness and Length Regression	
	Male	Female	Male	Female	Male	Female
Predicted Length at age 1(cm)	133.4	128.8	147.8	149.9	145.0	146.4
Monthly Growth Rate (cm/mo)	3.45	3.07	4.65	4.85	4.42	4.53

Table 5. Reproductive condition of 10 mature female *Lagenorhynchus obliquidens* collected in high seas driftnets during 1990 and 1991. The recent corpora condition categories for corpora albicantia (C.A.) Types 2 and 3 were based on criteria in Perrin *et al.* (1976), however, Type 3 represents all well-regressed corpora including the Perrin *et al.* (1976) Types 3 to 5.

Specimen Number	Date	Corpora Type	Ovary Mass	Milk?	Preg?
JHY 004	7/03/90	2 C.A.	7.1 g	Yes	No
BTS 011	7/13/91	2 C.A.	6.9 g	Yes	No
JBE 112	7/26/90	3 C.A.	7.8 g	Yes	No
JCL 010	7/29/91	2 C.A.	6.8 g	Yes	No
RAT 006	8/06/90	2 C.A.	6.8 g	Yes	No
RAT 007	8/06/90	C.L.	1.8 g	No	Yes
NWR 123	8/10/91	2 C.A.	5.7 g	Yes	No
SJW 132	8/21/91	C.L.	16.4 g	No	Yes
JBE 125	8/22/90	2 C.A.	4.8 g	Yes	No
JBE 135	9/24/90	C.L.	18.8 g	No	Yes

Table 6. Birth date distributions for *Lagenorhynchus obliquidens* taken in high seas driftnets using two alternative methods.

	Method A		Method B	
Month	Frequency	Percent	Frequency	Percent
January	19	20.9	3	6.1
February	12	13.2	5	10.2
March	22	24.2	9	18.4
April	17	18.7	8	16.3
May	10	11.0	8	16.3
June	9	9.8	14	28.6
July	2	2.2	2	4.1

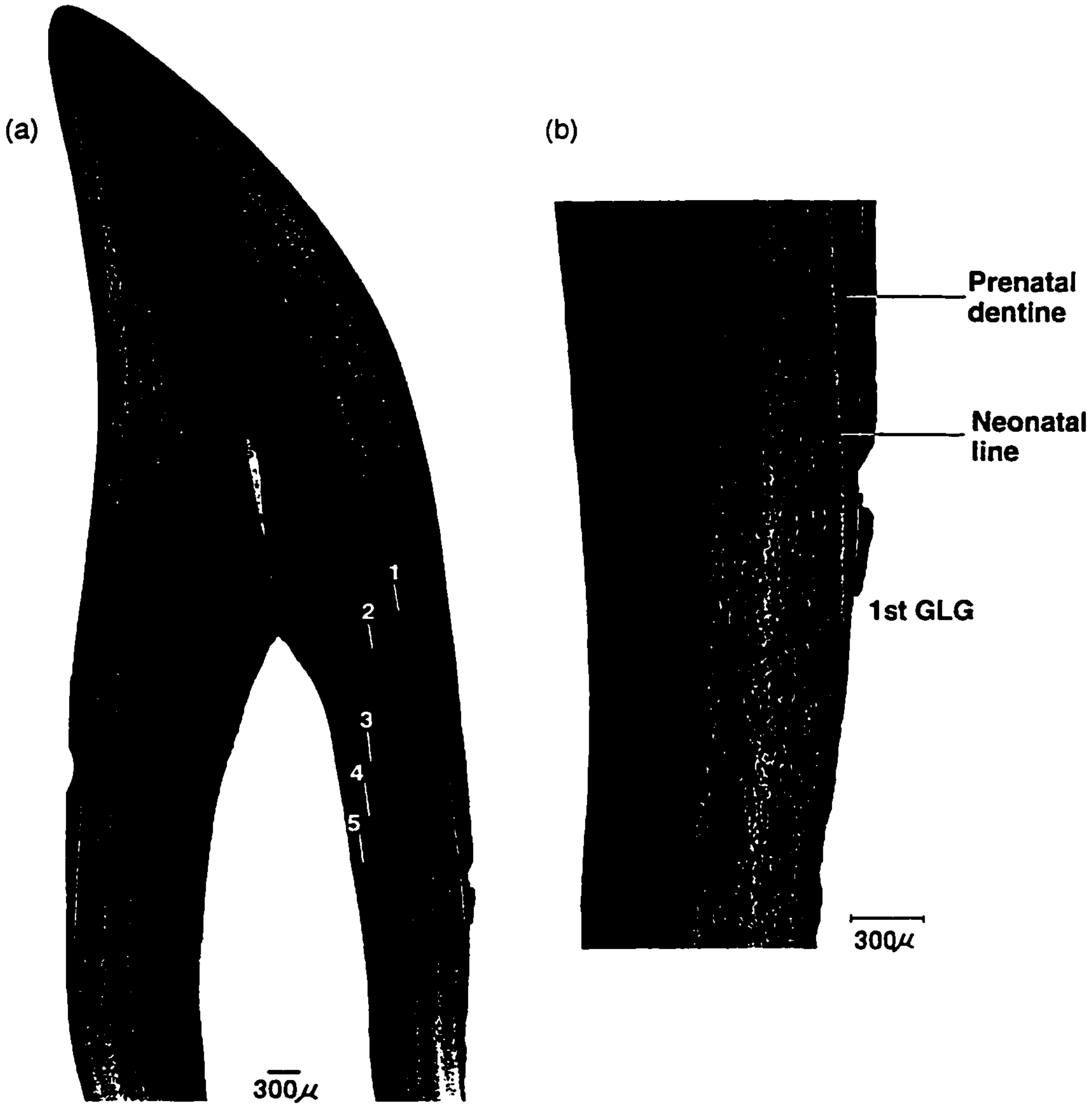


FIGURE 16: *Lagenorhynchus obliquidens* tooth section (a) from a male with 5 complete and one incomplete growth layer groups (GLG). The enlargement (b) of the same tooth shows the location of the first GLG thickness measurement.

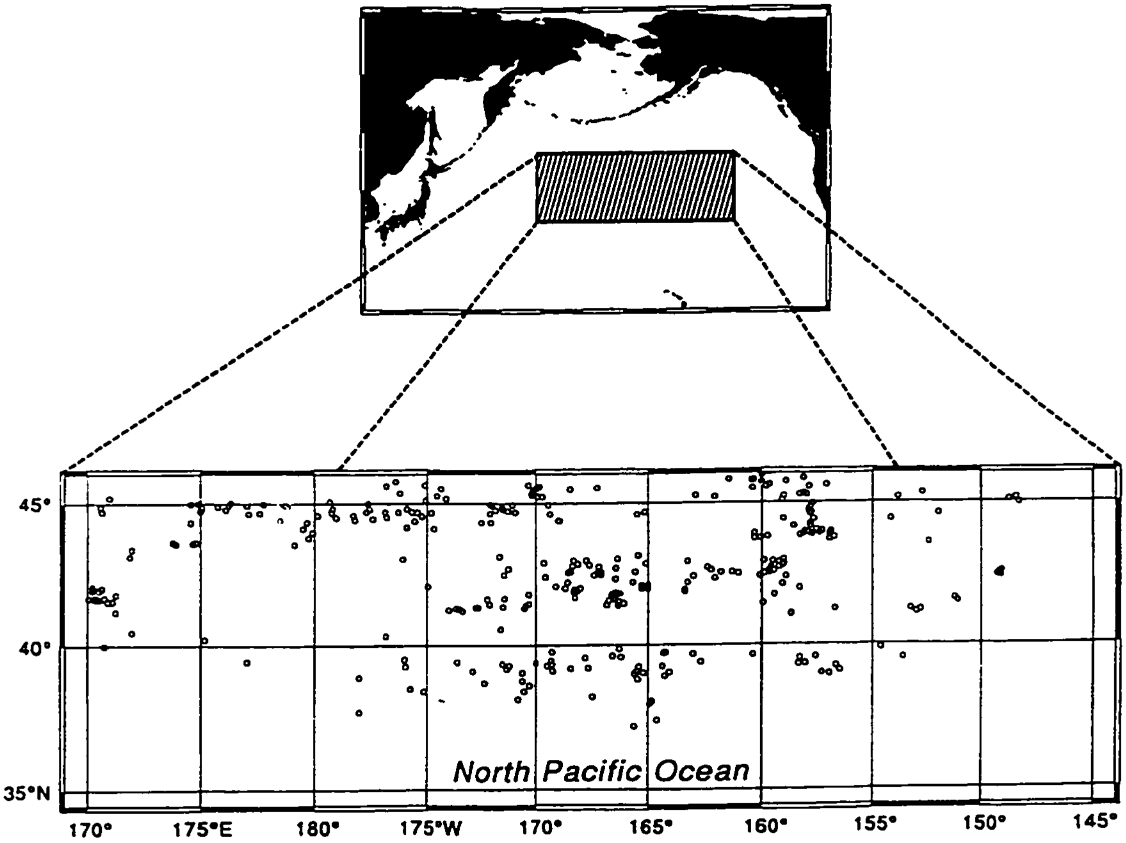


FIGURE 17: Sampling locations of 341 *Lagenorhynchus obliquidens* (171 males and 170 females) taken in high seas squid driftnets during 1990 and 1991.

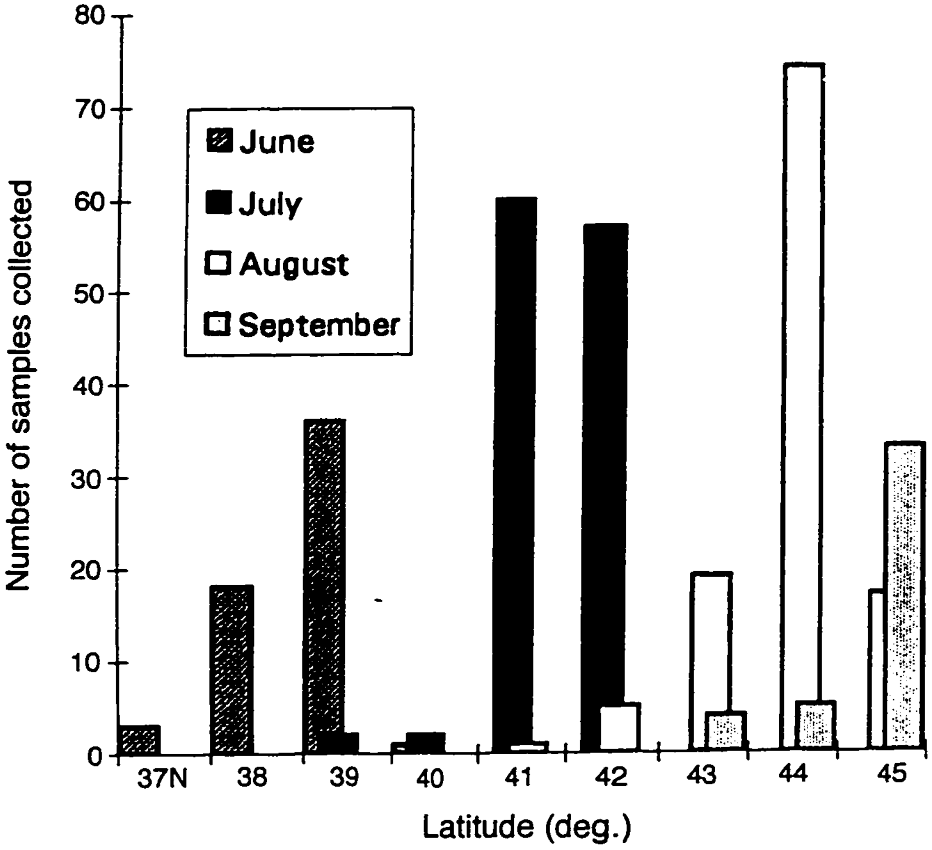


FIGURE 18: Latitudinal sampling frequency of 341 *Lagenorhynchus obliquidens* (171 males and 170 females) taken in high seas squid driftnets.

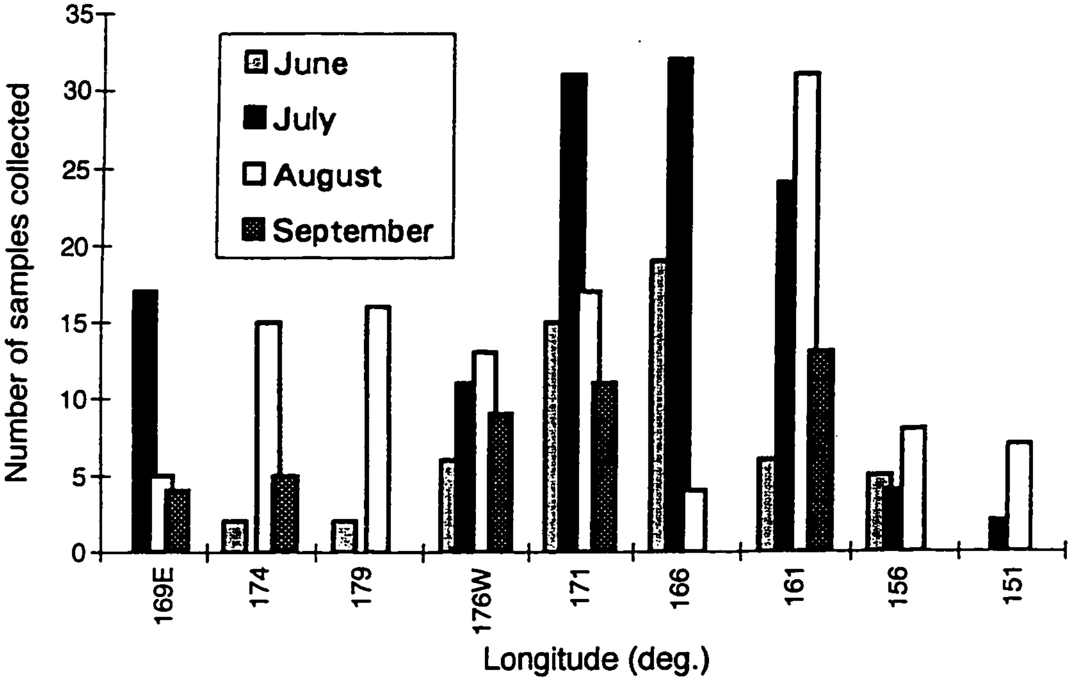


FIGURE 19: Longitudinal sampling frequency of 341 *Lagenorhynchus obliquidens* (171 males and 170 females) taken in high seas squid driftnets.

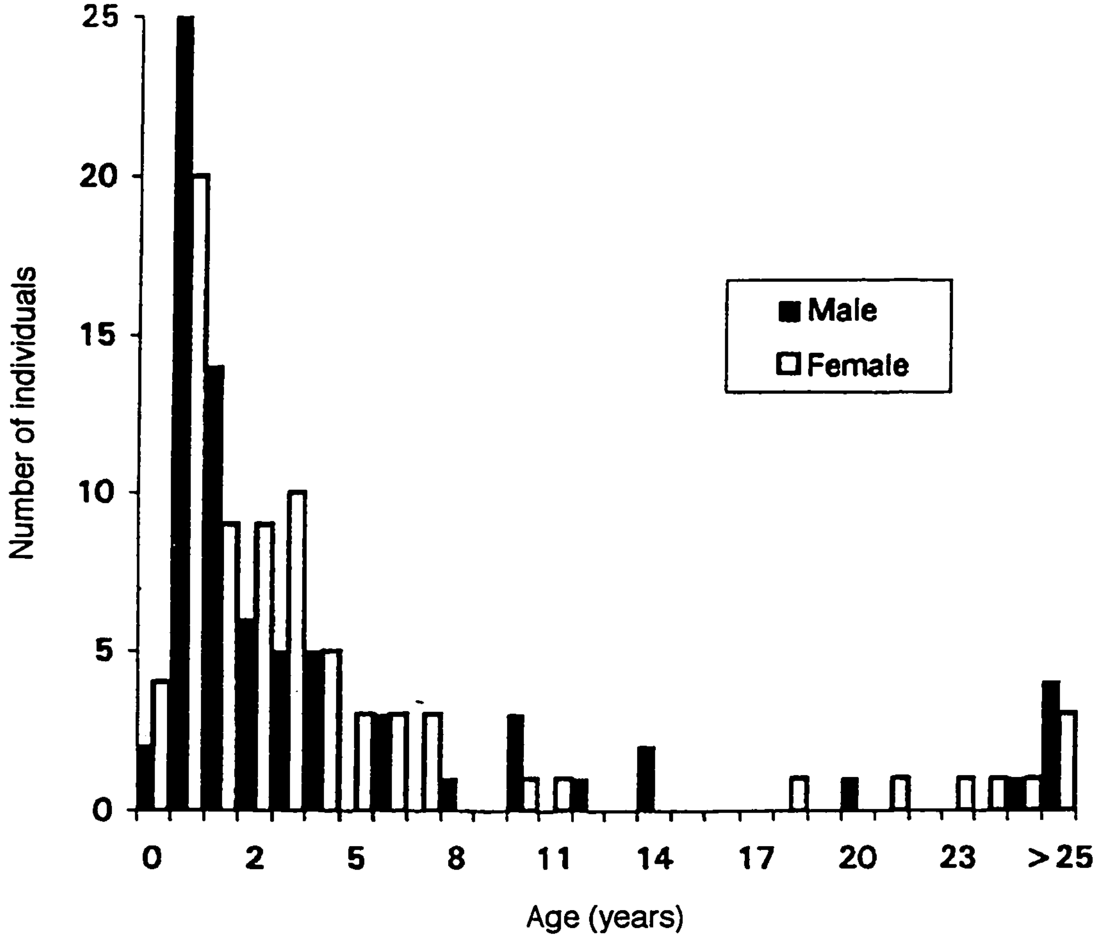


FIGURE 20: Age frequency distribution of 73 male and 76 female *Lagenorhynchus obliquidens* taken in high seas squid driftnets.

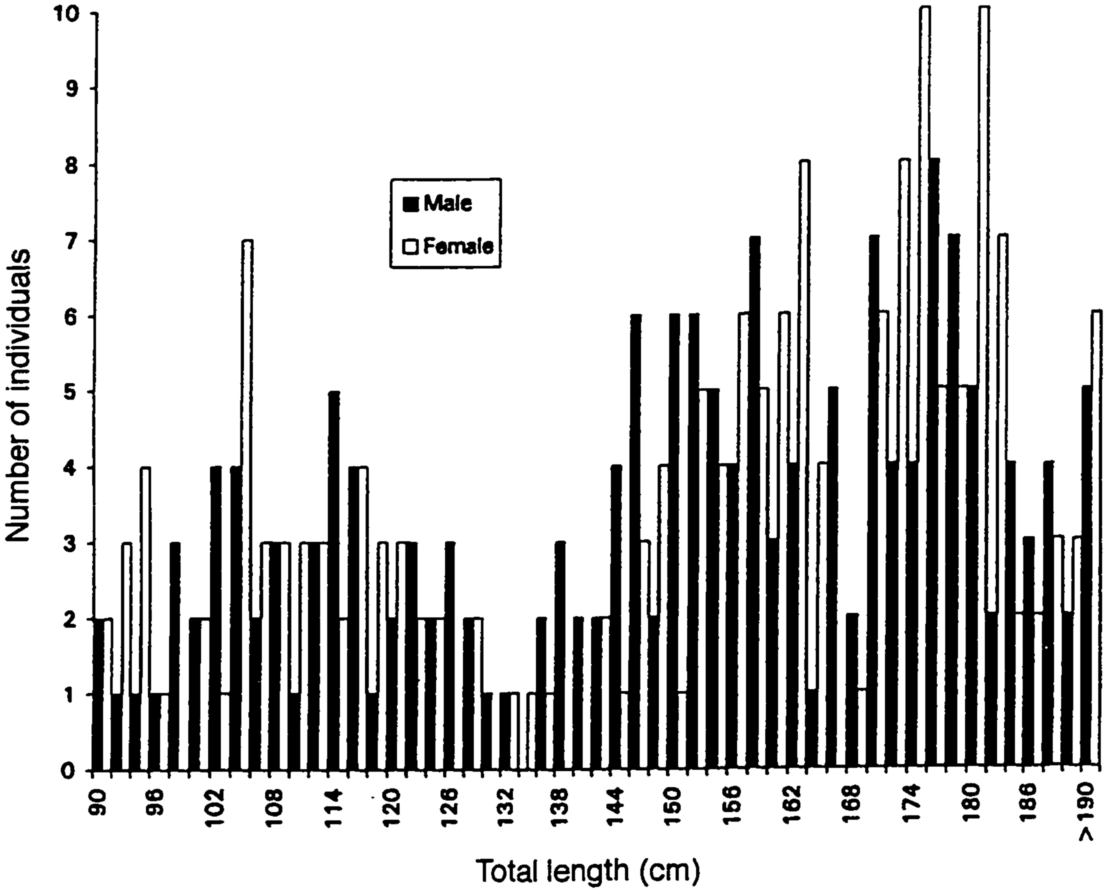


FIGURE 21: Length frequency distribution of 341 *Lagenorhynchus obliquidens* (171 males and 170 females) taken in high seas squid driftnets.

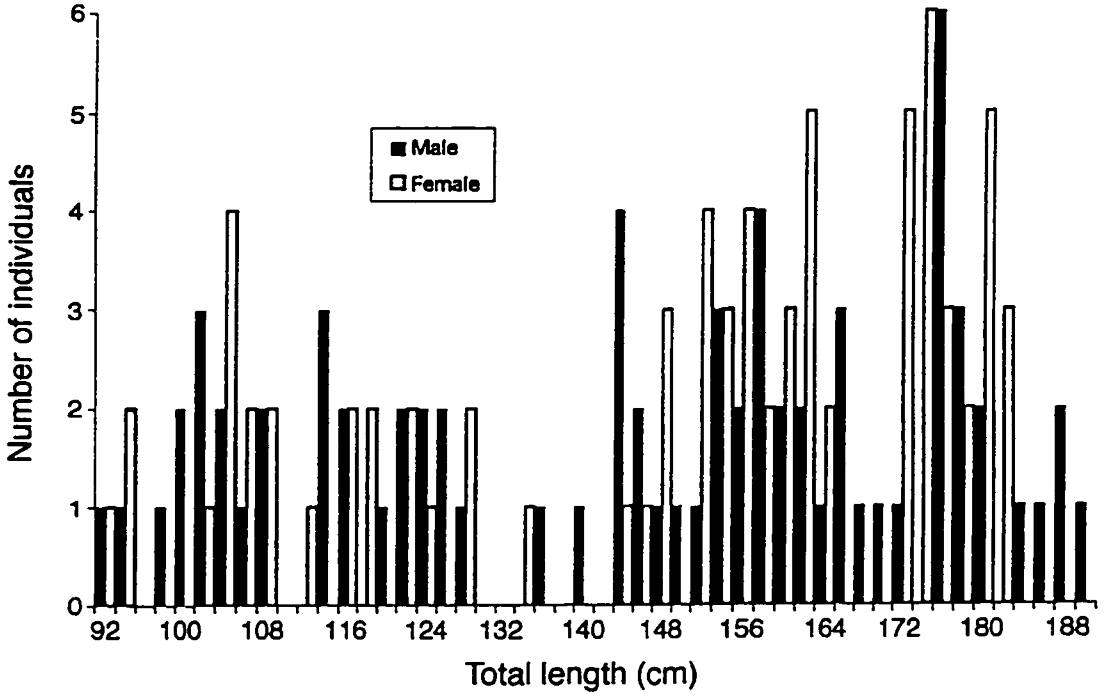


FIGURE 22: Length frequency distribution of the 73 male and 76 female *Lagenorhynchus obliquidens,* for which ages were determined, taken in high seas squid driftnets.

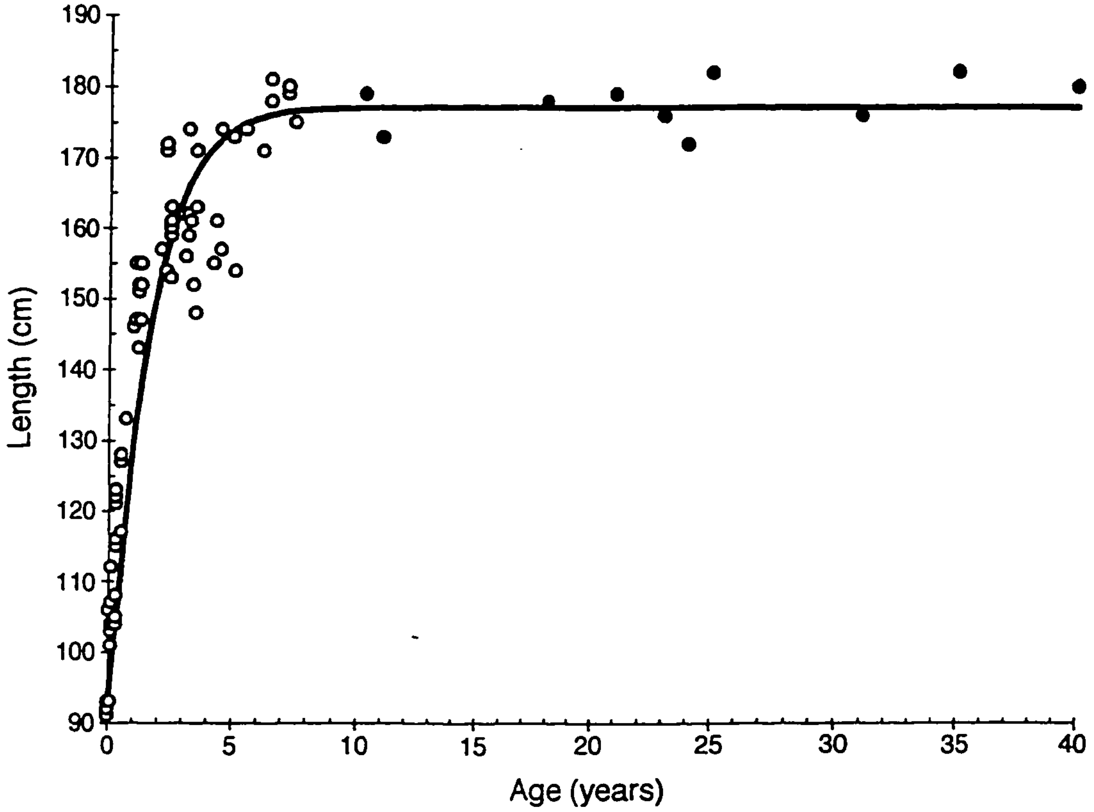


FIGURE 23: Length-at-age of female *Lagenorhynchus obliquidens* with fitted growth curves (Laird-Gompertz (1969) model). The open circles represent sexually immature animals; the closed circles represent mature animals.

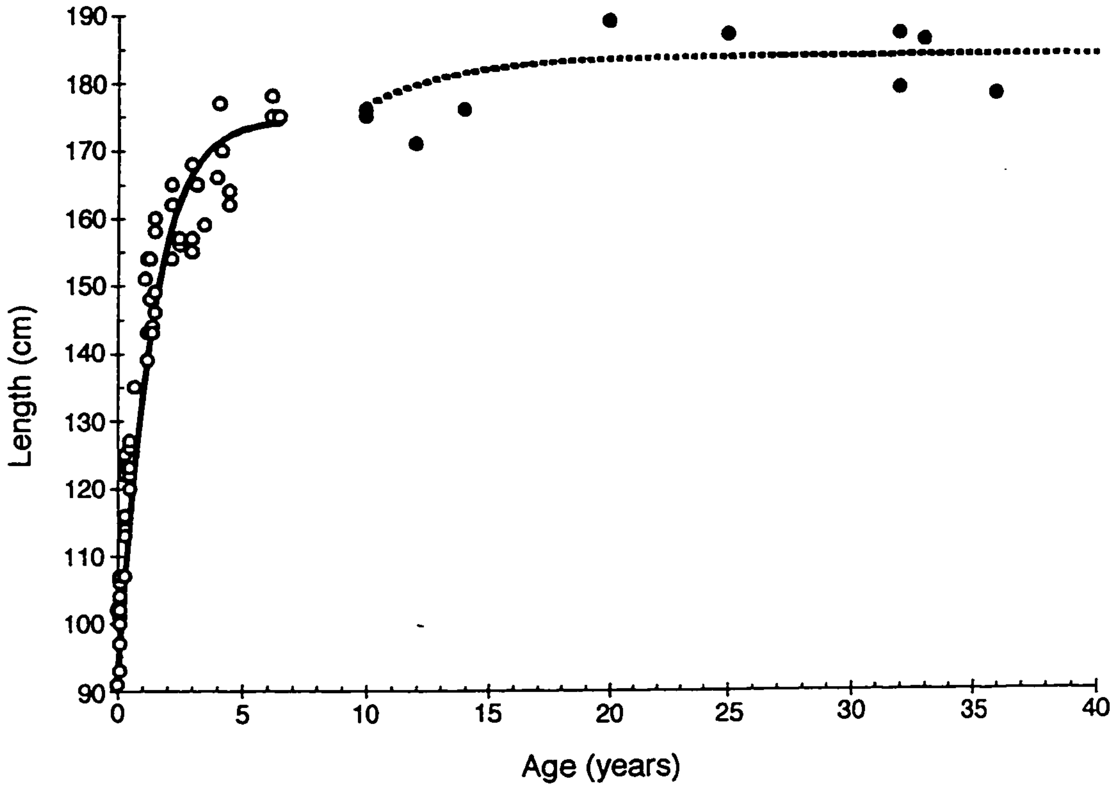


FIGURE 24: Length-at-age of male *Lagenorhynchus obliquidens* with fitted growth curves (2-phase Laird-Gompertz (1969) model). The open circles represent sexually immature animals; the closed circles represent mature animals.

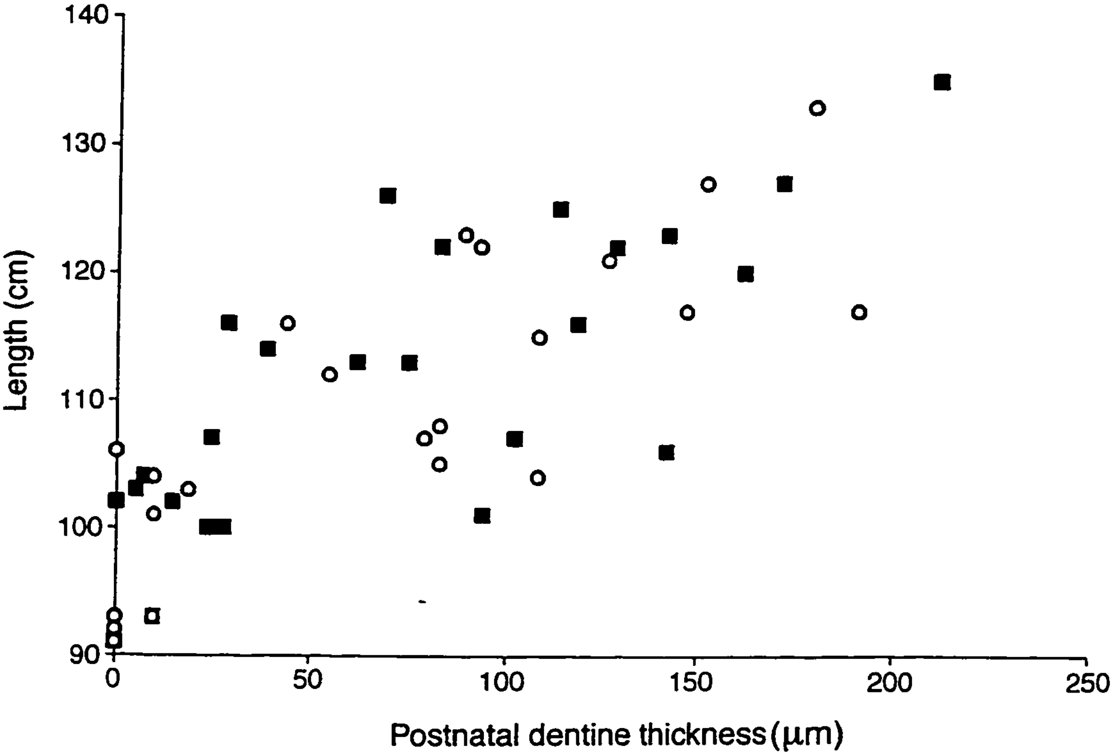


FIGURE 25: Scatterplot of postnatal dentine thickness (µm) and length (cm) for 47 *Lagenorhynchus obliquidens* (25 males and 22 females) with incomplete first dentinal growth layer groups (GLG). Simple linear regressions of length on postnatal dentine thickness yielded the equasions: y=101.0 + 0.1419x, for males, and y=98.4 + 0.1548x, for females. The closed squares represent males; the open circles represent females.

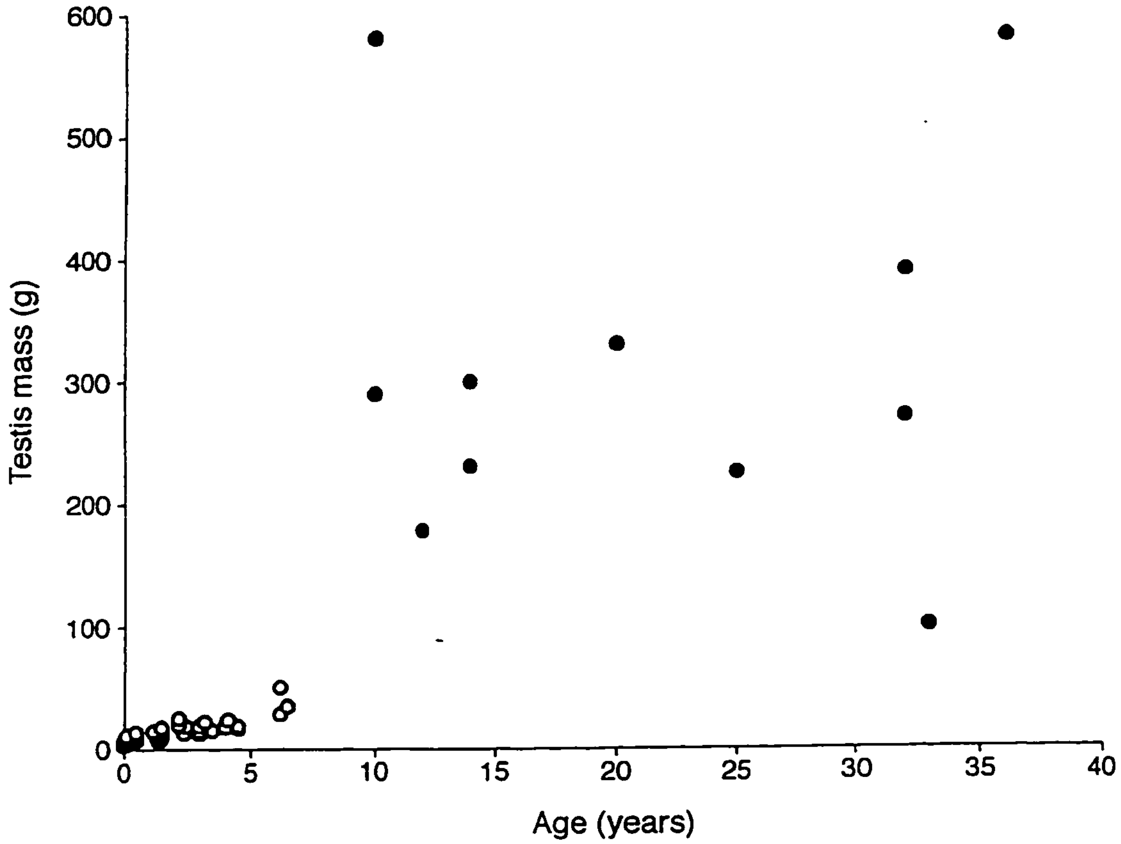


FIGURE 26: Scatterplot of age (years) and testis mass (g) for 73 *Lagenorhynchus obliquidens* males. The open circles represent sexually immature animals; the closed circles represent sexually mature animals.

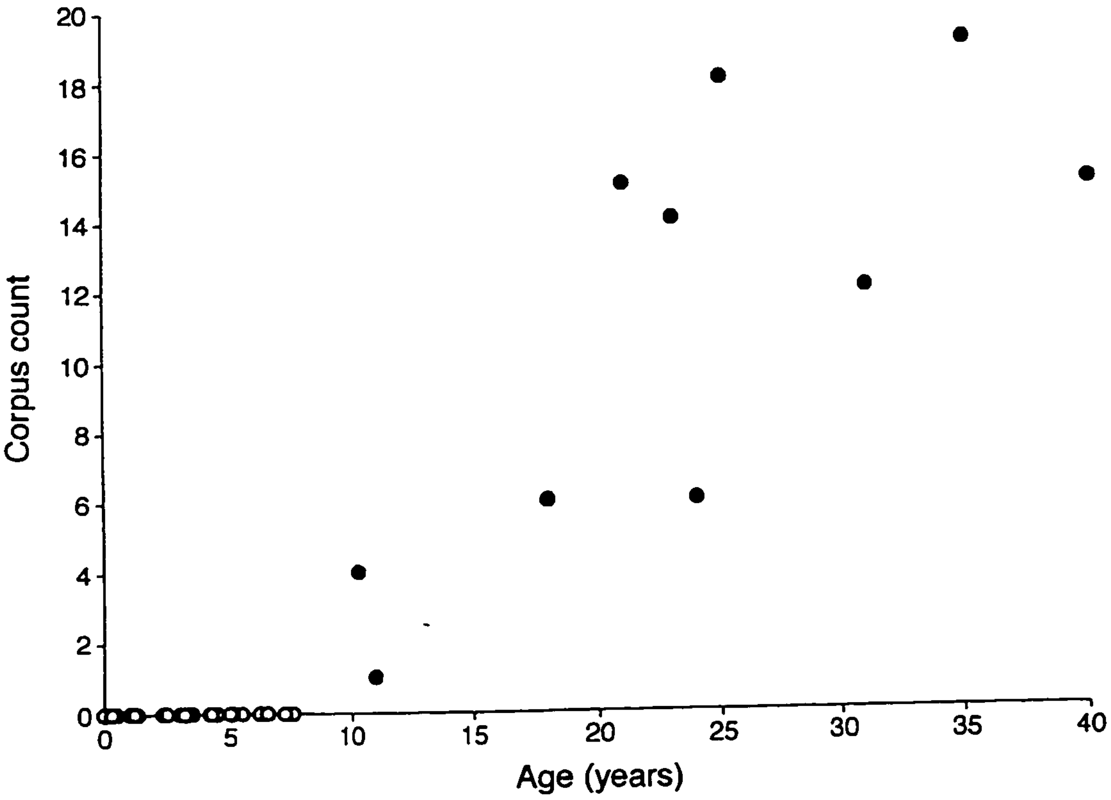


FIGURE 27: Scatterplot of age (years) and total corpus count for 76 *Lagenorhynchus obliquidens* females. The open circles represent sexually immature animals; the closed circles represent sexually mature animals.

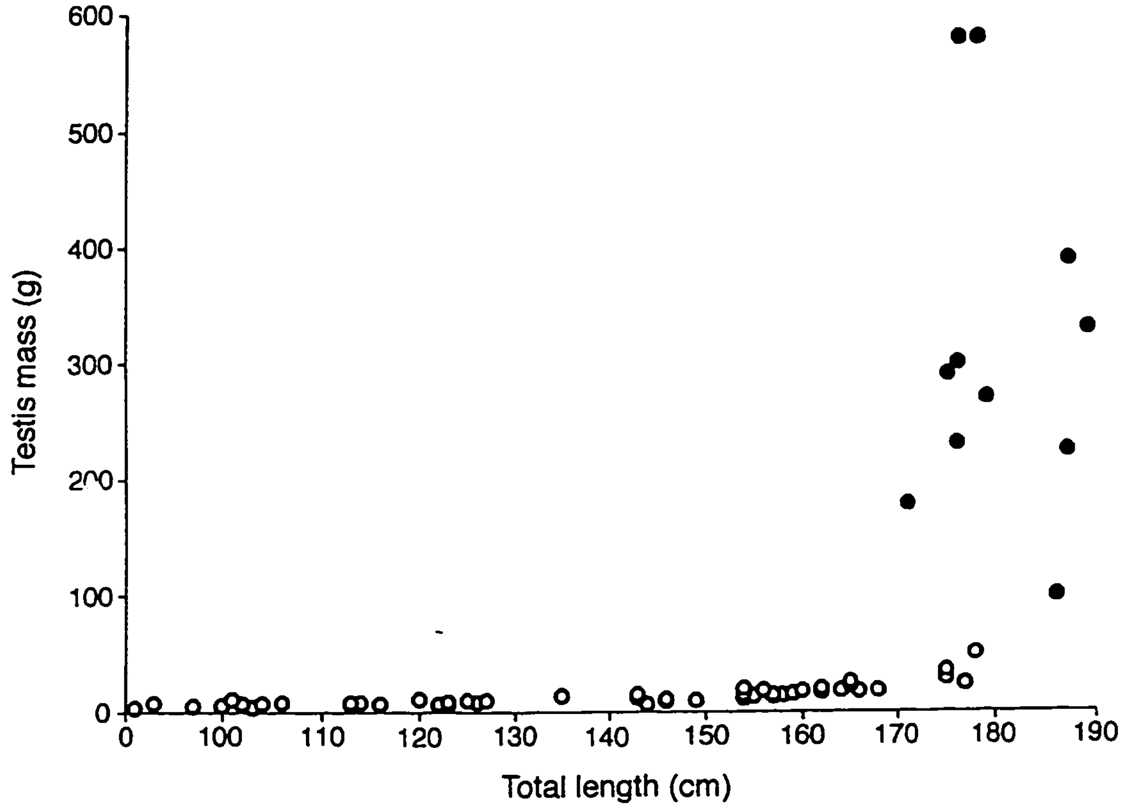


FIGURE 28: Scatterplot of length (cm) and testis mass (g) for 73 *Lagenorhynchus obliquidens* males. The open circles represent sexually immature animals; the closed circles represent sexually mature animals.

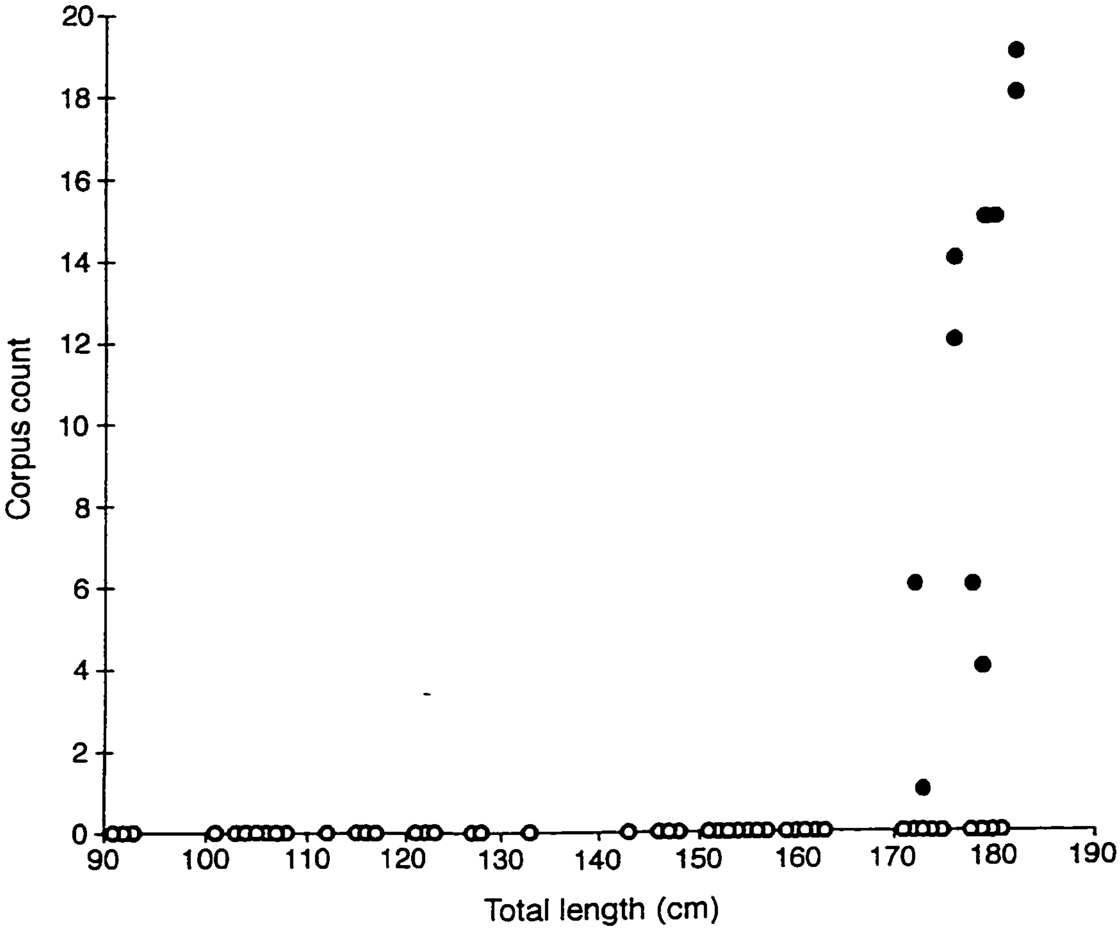


FIGURE 29: Scatterplot of length (cm) and total corpus count for 76 *Lagenorhynchus obliquidens* females. The open circles represent sexually immature animals; the closed circles represent sexually mature animals.

CHAPTER 3

Age, Growth and Reproductive Patterns of Dall's Porpoise (*Phocoenoides dalli*) from the Central North Pacific Ocean

Biological information on age, growth and reproductive parameters of Dall's porpoise (*Phocoenoides dalli*) have been published for populations inhabiting the coastal and offshore waters of Japan (Okada and Hyashi 1951, Kasuya 1978, Amano and Kuramochi 1992). Accounts of Dall's porpoise in the coastal waters of North America have been limited to calf sightings, descriptions of fetal samples and estimates of reproductive seasonality (Ridgway and Green 1967, Loeb 1972, Morejohn 1979, Jefferson 1987, 1989).

Literature containing information on biological parameters for *P. dalli* populations from the oceanic waters of the northwestern North Pacific Ocean and Bering Sea are numerous (Mizue and Yoshida 1965, Mizue *et al.* 1966, Kasuya 1978, Newby 1982, Kasuya and Jones 1984, Kasuya and Shiraga 1985, National Marine Fisheries Service 1987, Gosho 1990). Of these sources, Kasuya (1978) and Newby (1982) are the most comprehensive. These papers present analysis of age, growth and reproductive data and calculate estimates of life history parameters from samples taken by the Japanese high seas salmon driftnet fishery in the northwestern North Pacific Ocean and Bering Sea prior to 1981. However, both of these studies combined specimens from the oceanic region south of the western Aleutian Islands and Bering Sea in their analyses. More recent research on geographic variation in this species has indicated that the Bering Sea population may be a separate breeding stock (Kasuya and Ogi 1987, Walker 1990, Walker and Sinclair 1990, Amano and Miyazaki 1992). As a result, the combination of samples from the two regions in these earlier studies may have led to erroneous estimates of stock-specific life history parameters.

This study focuses on examination of age, growth and reproductive patterns in a unique sample of *P. dalli* taken south of the western Aleutian Islands in the Japanese high seas salmon mothership fishery between 1981 and 1987. Under auspices of the International North Pacific Fisheries Commission, a cooperative agreement between the United States and Japan provided for the placement of U.S. scientific observers on Japanese motherships and associated catcherboats to assess the impacts of salmon driftnets on *P. dalli*. U.S. observers remained onboard these vessels while fishing occurred inside the U.S. Fisheries Conservation Zone (U.S.F.C.Z.).

The present study and Newby's (1982) study were based on samples from the same research program, but the samples were wholly independent, partitioned by year of collection. In addition, this study only includes samples from south of the western Aleutian Islands (i.e., south of 53°N latitude) to avoid inclusion of specimens belonging to the Bering Sea stock. While portions of these data were summarized or subjected to limited analytical treatments during the active years of the program (i.e., prior to 1987), thorough analyses of the final seven years of Dall's porpoise life history data were not undertaken.

METHODS

Specimen Collection

U.S. scientific observers were stationed onboard Japanese motherships to collect biological samples from all Dall's porpoise caught incidentally in salmon gillnets. Catcherboats delivered porpoise carcasses to the motherships each morning during routine offloading of the previous night's catch.

Soon after arrival on the mothership, each porpoise was sexed, measured (total length to nearest 1.0 cm), weighed (to the nearest 1.0 kg), photographed twice (left lateral and ventral), and given a unique specimen number. The standard sampling protocol included collection of teeth and gonads, and examination of females for evidence of lactation. Other collections were added to the sampling plan as time allowed, including retention of stomachs from calves (to be examined for evidence of weaning) and thoracic vertebrae (to investigate physical maturity patterns).

The left lower jaw was removed intact, tagged and frozen. Teeth were later removed for ageing at the National Marine Mammal Laboratory (NMML). For males, the right testis and epididymis were collected whole, tagged, and preserved in 10% formalin. The ovaries and uteri for females were collected intact whenever possible. A tag was tied around the uterine horn, adjacent to the left ovary and the entire reproductive tract was preserved in 10% formalin. If the animal was pregnant or was recently postpartum, only the ovaries were collected. Fetuses were sexed and weighed to the nearest 1.0 g, and total body length was measured to the nearest 1.0 cm. Females were checked for evidence of lactation by longitudinal incision through the left mammary gland. When collected, calf stomachs were removed intact, tagged and frozen.

Examination of Reproductive Organs

Males

In the laboratory, right testes with epididymides were weighed to the nearest 0.01 g and measured to the nearest 0.1 cm. A 1 cm^3 block was removed from the center of each testis; a similar section of epididymis was removed at mid-length, and both were prepared histologically. Paraffin-embedded tissues were sectioned at 6 µm, stained with hematoxylin and eosin, and mounted on glass slides.

Testes and epididymides were examined for evidence of spermatogenesis using a compound microscope at 100X with transmitted light. Males were considered mature if spermatozoa were present in tubules of the central testicular tissue. "Maturing" specimens (i.e., those with spermatids or spermatocytes and where such spermatogenic activity was restricted to only a portion of the tubules examined) were considered immature for the purposes of parameter estimation. However, testicular changes associated with sexual maturation were examined separately by comparing a random sample of mean tubule diameters to testis masses across all maturity stages. Mean diameters were based on measurement of ten tubule cross sections and regressed on testis mass using a linear model.

Seasonal changes in testis condition among sexually mature specimens were examined by comparing the degree of spermatogenic activity among specimens collected at different times during the sampling period. Testes from 30 or more specimens from each of 4 two-week intervals were randomly selected. Spermatogenic activity was based on microscopic scans of approximately 100 tubules per specimen. The percentage of tubules producing spermatozoa was calculated and the condition categorized as “scant” if <20% of tubules were active, “heavy” if >80% were active or “moderate” for all intermediate values. Category limits were set disproportionately to emphasize differences between the two extreme conditions.

Females

Ovaries were weighed to the nearest 0.01 g. Maximum diameter of the left uterine horn was measured to the nearest millimeter where reproductive tracts were collected intact. Each ovary was sliced transversely into serial sections (≈1 mm thick) with a scalpel and examined for the presence of corpora lutea and corpora albicantia. Two measurements of corpus diameter, taken at right angles, were recorded for well-regressed corpora; three diameters were recorded for larger corpora. Total corpus counts included corpora albicantia and corpora lutea from both the right and left ovaries. Females were classified as sexually mature if at least one corpus was present on either ovary.

Corpora were examined externally for indications of regression, including color change (i.e., darkening), reduced size and surface furrowing, and classified by type following Perrin *et al.* (1976). On each ovary examined, the diameter of the largest intact follicle was measured to the nearest 0.1 mm and observations of ruptured follicles were noted.

Physical Maturity

Physical maturity was determined through examination of the degree of fusion in thoracic vertebral epiphyses. In the field, three adjacent vertebrae from the center of the thoracic cavity were removed from animals ≥180cm in length, tagged and frozen for subsequent laboratory examination. After cleaning in a dermestid colony or by maceration in standing water to remove surrounding tissue, the vertebral centra were split lengthwise with a cleaver. Epiphyseal fusion was graded as follows: 1 = epiphyseal suture open; 2 = partially fused (small pieces of intervertebral discs break free along suture line); 3 = fused (intervertebral disc is completely fused to the centrum, no evidence of suture remains). For purposes of analysis, epiphyseal conditions 2 and 3 were considered fused.

Stomach Contents

The food habits data presented in this paper related only to presence or absence of milk and solid food as indications of weaning. Each stomach chamber was opened and flushed into a pan with tap water. The fluid was filtered using a vacuum flask, and the filtrate was visually inspected for evidence of solid food.

Age Determination

Teeth were extracted from the center of the left lower jaw for age determination. After extraction, each tooth was placed in a vial of water for 1 to 5 d to soften the adhering gum tissue, then cleaned by hand. Processing of approximately one-third of the sample was done at NMML; the remainder were shipped to a commercial laboratory.

Teeth processed at NMML were decalcified using full-strength RDO (a commercially available rapid bone decalcifying agent) for 5 to 15 min depending on the size of the tooth, then rinsed for up to 24 h in running tap water. The decalcified teeth were sectioned (15 µm) longitudinally on a freezing microtome. The teeth were oriented on the microtome stage so that each cut section described the plane encompassing the crown apex and the approximate center of the root canal. After rinsing (up to 12 h) the sections were stained in Mayer's hematoxylin and mounted on glass slides.

The commercial laboratory decalcified the teeth in 5% nitric acid. Each tooth was embedded in paraffin and sectioned (15 µm) using a rotary microtome. As with the NMML preparations, the sections were stained in

Mayer's hematoxylin and mounted on glass slides. All slides were returned to NMML for age determinations.

Eight to 10 stained sections from the center of each tooth were examined under a compound microscope at 100X to 400X magnification with transmitted light. Dentinal layers were almost always indistinguishable in the tiny, often irregularly shaped Dall's porpoise teeth. The dentinal growth layer group (GLG) counting guidelines developed by Myrick *et al.* (1983) for *Stenella* spp., therefore, could not be used. Instead, following the general procedures in Kasuya (1978), cementum layers were read, assuming that each clear layer, apparent more or less continuously along the sides of the tooth below the gum line, represented 1 yr of growth (Fig. 30). Clear layers were often accompanied by accessory layers. These were identified by their localized nature (i.e., lack of persistence along the perimeter of the tooth).

Tooth sections were read at least twice by independent readers. All readings were recorded to the nearest whole year. Reader's best estimates were compared to determine a final age. Where readings differed by 1 yr or more, the readers re-examined the tooth together. If the cementum layering pattern proved too ambiguous to resolve, no age was assigned to the specimen.

RESULTS

The Sample

A total of 5,599 *P. dalli* (2,033 males and 3,566 females) were sampled during June and July 1981 to 1987 on the fishing grounds between 46°N and 53°N and 168°E and 175°E (Fig. 31). However, the number of samples available for most growth and reproductive analyses was smaller due to initiation of subsampling protocols during the active years of the field research program (Table 7). The subsamples were based on selection of specimens from 2 or more of the mothership fleets each year. Since the fleets operated in a very constrained area, and repeatedly exchanged fishing locations every few days, the structure of the porpoise population sampled was assumed to be essentially the same across fleets. To maximize sample sizes, additional ageing work and examination of reproductive tissues from the remaining unprocessed specimens were subsequently completed by the authors, although time constraints still limited access to the entire sample. Over 95% of the male reproductive tissue samples were examined, while 53.4% of the female reproductive tracts were processed. Likewise, of the available tooth samples, ages were determined for 40.0% of the males and 36.4% of the females. In all cases, reproductive data were available for specimens where ages were determined. Thus, sex, total length, mass, reproductive condition, collection date, and catch location were available for 1,941 males and 1,906 females. Of these, ages were determined for 813 males and 1,297 females.

All samples included in these analyses were collected during the same time period each year. With the exception of 1987, 4 Japanese mothership fleets, each containing 64 catcherboats fished inside the U.S.F.C.Z. during June and July. During 1987, only 3 mothership fleets fished. Each catcherboat set approximately 16.5 km of gillnet each night.

Age data (813 males and 1,297 females) were used to examine postnatal growth patterns (i.e., length and mass at age) and to estimate average age at sexual and physical maturation. Where age data were not critical to the analyses (e.g., estimation of total length or mass at sexual or physical maturation, and gestation period, and examination of reproductive seasonality patterns), the larger sample of known reproductive status specimens was used (1,941 males and 1,906 females). The sex ratios, however, were based on the total sample where sex and lengths were recorded (n=5,599). Comparisons of the length frequency distributions for each sex indicated that the reproductive and aged subsamples were in relative proportion to the total available sample (Figs. 32 and 33). Biases associated with subsampling were considered minimal.

Male *P. dalli* ranged from age 0 to 14 yr (n=813) (Fig. 34). Among the age-0 males (n=159), 67.3% had umbilical remnants or open umbilical condition (i.e., neonates, n=107), 6.3% had healed umbilical scars (i.e., calves, n=10) and 26.4% were undetermined (n=42). Yearling males represented 6.7% of the aged sample (n=131) and the rest were >2 years old. Female ages ranged from 0 to 15 yr (n=1,297) (Fig. 34). The age-0 females (n=160) contained 66.2% newborns (n=106) and 5% calves (n=8); 28.2% were undetermined (n=46). Yearling females represented 5.5% of the aged sample (n=71).

Lengths of males in the sample for which reproductive data were available ranged from 84 to 222 cm (Fig. 35). The females ranged from 86 to 211 cm (Fig. 35). The unimodal peaks in the male and female length frequency distributions below 130 cm (Figs. 32 and 33) and the corresponding peaks at age 0 in the age frequency distributions (Fig. 34) were consistent across all years. The gap between the lower mode and the remainder of the length frequency distribution corresponded to the time interval between sampling seasons (i.e., the growth interval between the age-0 and age-1 cohorts).

Growth

Length at Birth and Early Postnatal Growth

Mean length at birth was estimated using four different approaches. A modification of the DeMaster (1978) method and logistic regression following Hohn and Hammond (1985) were used to describe the length at which half of the combined sample of full-term fetuses and newborns had reached parturition. For comparison and to test for changes in length soon after birth, the mean lengths of the full-term fetuses and neonates were also calculated

(Perrin and Reilly 1984).

For the first two approaches, individuals were considered recent births if they showed no evidence of postnatal dentine. For the third method, fetuses longer than 80 cm, comprising over 95% of the fetal sample, were considered full term. For the last method, we identified four classes of umbilical condition as an index to the interval since birth because estimation of mean neonatal length was considered sensitive to bias associated with growth between birth and capture. The classes were: 1) umbilical remnants present, 2) umbilicus open but no remnants, 3) umbilical scar partly closed, and 4) umbilicus fully healed. A separate mean length estimate was generated for each umbilical condition subsample.

DeMaster's (1978) method, modified to use length rather than age (Ferrero and Walker 1993), was applied to 765 fetuses and 307 neonates for which lengths were indeterminâte with regard to birth status. The sample, grouped in 2-cm intervals, provided a length at birth estimate of 103.0 cm (SE=0.3466). Males and females were also examined separately, yielding estimates of 103.5 cm and 102.6 cm, respectively. The means for males and females were not significantly different (Student's t-test, P>0.05).

Logistic regression was used to estimate the mean length at birth as the point at which 50% of the combined sample of all full-term fetuses (n=939) and neonates (n=19) had reached parturition. A description of the logistic model is detailed under average age at sexual maturation (ASM). The mean length estimate for both sexes combined was 101.1 cm (95% Confidence Interval (CI) = 100.6-101.6 cm). Five percent of the sample had reached parturition at 90 cm, and 95% at 112.7 cm (Fig. 36).

Male and female fetal lengths ranged from 75 to 118 cm (n=939). The mean lengths, 92.1 cm (SE=0.3192) for males and 91.0 cm (SE=0.3069) for females were significantly different (Student's t-test, t=2.434, P<0.016). However, the difference was slight, effectively less than the precision of the field measurements on the fetuses in their folded position. Therefore, the male and female samples were combined and a single mean, 91.5 cm (SE=0.2214) calculated.

Mean neonatal lengths (sexes combined) were calculated for 102 specimens in umbilicus class 1, 80 specimens in class 2, 31 specimens in class 3 and 18 specimens in class 4 (Table 8). The resulting mean estimates of length at birth, 99.0, 102.7, 110.6 and 114.1 cm, respectively, were significantly different between adjacent umbilicus classes (ANOVA, F=61.36, P<0.0001). Linear regression of length on umbilicus class resulted in the equation:

$$y = 98.59 + 5.23x$$

suggesting that over 5 cm of growth could occur between stages of umbilical healing, even though all conditions occurred while no postnatal dentine accumulation was observed (slope significance: P<0.0001).

Birth Mass and Early Postnatal Growth

Average mass at birth was estimated using the same four methods used to estimate length at birth, substituting mass for length. DeMaster's (1978) method was applied to 890 fetuses and 161 neonates where masses were indeterminate with regard to birth status. The mass at which 50% of births had occurred was 14.8 kg (SE=0.1236). This estimate may have overstated the actual birth mass by inclusion of neonates in multiple umbilical classes.

Using logistic regression, the mean mass estimate for both sexes combined was 15.8 kg (95% CI=15.2-16.4 kg). Five percent of the sample had reached parturition at 12.7 kg, and 95% at 18.8 kg (Fig. 37).

Male and female fetal masses ranged from 6 to 18 kg (*n*=939). As with mean fetal lengths, the mean mass of male (11.6 kg, SE=0.1114) and female (11.2 kg, SE=0.3069) fetuses were significantly different (Student's t-test, t=2.515, P=.012), but the difference was less than the precision of the field measurements. The mean mass for both sexes combined was 11.4 kg (SE=0.0745).

Umbilical class 1 neonates (*n*=102) ranged from 8.0 kg to 26.0 kg, with a mean of 16.9 kg (SE=0.3084). Comparisons of mean mass across umbilical conditions showed a significant increase prior to the full healing of the umbilical scar. The mean masses of umbilical classes 2, 3 and 4 were 18.7 kg

(SE=0.7197), 22.1 kg (SE=0.6141) and 23.8 kg (SE=1.5306), respectively. The difference in mean masses across all four umbilical classes was significant (ANOVA, F=30.72, P<0.0001).

Linear regression of mass on umbilical class resulted in the equation:

$$y = 16.69 + 2.44x$$

indicating that an increase of over 2 kg occurred between umbilical classes (slope significance: P<0.0001). Evidence of such rapid growth immediately after birth suggested that the mean mass of the 939 fetuses more closely approximated birth mass than that of the umbilical class-0 neonates.

Gestation Period

The relationship between fetal length and gestation time described by Hugget and Widdas (1951) may be used to estimate the gestation period if a sample of fetuses at various stages of development are available. The *P. dalli* sample, however, contained only full-term fetuses, offering insufficient range in fetus lengths to allow the use of regression techniques to estimate the period of gestation. Instead, the relationship between size at birth and gestation period described for several species of delphinids by Perrin *et al.* (1977) was used as a proxy for the relationship between size at birth and gestation period for *P. dalli*. In the Perrin *et al.* (1977) regression equation:

$$Log(y) = 0.1659 + 0.4586\ Log(x)$$

x was substituted with the estimates of length at birth obtained, in turn, using logistic regression, the DeMaster (1978) method, and the mean length of newborns with umbilical remnants attached. The three length at birth estimates, 101.1, 103.0 and 99.0 cm, corresponded to gestation periods of 12.2, 12.3 and 12.0 mo, respectively.

Physical Maturity

Special collections of thoracic vertebrae during the 1982, 1983 and 1985 field seasons provided a total of 692 specimens (246 male and 446 female). The range of indeterminate length classes with regard to physical maturity status was very broad for both sexes. Among males, the smallest physically mature animal was 182 cm in length while the largest physically immature animal was 220 cm. The smallest physically mature female was 180 cm; the largest physically immature female was 205 cm. The mean length of physically mature specimens was 198.1 cm (n=83, SE=0.8566) for males and 189.7 (n=164, SE=0.4002) for females. These values, reflecting the asymptotic lengths for each sex, were significantly different (Student's t-test, t=8.854, P<0.0001).

Logistic regression of length on physical maturity status provided estimates of average length at physical maturity (LPM; see ASM for details of the model). Fifty percent of males sampled were physically mature at 202.6 cm (95% CI=201.3-203.9 cm) (Fig. 38), while half of the females were physically mature at 192.7 cm (95% CI=191.3-194.1 cm) (Fig. 39).

Of the 692 specimens from which thoracic vertebrae were collected, ages were determined for 165 porpoise (49 males and 116 females). For both sexes, the youngest physically mature animals were 5 yr old while the oldest physically immature animals were 8 yr old.

The average ages at physical maturity were calculated for each sex using logistic regression. Estimates of age where 50% of the porpoise had reached physical maturation were effectively identical for both sexes, i.e., 7.16 yr for males (95% CI=5.7-8.6 yr) and 7.24 yr for females (95% CI=6.3-8.1 yr) (Figs. 40 and 41).

Postnatal Growth

Length

The male and female growth curves were fitted to the length-at-age data separately using a nonlinear least-squares approach. The Laird-Gompertz formula (Laird 1969) was used as a base model:

$$L(t) = L_0 \exp\{a[1 - \exp(-\alpha t)]\}$$

where $L(t)$ is the length at age t, L_0 is the length at birth, t is the age, a is the specific rate of exponential growth, and α is the rate of decay of exponential growth.

For both sexes, the best growth model fits were obtained using two Laird-Gompertz curves. In each case, the first curve was fit to data from sexually immature individuals with its lower end (L_0) fixed at the average length at birth. Of the three length at birth estimates produced, the median value was chosen for use in the growth model (i.e., 101.1 cm). The second curve was fit to the sexually mature data with the asymptotic length fixed at the mean length of physically mature specimens examined. The transition point between the lower to the upper curves was allowed to float, ultimately marked by the intersection of the two curves.

For the males, the upper Laird-Gompertz curve was fitted with a fixed asymptote at 198.1 cm, corresponding to the mean size of physically mature specimens. Early postnatal growth was rapid, reaching a predicted length at age 1 of 148.5 cm. The transition point between the upper and lower curves was 165.3 cm at age 2.2 yr (Fig. 42).

The upper curve for the female model was fitted with a fixed asymptote at 189.7 cm. As with males, early postnatal growth was rapid, with a predicted length at age 1 of 146.3 cm. The transition point between the upper and lower curves was 162.9 cm at age 2.1 yr (Fig. 43). The secondary growth phase was slightly less pronounced for females compared with males.

Mass

The relationship between mass and age was examined by fitting the two-stage Laird-Gompertz growth model to mass-at-age data for each sex. For both sexes, the lower curve segment was fitted to the age classes that contained immature and indeterminate sexual maturity specimens, while the upper curve was fitted to those specimens in age classes containing the indeterminate and sexually mature specimens. Pregnant females carrying full term fetuses were not included. The break point between the upper and lower curves was based on the intersection of each individually fitted curve.

Male masses ranged from 8 kg to 190 kg. The largest increase in mean mass among males was between ages 0 and 1 (43.4 kg), after which growth moderated to age 2 (Fig. 44). A marked surge in growth began at age 3.4, corresponding to a mass of approximately 85 kg. Changes in mass-at-age beyond 7 yr were less obvious, with a predicted asymptote at approximately 157 kg. By comparison, the mean mass of physically mature animals was 145.2 kg (SE=1.6129).

Female masses ranged from 9 kg to 183 kg. As with males, the greatest increase occurred in the first year (42.5 kg) (Fig. 45). The secondary growth in mass began earlier than it did for males, at about age 3, although the increase was less pronounced. As with males, female increase in mass-at-age beyond age 7 was small; the predicted asymptotic mass was 122 kg. The mean mass of physically mature females was 120.1 kg (SE=1.1744).

Sexual dimorphism in adult mass was, therefore, apparent both in predicted asymptotes and in the mean weights of physically mature specimens. Despite the inclusion of postpartum females with enlarged reproductive tracts, the mean mass of physically mature males was still significantly greater than that of females (Students t-test, t=-12.4731, P<0.0001).

Reproduction

Sex Ratio

Sex ratios were estimated for three portions of the total postnatal sample (n=5,599) representing the age-0 cohort, age 1+ adolescents and sexually mature life stages. A separate estimate based on full-term fetuses (n=939) was also calculated. The age-0 cohort was comprised of all animals in the isolated mode of the length frequency distribution below 130 cm (Figs. 32 and 33). The sexually mature category was based on length cut-offs corresponding to the average lengths at sexual maturation for each sex. Thus, all males ≥179 cm and females ≥172 cm were included in the "mature" category. All males ≥130 cm but <179 cm, and females ≥130 cm but <172 cm were considered adolescents. The empirical logistic transform method (Cox and Snell 1989) was used to estimate sex ratio as

$$r = \frac{m + 0.5}{f + 0.5}$$

where *r* is the ratio of males to females, m is the number of males, and *f* is the number of females. The natural logarithm of *r* is normally distributed with variance,

$$var[\ln(r)] = \frac{(n+1)(n+2)}{n(m+1)(f+1)}$$

where *n* is the total number of males and females, *m* is the number of males, and *f* is the number of females. The sex ratios were 0.958 (SE=0.1104) for the age-0 cohort (160 males and 167 females), 0.830 (SE=0.0422) for adolescents (1,026 males and 1,236 females, and 0.392 (SE=0.0422) for "matures" (847 males and 2,163 females). Among fetuses, the sex ratio was 0.940 (SE=0.0653, 455 males and 484 females). Neither the fetal nor age-0 cohort ratios were significantly different from 1.0 (Exact Binomial Test, P=0.249 and P=0.740, respectively); however, both the age 1+ adolescent and mature sex ratios significantly favored females (Exact Binomial Test, P<0.0001 in both cases).

Age and Sexual Maturation

The average age at sexual maturation (ASM) was estimated using the DeMaster (1978) method, and by logistic regression. DeMaster's equation computes the mean age as

$$ASM = \sum_{=}^{k} a(f_a - f_{a-1}),$$

where f_a is the fraction of sexually mature animals in the sample aged a, j represents the age of the youngest sexually mature animal sampled, and k is the age of the oldest sexually immature animal in the sample.

The variance about the DeMaster method estimate is calculated as

$$var(ASM) = \sum_{a=j}^{k} \frac{f_a(1-f_a)}{(N_a-1)},$$

where N_a is the total number of animals aged a.

The logistic regression approach (Cox and Snell 1989) fits a sigmoid curve [$\mu(a)$], the probability that a porpoise of age a is sexually mature, to the distribution of sexually mature and immature animals by age as

$$\mu = \frac{e^{ab+c}}{1+e^{ab+c}},$$

where a is the age of the dolphin, b is the slope of the regression and c is the intercept. The logistic curve was fitted using a maximum likelihood and iteratively re-weighted least-squares algorithm (Chambers and Hastie 1992). The standard error for μ was obtained by transforming the standard error of the linear fit. The average age at sexual maturation was then estimated as the age where $\mu(a)=0.50$ such that ASM $=-c/b$.

Males

The sample of males with age and reproductive data contained 228 sexually mature and 585 sexually immature males. The youngest sexually mature specimen was 3 years old (testis mass 115.2 g); the oldest sexually immature male was 6 years old (testis mass 25.8 g). The average mass of a mature testis was 191.4 g (SE=4.8577) (Fig. 46).

Based on the DeMaster (1978) method, the average age at sexual maturation for males was estimated to be 5.0 years (SE=0.09419). Using the logistic regression approach, we obtained a slightly lower estimate of 4.5 years (95% CI=4.4-4.6 years), with 5% sexually mature by age 3.2 years(95% CI=2.9-3.3 years), and 95% sexually mature by age 5.8 years (95% CI=5.6-6.0 years) (Fig. 47).

Significant linear correlations were found between testes mass and age for both sexual maturity categories. Among the immature males, testes mass increased gradually at 3.7 g/yr, (SE=0.2419, $P<0.0001$). After reaching sexual maturity, the increase in testis mass averaged 9.3 g/yr (SE=2.4196, $P<0.001$). Despite the significant correlation in the sexually mature sample, individual variation in testis weight at age was pronounced ($R^2=0.059$).

Females

The sample of females with age and reproductive data contained 597 sexually mature and 700 sexually immature porpoise. The youngest sexually mature specimens were 3 years old while the oldest sexually immature female was 8 years old (Fig. 48).

Based on the DeMaster (1978) method, our estimate of average age at sexual maturation for females was 4.4 years (SE=0.0655). The logistic regression approach yielded a lower value, 3.8 years (95% CI=3.6-4.0 years), with 5% sexually mature by age 2.4 years (95% CI=2.0-2.6 years), and 95% sexually mature by age 5.2 years (95% CI=5.0-5.5 years) (Fig. 49).

Length and Sexual Maturation

Average length at sexual maturation was estimated both using the DeMaster (1978) method, adapted to estimate the average length instead of average age (Ferrero and Walker 1993) and by logistic regression. The DeMaster (1978) equation adapted for lengths was

$$LSM = \sum_{i=i_{\min}}^{i_{\max}} l_i(f_i - f_{i-1}),$$

where f_i was the fraction of sexually mature animals in the sample of length l, $i_{\min}$ was the index of the size class with the smallest mature animal, and $i_{\max}$ was the index of the size class with the largest immature animal.

The length interval width was 1 cm since the sample contained a sufficient number of specimens in indeterminate length classes to avoid binning. The variance estimate on LSM, therefore, followed the DeMaster

(1978) formulation for ASM, simply substituting length for age.

Males

The reproductive data sample contained 1,136 sexually immature and 805 sexually mature specimens. The smallest sexually mature male was 166 cm (testis weight 162.9 g); the largest sexually immature porpoise was 194 cm (testis weight 26.0 g) (Fig. 50).

According to the DeMaster (1978) method, the average length at sexual maturation was 179.7 cm (SE=0.3672). The logistic regression approach provided the same estimate, 179.7 cm (95% CI= 179.6-179.8 cm), with 5% of the sample maturing at 170.8 cm (95% CI=169.8-171.6 cm) and 95% mature at 188.6 cm (95% CI=187.8-189.4 cm) (Fig. 51).

Significant linear correlations between total length and testis mass were noted for both immature ($P<0.0001$) and mature ($P<0.0001$) males. Testis mass increased nominally prior to the onset of sexual maturity (0.246 g/cm), but increased sharply thereafter (2.56 g/cm). As with the age and testis mass relationship, individual variation in testis mass at length was highly evident ($R^2=0.1136$).

Of the 191 specimens for which tubule diameters were measured, 78 were immature, 19 were maturing and 94 were mature. The mean diameters for each group, 59.4 µm (S.E.=0.9465), 120.9 µm (S.E.=8.6760) and 172.8 µm (S.E.=2.4246) were significantly different (ANOVA, $F=3.044$, $P<0.001$). Linear regression indicated a significant increase in tubule diameter across maturity stages (P<0.001), although tubule diameter appeared to become asymptotic in the range of mature testis masses (Fig. 52). The correlation between tubule diameter and testis mass among matures was non-significant (P>0.5).

Females

In the reproductive sample, 845 females were sexually immature and 1,061 were sexually mature. Among the mature females, 1,028 were either near-term pregnant or postpartum; 33 were neither pregnant nor lactating (i.e., "resting").

The smallest sexually mature female measured 147 cm and was carrying a full-term fetus. The largest sexually immature female was 193 cm (Fig. 53). The average length at sexual maturation was estimated at 172.0 cm (SE=0.3386) by the DeMaster (1978) method. Logistic regression provided a similar estimate of 171.2 cm (95% CI=170.7-171.7 cm), with 5% of the sample mature at 158.7 cm (95% CI=157.2-160.0 cm), and 95% of the sample mature at 183.7 cm (95% CI=182.4-85.2 cm) (Fig. 54).

Ovulation Rate

An ovulation rate for *P. dalli* was estimated following methods used for *Stenella attenuata* in Perrin *et al.* (1976). All females with one or more corpus up to age 12 were grouped in 1-year intervals while females age 13 or older were pooled. The average reproductive age($\bar{A}$) in interval p was calculated as

$$\overline{A_P}=\frac{(\sum_{i}^{p} a_i*b_i)}{c},$$

where *a* is the percentage of females maturing in the *i*th interval, *b* is the average reproductive age in interval *p* of females which matured in *I* and *c* is the percent mature in interval *p*.

The average corpus count in each age group was estimated by dividing the sum of corpora counted in interval *I* by the number of mature females in interval *I*. The average corpus count was then regressed on the average reproductive age using a simple linear model (Fig. 55).

The maximum number of corpora present in *P. dalli* specimens examined was 19 in a 2 year old. The linear regression indicated a significant slope of 0.914 ovulations/average reproductive year ($P<0.0001$, $R^2=0.9726$).

Seasonality

The temporal pattern of calving activity was explored by relating the timing of sampling periods, the length frequency distribution, and the reproductive condition of mature specimens. Several features of the *P. dalli* sample provided evidence of a strong temporal concentration of calving activity within the study period each year. The length frequency distribution (Figs. 32 and 33) contained a distinct grouping of small animals separated by a gap from about 125 to 135 cm. The lower edge of the gap marks the length not yet attained by the age-0 cohort before July 31, the latest possible sampling date, while the upper edge represents the greatest length already surpassed by the previous cohort as of the earliest possible sampling date in early June. The consistent existence of a gap in length class representation appeared in each of the 7 years sampled, suggesting little inter-annual variation in the timing or duration of the calving period.

In the sample for which reproductive data were available, nearly all mature females were either pregnant or postpartum. Examination of changes in female reproductive condition across the field season indicated no births had occurred by the onset of sampling, while no pregnant animals were observed after the third week in July. Using logistic regression of pregnancy status (i.e., pregnant vs. postpartum) on date of collection, we predicted July 3 (95% CI +/- one day) as the point at which 50% of births had occurred (all years combined) (Fig. 56). Similarly, we predicted the length of the calving period to be approximately 6 weeks, based on the dates when 5 and 95% of births had occurred (11 June and 24 July, respectively).

Simple linear regression of ovarian mass on date of collection indicated a significant decrease of 0.19 g/day ($P<0.0001$) across the predicted calving period. Likewise, the number of females with corpora lutea was highest in June while the number with stage 2 corpora albicantia were highest in July (Fig. 57).

Examination of mammary activity also provided indications of a consistent peak in calving activity. Of the 1,028 reproductively active females examined, 117 were pregnant with no mammary activity, 320 were pregnant and producing colostrum, 55 were pregnant and lactating, and 536 were postpartum (lactating) (Table 9). Colostrum production was highest during the second and third weeks in June, then decreased with increasing frequency of postpartum conditions (Fig. 58). Lactation among pregnant females neither increased nor decreased during the sampling period. Instead, pregnant and lactating females represented 3.9 to 12.4% of the total number of reproductively active females sampled during any 5-day period. Limited observations of the pregnant and lactating condition may have reflected its short duration immediately prior to parturition. Colostrum production, in comparison, represented a more persistent stage of mammary activity, although its relationship to milk production in small cetaceans is poorly understood.

The timing or duration of weaning could not be determined with this sample. The examination of 69 neonatal stomachs revealed no evidence of solid food, indicating only a lower limit of at least two months for the nursing period.

Further indications of a highly modal reproductive cycle and signs of imminent breeding activity were indicated by other changes in gonadal activity. Among females, maximum follicle diameter in early June through the third week in July averaged 1.7 mm (S.E.=0.0752), while the largest follicle observed during this period was 9.5 mm (Fig. 59). In late July, the mean of largest follicle diameter, 5.3 mm (S.E.=0.3659), was significantly greater

(Student's t-test, t=9.635, P<0.0001). Over 30 specimens had follicles greater than the maximum size recorded during the earlier period, ranging in size to 17.7 mm. In addition, 6 cases of newly ruptured follicles were observed after 22 July.

Among mature males, spermatogenic activity increased across the sampling period (Fig. 60). The frequency of specimens in the "scant" activity category decreased from 25% to 12.5%, while the frequency of specimens ranked "heavy" increased from 12.5% to over 42% by mid-July.

DISCUSSION

Collectively, the *P. dalli* growth and reproductive analyses illustrate a unique life history pattern, atypical of most other small cetaceans. Most notably, the very early onset of sexual maturation, annual reproductive interval and short life span contrast with the protracted maturation and reproductive schedule of most other small cetacean species (Perrin and Reilly 1984). Only the harbor porpoise, *Phocoena phocoena,* (Mohl-Hansen 1954, Hohn and Brownell 1990, Kinze *et al.* 1990, Read 1990, Read and Gaskin 1990, Lockyer and Walton 1995, Read and Hohn 1995) and the vaquita, *Phocoena sinus,* (Hohn *et al.* 1996) demonstrate similar life history strategies. These features, as well as strong indications of very rapid growth potential, suggested that *P. dalli*, while sharing K-selected species characteristics with other cetaceans overall, would rank a step in the direction of r-selection on a continuum of life history strategies.

Early Onset of Sexual Maturation

Female *P. dalli* were sexually mature as early as age 3, although mean ASMs, 3.8 and 4.4 years, varied by estimation method. DeMaster (1984) noted that different estimators of ASM would produce different values, none of which were necessarily invalid. However, in this study, the frequency distribution of ages contained a long tail to the right (i.e., a small number of older immatures) suggesting that a median-type estimator, like logistic regression, was preferable to a mean-type estimator (e.g., the DeMaster (1978) method). The higher estimate using DeMaster (1978) was sensitive to the persistence of 10 sexually immature females at ages over 6 years old which contributed nearly 0.5 years to the ASM estimate. Similar differences between the estimates of male ASM and female LSM were also noted. The Newby (1982) estimate of ASM for *P. dalli* females compares closely with our preferred estimate of about 3.8 years. His male ASM estimate (5.67 years), however, is considerably higher than ours (4.5 years). The apparent discrepancy may be a result of the low representation of mature animals, aged 5 and under (n=4), in the Newby (1982) sample. Our estimates of ASM also fall within the range of 4-5 years presented by Kasuya (1978) for both sexes.

The ASMs for *P. dalli* from both the present and previous studies were lower than reported for many delphinid cetaceans (Perrin and Reilly 1984, Myrick *et al.* 1986, Ferrero and Walker 1993, Kasuya and Tai 1993, Ferrero and Walker 1995, 1996). However, both male and female *P. dalli* ASM estimates compared closely to those of *Phocoena phocoena* (van Utrecht 1978, Gaskin *et al.* 1984, Melin *et al.* 1990, Read and Hohn 1995).

Annual Reproductive Interval

The interval between pregnancies was inferred through the estimated ovulation rate (0.914 ovulations/reproductive year, see Fig. 53), and the reproductive condition of mature females, both of which suggested an annual cycle. Location of the ovulation rate regression line above an intersection with the origin was likely due to multiple ovulations in the first year (or years) of sexual maturity, and the persistence of those corpora throughout the life of the animal (Fig. 53).

Over 97% of the mature females sampled in all 7 years of collections were either pregnant or lactating, while no fetus smaller than full-term size was ever encountered. The predominance of a common reproductive condition suggested rigid adherence to a modal pattern of annual breeding. In addition, lactation was accompanied in all cases by recently active corpora (either stage 1 or stage 2 corpora albicantia) offering no evidence that lactation had resulted from a birth prior to the sampling period or during the previous year.

Previous estimates of the calving interval for *P. dalli* were consistent with our interpretation of an annual cycle. An annual reproductive cycle was also reported by Newby (1982); however, we could not determine the rationale for his assertion that delayed implantation played a role in the timing of breeding and the subsequent calving mode.

Evidence of Short Lifespan

The age frequency distribution provides indications that *P. dalli* are short-lived, both by the lack of any individual with more than 15 cementum layers and the progressive reduction in the number of animals age 6 and older. Age frequency distributions in Newby (1982) and Kasuya (1978) showed similar patterns. The single 22-year-old specimen reported by Newby (1982) represents an outlier when compared to all other sources of existing *P. dalli* age data. However, preliminary examination of the *P. dalli* age structure by Gosho (1990) noted that age agreement among readers was lower for larger total length classes than smaller ones. Similar concerns that samples may under-represent older age classes were expressed by Kasuya and Shiraga (1985). Failure to detect older age groups could be related to the limitations of the cementum-based ageing technique although these and previous references to *P. dalli* problems in estimating age (Perrin and Myrick 1980) focused on interpretation and resolution of disparate reader counts, not a systematic failure to detect the oldest age groups.

The likelihood that the sample did capture the upper end of the age distribution was supported by the analyses of physical maturity. The relationship between average length at physical maturity and average age at physical maturity contrasted sharply. Unlike age, length was a poor predictor of physical maturity, reflecting the high degree of individual variation in total length at age possible for the species. Similar variation in length at age was also reflected in the scatter around the fitted growth curves. Given such variability, it was likely that only a portion of the unaged specimens of concern to Gosho (1990) and Kasuya and Shiraga (1985) were actually among the oldest in the samples.

Growth Patterns

Assuming that some minimal body size is necessary for females to carry a fetus to term, individuals need to grow rapidly in both length and mass prior to the onset of sexual maturation. For both sexes we identified a marked increase in length, followed by a similar increase in mass 1 to 2 yrs later. Both events preceded the onset of sexual maturity. In our sample, female *P. dalli* attained 90% of their projected asymptotic length and mass by ages 3 to 4.

The pattern of annual reproduction may also have been fostered by rapid prenatal growth potential. Using the Perrin *et al.* (1977) relationship between average length at birth and gestation period developed for delphinids, the estimated gestation period was slightly over 12 mo. However, the findings strongly point to an annual cycle with births in June and July. By late July, enlarged follicles were becoming more common and the first cases of recent ovulation were encountered. This coupled with concurrent increases in spermatogenic activity suggested that the beginning of a breeding season was close at hand. If so, then the gestation period would have been more on the order of 10 to 11 mo. The combination of a 100 cm birth length over a 10-month period results in a prenatal growth trajectory much steeper than that predicted by the Perrin *et al.* (1977) relationship.

We note that one of the average length at birth estimates, the mean of the full-term fetuses (91.5 cm) would have suggested a shorter gestation period, closer to 11 months. However, this estimate of length at birth should be viewed with caution, as the lengths of fetuses in the folded position may not be fully comparable to straight line measurements of postnatal specimens. Furthermore, changes in length may occur as the spinal column assumes its linear configuration after birth.

Rapid early postnatal growth was also evident in the comparisons of weight and length from birth through the point of umbilical healing. Although we could not express the intervals between birth and the four classes of umbilical condition in exact temporal terms, all four classes were observed during sampling period. Therefore, the average increase in length and mass of approximately 14 cm and 10.3 kg, occurred over a 6-week period, the typical length of our field seasons. Such rapid early growth may have allowed a shorter weaning period, which in turn would allow greater allocation of maternal energy to fetal development.

These estimates of early postnatal growth rate did not approximate the growth model projections of length at age 1 or observations of mean mass at that age. The length-based growth model fit was nearly linear in the interval between ages 0 and 1, with projected lengths at age 1 of 148.5 and 146.3 cm for males and females, respectively. However, a sustained rate of growth based on changes during the first 2 months after birth would have resulted in projected lengths at age 1 exceeding 170 cm for both sexes. Likewise, projections of mass at age 1 based on observed differences among the neonatal specimens would have exceeded the observed means (62.7 kg for males and 60.4 kg for females) by over 20 kg. The discrepancy may have been due to the overly simplistic fit of length at ages 0 to 1 year. Differences in nutrition before, during and after weaning may have been the biological basis for these observed changes in growth rate. Likewise, events related to the weaning process may represent a rationale for consideration of alternative approaches to modeling early postnatal growth. In the present sample of *P. dalli*, umbilical condition provided the temporal index needed to examine growth at a finer resolution. However, similar conclusions were reached in examinations of *Lagenorhynchus obliquidens* early growth patterns, where measurements of partially formed first dentinal growth layer groups were possible (Ferrero and Walker 1996).

Segregation and Sample Limitations

Although the *P. dalli* specimen collections provided the means to estimate benchmarks for most growth and reproductive parameters specific to the central North Pacific stock, the spatial compression of sampling, coupled with *P. dalli* use of the fishing area as a calving grounds indicated that the sample probably did not reflect the actual maturity status and reproductive class frequencies of the stock across its entire range. Application of the sample to analyses beyond those undertaken, therefore, was not warranted. Previous examinations of *P. dalli* catch composition in this fishery also showed evidence of population segregation; the catch per unit effort of mature females was higher in July than in June during 1980 to 1984, while the trend among immature porpoise of both sexes was the opposite (Ferrero and Jones 1986).

Inflated frequencies of sexually mature and reproductively active females would have resulted in positively biased reproductive rate estimates. Similarly, if reproductively inactive females (so called "resting" females) did not select the sampling area in proportion to their reproductively active counterparts, then estimates of annual pregnancy rate also would have been biased upward. Lacking sampling effort outside the U.S.F.C.Z, the potential segregation issue could not be resolved and no attempt was made to estimate these parameters.

In previous examinations of small cetacean age structure in gillnet fisheries, the nets were presumed to provide a non-selective sample of the population structure specific to the time and area coincident with fishing operations. However, despite the nearly complete spatial and temporal overlap between *P. dalli* calving and the mothership fishery, the ratio of calves to postpartum females was much lower than expected (319 neonates to 1,099 postpartum females versus an expected ratio closer to 1:1). Lacking observations of *P. dalli* mothers or calves in the vicinity of the nets, the relative importance of their behaviors in terms of either differential avoidance or attraction to the gear could not be determined. Observer catch records did indicate, however, that the drop out rate (i.e., disentanglement of dead animals prior to their coming onboard) was slightly higher for "young" animals. Perhaps owing to limited mobility early in life, *P. dalli* neonates may not have been as susceptible to gillnet entanglement as their older counterparts.

Table 7. Breakdown of *Phocoenoides dalli* sample sizes, by type, used to estimate life history parameters.

Data Available for Analyses	Number of Male Samples	Number of Female Samples	Total	Parameters
(1) Sex, length, mass, collection date and location	2,033	3,566	5,599	Sex Ratios
(2) Reproductive status and all items in (1) above	1,941	1,906	3,847	Average Length at Sexual Maturation Ovulation Rate
(3) Age and all items in (1) and (2) above	813	1,297	2,110	Growth Curves Average Age at Sexual Maturation
(4) Fetuses associated with (1) above	455	484	939	Fetal Sex Ratio
(5) Physical maturity status	246	446	692	Average Length at Physical Maturation
(6) Ages and (5) above	49	116	165	Average Age at Physical Maturation

Table 8. Umbilicus class for age-0 *P. dalli* taken in Japanese high seas salmon gillnets in the U.S.F.C.Z., south of the western Aleutian Islands, 1981-1987.

Class	Males	Females	Total
1	51	51	102
2	37	43	80
3	19	12	31
4	10	8	18
Undetermined	42	46	88
Total	159	160	319

Table 9. Reproductive status for 1,906 female *Phocoenoides dalli* where ovaries were collected and examined.

Number of Samples by Reproductive Condition		
845 Immature 1,061 Mature.... 1,906 Total	33 Resting 1,028 Active....	120 Pregnant (only) 55 Pregnant and lactating 321 Pregnant with colostrum 532 Postpartum (lactating)

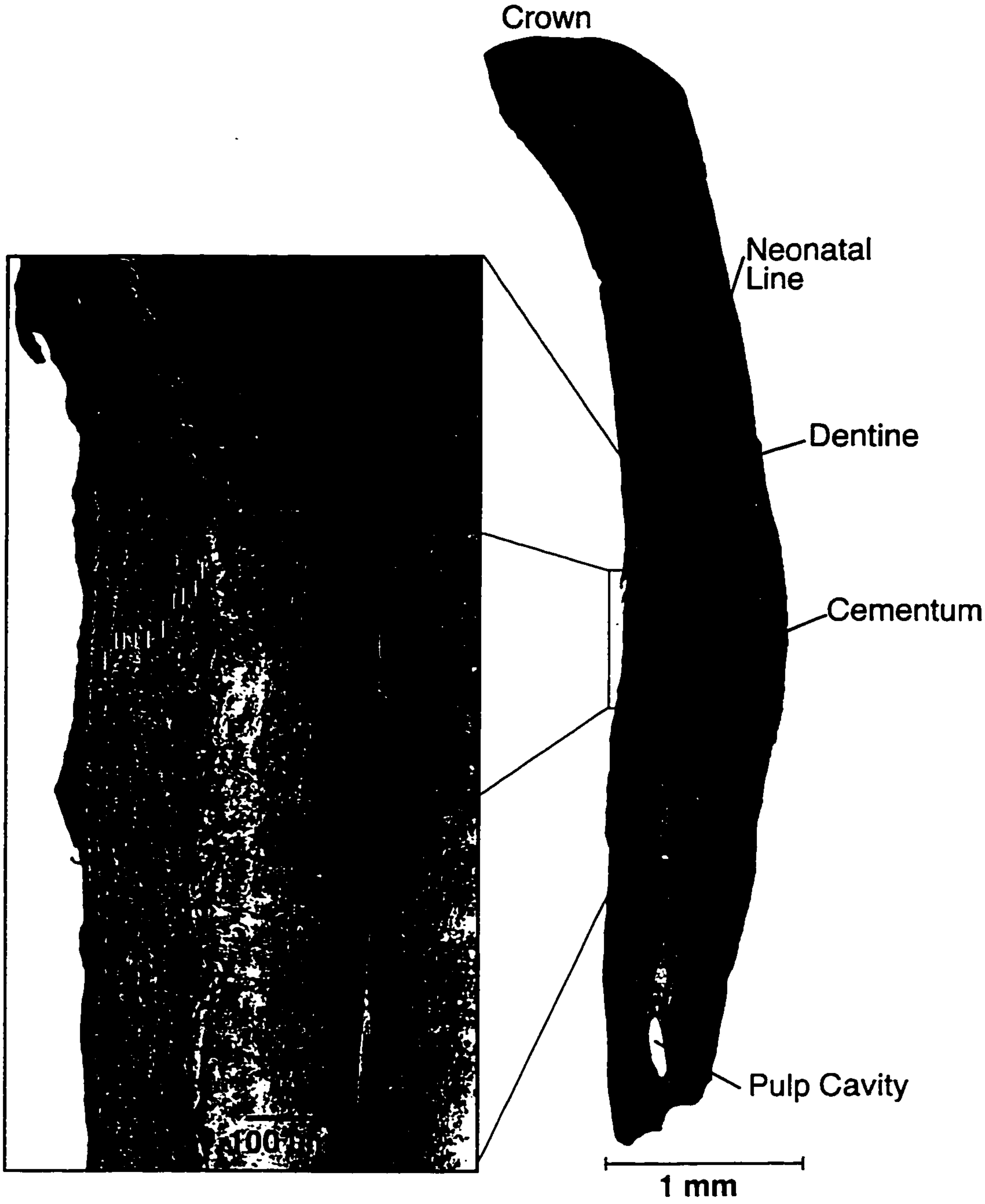


FIGURE 30: Longitudinal cross section of a Dall's porpoise (*P. dalli*) tooth showing principle features. The white dashes indicate cementum annuli.

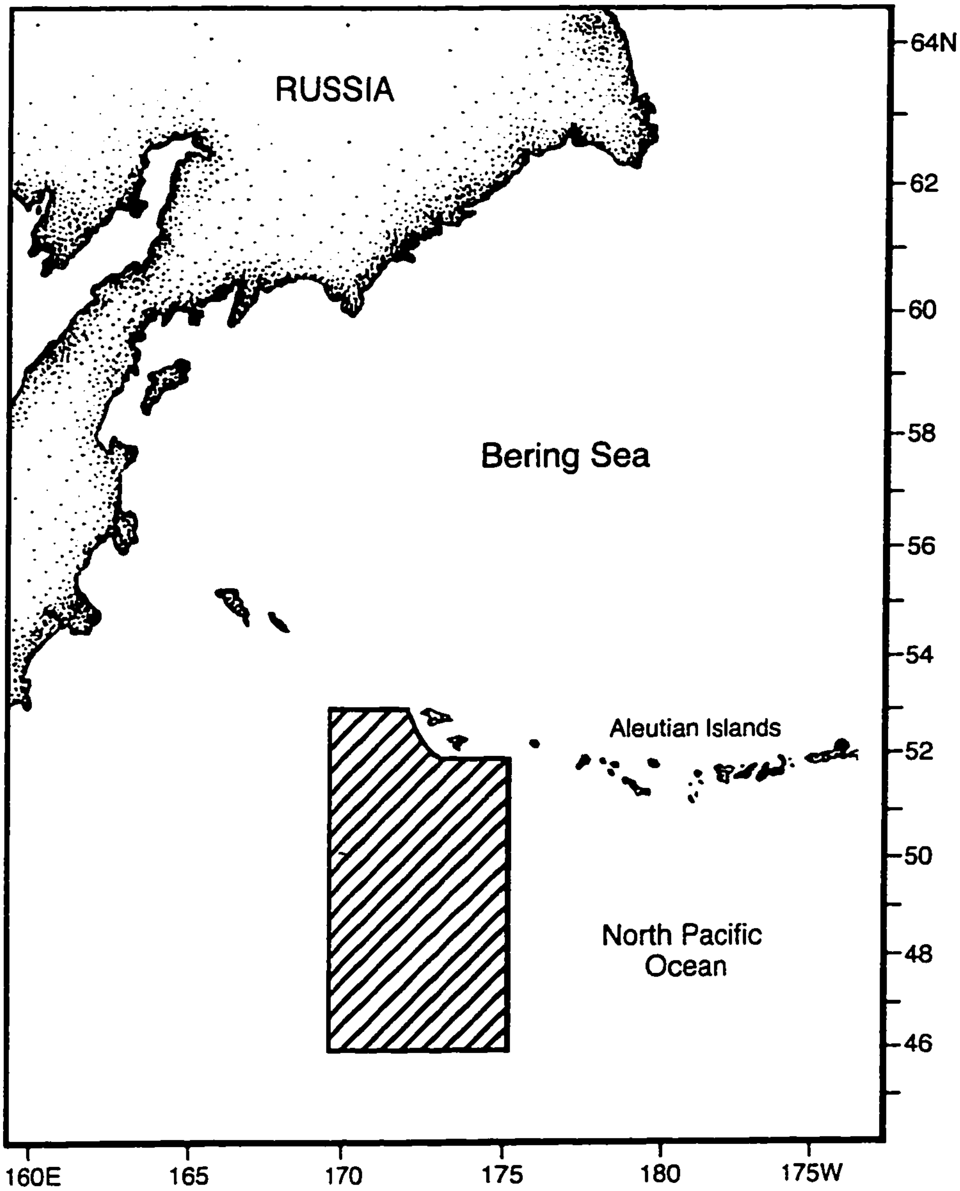


FIGURE 31: Area fished by the Japanese high seas salmon mothership fishery during June and July 1981-1987. All Dall's porpoise (*P. dalli*) samples included in the life history analyses were collected in this zone.

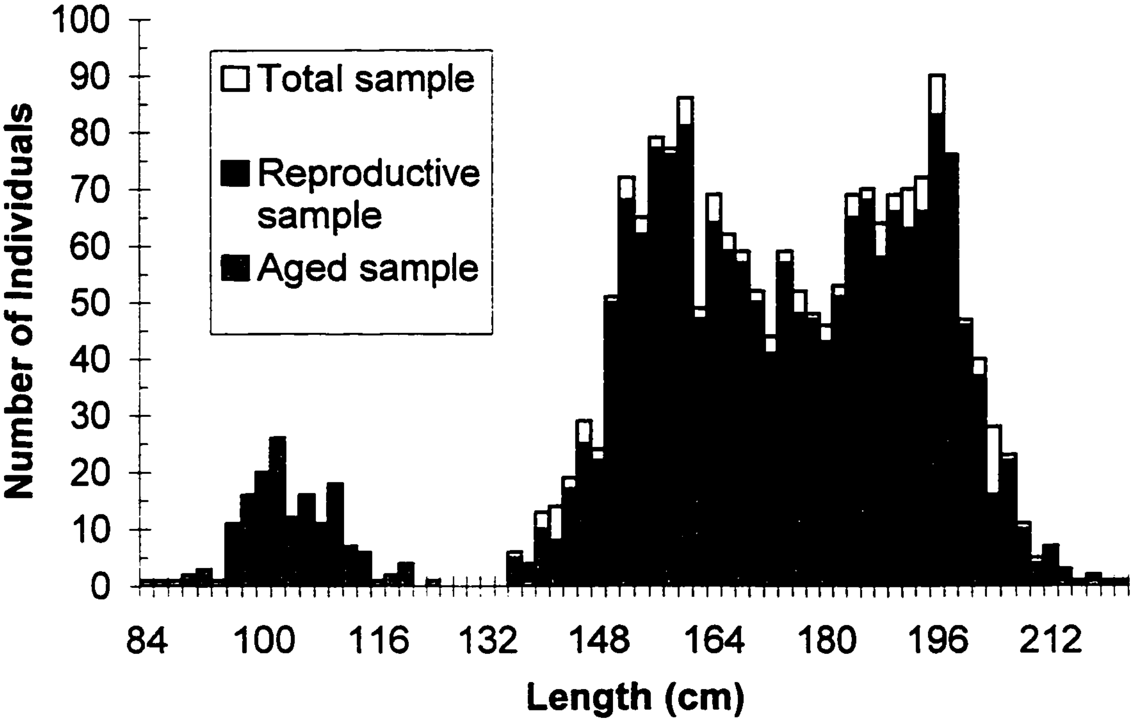


FIGURE 32: Comparison of length frequency distributions for male *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The total sample contained 2,033 males; reproductive data were available for 1,941 of those; 813 were aged.

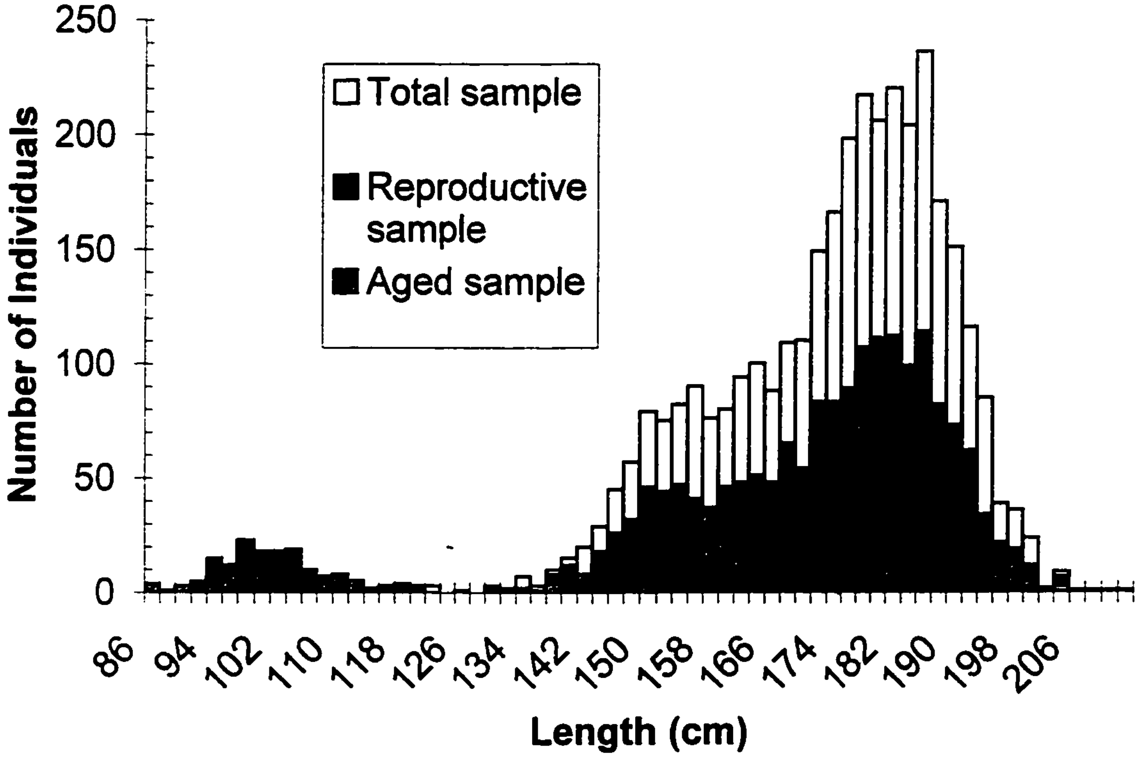


FIGURE 33: Comparison of length frequency distributions for female *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The total sample contained 3,566 females; reproductive data were available for 1,906 of those; 1,297 were aged.

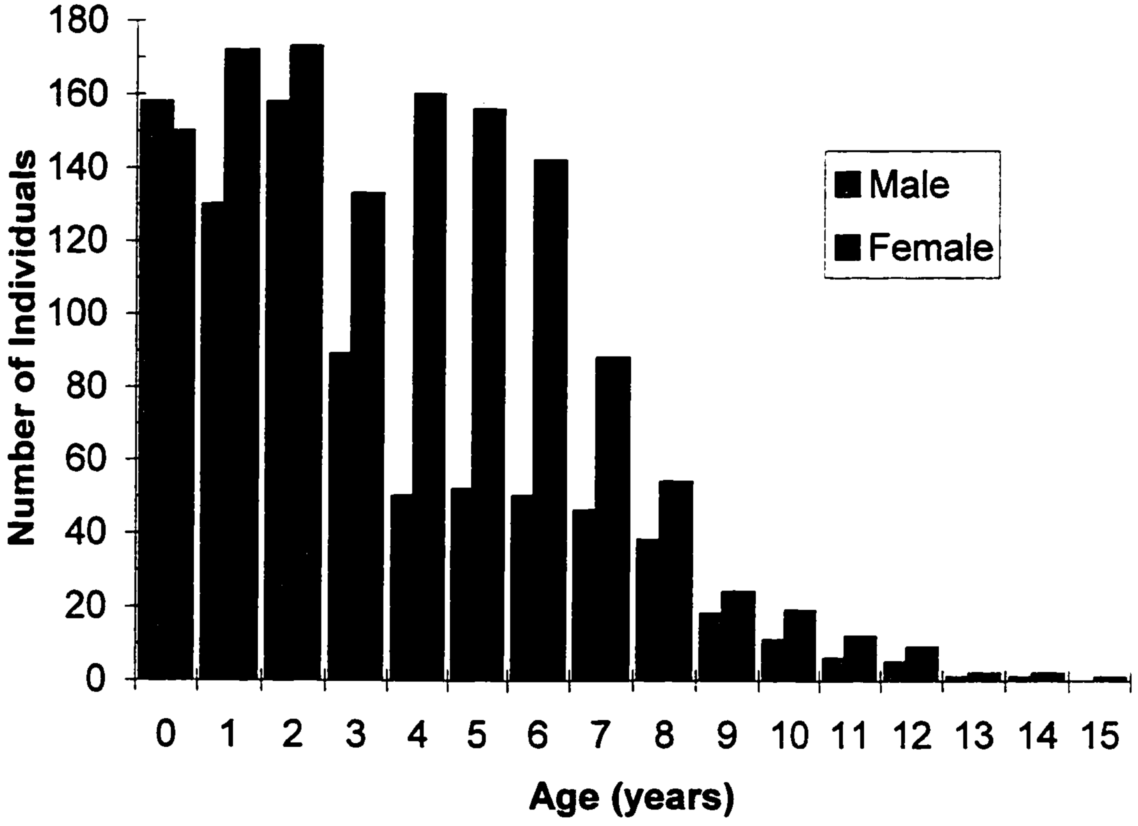


FIGURE 34: Age frequency distribution for 813 male and 1,297 female *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987.

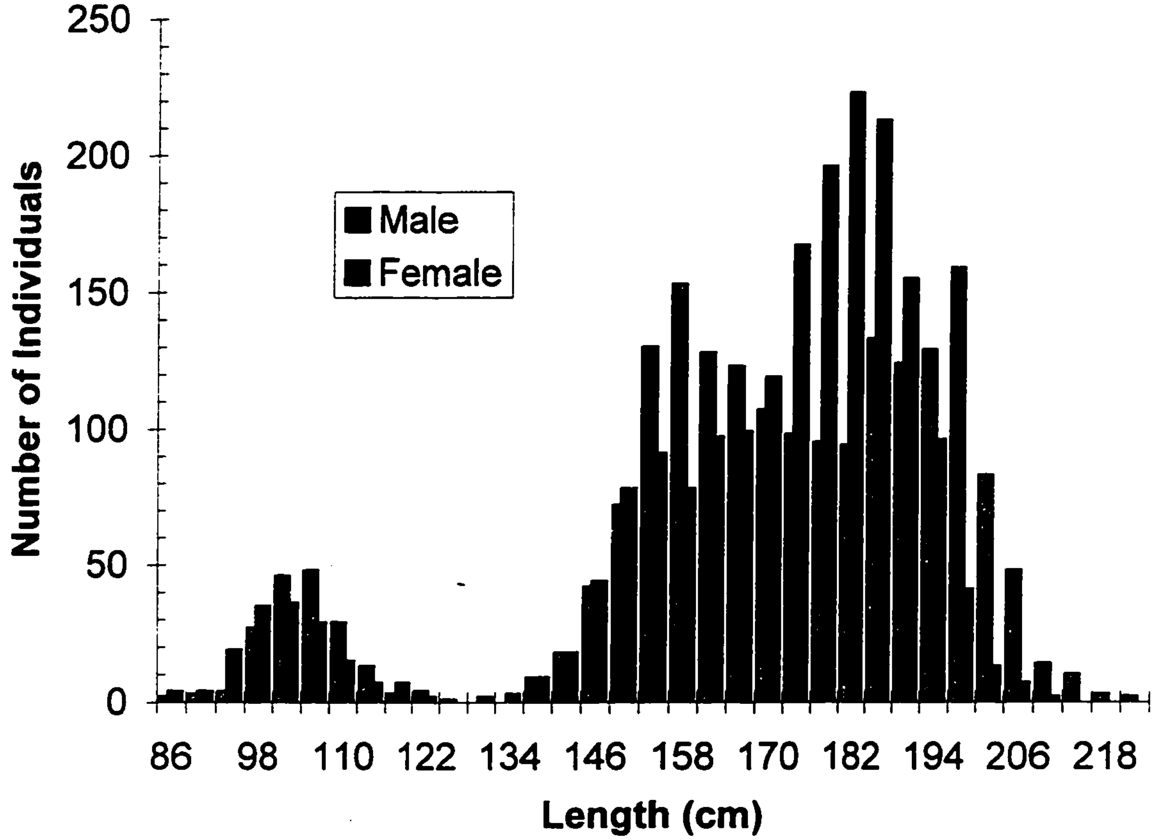


FIGURE 35: Length frequency distribution for 1,941 male and 1,906 female *P. dalli* (i.e., the sample for which reproductive data were available) taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987.

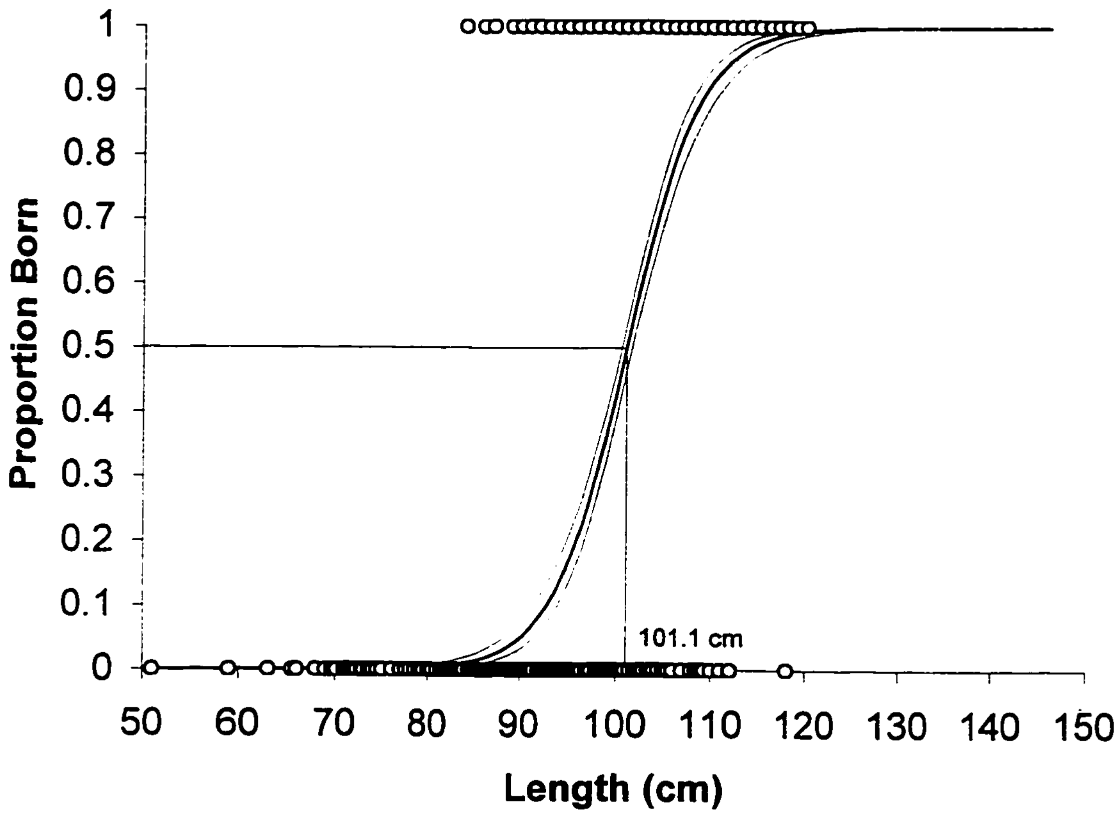


FIGURE 36: Logistic curve fitted to length and birth status (both sexes) for *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The light lines represent the 95% confidence limits on the fitted curve. The points represent individual samples.

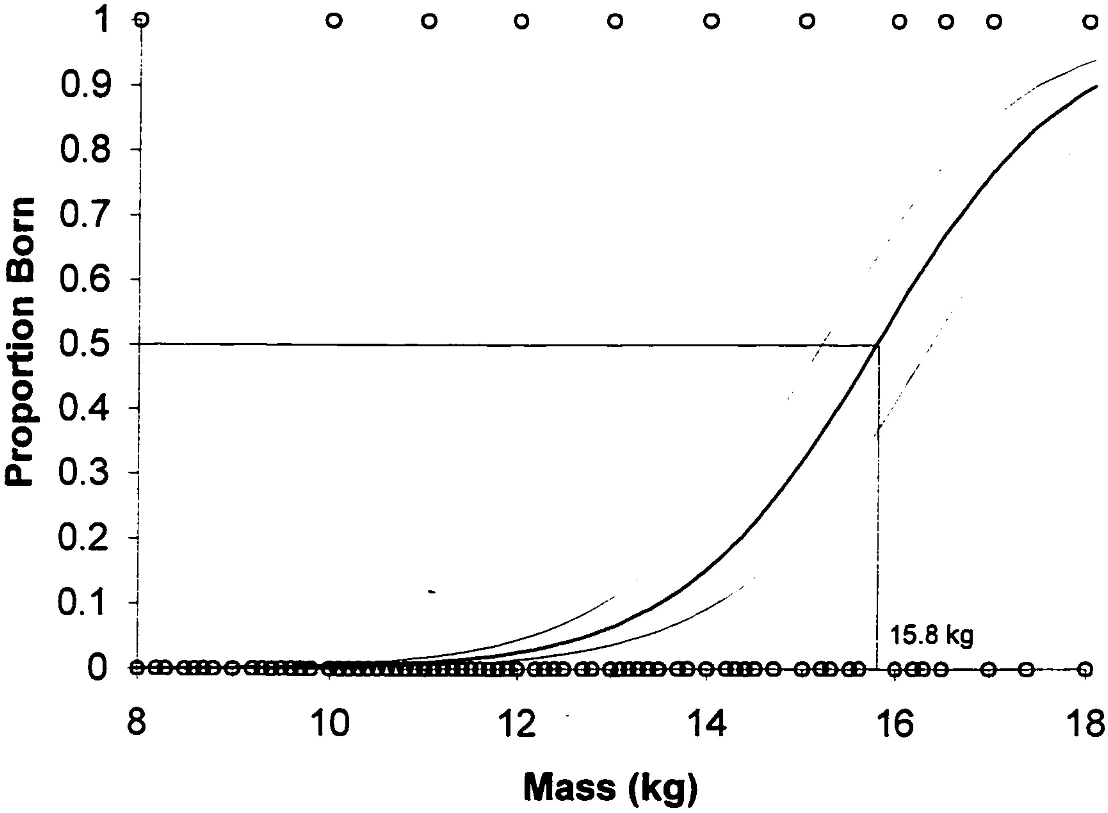


FIGURE 37: Logistic curve fitted to mass and birth status (both sexes) for *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The light lines represent the 95% confidence limits on the fitted curve. The points represent individual samples.

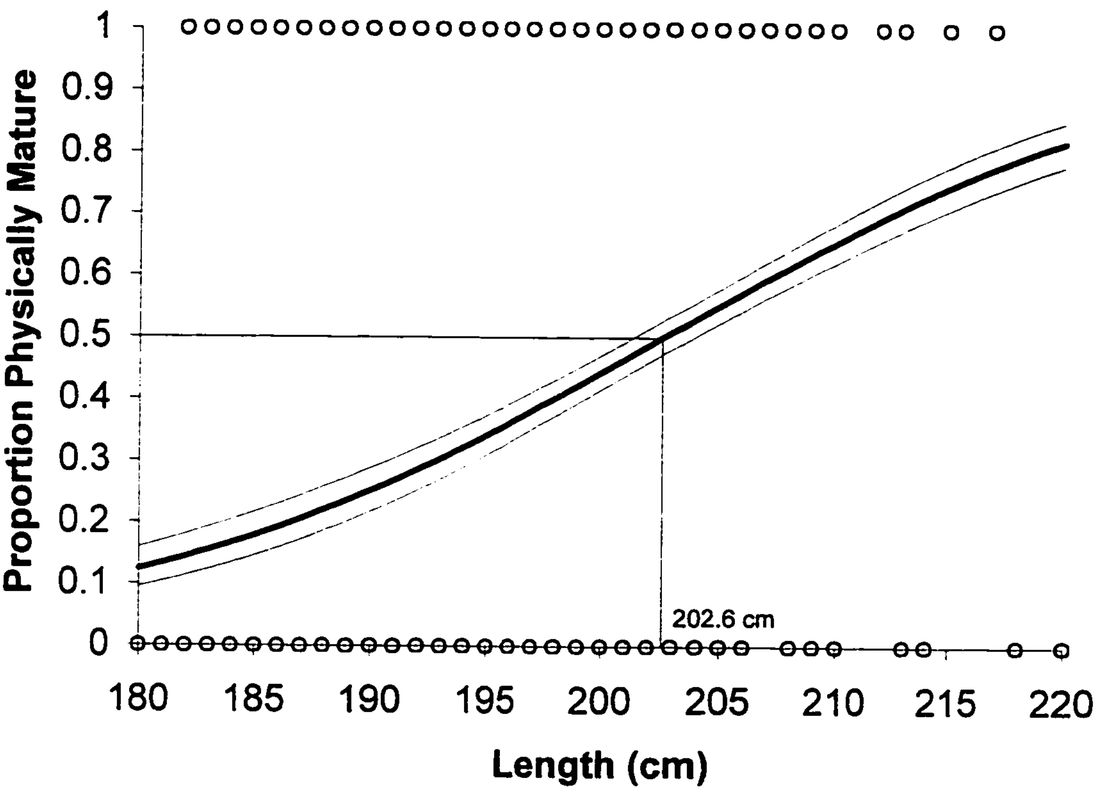


FIGURE 38: Logistic curve fitted to length and physical maturity status for male *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The light lines represent the 95% confidence limits on the fitted curve. The points represent individual samples.

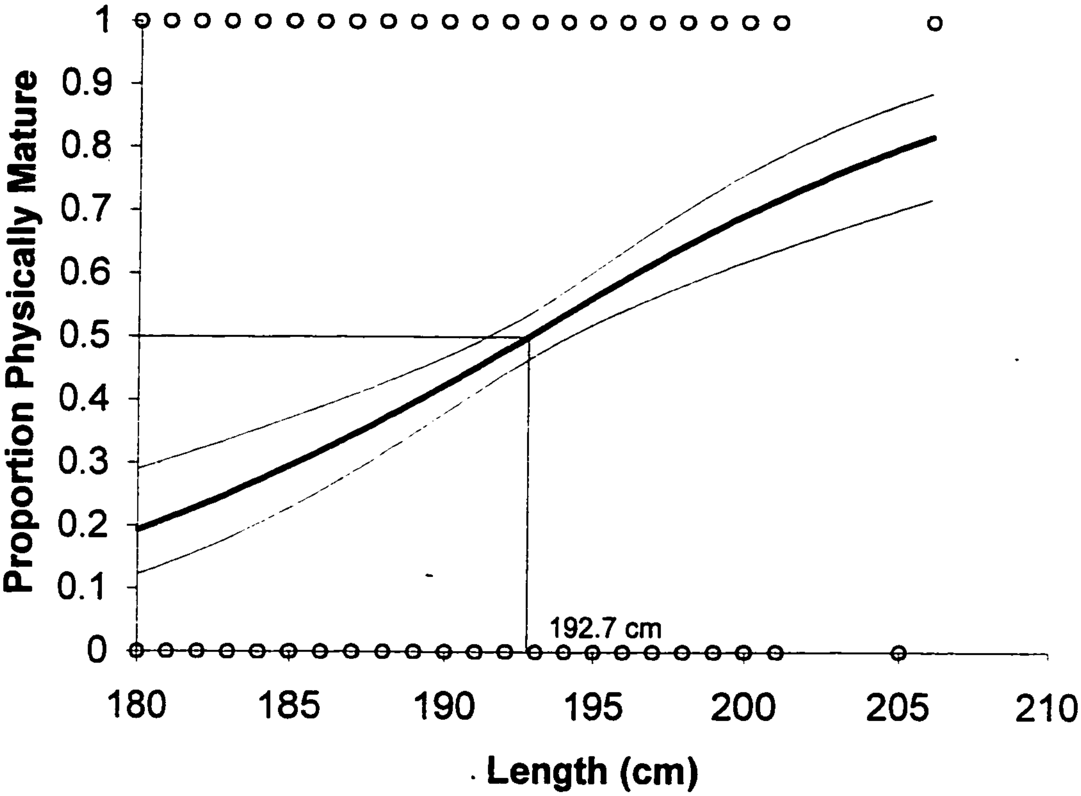


FIGURE 39: Logistic curve fitted to length and physical maturity status for female *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The light lines represent the 95% confidence limits on the fitted curve. The points represent individual samples.

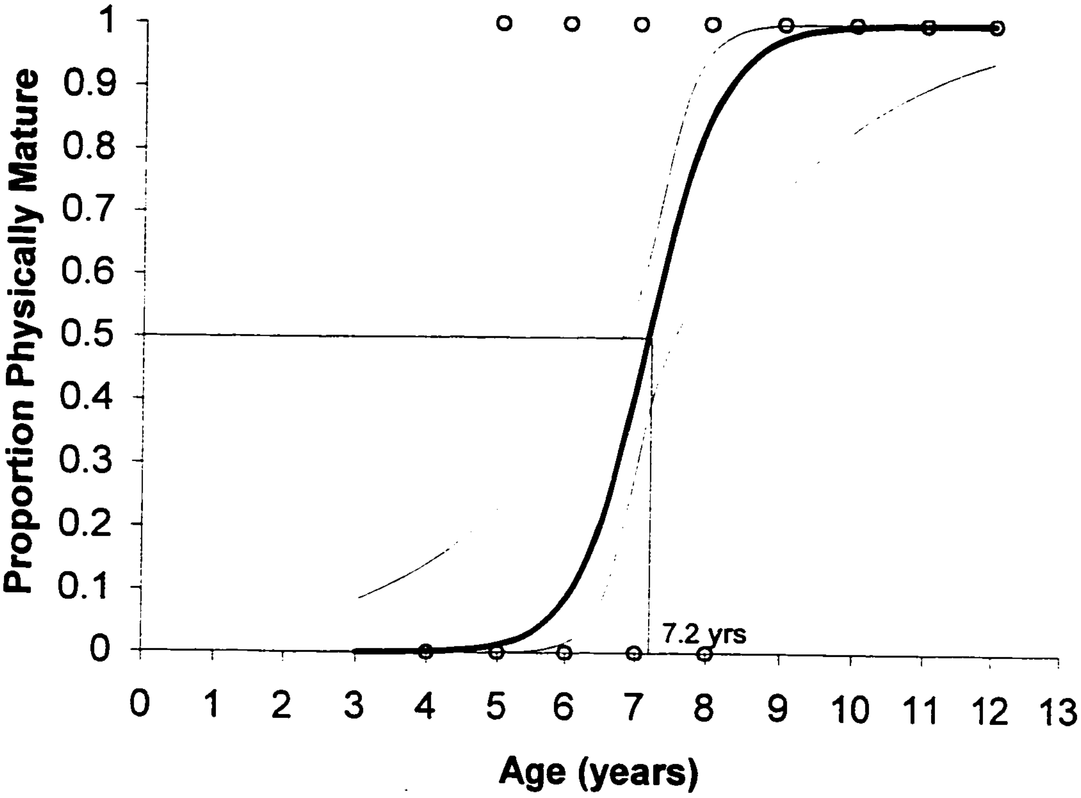


FIGURE 40: Logistic curve fitted to age and physical maturity status for male *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The light lines represent the 95% confidence limits on the fitted curve. The points represent individual samples.

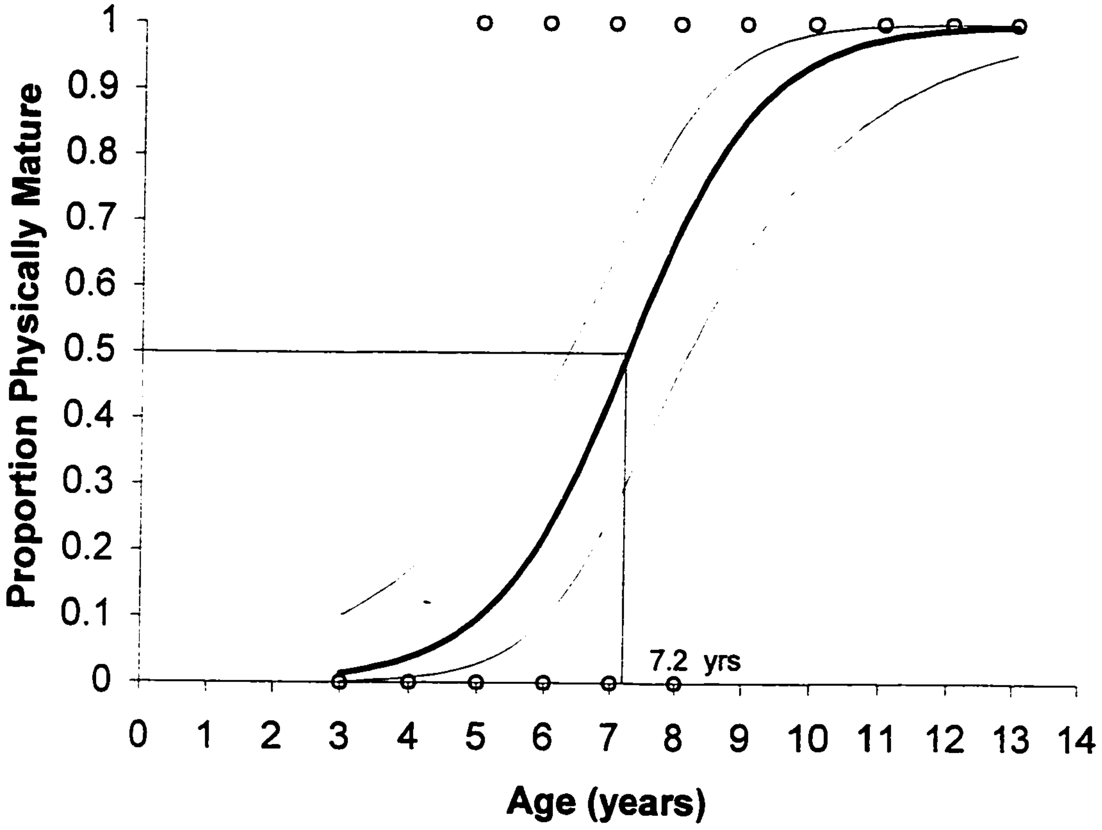


FIGURE 41: Logistic curve fitted to age and physical maturity status for female *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The light lines represent the 95% confidence limits on the fitted curve. The points represent individual samples.

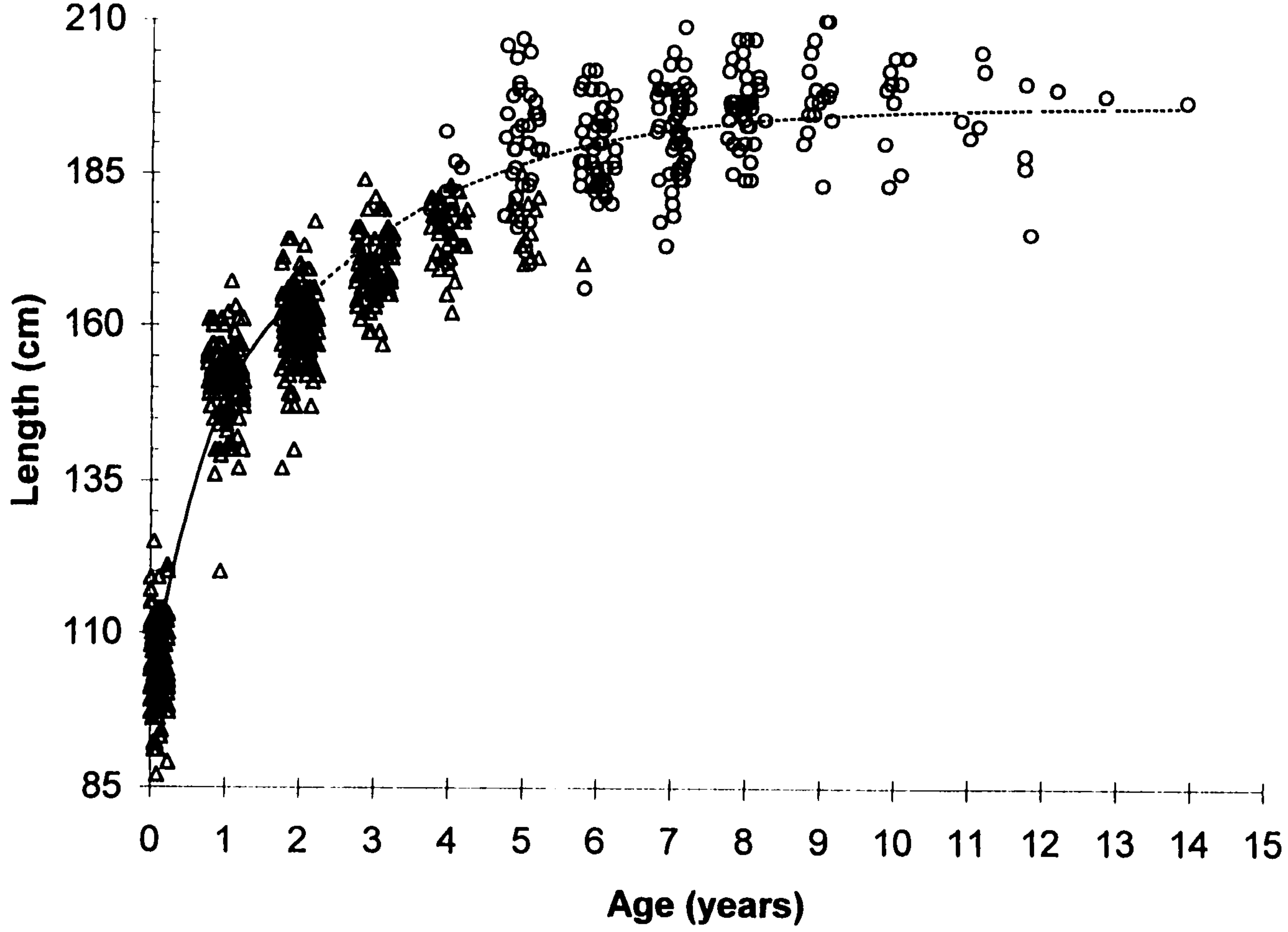


FIGURE 42: Length-at-age of male *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987 with fitted growth curves (two-phase Laird-Gompertz model). Triangles represent immatures; circles represent matures. Ages were recorded to the nearest whole year, but plotted as randomly jittered points to show the sample distribution.

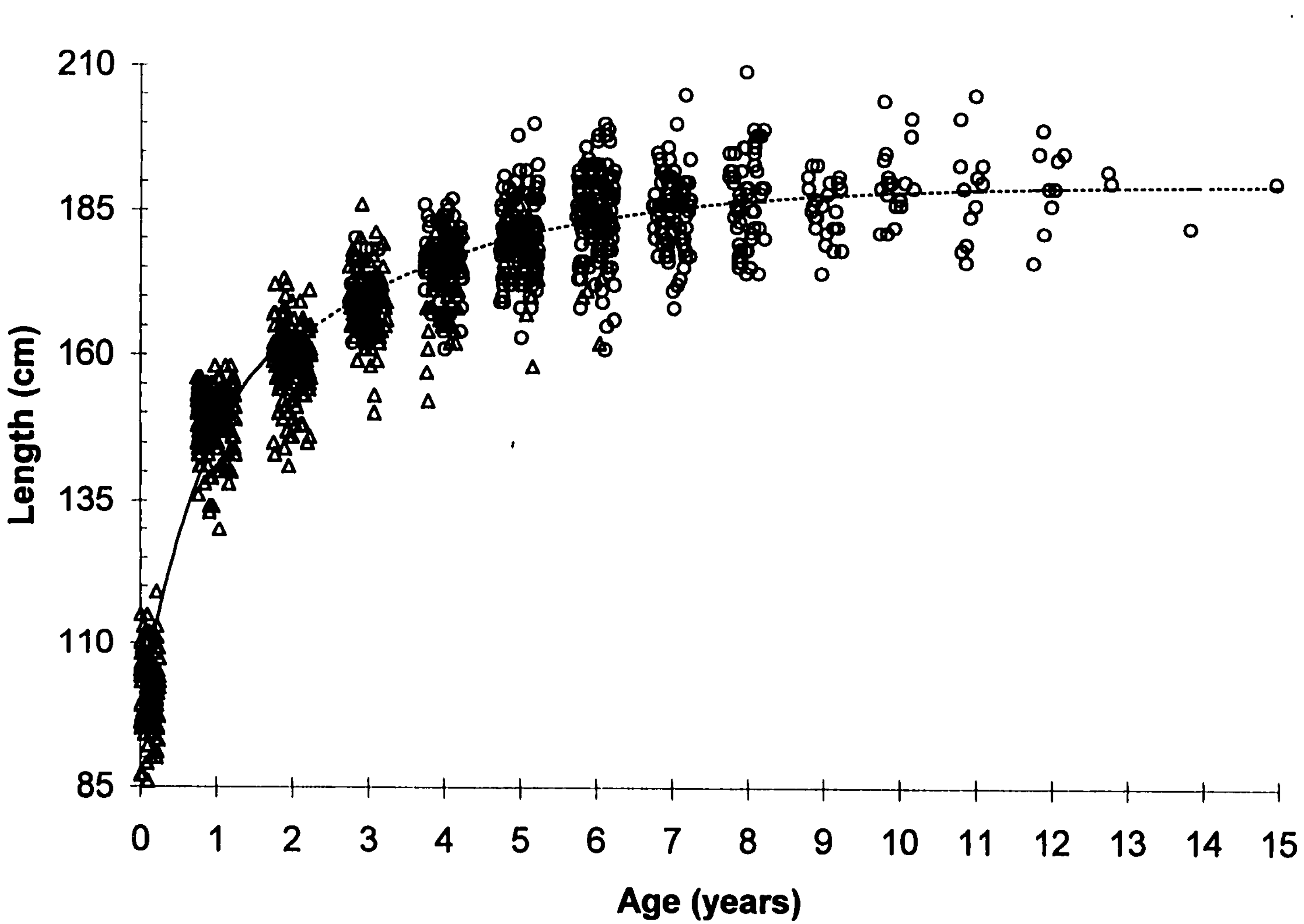


FIGURE 43: Length at age of female *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987 with fitted growth curves (two-phase Laird-Gompertz model). Triangles represent immatures; circles represent matures. Ages were recorded to the nearest whole year, but plotted as randomly jittered points to show the sample distribution.

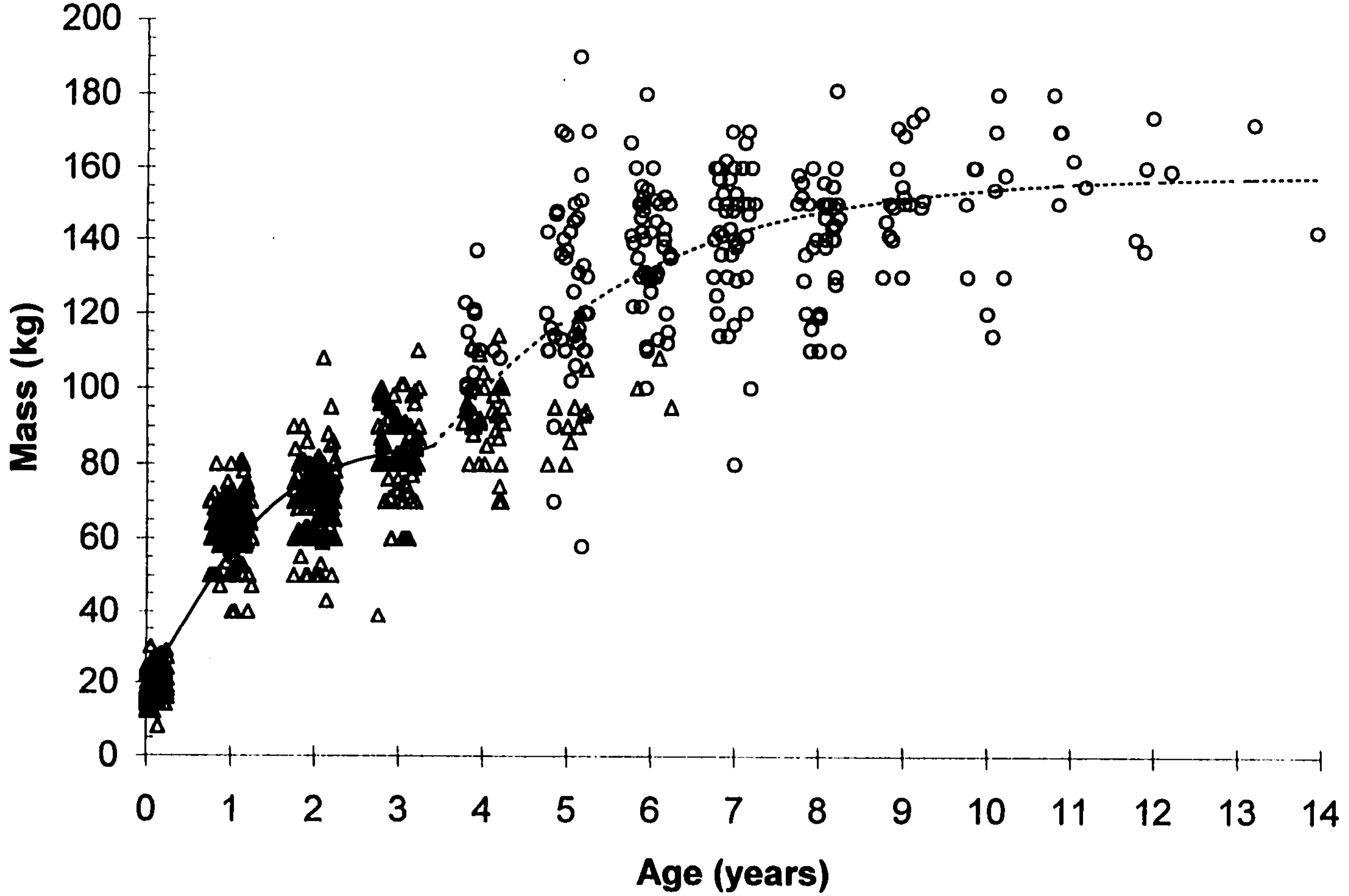


FIGURE 44: Mass at age of male *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987 with fitted growth curves (two-phase Laird-Gompertz model). Triangles represent immatures; circles represent matures. Ages were recorded to the nearest whole year, but plotted as randomly jittered points to show the sample distribution.

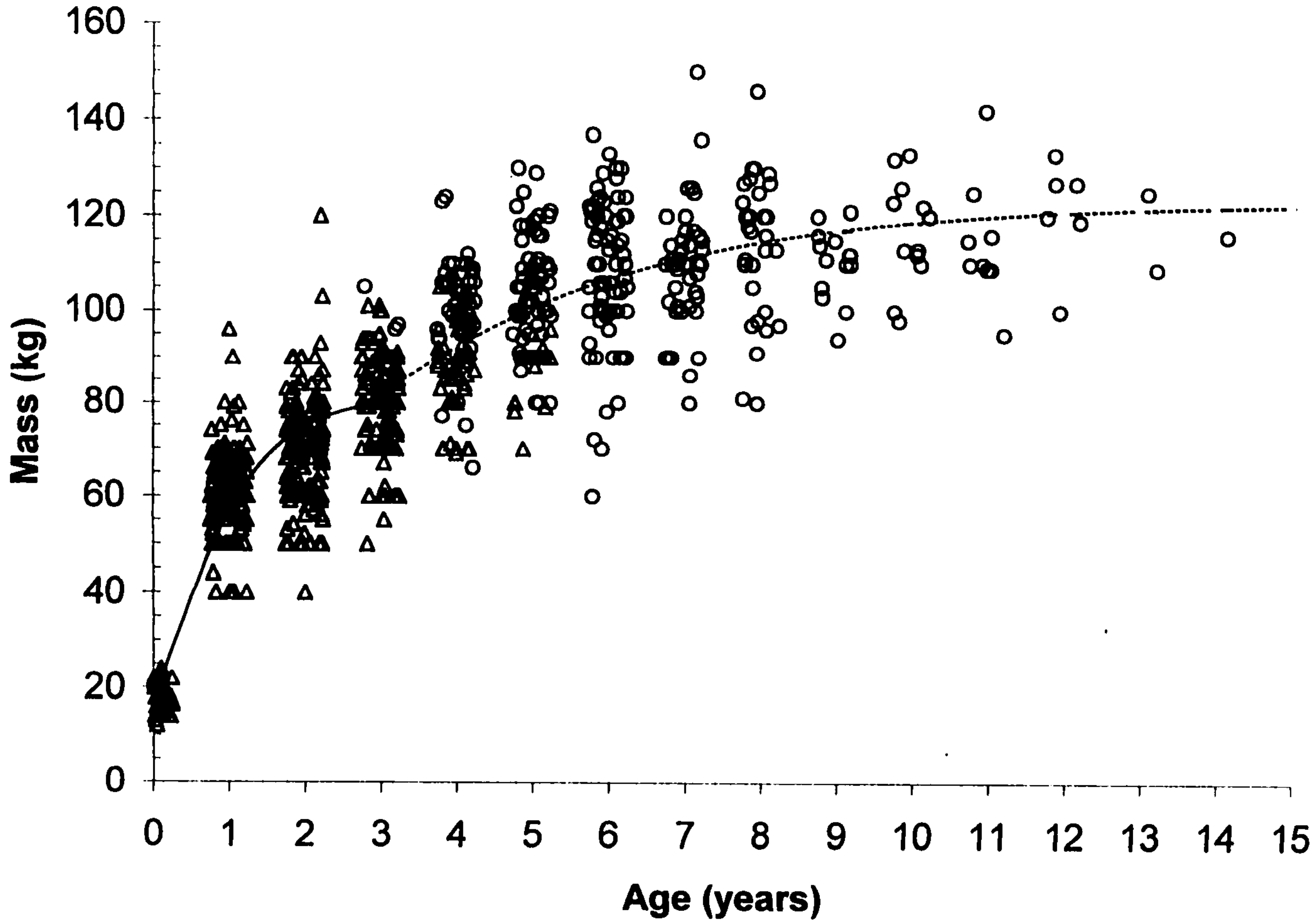


FIGURE 45: Mass at age of female *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987 with fitted growth curves (two-phase Laird-Gompertz model). Triangles represent immatures; circles represent matures. Ages were recorded to the nearest whole year, but plotted as randomly jittered points to show the sample distribution.

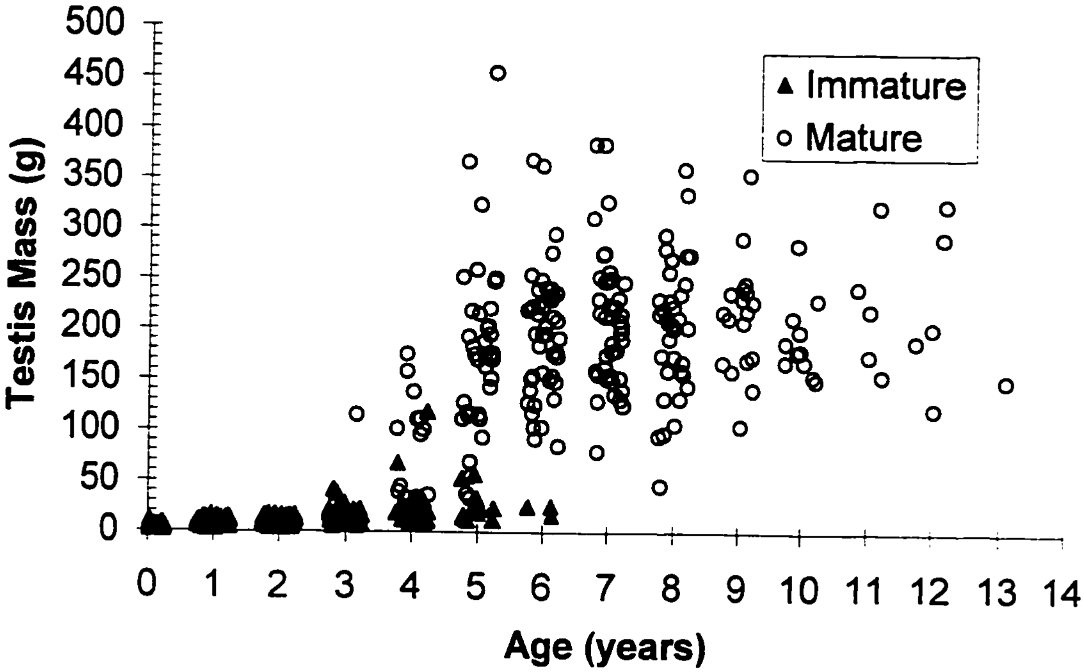


FIGURE 46: Scatterplot of age (years) and testis mass (g) for 1,941 male *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The triangles represent immature animals; the circles are mature animals.

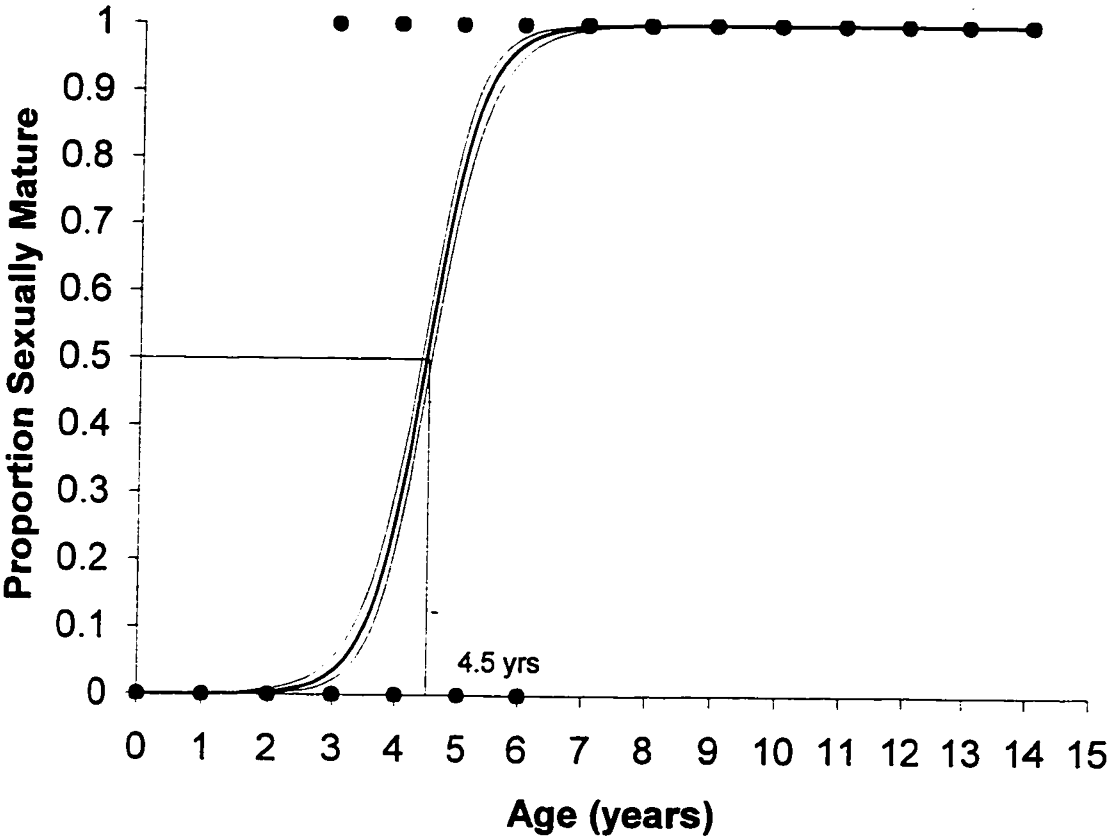


FIGURE 47: Logistic curve fitted to age and sexual maturity status for male *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The light lines represent the 95% confidence limits on the fitted curve. The points represent individual samples.

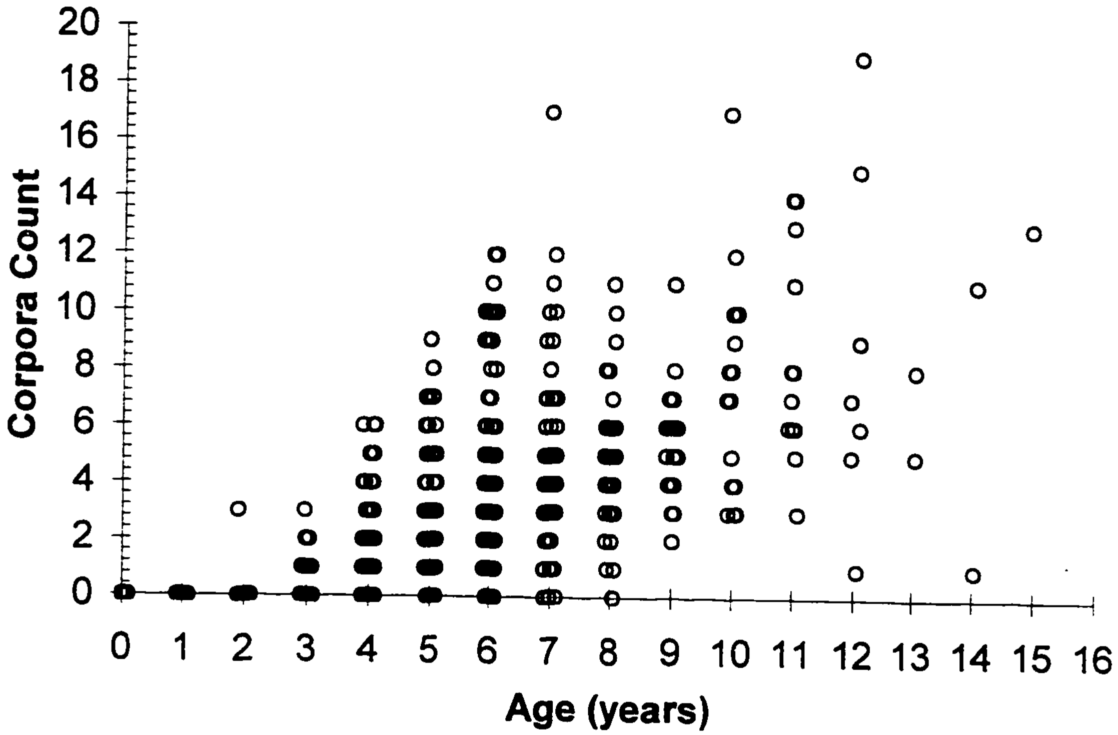


FIGURE 48: Scatterplot of age (years) and total corpora count for 1,906 female *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987.

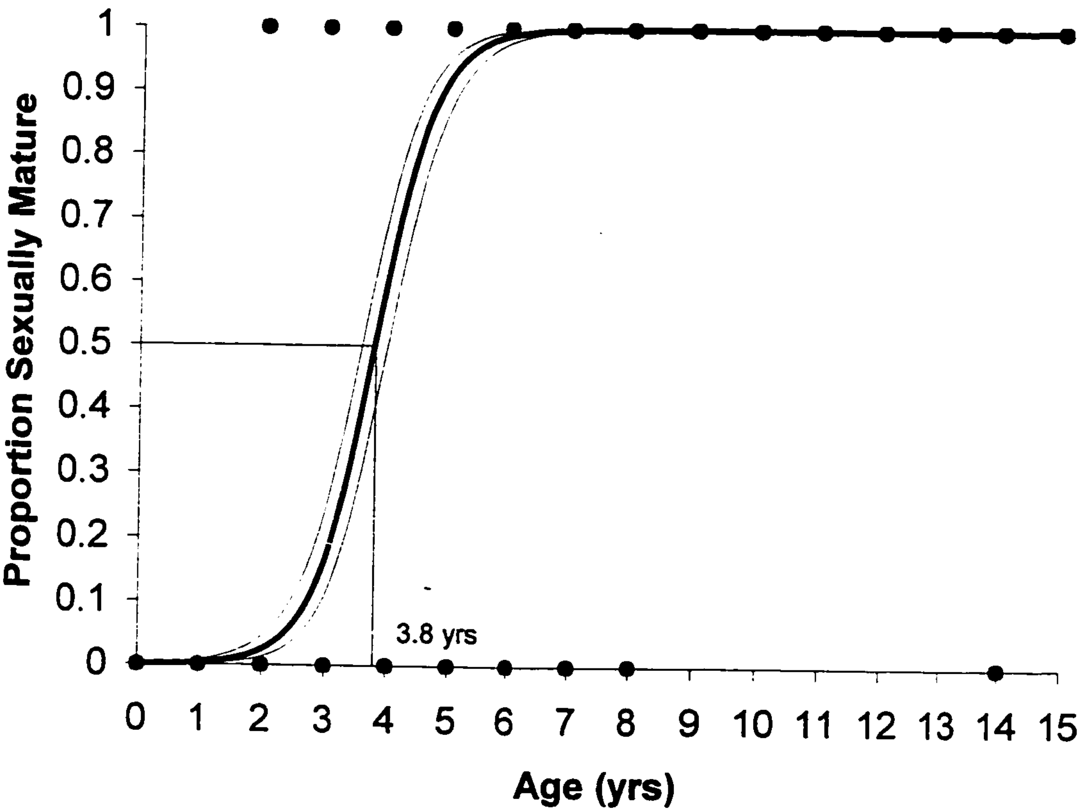


FIGURE 49: Logistic curve fitted to age and sexual maturity status for female *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The light lines represent the 95% confidence limits on the fitted curve. The points represent individual samples.

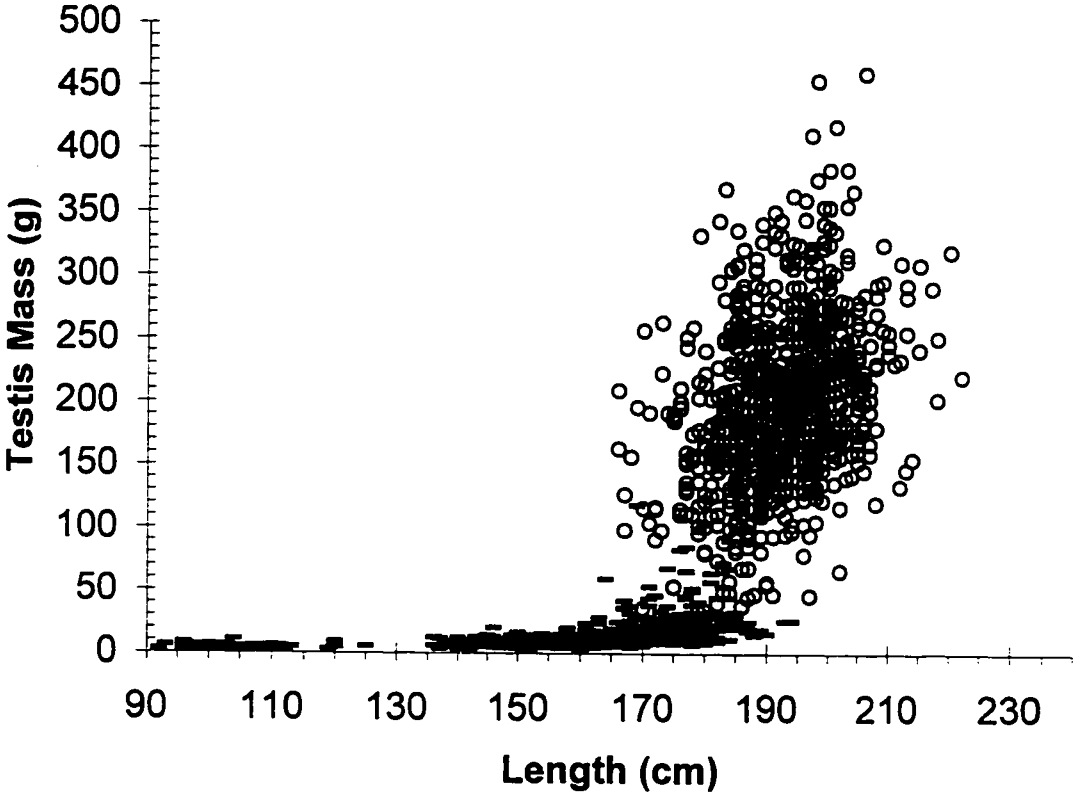


FIGURE 50: Scatterplot of length (cm) and testis mass (g) for 1,941 male *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The dashes represent immature animals; the circles are mature animals.

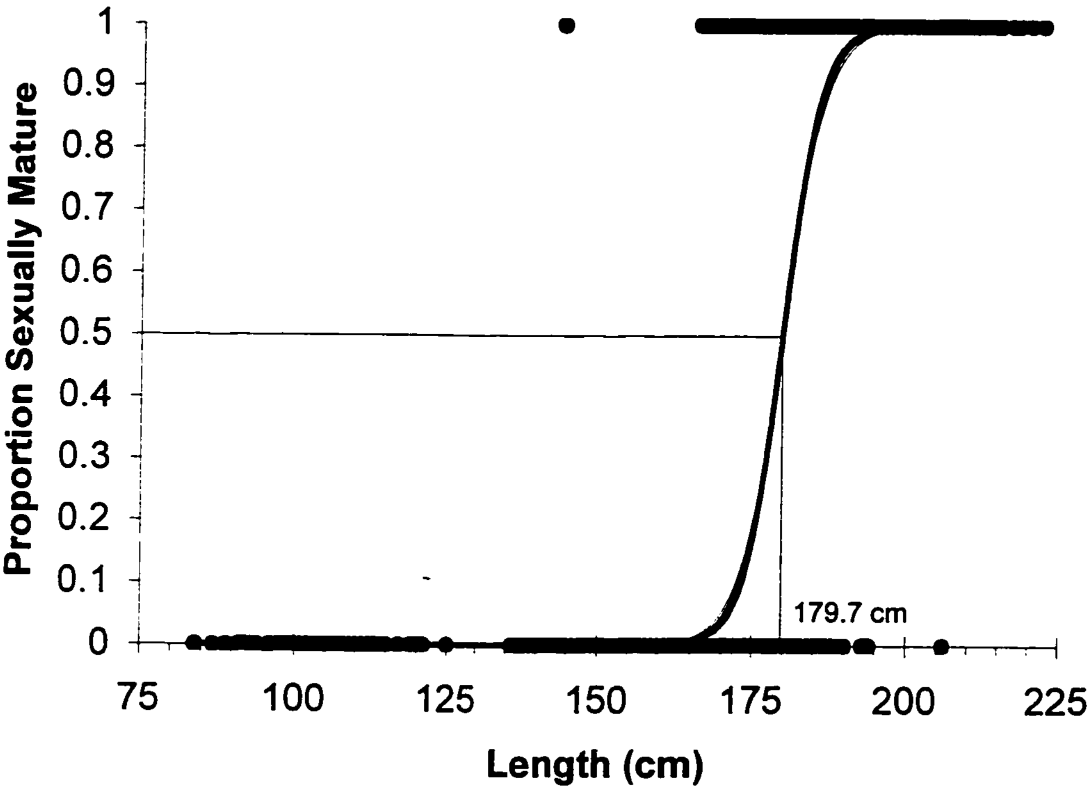


FIGURE 51: Logistic curve fitted to length and sexual maturity status for male *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The light lines represent the 95% confidence limits on the fitted curve. The points represent individual samples.

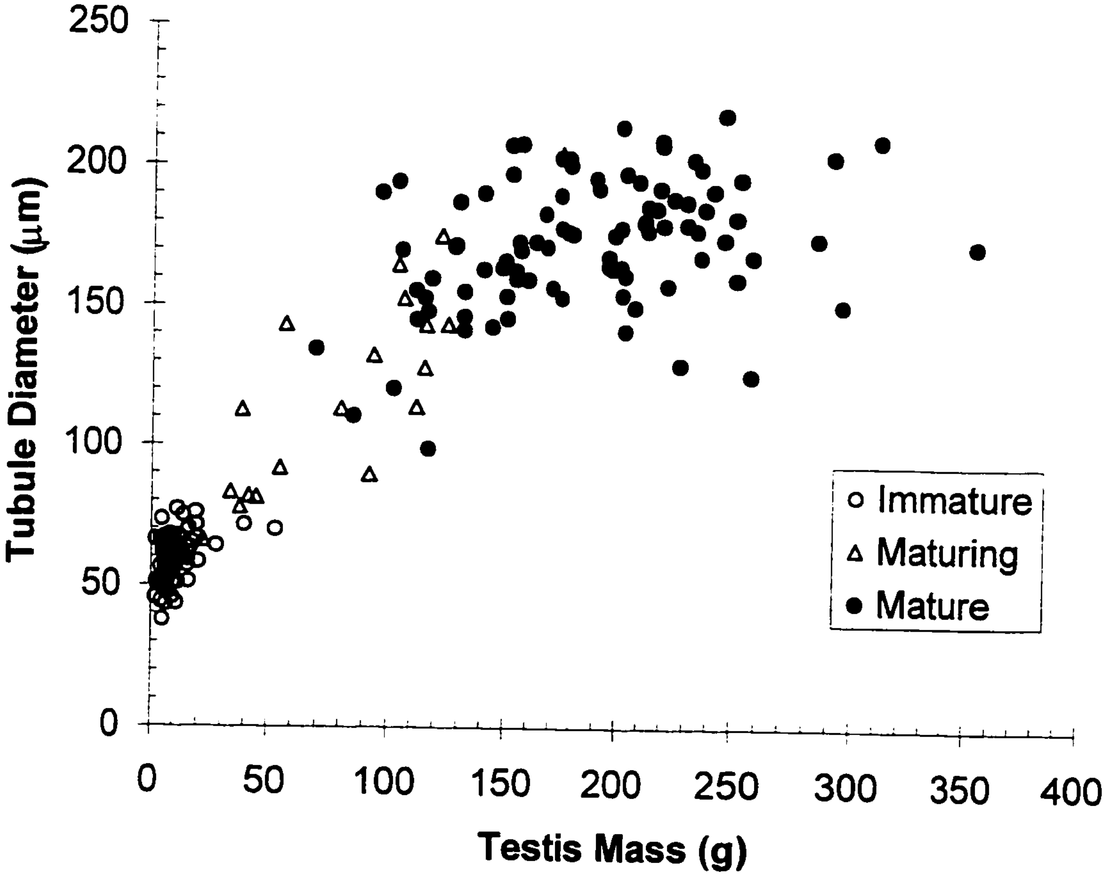


FIGURE 52: Scatterplot of testis mass (g) and tubule diameter (μm) for 191 male *P. dalli* taken in the Japanese high seas salmon mothership fishery during July 1981-1987.

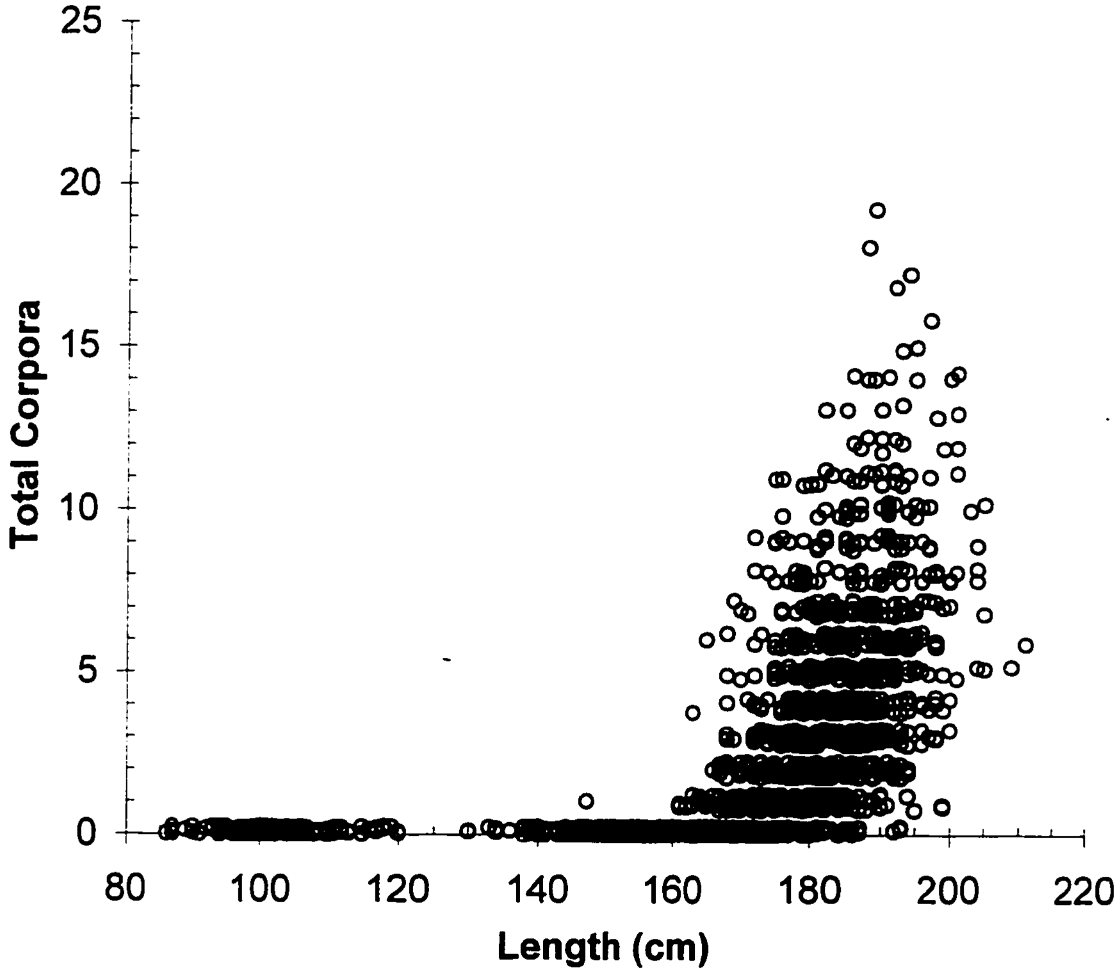


FIGURE 53: Scatterplot of length (cm) and total corpora count for 1,906 female *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987.

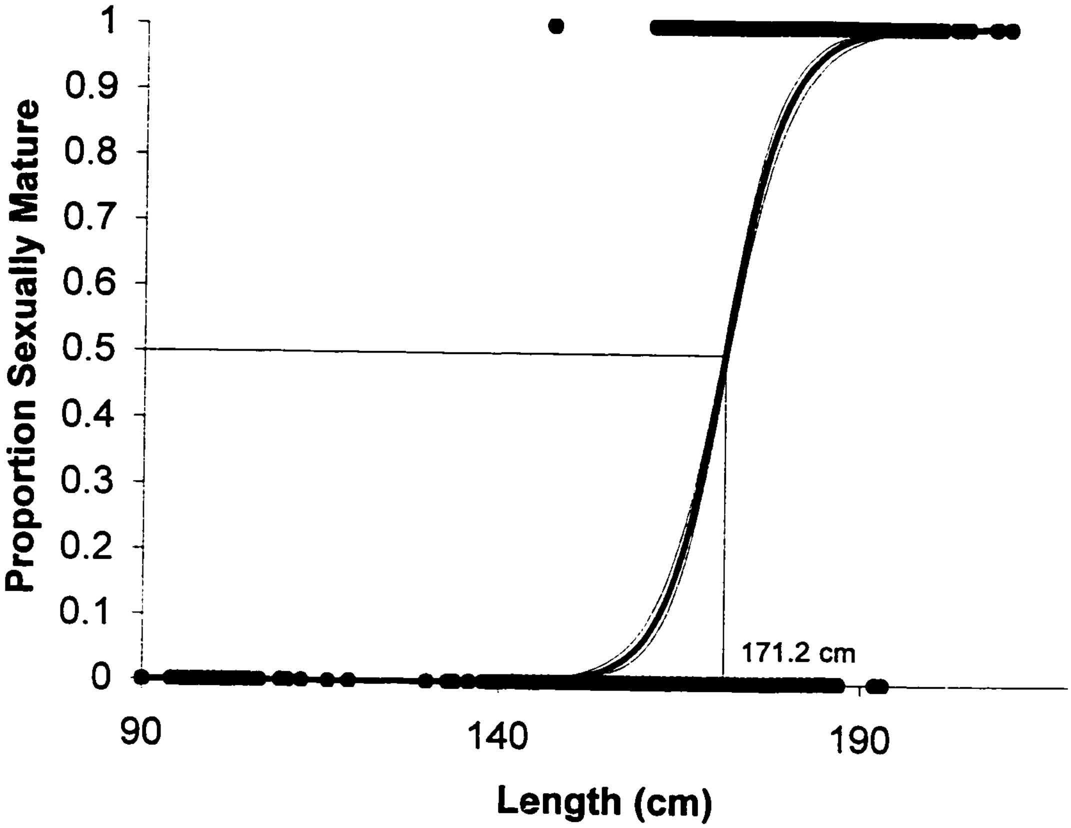


FIGURE 54: Logistic curve fitted to length and sexual maturity status for female *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The light lines represent the 95% confidence limits on the fitted curve. The points represent individual samples.

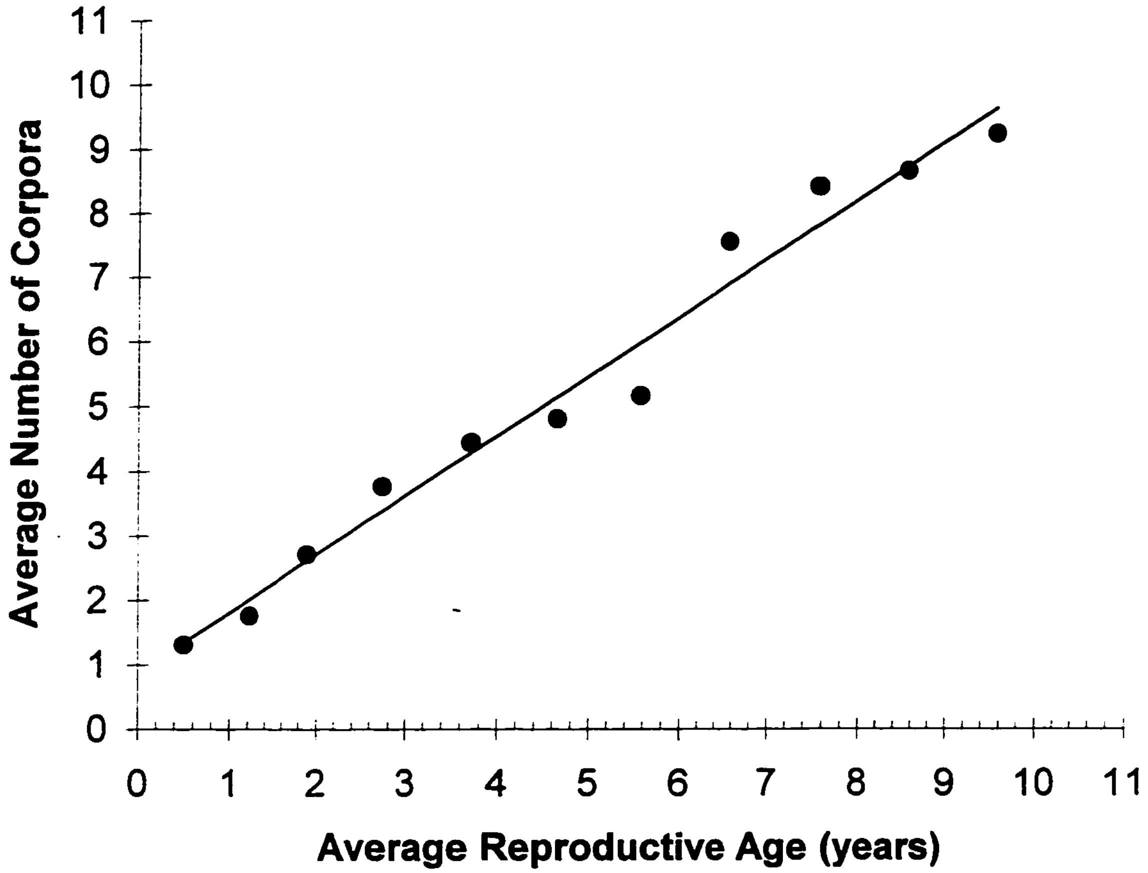


FIGURE 55: Linear regression of average corpora count on average reproductive age (years), where the slope estimates the ovulation rate. The regression equation was y = 0.894 + 0.914x.

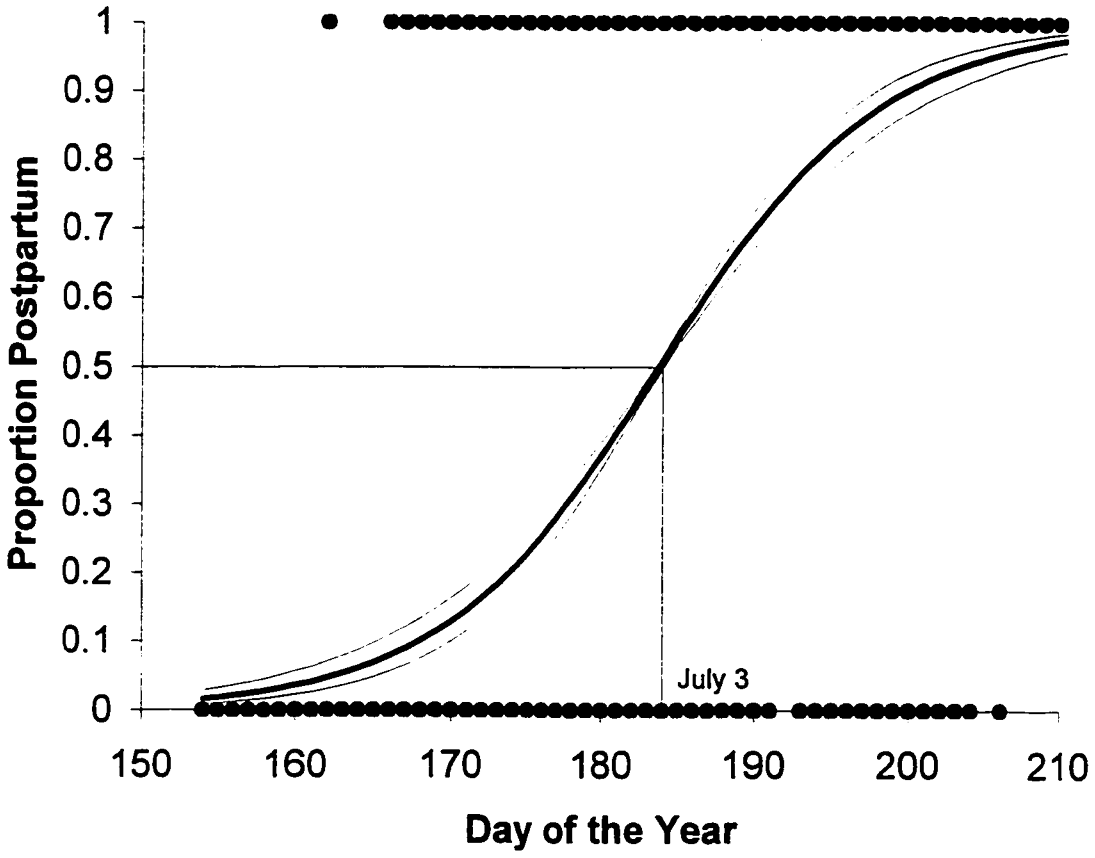


FIGURE 56: Logistic curve fitted to birth status and day of the year for *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The peak of the calving period is (July 3) indicated by the point at which 50% of reproductively active females were postpartum. The light lines represent the 95% confidence limits on the fitted curve.

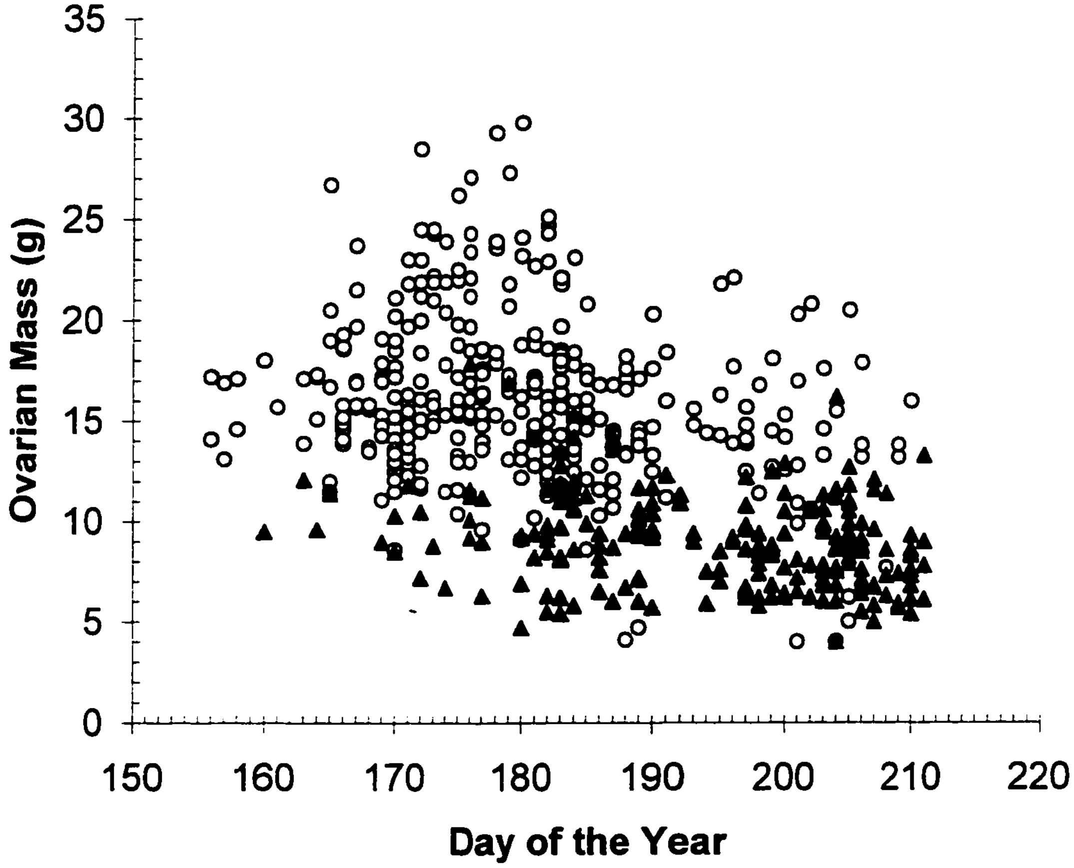


FIGURE 57: Scatterplot of ovarian mass (g) (i.e., right and left) on day of the year for 1,028 reproductively active female *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987. The simple linear regression equation was $y = 48.37 - 0.19x$. Circles represent specimens where corpora lutea were present; triangles represent presence of stage 2 corpora albicantia.

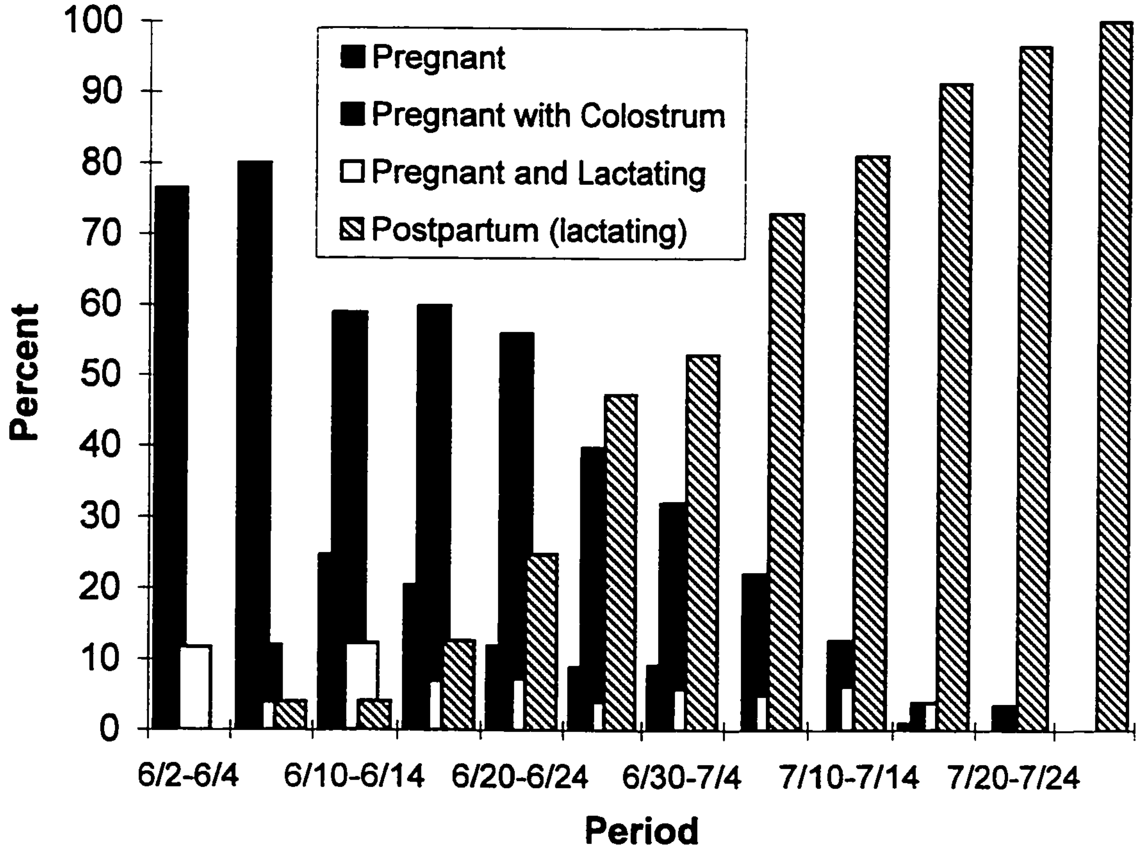


FIGURE 58: Comparative frequency distributions for four female reproductive conditions observed in *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987.

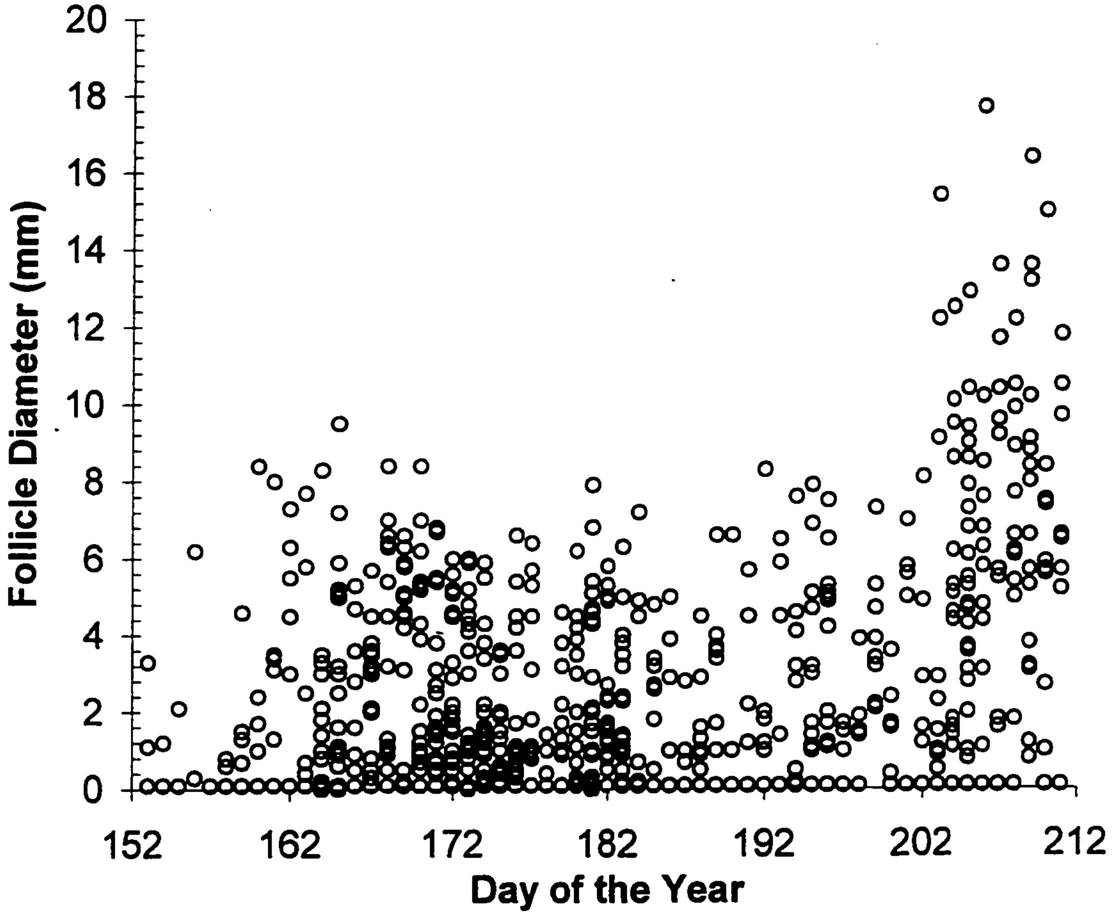


FIGURE 59: Scatterplot of date (day of the year) and follicle diameter (mm) for 1,028 reproductively active *P. dalli* females taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987.

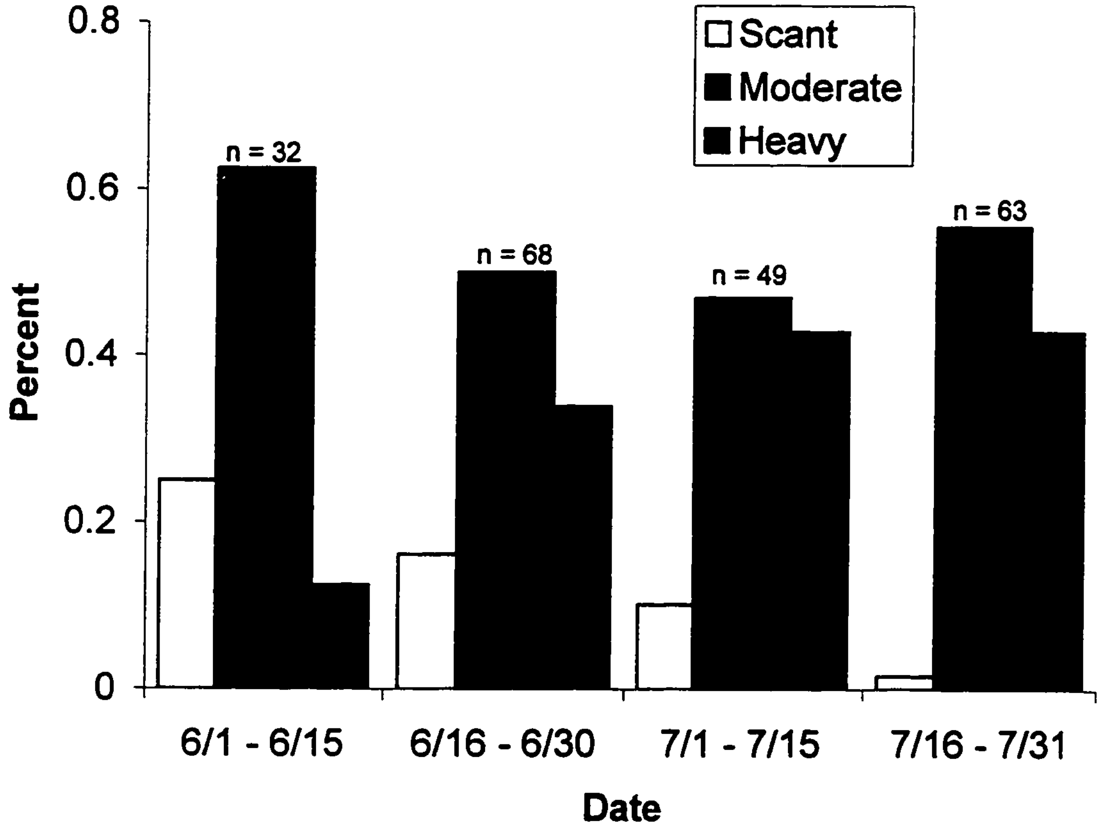


FIGURE 60: Comparative frequency distributions for three categories of spermatogenic activity by 2-week period observed in sexually mature *P. dalli* taken in the Japanese high seas salmon mothership fishery during June and July 1981-1987.

CHAPTER 4

Comparative Habitat Preference and Community Association Patterns Among Small Cetaceans in the Central North Pacific Ocean

Three species of small cetacean, the northern right whale dolphin (*Lissodelphis borealis*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and Dall's porpoise (*Phocoenoides dalli*), share overlapping distributions across much of the central North Pacific Ocean (Fig. 61). Dall's porpoise, principally a cold temperate and subarctic species of the North Pacific Ocean and adjacent seas, ranges from the Bering Sea, south to 41°N in pelagic waters (Morejohn 1979, Kasuya and Jones 1984). The Pacific white-sided dolphin is distributed widely across temperate Pacific waters, to latitudes as low or lower than 38°N, and northward to the Bering Sea (Leatherwood *et al.* 1984, Walker *et al.* 1986) and coastal areas of southeast Alaska (Dahlheim and Towell 1994). The northern right whale dolphin is endemic to the North Pacific Ocean, ranging from approximately 30°N to 50°N in the eastern Pacific Ocean (Leatherwood and Walker 1979) and 35°N to 51°N in the western Pacific Ocean (Sleptsov 1961, Nishiwaki 1967, Kasuya 1971). Kajimura and Loughlin (1988) reported northern right whale dolphins as far north as 52°N in the western Aleutian Islands.

Over the past three decades, opportunistic sighting surveys and research efforts associated with high seas driftnet fisheries have provided platforms for several studies of population abundance and distribution for all three species

(Turnock and Buckland 1995, Turnock *et al.* 1995, Hiramatsu 1993, Buckland *et al.* 1993, Miyashita 1993, Tanaka 1993). Movement patterns and stock identification for Dall's porpoise (Kasuya and Jones 1984; Ferrero and Jones 1986; Walker and Sinclair 1990) and Pacific white-sided dolphin (Miyazaki and Shikano 1989) have also been studied. Despite these efforts, published information on habitat preferences for any of the three species does not exist. Consequently, the basic ecological question of how these three species share or partition habitat has not been explored. As noted in the Introduction, contem-porary notions of niche partitioning have grown beyond the Hutchinsonian *n*-dimensional niche theory (Hutchinson 1957) based on competitive exclusion principles to embrace the importance of many dynamic processes operating at the ecosystem level which promote disequilibrium. Among these are natural disturbance, predation, parasitism, mutualism, founder effects and related uncertainties of population responses. While all of these processes may directly contravene the formation and maintenance of Hutchinsonian niches, observable differences in species distributions to measured biological or physical habitat features represent an important first view to the community ecology of the species. While recognizing the importance of more dynamic processes promoting disequilibrium, the objective of this study was to determine whether partitioning mechanisms could be detected for these three species, specific to their area of overlap, using life history and fisheries statistics data collected on Japanese driftnet vessels fishing the central North Pacific Ocean during 1990 and 1991.

Anecdotal evidence from preliminary food habits studies and sightings data suggest that habitat differences between Dall's porpoise and the other two species may be more pronounced than the distinctions between northern right whale dolphin and Pacific white-sided dolphin. Dall's porpoise consume somewhat different prey than the other two species, principally a different suite of Myctophid fish species (Crawford 1981, Walker and Jones 1993). Furthermore, they are seldom seen in association with either of the other two species. Conversely, the northern right whale dolphin and Pacific white-sided dolphin consume nearly identical prey, and both species are commonly observed in mixed schools (Leatherwood *et al.* 1984, Leatherwood and Walker 1979, Leatherwood *et al.* 1982).

The techniques for exploring species/habitat relationships have only recently been applied to marine mammals. The multivariate ordination techniques developed for analyses of plant communities known as Canonical Correspondence Analysis (CCA) (ter Braak 1986) formed the basis for these investigations. Reilly and Fiedler (1994) used sighting survey abundance data and oceanographic observations to compare habitat preferences among dolphin species in the Eastern Tropical Pacific. More recently, the same approach has been used to explore cetacean habitat partitioning in the California Current (Reilly *et al.* 1997), and in the Western Tropical Indian Ocean (Ballance *et al.* 1997).

This study, though similar to the previous research, differs in three ways. First, rather than using sightings data, mortality data (incidental kills in high seas driftnets) were used as the measure of relative abundance. Second, the results of life history investigations on each of the three marine mammal species are used to differentiate population components based on sex and reproductive status. By doing this, expressions of habitat preference both between and within species are explored. Third, a separate set of analyses based on a modification of the conventional multivariate ordination approach was used to examine community association patterns. All analyses are exploratory in nature, and intended to detect potential species/habitat relationships which can then provide a basis for future study.

METHODS

Scientific observers stationed onboard Japanese squid driftnet vessels during 1990 and 1991 were trained to collect a standardized suite of data on each driftnet operation monitored (Fitzgerald *et al.* 1993). The data elements included spatial and temporal reference points for the beginning and ending of sets and retrievals, the amount of gear fished, target species and bycatch tallies, and simple oceanographic and environmental measures: sea surface temperature (SST), wind speed (Beaufort stage), wind direction, and swell height.

From June 1 to September 30, 1990 and 1991, 1,019 driftnet operations monitored by observers in the central North Pacific Ocean from 36°N and 46°N, and 170°E and 149°W resulted in catches of northern right whale dolphin, Pacific white-sided dolphin or Dall's porpoise. Northern right whale dolphins were most frequently caught, followed by Pacific white-sided dolphin and Dall's porpoise (Table 10).

Biological data and specimen materials were collected from all marine mammals entangled and brought onboard dead. All entangled animals, still alive when brought onboard, were released immediately. Species identification, total length and sex were recorded for each specimen. Biological specimens including reproductive organs were also collected in cases where the observer had been specially trained and assigned marine mammal necropsy duties. Collection protocols, and laboratory examination of reproductive samples for determination of sexual maturity status followed procedures in Perrin *et al.* (1976) and Ferrero and Walker (1993).

The composition of the pelagic communities represented by the catches in driftnet sets were related to habitat conditions using CCA. The CCA routine included in the computer program CANOCO version 3.1 (ter Braak 1988) was used in all analyses. The CCA model and algorithm documentation are detailed in ter Braak (1986) and Reilly and Fiedler (1994) summarized the technique in their application with marine mammals. In general, CCA extracts orthogonal axes of variation in indices of abundance for multiple species collected at multiple locations. For the present case, each gillnet operation where at least one northern right whale dolphin, Pacific white-sided dolphin or Dall's porpoise was caught was considered one sampling unit. Differences in the amount of gear set per operation were compensated for by expressing all abundance measures as catch per unit effort (CPUE):

$$\mathrm{CPUE} = (C_{x,y}/T_y)^{*}\ 1000$$

where C_x is the total catch of species x in set y and T_y is the total number of tans of net fished in set y (a tan is equal to a 50 m long by 12 m deep panel of gillnet). Since each gillnet operation employed approximately 60 km of gillnet, this distance set the lower limit on the scale of environmental features that could be described in the study.

"Species" in the Data Sets

Using the available life history information, both inter- and intraspecific species-environmental relationships were examined. For each of the three species, sex and sexual maturity status were incorporated by classifying each specimen into one of four groups (male or female x sexually mature or immature). A neonatal category was also included since it partitioned calf and adolescent life stages. Thus, a total of 15 "species categories" based on three taxa, two sexes and three within-taxa life stages were used.

Where reproductive organs had been collected, the results of laboratory examinations of gonadal tissues determined sub-taxa category placement.

However, in order to include as many cases where both marine mammal catch and associated environmental and bycatch data were available, specimens with known species identification, length and sex were also classified. For these cases, species and sex specific estimates of average length at sexual maturity (LSM) were used as the grouping criteria. To reduce classification error, specimens with lengths +/- 5 cm of LSM were not included although less than 5% of all length measurements fell in this interval. The calculation of LSM is detailed in Chapter 1. The LSM estimates for northern right whale dolphin, Pacific white-sided dolphin and Dall's porpoise were based on estimates from Chapters 1, 2 and 3, respectively.

Research Design

The overall study was organized into two separate sets of CCA runs. One focused on physical factors driving observed distribution patterns; this was analogous to the analytical approach presented in the studies previously noted. The second set used bycatch data in place of the environmental variables to explore the role of other species presence in explaining the small cetacean abundance patterns. Here, the primary objective was to identify the strongest species/bycatch relationships and to compare them both within and among taxa.

Each of the two analytical approaches incorporated five separate ordinations, one overall, including all available data, and one for each month, June to September. In the overall runs, the original 15 species categories (3 species x 5 sub-taxa categories) were coded by month so that a total of 60 new species categories were created. This allowed identification of the strongest relationships encountered season-wide, taking into account possible differences in time (or because of fisheries movements, its covariate, latitude). Less dominant, but perhaps relevant relationships, both among and within species, were addressed in the separate monthly runs.

The monthly stratification was based on shifts in the fishing area which occurred in response to regulatory openings or closings effective the first day of each month (Yatsu *et al.* 1993) (Fig. 62). The corresponding capture locations mirrored the monthly redistribution of the fishing fleets (Fig. 63). The movement of sampling area across months was considered as an opportunity to detect differences in species habitat use and community association patterns in the context of these known spatial and temporal gradients.

Environmental Gradient Runs

The first set of CCA runs was designed to identify gradients in the physical environment as the basis for comparing habitat use patterns among and within marine mammal taxa. Here, the species matrix for CANOCO consisted of the CPUE for each of the species categories by driftnet operation (the "sample" unit). The environmental matrix contained the values for each of the nine environmental variables, by driftnet operation.

To examine the relative isolation or overlap of species locations in ordination space, the tolerance values provided by CANOCO were used to generate a matrix of all pair-wise species comparisons. Tolerance was conceived as a measure of niche width (ter Braak 1988). The tolerance values were used to measure habitat overlap (HO) between all possible pair-wise species categories in the algorithm

$$HO=EXP((x_1-x_2)^2/(tx_1^2+tx_2^2)+(y_1-y_2)^2/(ty_1^2+ty_2^2))$$

where x_1 and x_2 were the Axis 1 eigenvalues for species 1 and 2, y_1 and y_2 were the Axis 2 eigenvalues for species 1 and 2, tx_1 and tx_2 were the Axis 1 tolerance values for species 1 and 2, ty_1 and ty_2 were the Axis 2 tolerance values for species 1 and 2. Overlap values ranged from 0 to 1.0, with strong partitioning indicated by values approaching zero.

Environmental Variables

Ideally, the environmental variables included in the CCA should reflect the most characteristic habitat features influencing community structure (ter Braak 1986). While the best set of environmental variables to describe the small cetacean habitats in this study were unknown, Reilly and Fiedler (1994) used six fundamental oceanographic parameters to describe habitat characteristics at regularly located sampling stations. Unfortunately, similar oceanographic data collected on research vessels in the central North Pacific in 1990 and 1991 were insufficient to reflect prevailing conditions associated with particular driftnet operations at compatible spatial and temporal scales. Instead, the observers' records, specific to each fishing operation, were used to define environmental parameters.

1) Sea surface temperature (SST)

Sea surface temperature was recorded directly by observers from the ship's thermograph at the beginning and end of each retrieval operation. The mean value was used if readings were different. The sensors were generally located near the ship's keel, at a depth of about 3 - 4 m.

2) Delta SST

Delta sea surface temperature was the difference in the temperature readings from one end of the net to the other. A large difference in sea surface temperature across the 60 km (maximum) net (e.g., >5.0°C) was considered an indication that the net crossed an oceanographic front.

3) Current Speed

The current speed was calculated using the starting and ending times and positions of a chosen buoy marking a net end. The drift of that particular bouy was assumed to represent the general speed of the water mass containing the net.

4) Current Direction

Current direction was broken into two components (east/west and north/south) because the non-linear measurement from 0 to 359 degrees would represent a confounded gradient in the CCA (i.e., both ends of the scale, 0 and 359 degrees represented virtually the same wind direction). Instead, since the mean current direction in the study area was eastward, corresponding to the dominant flow of the North Pacific Current (Pickard and Emery 1991), variations from this norm, suggesting possible eddies or counter-currents, were considered potentially important habitat features. The east/west aspect was calculated as the cosine of the angular direction. Strong deviation from an easterly flow would suggest a counter-current. The north/south aspect was characterized, without regard to direction, as the absolute value of the sine of angular direction. This approach assumed that currents flowing northward rated the same importance as currents flowing southward as habitat features.

5) Wind Velocity

Wind velocity was recorded by observers on the Beaufort scale at the beginning of the net retrieval operation and up to 4 additional times thereafter. When conditions changed during the operation, an average value, rounded to the nearest whole number, was used. Higher wind velocities were considered indicative of local storm activity which could give rise to greater surface mixing.

6) Wind Direction

Wind direction was broken into north/south and east/west components following the same logic described for current direction. The prevailing winds in the study area were from the west, so that winds from the north, south or east deviating from the norm, were considered possible stimuli for enhanced surface mixing. Like current direction, the east/west aspect was calculated as the cosine of the angular direction and the north/south aspect as the absolute value of the sine.

7) Swell Height

Swell height was estimated directly by observers and recorded as distance from trough to crest. It provided an index to storm activity beyond the local area and up to several days earlier. Its local effect would have been an increase in surface mixing.

These definitions resulted in nine environmental parameters (including both the north/south and east/west aspects of numbers 4 and 6) that could be quantified and included in all CCA runs. Although several were all considered potential causes of enhanced surface mixing and higher productivity levels, they were treated as separate parameters to explore possible differences in their relative importance.

Community Association Runs

The second set of analyses focused on association patterns between the marine mammals and other marine organisms caught in the driftnets, including fish, cephalopods, marine birds, sea turtles and other marine mammals. The species composition of the sample was restricted to those species susceptible to entanglement in surface nets (15 m deep), in mesh sizes no less than 120 mm; thus, only a portion of the community could be sampled (Table 11).

The design of the species matrix for the community association runs was identical to the previous analysis. The environmental matrix, however, contained the CPUE of all bycatch, by species, by driftnet operation. The CPUE of the bycatch species differed by one or more orders of magnitude, therefore, the values were log transformed prior to the analysis. The nine environmental variables were not used. Overlap or partitioning between species on the basis of these associations complemented interpretation of the ordinations based on directly measured environmental gradients.

Identification of associations was based on comparison of bycatch vector magnitudes and species category eigenvalues. First, the bycatch species represented by the longest (i.e., most influential) vectors were identified (generally including 20-30% of all vectors plotted). Next the species categories located within a 10° angle centered on each of those vectors were determined. Then, the species categories farthest from the origin along the bycatch vector were considered to be most associated with it. In other words, the focus was on the most obvious cases of association, defined by greatest species/vector correlations along the most dominant gradients. Species tolerance values were not used in these runs.

RESULTS

Environmental Gradient Runs

Overall Run

The CCA run including all species categories present in all months indicated nearly 62% of the variance in the species-environmental relation was explained by the first two axes (Fig. 64). The first axis, explaining 50.9 % of the variance, was significantly correlated with SST ($r=0.9555$, $P<0.05$). All correlations reported hence forth were also significant with $P<0.05$. The second axis, explaining an additional 11.0% of the variance, was most strongly correlated with current velocity ($r=0.6710$) and north/south deviations in wind direction ($r=0.5346$). Axes 3 and 4 contributed 10.9% and 7.3%, respectively, to the variance explained, but species eigenvalues were grouped near the origin of axis 3 and 4 plots. Interpretation of Axis 3 and 4 explanatory value, therefore, was unclear, and scores beyond the first two canonical axes were not considered further.

The species scores loaded along Axis 1 in monthly clumps, with the most positive values associated with June and becoming progressively smaller with time; September values were all negative. Within each monthly group, the three species of small cetaceans appeared in a consistent order, with northern right whale dolphin tending toward the right (higher eigenvalues correlated with higher SSTs), Dall's porpoise tending left, and Pacific white-sided dolphin situated in between. Dispersion of Axis 2 scores did not suggest strong species preferences along any particular gradient. Intraspecies comparisons were not addressed in lieu of the better resolution possible via separate monthly ordinations.

June

During June, over 95% of the 143 fishing operations sampled were made between 38°N and 40°N (Fig. 62). The analysis included all species categories except immature and neonatal Dall's porpoise for which the sample sizes were zero. The variance explained by Axis 1 and Axis 2 was 31.5% and 22.1%, respectively. Axis 1 showed a strong negative correlation with SST (r=-0.7452). Each of the three categories of Dall's porpoise occupied positive Axis 1 eigenvalues, indicating their preference for cooler waters (Fig. 65). The mature female Dall's porpoise occupied the most extreme (cold) position along the SST gradient. The opposite side of the SST gradient, corresponding to warmer waters, was populated by all categories of northern right whale dolphin. Pacific white-sided dolphins loaded between the other two species, suggesting a broader range of SST preferences including both the upper extreme for Dall's porpoise and lower extreme for northern right whale dolphin.

Axis 2 was most strongly correlated with Beaufort (r=0.5815) and north/south deviations in wind direction (r=0.4114). Northern right whale dolphin eigenvalues were all positive. With the exception of mature females, all Pacific white-sided dolphin eigenvalues were negative. The species tolerance values indicated no cases of complete habitat partitioning between them along either axis. No cases of intraspecific partitioning occurred either.

All Dall's porpoise categories were partitioned from at least two other species categories on the opposite side of the SST gradient. The mature classes of Dall's porpoise were the most isolated. In addition, the mature female Dall's porpoise were completely partitioned from all other categories along Axis 2, suggesting they were sampled in calmer sea conditions in areas with prevailing westerly winds compared to other categories.

July

In July, the fishery moved northward to a band extending 41°N - 43°N east of 170°W and 41°N - 42°N west of 170° W. Of the 384 operations sampled, only 6 occurred in areas fished the previous month (Fig. 62). All species categories were present.

The first and second canonical axes explained 46.7% and 13.8% of the variance in the species-environment relation. As in June, the dominant environmental gradient was SST, negatively correlated with Axis 1 (r=-9588)

(Fig. 66). Axis 2 was positively correlated with Beaufort (r=0.5821) and swell height (r=0.5581), but negatively correlated with north/south deviations in wind direction (r=-0.4969).

The order of species positions along the SST gradient was consistent with the June analysis (Fig. 65), although the degree of overlap in preferred habitat between Dall's porpoise and Pacific white-sided dolphin was more pronounced in July. Conversely, northern right whale dolphin categories were more removed from the Pacific white-sided dolphins; the former scoring all negative eigenvalues and the latter all positive values. The neonatal northern right whale dolphin category occupied the extreme position on the SST gradient, in the warmest waters sampled that month.

Along Axis 2, Pacific white-sided dolphin scored only positive eigenvalues while northern right whale dolphins and Dall's porpoise scored predominantly negative eigenvalues. The Pacific white-sided dolphin appeared to prefer more extreme wind and swell conditions which were not the result of local storm systems.

Accounting for species tolerance scores, neonatal northern right whale dolphins were completely partitioned from immature Dall's porpoise (both sexes) and immature female Pacific white-sided dolphins. No other cases of complete partitioning were noted this month.

August

In August, the fishery reached its northern limit, extending to 46°N east of 170°W, and to 45°N west of 170°W (Fig. 62). Only three of the 273 operations were conducted in the area fished during July. All species categories except neonatal Dall's porpoise were contained in the sample.

The first two canonical axes explained 49.4% and 15.9% of the variance in the species-environment relation. Axis 1 was highly correlated with positive values of SST (r=0.8679), while Axis 2 was negatively correlated with swell height (r=-0.7666) and Beaufort (r=-0.6845) (Fig. 67). Once again, all categories of northern right whale dolphin were located in the higher range of SST values, while Dall's porpoise and Pacific white-sided dolphins co-occurred in a moderate to lower range of sea surface temperatures. Along Axis 2, neonatal and mature female Pacific white-sided dolphins occupied the most extreme locations representing the lowest Beaufort and swell conditions observed during the month.

Unlike either June (Fig. 65) or July (Fig. 66), the August ordination showed a high degree of habitat partitioning, both inter- and intra-species, when tolerance values were considered. In fact, 5 species categories (immature and neonatal northern right whale dolphins, neonatal and mature female Pacific white-sided dolphins, and immature female Dall's porpoise) were completely partitioned from each other and all other categories.

September

In September, the fishery shifted to the west in response to opening of the area between 45°N and 46°N west of 170°W, and to the southwest as vessels began moving toward home ports in Japan. Of the 140 operations sampled, over 75% occurred in areas not fished in August, and over 50% were south of 44°N (Fig. 62). All species categories except neonatal Dall's porpoise were encountered.

The first two canonical axes explained 30.1% and 22.7% of the variance in the species-environment relation, respectively. Consistent with earlier months, SST was the dominant gradient, strongly correlated with Axis 1 (r=0.7435). Axis 2 was correlated with swell height (r=0.5346), deviations in wind direction (r=0.5334), and Beaufort (r=0.4106) (Fig. 68).

The pattern of species loading along Axis 1 in the September ordination was similar to the previous months, with northern right whale dolphin occupying the warmest waters, Dall's porpoise in the coolest and Pacific white-sided dolphin in between. The intermixing of Pacific white-sided dolphin and Dall's porpoise categories was more similar to the July and August runs than to June, with members of both species (immature female Dall's porpoise and mature female Pacific white-sided dolphins) selecting particularly cool waters.

The distribution of eigenvalues along Axis 2 placed females and neonates of all species in the positive range of values, and nearly all males in the negative range. However, despite these tendencies, no cases of complete habitat partitioning were expressed in the species tolerance scores.

Community Association Patterns

Overall Run

The variance explained in the species environment relationship in the overall community association CCA was low in comparison to the runs in the first series; 15.8% for Axis 1 and 12.9% for Axis 2. The lack of a dominant gradient corresponding to either axis reflected the plurality of associations possible given the number of marine mammal categories and bycatch species being compared. Identification of more specific relationships was reserved for the separate monthly analyses (Fig 69). However, the relative strengths of all possible associations taken together were identifiable.

In addition, the impact of the temporal component of the sampling regime was reflected in the grouping of species categories by month. Using a clock analogy, June categories loaded between 1 and 3 o'clock, July between 4 and 8, August between 8 and 10, and September between 10 and 1 (Fig. 69). The strongest overall associations occurred in June and involved yellowtail (*Seriola lalandi*) and blue shark (*Prionace glauca)* with northern right whale dolphin and Pacific white-sided dolphin. Dall's porpoise associations in June, by comparison, were weaker and less focused on any particular bycatch species.

The July categories were more dispersed, with northern right whale dolphin focused in one tight group, and Dall's porpoise and Pacific white-sided dolphin loosely positioned in another. The Dall's porpoise associations with salmon shark (*Lamna ditropis*) and coho salmon (*Oncorhynchus kisutch*) were most apparent. Pacific white-sided dolphin may also have shared this association, but their positions closer to the origin suggested a less compelling case. Northern right whale dolphin was most closely associated with Louvar (*Luvarus imperialis*) in July.

The August categories were tightly grouped (except for mature male P. dalli) along the sooty shearwater (*Puffinus griseus*) and Pacific pomfret (*Brama japonica*) vectors, with Pacific white-sided dolphin and Dall's porpoise species categories showing the stronger associations with them.

The positions of the September categories reflected possible intraspecific differences in community association patterns where the mature female Pacific white-sided dolphin were closely aligned with Pacific saury (*Cololabis saira*) and skipjack tuna (*Katsuwonus pelamis*) but none of the other Pacific white-sided dolphin constituents expressed that association. Northern right whale dolphin appeared in association with Pacific saury and skipjack tuna, and perhaps Japanese butterfish (*Hyperoglphes japonica*).

June

The June analysis provided considerably better resolution in the community association patterns both within and between species compared to the overall ordination. The variance in the species-environment relation explained by Axes 1 and 2 was slightly higher than in the overall ordination, 19.2% and 16.1%, respectively.

As in the overall ordination, mature female northern right whale dolphins were closely associated with yellowtail and blue shark, but their conspecifics were not (Fig. 70). Instead, the immature male and female northern right whale dolphins were more closely aligned with leatherback turtle (*Dermochelys coriacea*) and black-footed albatross (*Diomedea nigripes*), while mature males showed no pronounced appearance with any particular bycatch species. Pacific white-sided dolphin constituents occupied the middle ground between northern right whale dolphin and Dall's porpoise with pelagic armorhead (*Pseudopentaceros wheeleri*) and Pacific pomfret representing the more important bycatch associates, at least for the female components. Mature male Pacific white-sided dolphin were associated with northern bluefin tuna (*Thunnus thynnus*).

Dall's porpoise loaded along the strongest gradients encountered, those representing the coho and chum salmon (*Oncorhynchus keta*), salmon shark, Pacific saury and sooty shearwater. The placement of the Dall's porpoise eigenvalues well away from the origin along these gradients suggested that they also represented the strongest associations encountered for the month.

July

The variance explained in the July species-environment relation by axes 1 and 2 was higher than the previous two runs, 28.3% and 14.1%, respectively. The association patterns were slightly different than the previous month, although several characteristics persisted. Each of the three small cetacean species appeared in discrete clusters, with northern right whale dolphin constituents loaded most closely together (Fig. 71). At the species level, northern right whale dolphins associated with a wider variety of species than previously encountered. These included albacore tuna (*Thunnus alalunga*), yellowtail, blue shark, northern bluefin tuna, daggertooth (*Anotopterus pharao*) and Louvar. As in June, the mature female northern right whale dolphins were associated with yellowtail and blue shark, although albacore tuna became the dominant bycatch associate for both the mature males and females. The immature northern right whale dolphin constituents were aligned with blue shark, northern bluefin tuna and Louvar.

All categories of Pacific white-sided dolphins appeared more or less equally associated with sooty shearwater, common thresher shark (*Alopias vulpinus*) and medusa fish (*Icychtys lockingtoni*).

The Dall's porpoise constituents showed the greatest dispersion in ordination space, and reflected the greatest intraspecies differences as well. Both mature and immature males were strongly associated with chum and coho salmon, steelhead (*Oncorhynchus mykiss*) and northern fur seal

(*Callorhinus ursinus*). Mature females were more closely aligned with salmon shark. The small sample of neonates appeared strongly associated with eight armed squid (*Gonotopsis borealis*) and boreal clubhook squid (*Onychoteuthis borealijaponica*). Spiny dogfish (*Squalus acanthias*) and Pacific pomfret were also included in association with Dall's porpoise at the species level.

August

In August, the variance explained in the species-environment relation by Axes 1 and 2 was 21.1% and 17.1%, respectively. As in July, northern right whale dolphin constituents formed a tight group compared to the other two species, within which mature females were slightly separated (Fig. 72). The mature females were associated with blue shark, albacore tuna and longnose lancetfish (*Alepisaurus ferox*), while the other northern right whale dolphins aligned with ocean sunfish (*Mola mola*), Pacific pomfret, common thresher shark and pale-footed shearwater (*Puffinus carneipes*). By comparison, Pacific white-sided dolphin eigenvalues were more dispersed, with the mature female and neonatal components loading very close to the origin, expressing little association with any particular bycatch species. The remaining Pacific white-sided dolphin constituents were associated most strongly with northern fur seal, chum salmon, ragfish (*Icosteus aenigmaticus*) and Buller's shearwater (*Puffinus bulleri*). Among the Dall's porpoise categories, the mature males exhibited the strongest association of the period with short-tailed shearwater and Japanese anchovy. The female and immature male Dall's porpoise were associated with salmon shark and boreal clubhook squid.

September

The variance explained in the September species-environment relation by Axes 1 and 2 was 20.4% and 14.6%, respectively. The degree of eigenvalue dispersion within species groups was the greatest of any month examined (Fig. 73). Likewise, the degree of subtaxa category overlap between species was greater than previously observed. Among the northern right whale dolphin constituents, the neonatal component was associated with several species, including albacore tuna, swordfish (*Xiphias gladius*), striped marlin (*Tetrapturus audax*), spiny dogfish, and pelagic stingray (*Dasyatis violacea*). Female northern right whale dolphins were allied with skipjack tuna, blue shark and Japanese butterfish, while the mature males, like the mature male Dall's porpoise, were more closely associated with ragfish, Laysan Albatross (*Diomedea immutabilis*), ocean sunfish and Louvar. The remaining categories of Dall's porpoise and mature male Pacific white-sided dolphin were found with steelhead and longnose lancetfish. The Pacific white-sided dolphins, other than mature males, associated with northern fur seal, pelagic armorhead, skilfish (*Erilepis zonifer*) and salmon shark.

DISCUSSION

Canonical correspondence analysis has considerable power to reduce the dimensions of a large multivariate data set with direct application to relationships in the marine environment. The results, however, were noted to be sensitive to the type and quality of input data. For instance, temporal stratification (by month) was necessary to detect patterns otherwise obscured by the most dominant relationships in aggregate ordinations. Partitioning of ordination runs on the basis of recognized distinctions in habitat dimensions was also used by Reilly *et al.* (1997) to examine separately geographic and oceanographic effects on cetacean habitat in the California Current.

In addition, it was necessary to visualize how the data might be interpreted prior to their inclusion in the environmental data set and to adjust them accordingly. In particular, directional data (i.e., wind and current direction) were problematic because they required transformation from circular measure into monotonic gradients of importance to the species. The adjustments were based on the assumption that the most important information contained in the directional data was the magnitude of deviations from the eastward wind driven transport, regardless of whether they were to the north or south. The absolute value of north/south deviations best represented these concerns by placing all cases of large departures on the same end of the gradient.

Another decision faced in developing these analyses was whether to include the other bycatch in the species side of the analysis or to consider them as environmental components. Once again, the choice was based on the intended interpretation. In this study, definition of habitat preferences for non-cetacean species was not of interest, but rather the goal was to explore their associations with marine mammals as though they were features of the marine mammals' environment. Putting the bycatch species into the environmental data matrix of the CCA, in a separate set of ordination runs, therefore, provided a means to identify correlations within the bycatch species specifically as they were related to the marine mammals. In other words, the underlying relationships between the bycatch species and their environment did not affect the location of marine mammal species categories in ordination space.

In terms of explaining variance in the species-environment relation, mortality data compared favorably to studies based on marine mammal sightings (e.g., Reilly and Fiedler 1993). This suggested that the technique may be tried where either of the two more common sources of marine mammal distributional data are available. The mortality data, however, should reflect the relative abundance of subject animals in the study area as has been argued for studies based on pelagic driftnet collections (Ferrero and Walker 1993).

Species-Environment Relationships

Although the driftnet fisheries data available for the multivariate analyses lacked the detail necessary to describe oceanographic habitats in specific technical terms, they were sufficient to represent contrasts in environmental conditions and provide a basis for detecting habitat selection patterns. Differences in habitat selection preferences were suggested both between species and among species constituents. Not surprisingly, the most influential environmental gradient reflected in inter-species placement in ordination space was SST. Yatsu *et al.* (1993) reported temperature related differences in catch per unit effort among several fish and cephalopods caught in the Japanese squid driftnet fishery. Likewise, recent efforts to model the North Pacific transition zone and identify associations among taxa (MBC 1994) incorporated stratification by temperature.

The environmental variables other than SST were included as possible indicators of mesoscale habitat features, namely fronts (DSST), eddies (current speed and direction) and atmospherically induced areas of increased surface mixing. Only minor importance of the first two categories in explaining variance in the species-environment relation was detected, but observed consistency in the correlations between Beaufort and swell height with Axis 2. While this suggests that local mixing of surface waters may be a dominant habitat feature, we note that our ability to characterize the complex features like fronts and eddies was probably very low, and that they may still represent important features. Furthermore, since the direction of drift of nearly all driftnet sets was east/west, the analyses suffered a low probability of detecting latitudinal temperature gradients. For the purposes of these exploratory analyses, therefore, SST and surface layer mixing, regardless of its cause, are suggested to be among the habitat features of relevance to small cetaceans in the area studied.

The monthly habitat preference analyses indicated that some patterns were robust to time and area sampled, while others were more ephemeral. Clearly, the most robust pattern related to SST preference. Northern right whale dolphins consistently occupied the warm water extremes regardless of time or location sampled, while fidelity to cooler waters was characteristic of Dall's porpoise. Pacific white-sided dolphin SST preferences fell in between the other species, but with greater similarity to Dall's porpoise than to northern right whale dolphin.

Finer scale differences in habitat preference were detectable by comparing ordinations across months. In June, sampling occurred at the lowest latitudes included in the analyses. Here, Dall's porpoise were present only in low numbers, and they were well partitioned from those of the other two species in ordination space. It was likely that this area simply represented the southern fringe of Dall's porpoise habitat, but was within the core range the other two species. As the fishery advanced northward in succeeding months, the partitioning of Dall's porpoise disappeared, and the relative isolation of northern right whale dolphin took its place. This pattern contrasted with the apparent close association between northern right whale dolphin and Pacific white-sided dolphin suggested by previously noted anecdotal information.

Just as the isolation of Dall's porpoise in June probably reflected their more limited selection of habitats at the fringe of their range, so too the isolation of northern right whale dolphin in subsequent months may reflect a more southerly distribution and more pronounced selection of habitats at higher latitudes. Alternatively, northern right whale dolphin habitat preferences may relate to their reproductive activity at the time of sampling. Ferrero and Walker (1993) described a distinct calving mode for northern right whale dolphin in July and August, whereas neither of the other two species showed any indications of parturition at that time, in those areas. The northern right whale dolphin neonatal component was well partitioned from the other species in June, and relative to the SST gradient was positioned in the warmest waters. Northern right whale dolphin may, therefore, be selecting habitats in summer that are specific to calving or mating, while the other species are using the area more generally.

Lack of adherence of the northern right whale dolphin mature female and neonatal components across the calving period may be an artifact of the categorization process which only reflected sexual maturity, not reproductive activity. Northern right whale dolphins are not annual breeders, so the mature female category contains both reproductively active and inactive individuals.

One of the greatest contrasts in the monthly ordinations was in the relative isolation of species categories based on species tolerance values in August. A probable explanation for the difference was based on the location of sampling and the diversity of habitats available for selection in those locations. In June and July, the sampling was situated in the North Pacific transition zone, south of the subarctic boundary (Roden 1991, Pearcy 1991). In comparison, by August, the fishery probably crossed into the subarctic water mass where environmental conditions, as described by the available environmental parameters, were much more varied. It is unknown whether the tighter habitat selection patterns observed in August reflected biological phenomena, or were simply the result of having more possible combinations of apparent habitat types over which to distribute the species abundance data. Either way, the fishery retreated to the south and west in September and the degree of habitat sharing returned to levels observed in June and July. Therefore, regardless of the relevance of the selection pattern in August, its contrast to the surrounding months likely demonstrated CCA's ability to at least detect differences in habitat conditions between areas.

Community Associations

The community association analyses suggested patterns that were complementary to the species-environment runs. Like the previous analyses, the most robust marine mammal/other marine organism associations were identifiable. In addition, differences in association patterns between species constituents were detected, suggesting that a significant level of intraspecies segregation may be common to all three species. Like the environmental variables used in the first analyses, the community constituents may not actually define habitat features, but can suggest the places to look for differences in habitat selection both among and within species groups.

At the species level, Dall's porpoise and northern right whale dolphin were associated with nearly distinct marine communities over most of the areas sampled. Northern right whale dolphin were typically found with warm temperate fish species such as yellowtail, blue shark and albacore, while Dall's porpoise associated with the subarctic varieties, including salmon shark, coho and chum salmon, steelhead and Pacific saury. Such partitioning apparently occurred at relatively fine scales, as the juxtaposition of species sampling dates and locations were well mixed during each sampling period. Pacific white-sided dolphin associations included species common to both Dall's porpoise and northern right whale dolphin, but in very few cases did they overlap in the same sampling period. A temporal or spatial element to the community association fidelity, thus, was also implicated.

The greatest consistency in the composition of community associations for any sub-taxon category occurred in the case of mature female northern right whale dolphin and involved blue shark in every month and yellowtail in June and July. Within monthly periods, most other sub-taxon groups also showed differing association tendencies. For instance, the associations involving immature components tended to be distinct from their mature counterparts. This may be considered consistent with observations that immature small cetaceans are more broadly distributed and so may select habitat less specifically than the reproductively active portion of the population. Conversely, mature male northern right whale dolphins shared the same associations with mature females in July and August, but not in September. This behavior was again consistent with the results of life history analyses suggesting that northern right whale dolphin breeding may coincide with the calving period. (Ferrero and Walker 1993). These more fluid association patterns, therefore, also may be useful for detecting seasonal differences in species behavior.

Few previous analyses of community structure in the central North Pacific Ocean have dealt with marine mammals, thus limiting comparisons with our results. McKinnel and Waddell (1993) used Principle Components Analysis to identify groupings of epipelagic taxa caught in Japanese squid driftnets analogous to our community association runs. In the first of two groups identified, northern right whale dolphins were placed with yellowtail, blue shark and albacore among others. Their second group placed both Dall's porpoise and Pacific white-sided dolphin in association with salmon shark, pelagic armorhead, Pacific pomfret and salmonids. While the McKinnel and Waddell (1993) groupings were generally consistent with our findings, finer level distinctions, particularly between Dall's porpoise and Pacific white-sided dolphin were not detected.

Table 10. Numbers of marine mammals, by species, by category, by month included in CCA.

	Month				
Species	June	July	August	September	Total
L. borealis					
Mature males	13	63	35	32	
Immature Males	33	116	65	42	
Mature Females	26	137	94	62	
Immature Females	27	102	49	33	
Neonates	2	9	34	29	
Total	101	427	277	198	1003
L. obliquidens					
Mature males	13	21	22	5	
Immature Males	18	41	45	27	
Mature Females	12	19	23	12	
Immature Females	18	38	50	21	
Neonates	37	46	18	3	
Total	98	165	158	68	489
P. dalli					
Mature males	7	42	17	11	
Immature Males	0	42	20	5	
Mature Females	3	6	15	15	
Immature Females	3	24	27	9	
Neonates	0	3	0	0	
Total	13	117	79	40	249
Grand Total	212	709	514	306	1741

Table 11. Marine organisms caught in pelagic driftnets that were used in the Community Associations aspect of the CCA.

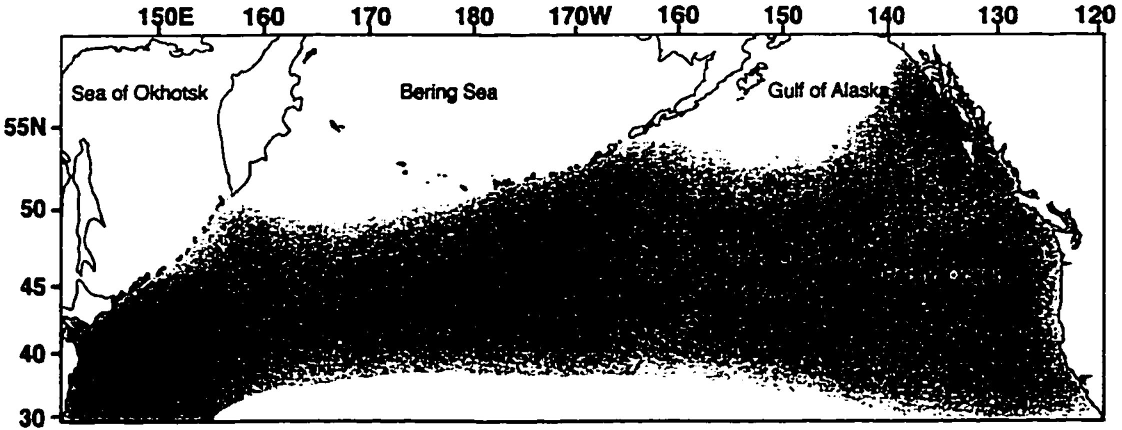
Common Name	Scientific Name
neon flying squid	*Omastrephes bartrami*
8 - armed squid	*Gonatopsis borealis*
boreal clubhook squid	*Onychoteuthis borealijaponica*
purpleback flying squid	*Sthenoteuthis oualaniensis*
chum salmon	*Oncorhynchus keta*
coho salmon	*Oncorhynchus kisutch*
pink salmon	*Oncorhynchus gorbuscha*
steelhead	*Oncorhynchus mykiss*
blue shark	*Prionace glauca*
salmon shark	*Lamna ditropis*
common thresher shark	*Alopias vulpinus*
short-finned mako shark	*Isurus oxyrinchus*
spiny dogfish	*Squalus acanthias*
pelagic stingray	*Dasyatis violacea*
albacore tuna	*Thunnus alalunga*
skipjack tuna	*Katsuwonus pelamis*
northern bluefin tuna	*Thunnus thynnus*
yellowfin tuna	*Thunnus albacares*
swordfish	*Xiphias gladius*
striped marlin	*Tetrapturus audax*
shortnose spearfish	*Tetrapturus angustrirostris*
longnose lancetfish	*Alepisaurus ferox*
daggertooth	*Anotopterus pharao*

Table 11 (cont.)

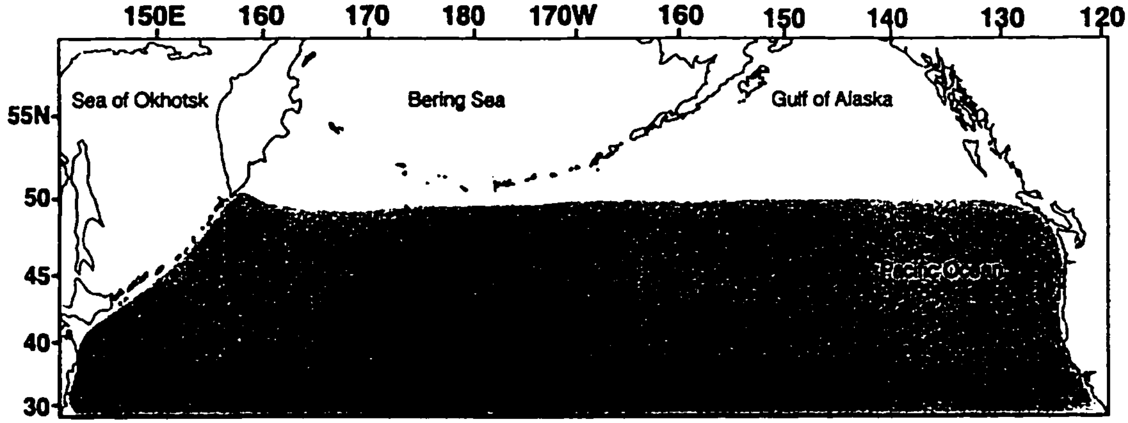
Pacific saury	*Cololabis saira*
opah	*Lampris guttattus*
skilfish	*Erilepis zonifer*
pilotfish	*Naucrates ductor*
yellowtail	*Seriola lalandi*
mahi mahi	*Coryphaena hippurus*
Pacific pomfret	*Brama japonica*
pelagic armorhead	*Pseudopentaceros wheeleri*
oilfish	*Ruvettus pretiosus*
smalleye squaretail	*Tetragonurus cuvieri*
louvar	*Luvarus imperialis*
ragfish	*Icosteus aenigmaticus*
medusafish	*Icychthys lockingtoni*
ocean sunfish	*Mola mola*
blackrag	*Psenes pellucidus*
rough pomfret	*Taractes asper*
Japanese butterfish	*Hyperoglphes japonica*
cigarfish	*Cubiceps squamiceps*
barricudina	*Paralepis atlantica*
Japanese anchovy	*Engraulis japonicus*
Laysan albatross	*Diomedea immutabilis*
black-footed albatross	*Diomedea nigripes*
northern fulmar	*Pterodroma solandri*
pale-footed shearwater	*Puffinus carneipes*
Buller's shearwater	*Puffinus bulleri*

Table 11 (cont.)

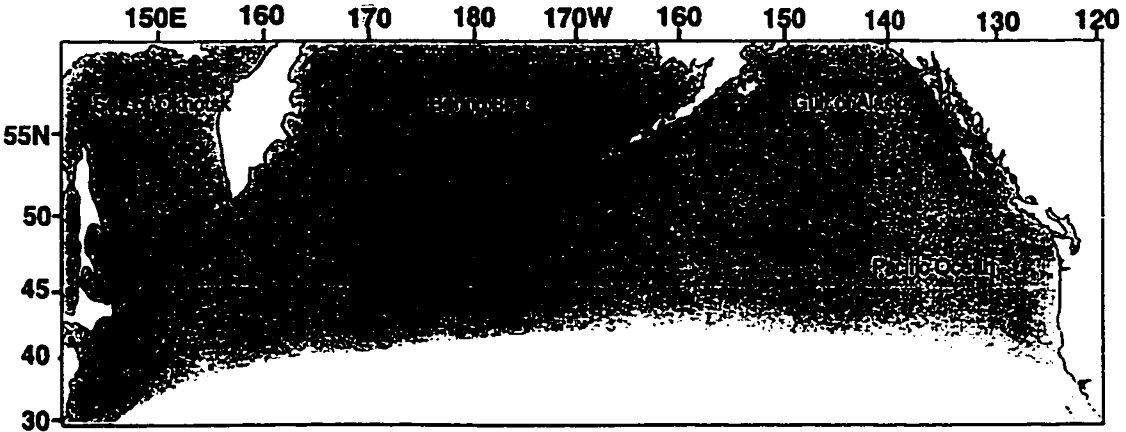
sooty shearwater	*Puffinus griseus*
short-tailed shearwater	*Puffinus tenuirostris*
fork-tailed storm petrel	*Oceanodroma furcata*
horned puffin	*Fratercula corniculata*
northern fur seal	*Callorhinus ursinus*
common dolphin	*Dephinus delphis*
leatherback turtle	*Dermochelys coriacea*



Pacific white-sided dolphin



Northern right whale dolphin



Dall's porpoise

FIGURE 61: Approximate pelagic distributions of Pacific white-sided dolphin, northern right whale dolphin, and Dall's porpoise in the North Pacific Ocean.

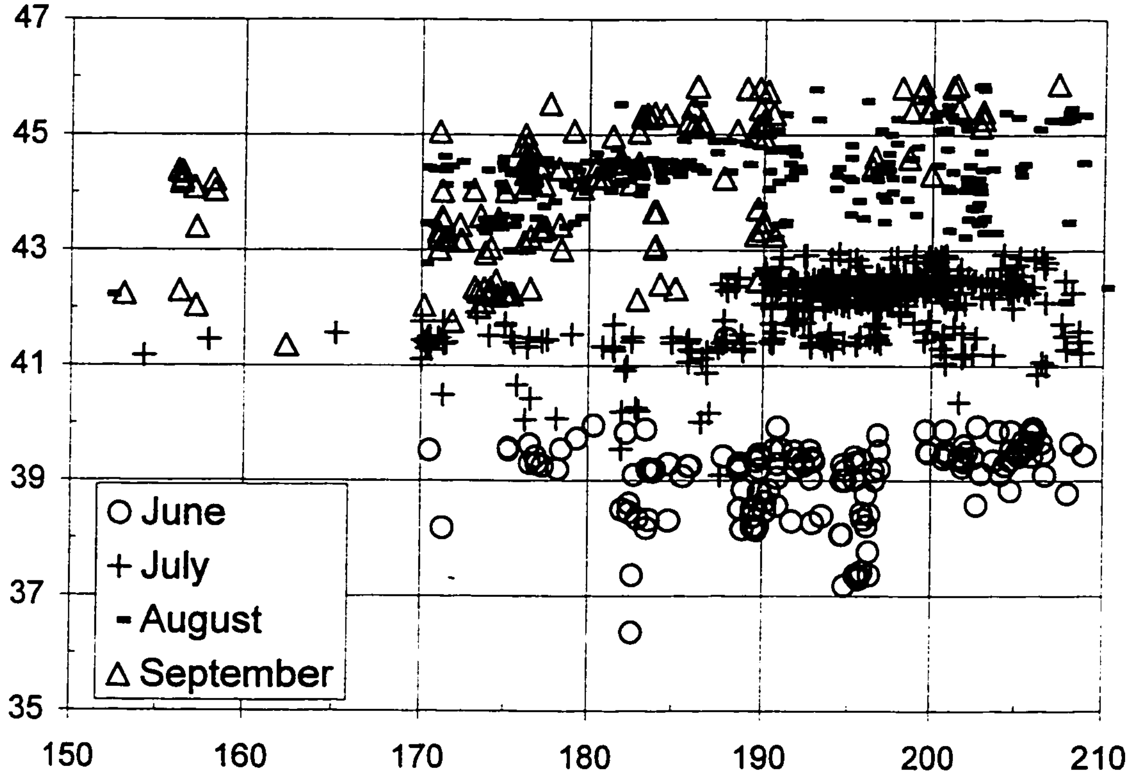


FIGURE 62: Squid driftnet fishing locations, by month, where Dall's porpoise, Pacific white-sided dolphin and northern right whale dolphins were collected.

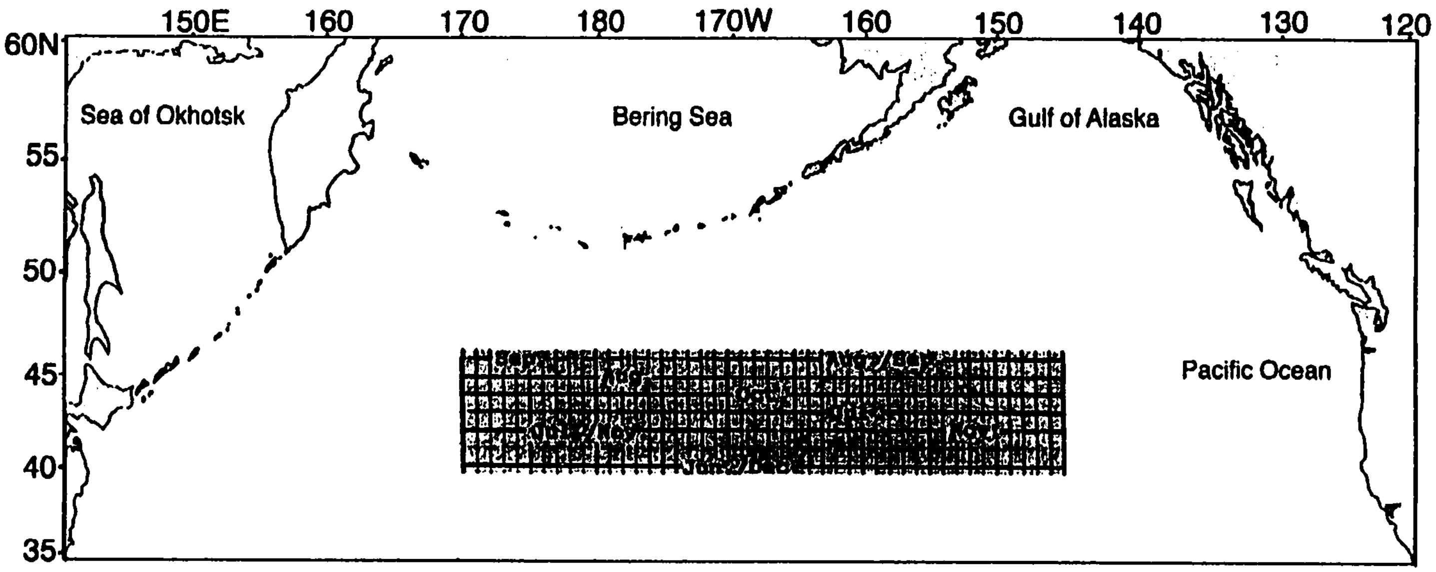


FIGURE 63: Squid driftnet fishing area boundaries showing northward progression of the fishing area across the summer months.

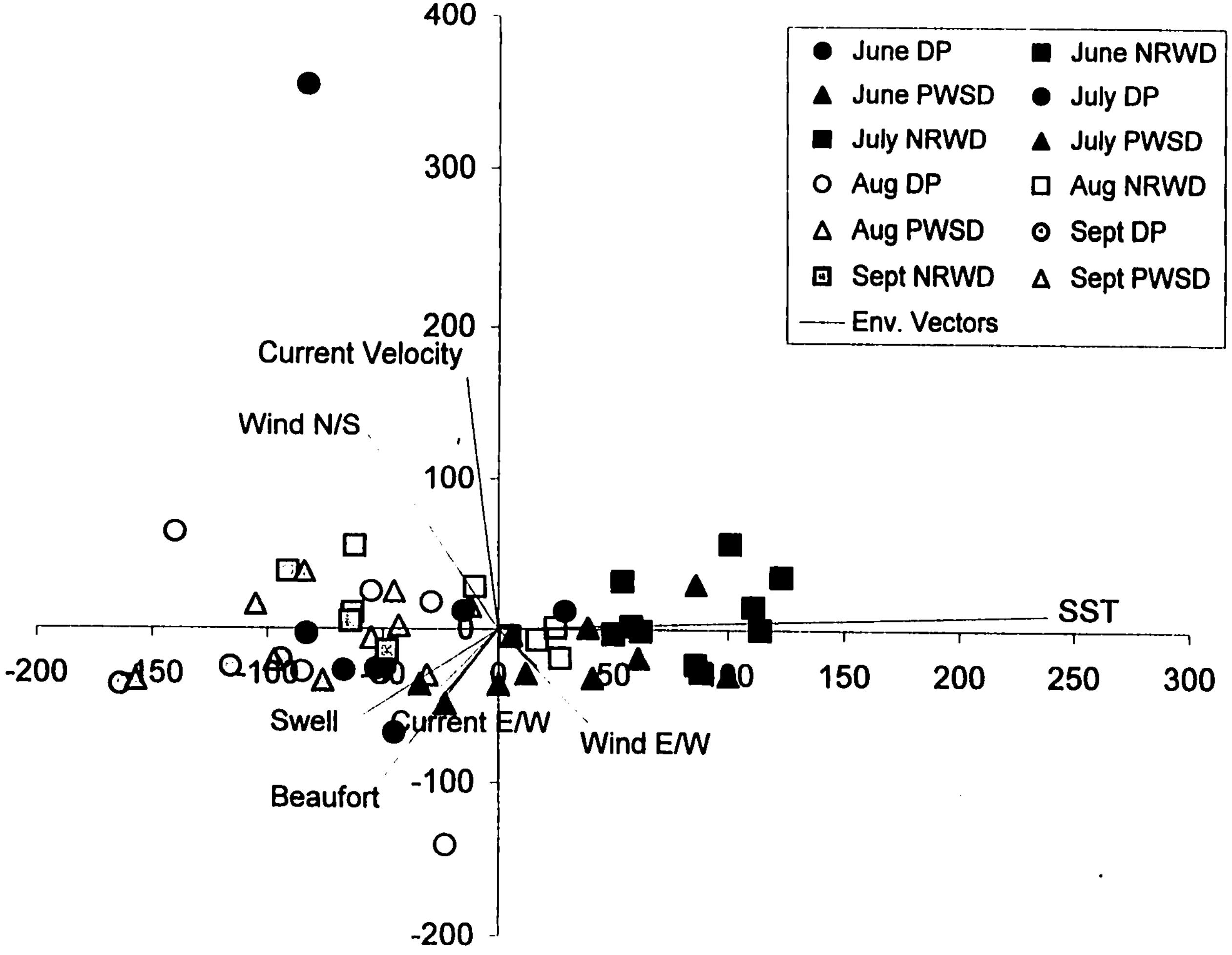


FIGURE 64: Ordination diagram for the overall environmental gradient run based on CCA. The abbreviations DP, NRWD and PWSD stand for Dall's porpoise, northern right whale dolphin and Pacific white-sided dolphin, respectively.

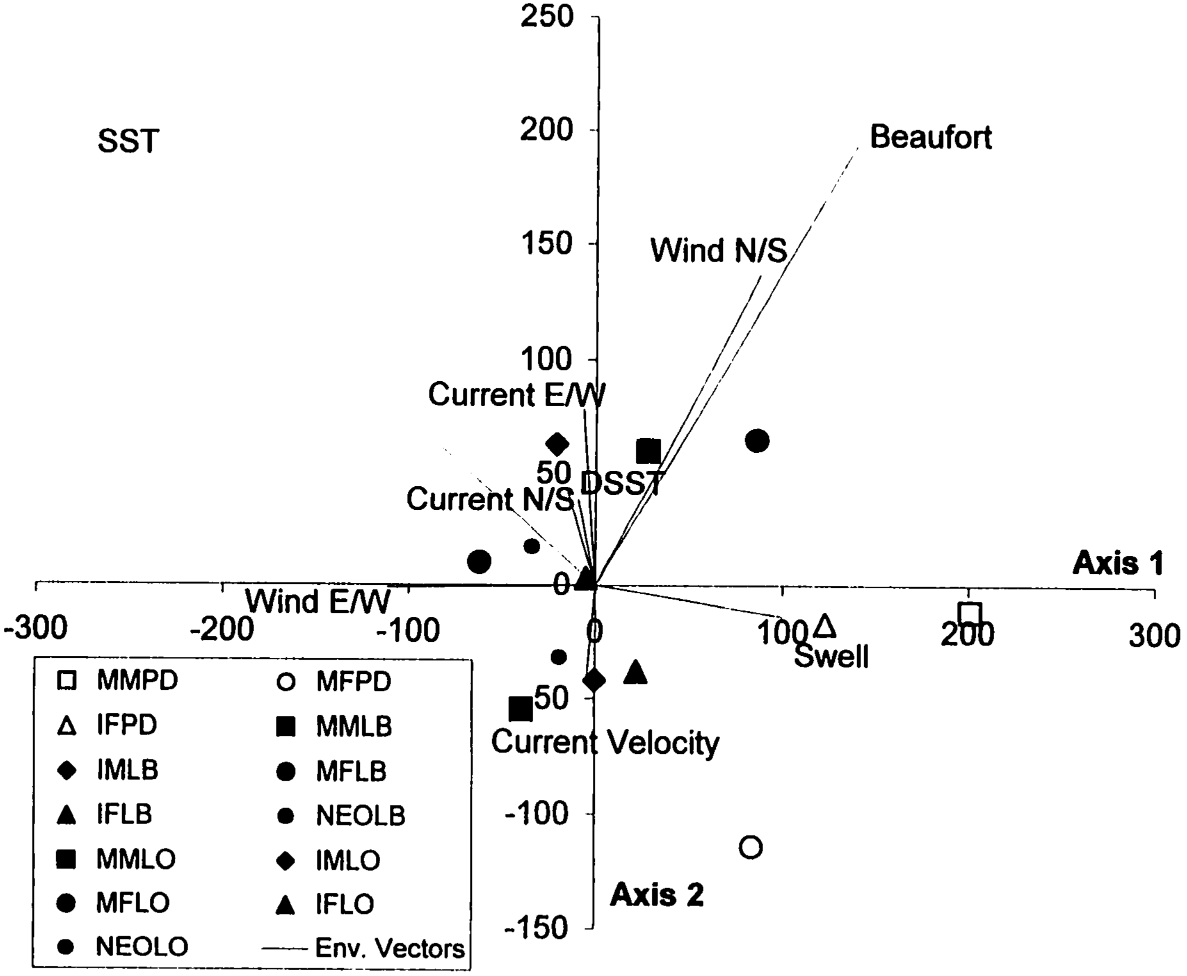


FIGURE 65: Ordination diagram for the June environmental gradient run based on CCA. The abbreviations DP, NRWD and PWSD stand for Dall's porpoise, northern right whale dolphin and Pacific white-sided dolphin, respectively.

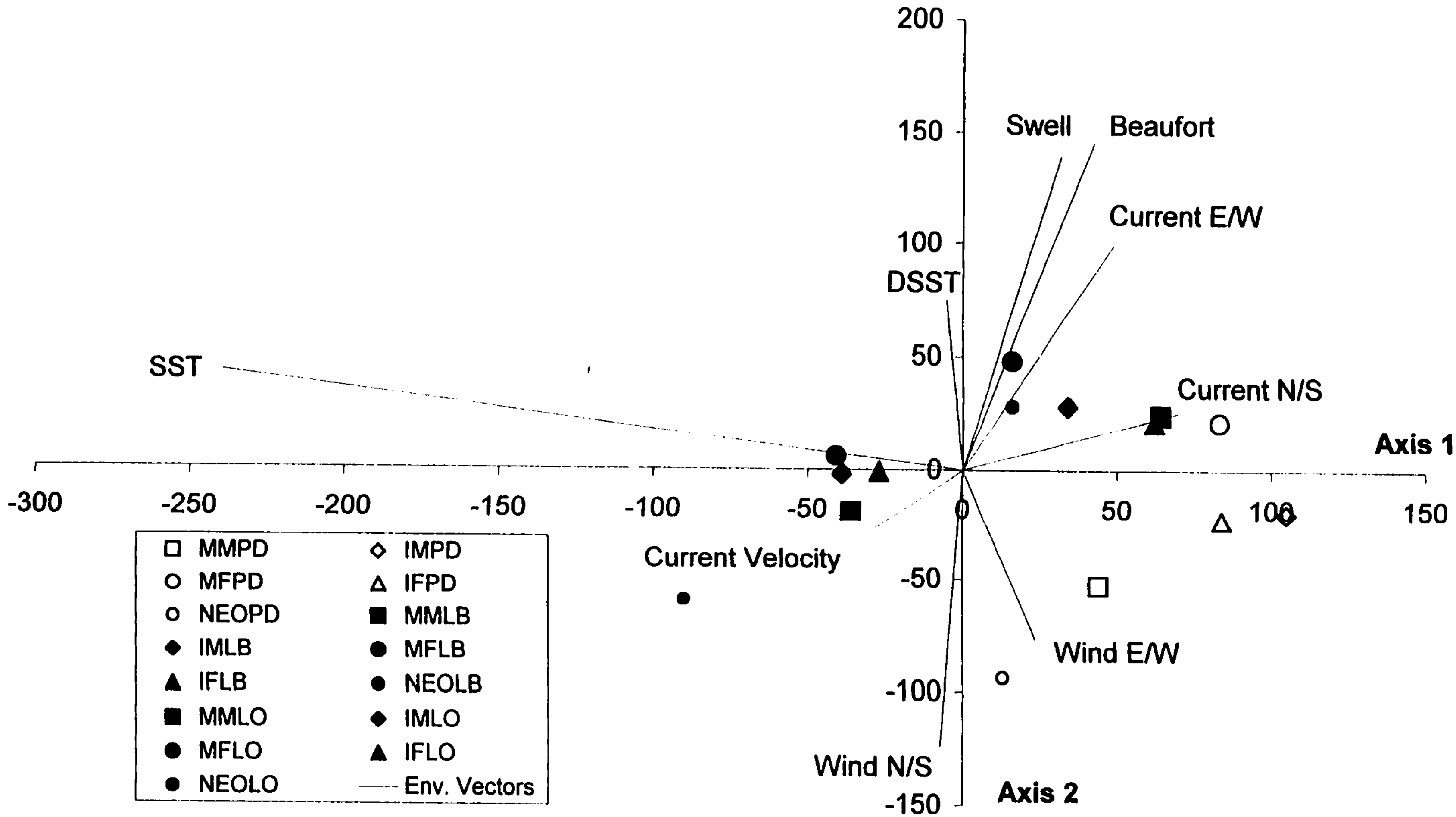


FIGURE 66: Ordination diagram for the July environmental gradient run based on CCA. The abbreviations DP, NRWD and PWSD stand for Dall's porpoise, northern right whale dolphin and Pacific white-sided dolphin, respectively.

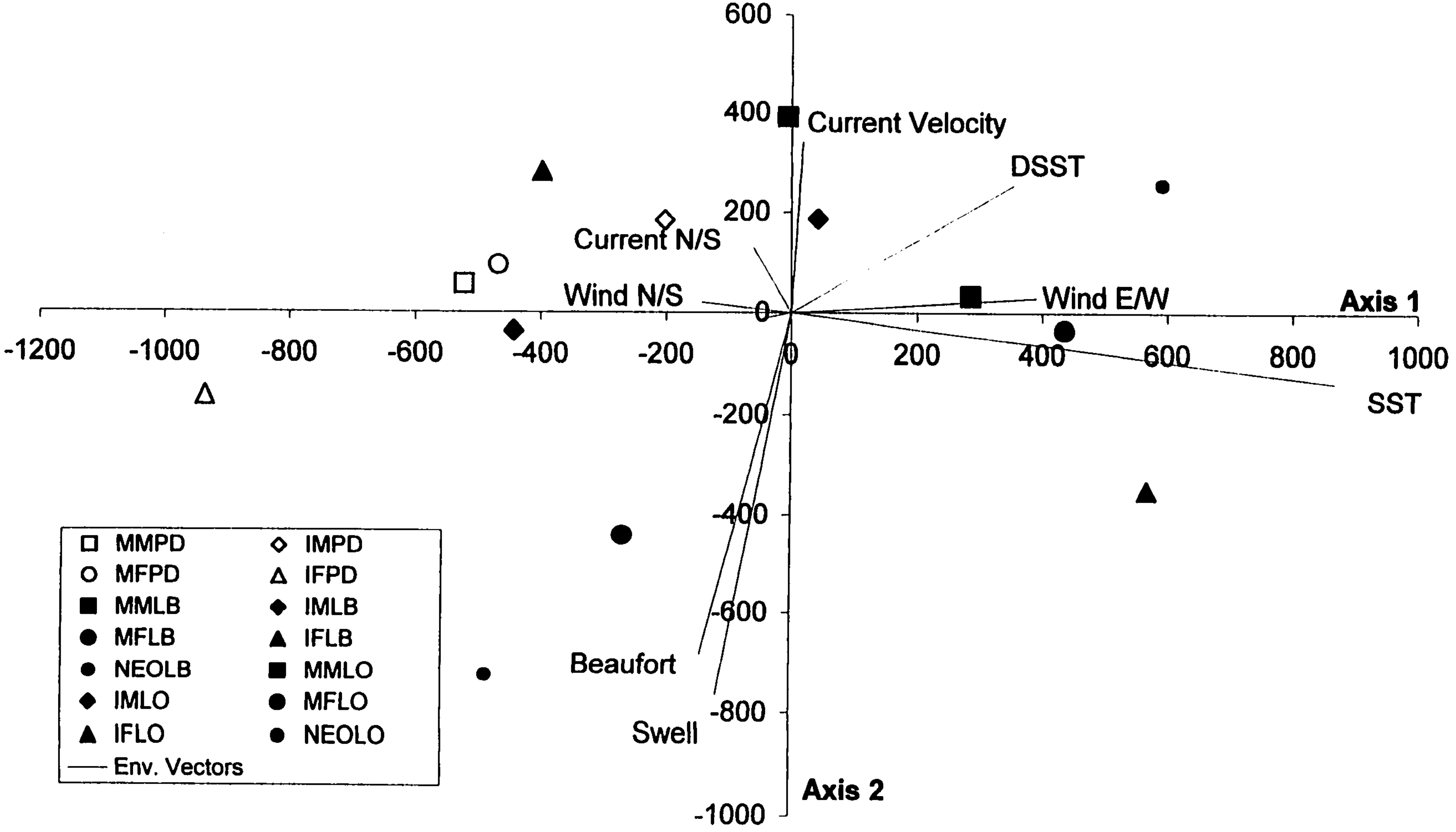


FIGURE 67: Ordination diagram for the August environmental gradient run based on CCA. The abbreviations DP, NRWD and PWSD stand for Dall's porpoise, northern right whale dolphin and Pacific white-sided dolphin, respectively.

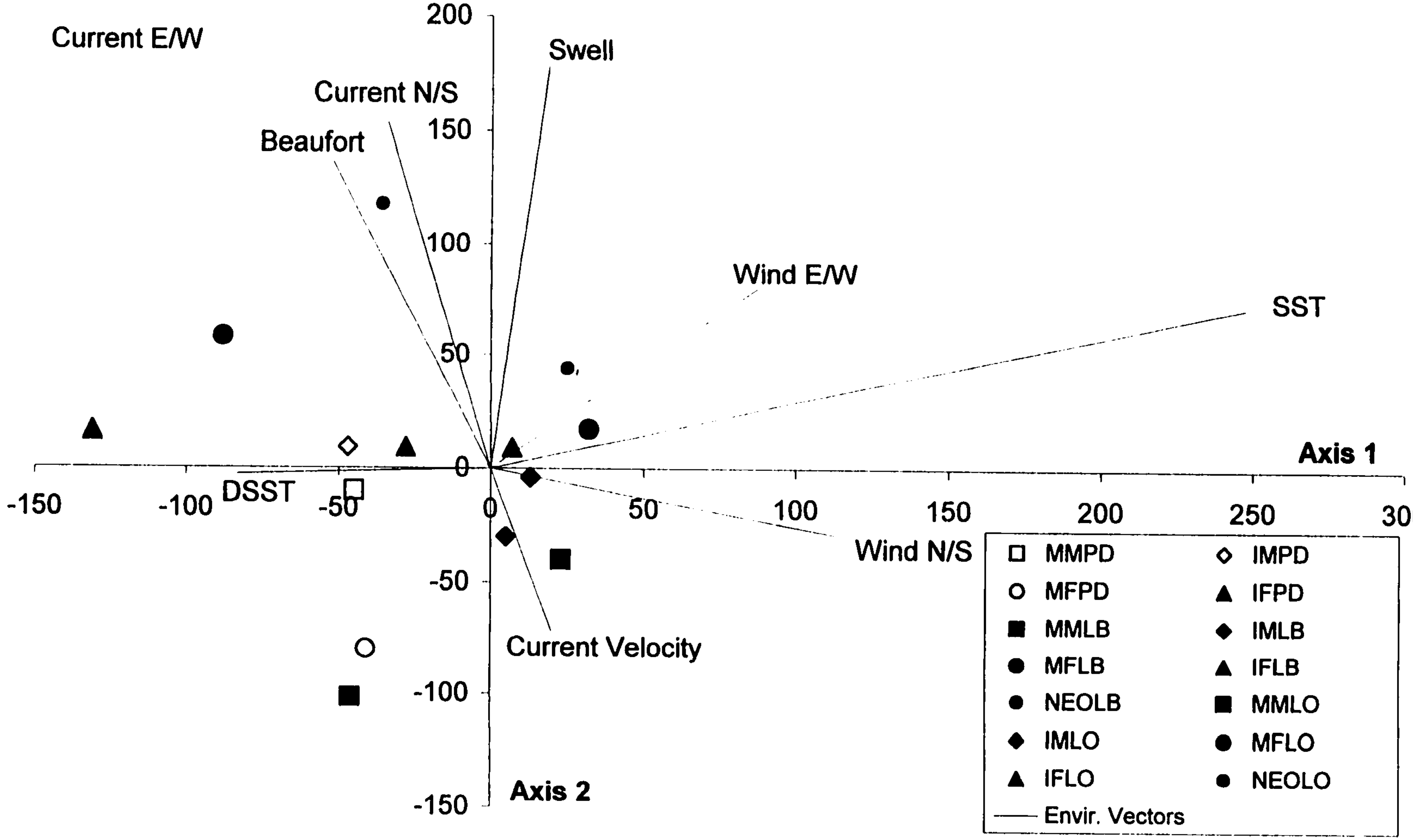


FIGURE 68: Ordination diagram for the September environmental gradient run based on CCA. The abbreviations DP, NRWD and PWSD stand for Dall's porpoise, northern right whale dolphin and Pacific white-sided dolphin, respectively.

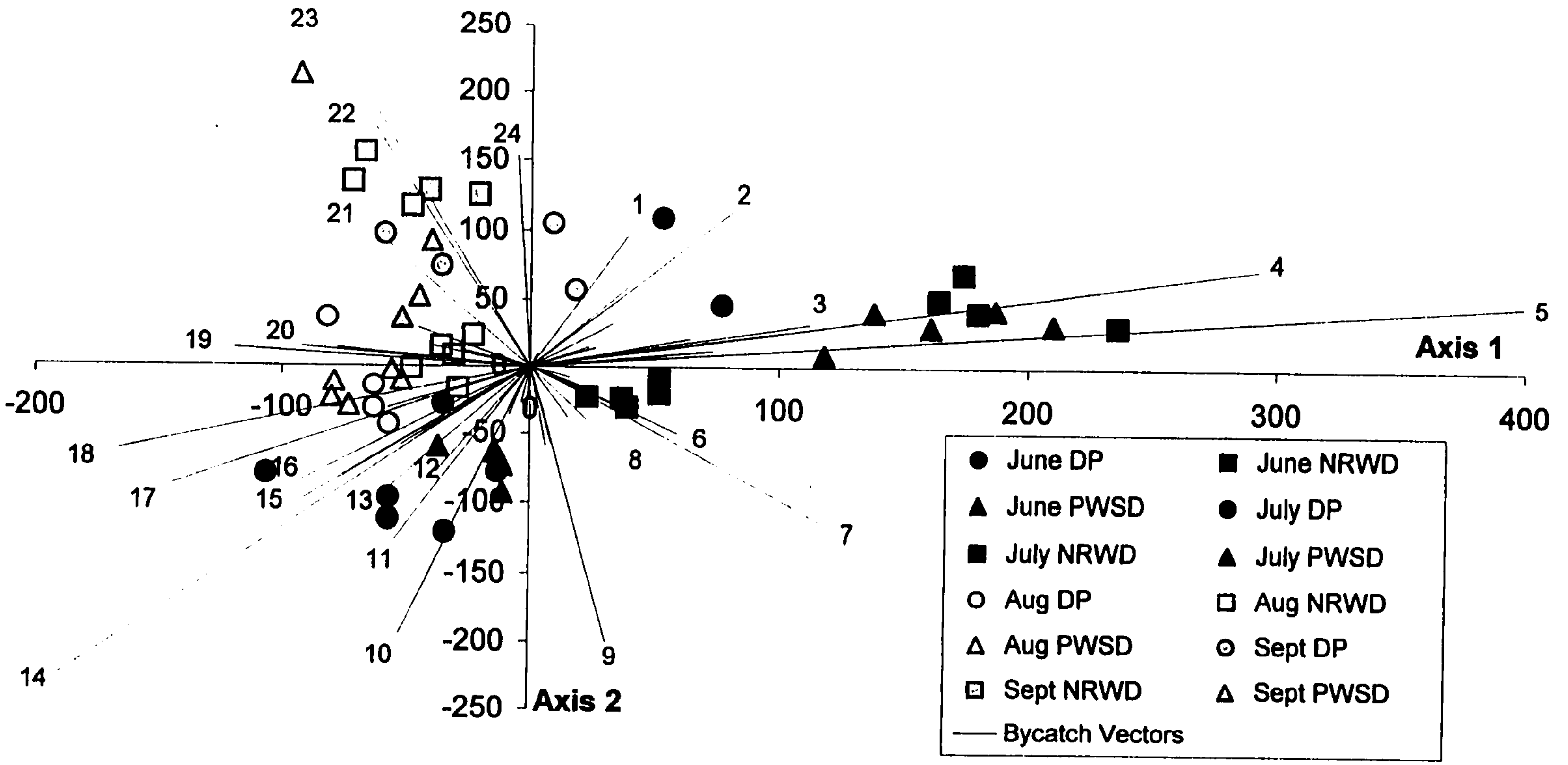


FIGURE 69: Ordination diagram for overall the community association run based on CCA. The abbreviations DP, NRWD and PWSD stand for Dall's porpoise, northern right whale dolphin and Pacific white-sided dolphin, respectively. Numerical codes for selected bycatch vectors are: 1. swordfish, 2 albacore, 3. cigarfish, 4. blue shark, 5. yellowtail, 6. bluefin tuna, 7. louvar, 8. opah, 9. longnose lancetfish, 10. coho salmon, 11. pelagic armorhead, 12. pink salmon, 13. steelhead, 14. salmon shark, 15. northern fur seal, 16. neon flying squid, 17. Pacific pomfret, 18. sooty shear-water, 19. Buller's shearwater, 20. Laysan albatross, 21. short-tailed shearwater, 22. Pacific saury, 23. skipjack, and 24. Japanese butterfish.

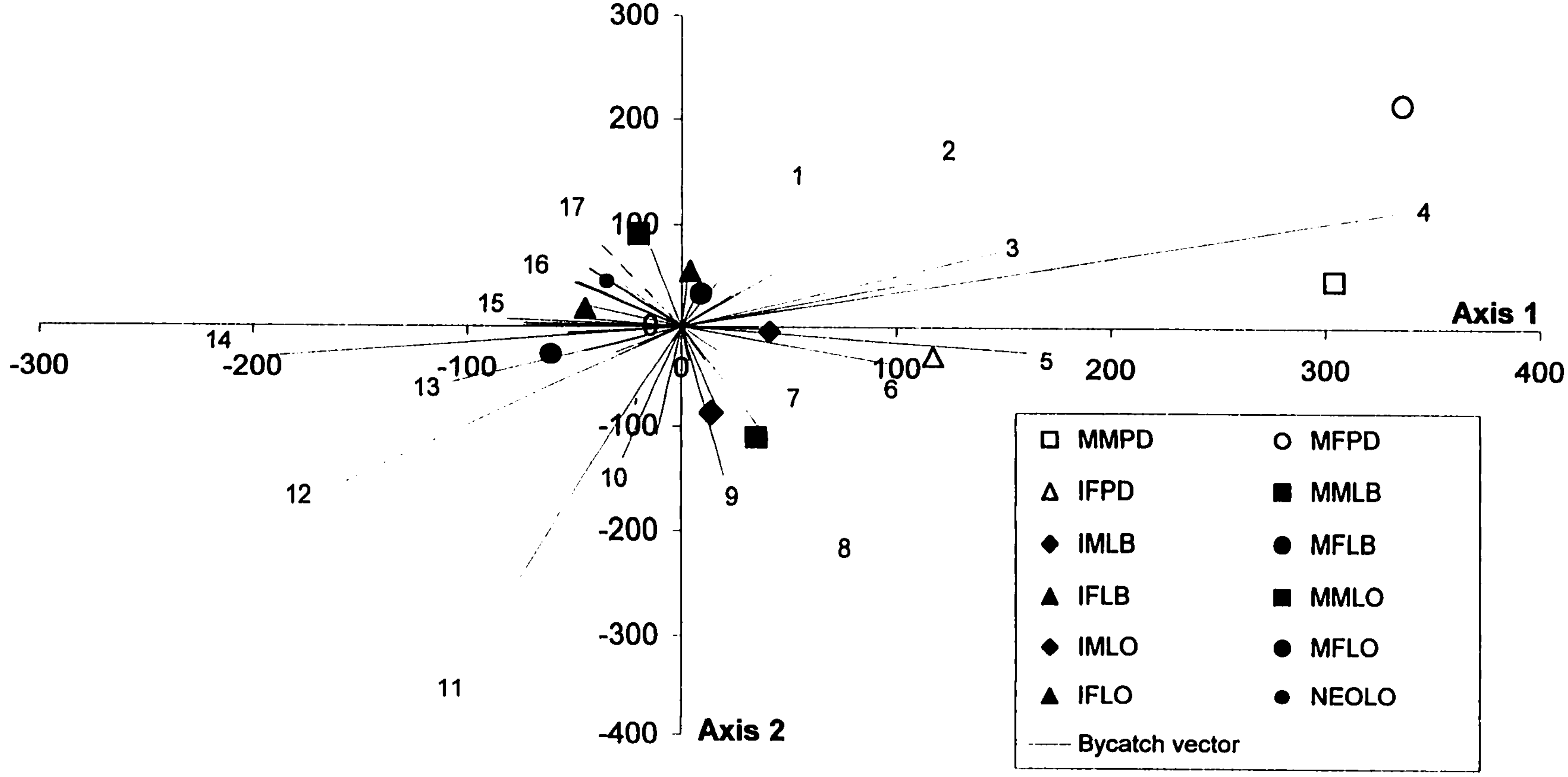


FIGURE 70: Ordination diagram for the June community association run based on CCA. The notations MM, MF, IM, IF, NEO, PD, LB and LO stand for mature male, mature female, immature male, immature female, neonate, Dall's porpoise, Pacific white-sided dolphin and northern right whale dolphin, respectively. Numerical codes for selected bycatch vectors are: 1. pelagic armorhead, 2. Pacific pomfret, 3. salmon shark, 4. chum salmon, 5. coho salmon, 6. sooty shearwater, 7. northern fur seal, 8. black-footed albatross, 9. leatherback turtle, 10. swordfish, 11. albacore, 12. blue shark, 13. louvar, 14. yellowtail, 15. striped marlin, 16. opah, and 17. northern bluefin tuna.

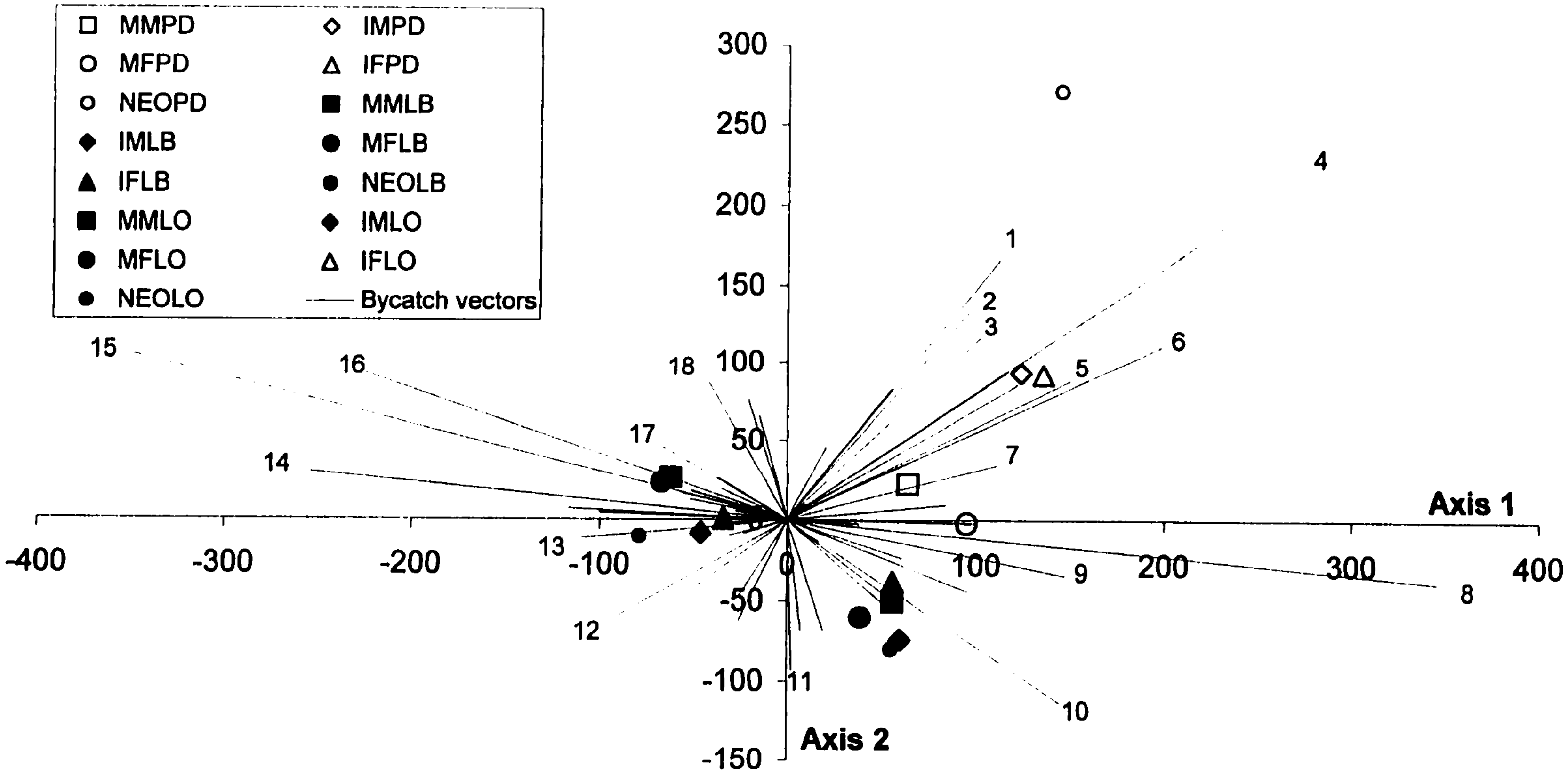


FIGURE 71: Ordination diagram for the July community association run based on CCA. The notations MM, MF, IM, IF, NEO, PD, LB and LO stand for mature male, mature female, immature male, immature female, neonate, Dall's porpoise, Pacific white-sided dolphin and northern right whale dolphin, respectively. Numerical codes for selected bycatch vectors are: 1. 8-armed squid, 2. boreal club-hook squid, 3. spiny dogfish, 4. coho salmon, 5. steelhead, 6. chum salmon, 7. Pacific pomfret, 8. salmon shark, 9. Laysan albatross, 10. sooty shearwater, 11. shortnose spearfish, 12. ocean sunfish, 13. louvar, 14. blue shark, 15. albacore, 16. yellowail, 17. daggertooth, and 18. Pacific saury.

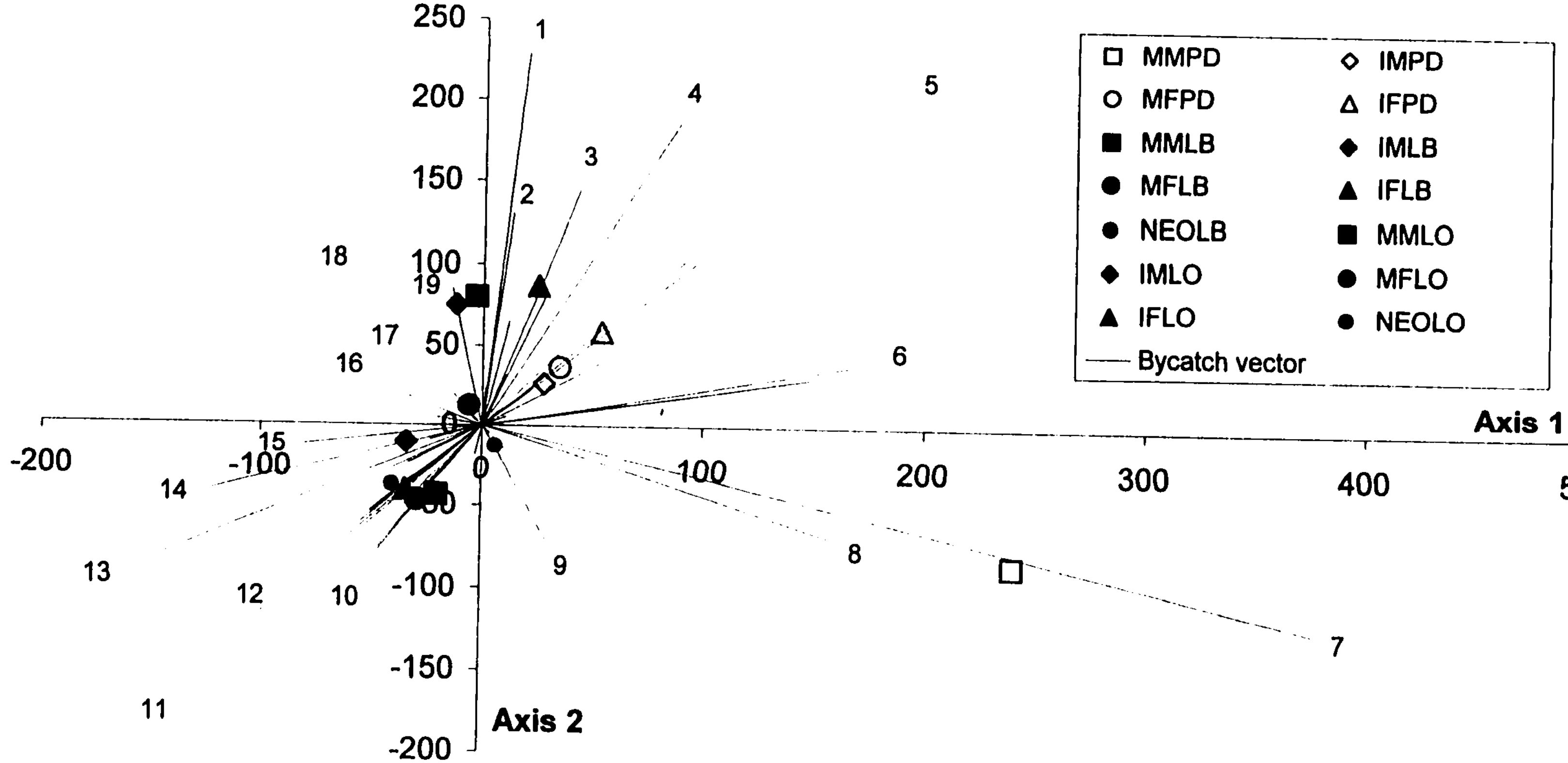


FIGURE 72: Ordination diagram for the August community association run based on CCA. The notations MM, MF, IM, IF, NEO, PD, LB and LO stand for mature male, mature female, immature male, immature female, neonate, Dall's porpoise, Pacific white-sided dolphin and northern right whale dolphin, respectively. Numerical codes for selected bycatch vectors are: 1. northern fur seal, 2. chum salmon, 3. ragfish, 4. Buller's shearwater, 5. salmon shark, 6. steelhead, 7. short-tailed shearwater, 8. anchovy, 9. Laysan albatross, 10. thresher shark, 11. ocean sunfish, 12. pomfret, 13. blue shark, 14. albacore, 15. longnose lancetfish, 16. louvar, 17. pink salmon, and 18. pelagic armorhead, and 19. mako shark.

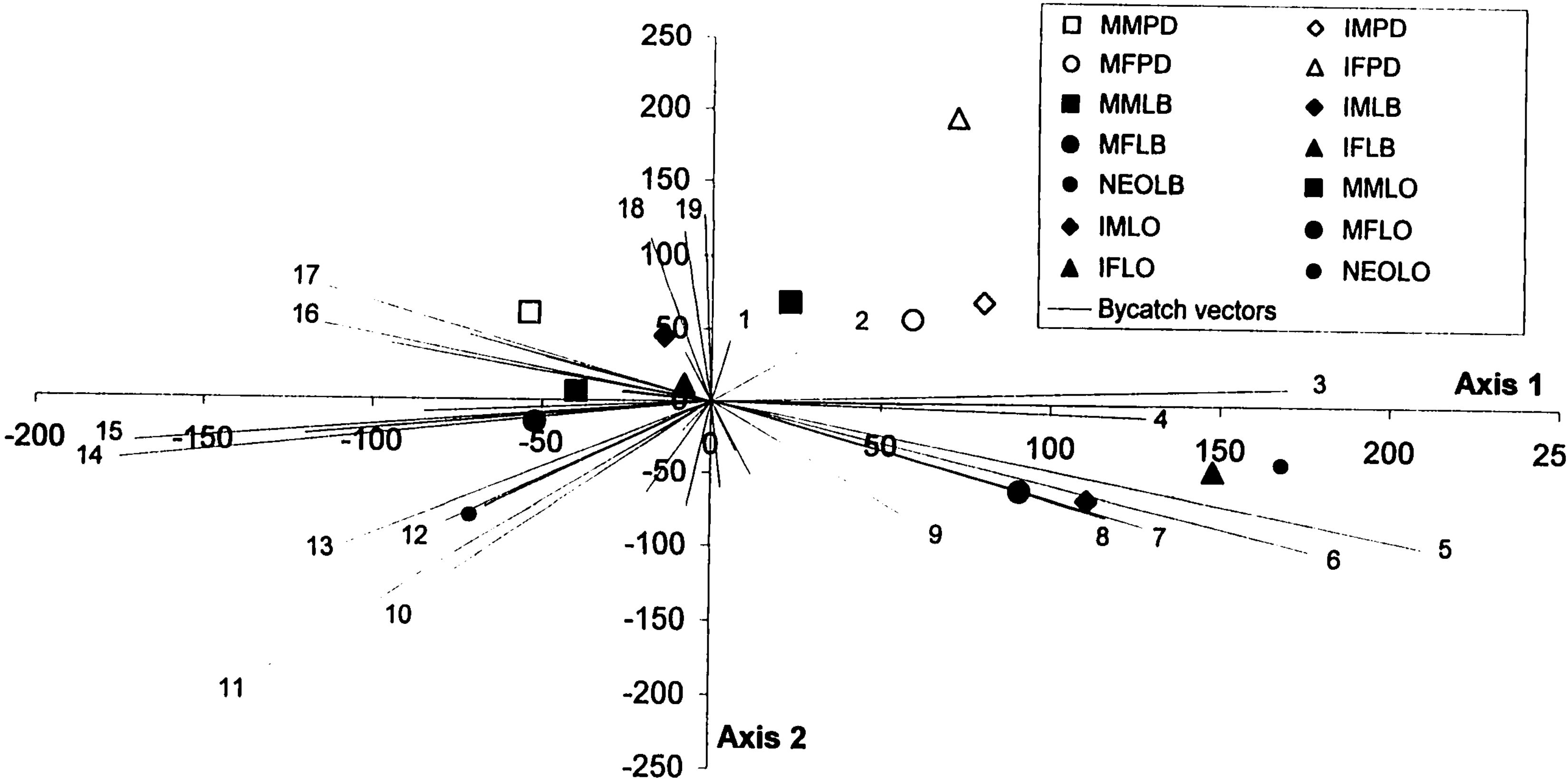


FIGURE 73: Ordination diagram for the September community association run based on CCA. The notations MM, MF, IM, IF, NEO, PD, LB and LO stand for mature male, mature female, immature male, immature female, neonate, Dall's porpoise, Pacific white-sided dolphin and northern right whale dolphin, respectively. Numerical codes for selected bycatch vectors are: 1. longnose lancetfish, 2. steelhead, 3. short-tailed shearwater, 4. black-footed albatross, 5. northern fur seal, 6. pelagic armorhead, 7. skilfish, 8. salmon shark, 9. chum salmon, 10. pelagic stingray, 11. albacore, 12. striped marlin, 13. swordfish, 14. skipjack, 15. blue shark, 16. Laysan albatross, 17. ragfish, 18. pilotfish, and 19. northern bluefin tuna.

CHAPTER 5

Summary and Conclusions

The Study Objective Revisited

Relative to the primary objective of this study, i.e., whether habitat selection preferences or niche partitioning mechanisms can be detected for Pacific white-sided dolphin, northern right whale dolphin and Dall's porpoise using the available life history and fisheries data, both the qualitative and quantitative approaches used in this dissertation suggest that the answer is yes. Comparisons of life history analyses in Chapters 1-3 indicate that habitat distinctions may be related to differences in reproductive biology. The multivariate analyses (i.e., the CCA) complement these findings given that one of the strongest cases of species separation in ordination space involved northern right whale dolphins during their summer calving mode. Furthermore, the CCA identified at least one physical parameter to which all three species responded differently.

The life history analyses provide the basis for proposing that habitats used for calving are partitioned spatially, temporally or both among the three species. The Dall's porpoise calving period was characterized by a consistent mode in early July based on samples collected in the Japanese salmon mothership fishery during 1981 to 1987. Each year, calving was evident as early as the second week in June, but was essentially completed by the end of July. The location of this activity, latitudinally, was between the western

Aleutian Islands (approx. 53°N) and 49°N. However, calving activities were not detected among Dall's porpoise collected on the squid driftnet fishing grounds from 46°N and southward. The field studies in the squid driftnet fishery were conducted not only during June and July, but for at least two months before and after, such that the probability of detecting evidence of calving or nursing activity, if it had occurred in those areas, was high. Thus virtually all Dall's porpoise encountered, coincident with Pacific white-sided dolphins and northern right whale dolphins on the squid driftnet fishing grounds, were immature males and females, mature males or mature females neither pregnant nor lactating.

In contrast, the northern right whale dolphins collected in the squid driftnet fishery strongly suggested a peak in calving activity during July and August. The frequency of parturient females in the sample trended downward across early summer while the number of lactating females and neonates increased. As noted above, no pregnant or lactating Dall's porpoise were ever encountered with the reproductively active northern right whale dolphins, nor were northern right whale dolphins ever caught in the area farther north used by Dall's porpoise as a calving area. While the calving activity exhibited by both species was nearly coincident in time, the locations were separated by at least 4 degrees of latitude. Thus, a spatial dimension which separates calving/nursing areas may be considered a niche partitioning mechanism for northern right whale dolphins and Dall's porpoise although the reasons for this separation can not be identified at present.

As with northern right whale dolphins, Pacific white-sided dolphins were only encountered in the squid driftnet fishery, and never in the salmon driftnet fishery farther north. While no parturient Pacific white-sided dolphins were collected, approximately 40% of the mature females were lactating. In addition, the highest frequency of calves in the sample were Pacific white-sided dolphins, most between three and six months old. Back calculation of birth dates based on early post-natal growth rates relative to the average length at birth indicated a calving mode in late winter or early spring. While the location of the Pacific white-sided dolphin calving area is unknown, its timing was earlier than either northern right whale dolphin or Dall's porpoise, suggesting time as the second niche partitioning mechanism, again focused on separation of calving/nursing activities.

When these findings are combined, the partitioning of calving and nursing activities operate: a) *spatially* between Dall's porpoise and northern right whale dolphin, b) *temporally* between northern right whale dolphin and Pacific white-sided dolphin, and c) both *spatially and temporally* between Pacific white-sided dolphin and Dall's porpoise.

Given that this pattern of habitat partitioning only applies to parturient or lactating females (and neonates) of these three species, it may be hypothesized that the resources available to the remaining segments of these populations (i.e, male and female immatures, mature males and nonpregnant/non-lactating females) are sufficiently abundant so as to negate the need for similar partitioning mechanisms. The strategy, therefore, appears to limit competition only between the population constituents with the highest energy demands during a particularly critical life stage. The avoidance of competition between parturient and lactating females of different species may relate to selection of high productivity foraging areas to meet the energetic demands during pregnancy and lactation, as well as constraints posed by limited mobility of neonates and young calves. Although captive animals have been shown to begin swimming efficiently within hours after birth (Travolga and Essapian 1957), anecdotal observations of young calves at sea (NMFS unpublished data) suggest that their swimming abilities do not equal those of the mother until much later. If calves limit the mother's foraging range, then the resource patches selected by the mother must not only be productive enough to minimize the duration of foraging excursions, but also persistent enough to last until the calf matures and gains greater mobility. Thus, while parturient females may attempt to position themselves near persistent and productive resource patches (and remain there postpartum), their conspecifics and members of other species would be free to move through a wider variety of more dispersed, but still adequate, prey distributions.

The multivariate analyses tend to complement this hypothesis given the high degree of niche overlap (based on tolerance values) displayed both among and within species not directly engaged in calving activities. More importantly, the CCA runs for the month of July resulted in the isolation of the northern right whale dolphin neonates in the warmest waters encountered along the sea surface temperature gradient. This coincides with the period identified in the life history analyses as the peak calving period. While it is unclear what the relationship between warmer waters and selection for productive and persistent foraging areas might be, it does indicate that the environmental conditions in areas used for nursing soon after parturition were distinct from habitats used by other small cetaceans. The lack of selection for warmer waters by neonatal or mature female northern right whale dolphins in August when the fishery operated north of the July fishing grounds may reflect the more southerly distribution of this species, and a tendency for calving areas to remain more central to its range.

The CCA also indicated a link between the needs of parturient and postpartum females. The only population segment that displayed a particularly strong fidelity to a community guild structure was the mature female northern right whale dolphin. In this case, the associations with blue shark and yellowtail were observed across the summer season. While the nature of relationships among these particular species remains unknown, the fact that the association persisted is consistent with the hypothesis that habitat preference by reproductively active females is more narrowly focused than other age and sex classes for these species.

The Similarity Paradox

At the onset of this study, the three species of small cetaceans considered were described as being outwardly similar, at least in terms of their distribution, association patterns and diet. The apparent similarities between Pacific white-sided dolphin and northern right whale dolphin life histories were most noticeable, given their tendencies to school together and their nearly complete overlap in prey consumption. The life history analyses in Chapters 1-3 tend to confirm that Pacific white-sided dolphins and northern right whale dolphins share similar life history characteristics but demonstrate that Dall's porpoise exhibits a much different reproductive strategy.

A brief comparison of selected growth and reproductive parameters illustrates the overall findings (Table 12). The estimates of average age at sexual maturity (ASM), reproductive interval, early postnatal growth rate, calving season pattern, gestation period and longevity show that northern right whale dolphins and Pacific white-sided dolphins take longer to mature, breed less often but live twice as long as Dall's porpoise. Likewise, their corresponding growth rates, both pre- and postnatal appear to be more gradual than Dall's porpoise. The Pacific white-sided dolphin and northern right whale dolphin strategy is typical of other pelagic delphinids such as spotted dolphin (*Stenella attenuata* (Perrin et al. 1976), striped dolphin (*Stenella coeruleoalba*) (Kasuya 1972), eastern spinner dolphin (*Stenella longirostris*) (Perrin *et al*. 1977). and common dolphin (*Delphinuus delphis*) (Ferrero and Walker 1995). Conversely, Dall's porpoise may have the highest annual reproductive potential of any small cetacean.

If only the the information on reproductive seasonality were available as a basis for predicting differences in habitat use patterns, one may conclude that any apparent similarities between Dall's porpoise and the other two species expressed at the onset were misconceptions. In other words, from the perspective of reproductive biology, Dall's porpoise life history and associated habitat preferences (at least in terms of selection for calving grounds) appear to be distinct from either Pacific white-sided dolphins or northern right whale dolphins.

However, if the three species are compared without considering the spatial and seasonal characteristics of the calving activities, a different hypothesis about the relative degree of niche dimension overlap could be based on the multivariate analyses in Chapter 4. In nearly all CCA species-environmental parameter runs Dall's porpoise and Pacific white-sided dolphin eigenvalues are closer to one another along the sea surface temperature gradient than either are to northern right whale dolphins. In these cases, Dall's porpoise occupied the coolest waters available while Pacific white-sided dolphins exhibited greater niche overlap (measured by tolerance values in Ter Braak 1988) with them than with northern right whale dolphins. This pattern suggests that despite the apparent similarities in Pacific white-sided dolphin and northern right whale dolphin reproductive biology, other mechanisms such as the conditions associated with differing seas surface temperatures may also be acting to limit interspecific competition (Tilman 1987). Thus, any number of niche partitioning mechanisms may operate among species, the detection of which may be constrained by the analytical methods used. While reproductive biology suggests that the niches occupied by Pacific white-sided dolphins and northern right whale dolphins are similar, and unique compared to Dall's porpoise, their SST preferences express greater niche similarity between Pacific white-sided dolphins and Dall's porpoise. Likewise, the CCA community association runs indicated that the pelagic communities common to both Dall's porpoise and Pacific white-sided dolphins tend to reflect cooler water preferences than northern right whale dolphin.

In essence, these circumstances point out the difficulty in predicting relationships between species and their corresponding habitat selection patterns when either the data or the methodologies are limited (Legendre *et al.* 1997). Multiple dimensions such as sea surface temperature, or location and timing of reproductive events contribute to the definition of niches occupied by Dall's porpoise, Pacific white-sided dolphins and northern right whale dolphins, but the interactions between these mechanisms are beyond the scope of exploratory analyses. Assuming that some form of experiment could be designed to test the significance of interspecific competition relative to potential niche partitioning mechanisms (examples of which are summarized in Schoener 1983), the effects of disturbance at various scales, changes in population density or fluctuations in carrying capacity may have profound impacts on the form and intensity of habitat selection and niche partitioning patterns.

Table 12. Comparison of selected life history parameters for three species of small cetaceans in the central North Pacific Ocean.

Parameter	Dall's porpoise	Pacific white-sided dolphin	Northern right whale dolphin
ASM (females)	4.4 yr	8.3 - 11.0 yr	9.7 yr
Reproductive Interval	annual	biennial or longer	biennial or longer
Percentage of adult size at age 1 (females)	76.8	72.9	73.8
Gestation period	10 mo	12 - 13 mo	12 - 13 mo
Calving Pattern	modal (2 mo)	modal (2 mo)	protracted (3-5 mo)
Longevity	≤15 yr	30+ yr	30+ yr

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Education:

1998	Ph.D. Wildlife Science University of Washington, Seattle, WA
1985	Master of Marine Affairs, Marine Resource Management University of Washington, Seattle, WA
1980	B.S. Wildlife Management University of Maine, Orono, ME

Research experience:

1983 to present	Fishery Biologist (Research), Small Cetacean Life History Task Leader National Marine Mammal Laboratory Alaska Fisheries Science Center National Marine Fisheries Service Seattle, WA
1983	Fisheries Biologist, High Seas Observer (Dall's porpoise) Fisheries Research Institute University of Washington Seattle, WA
1982	Fish and Game Technician (white-tail deer program) State of Maine, Department of Inland Fisheries and Wildlife Orono, ME
1982	Biological Technician (Fisheries), High Seas Observer (Tuna/Porpoise program) National Marine Fisheries Service San Diego, CA
1981	Forestry Technician, Timber Marker U.S. Forest Dervice, Umatilla National Forest Heppner, OR
1981	Biological Aid (Wildlife), Refuge Assistant Lake Ilo National Wildlife Refuge Dunn Center, ND

1980	Fish and Game Technician - waterfowl Capture/Banding State of Maine, Department of Inland Fisheries and Wildlife Orono, ME

Professional memberships:

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Awards and honors:

Alice and Byron Lockwood Fellowship, University of Washington, 1997
Commendation - Exxon Valdez oil spill response, 1989
Commendation - Implementation of squid gillnet observer program, 1989
Commendation - Celebration of public service, Steller sea lions, 1995
Commendation - NPFMC, Gulf of Alaska Plan Team Member, 1994
Outstanding Performance Recognition, NMFS 1985-89, 92, 94, 96 & 97

Publications:

Bouchet, G.C., R.C. Ferrero, and B.J. Turnock. 1986. Estimation of the abundance of Dall's porpoise (Phocoenoides dalli) by shipboard sighting surveys. Document submitted to the Scientific Subcommittee, Ad Hoc Committee on Marine Mammals, International North Pacific Fisheries Commission, March 1986. 50p.

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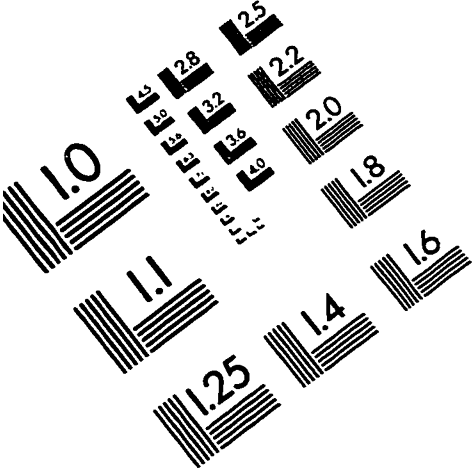

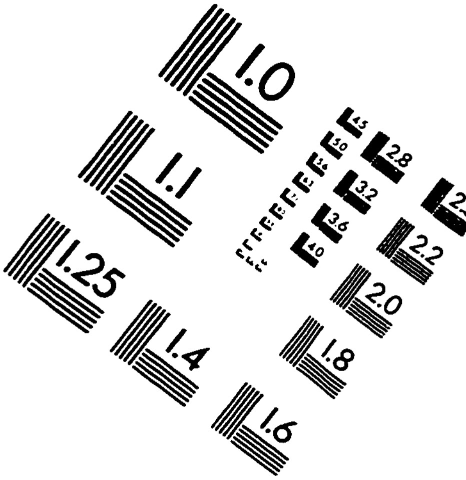

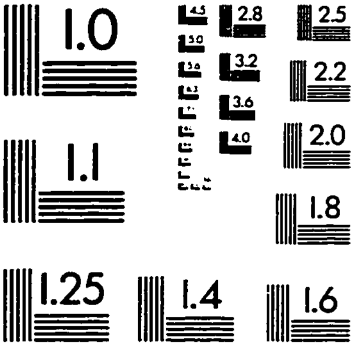

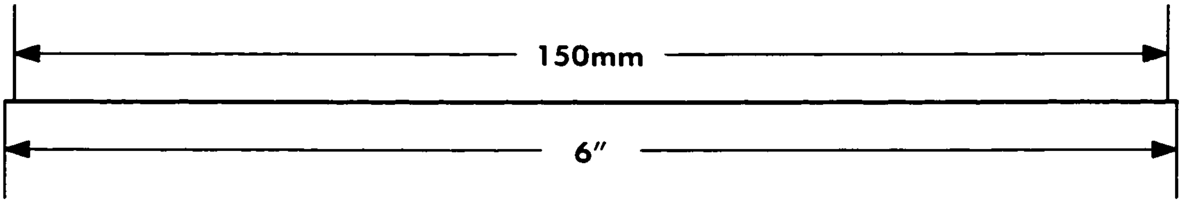

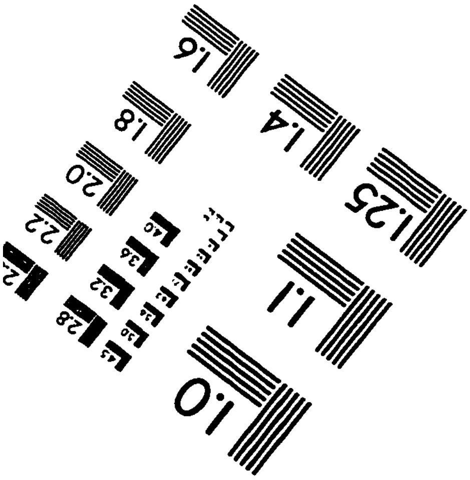

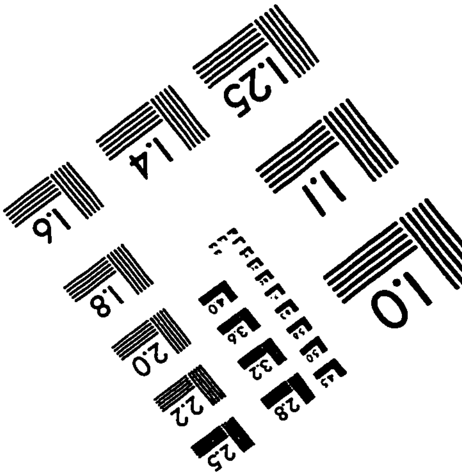

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