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Life History and Population Dynamics of Resident Killer Whales (*Orcinus orca*) in the Coastal Waters of British Columbia and Washington State

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ABSTRACT

Life history parameters are derived for the resident form of killer whale in the coastal waters of British Columbia and Washington State based on the demographic changes observed in two communities (closed to immigration and emigration) that were monitored between 1973–4 and 1987. Females have a mean life expectancy of 50.2 years, typically give birth to their first viable calf at 14.9 years of age, produce an average of 5.35 viable calves over a 25.2 year reproductive lifespan and have a maximum longevity of about 80–90 years. Calving is diffusely seasonal with most births occurring in October-March. Neonate mortality is approximately 43%. The estimated proportion of mature females pregnant varies from 0.274 in April to 0.411 in September. Males have a mean life expectancy of 29.2 years, typically attain sexual maturity at 15.0 years and physical maturity at 21.0 years of age, and have a maximum longevity of about 50–60 years. Mortality curves are U-shaped for both females and males, but the curve is narrower for males. There is no evidence of density dependence in the life history parameters as a result of cropping prior to the start of the study or as the populations increased during the study.

The derived life history parameters are used to develop a sex- and age-specific matrix population model and to calculate life tables. The model accurately emulates the demographic changes observed during the study. Population projections indicate that both communities represent stable populations below their carrying capacity. These populations had a finite annual rate of increase of 2.92% and were composed of 50% juveniles, 19% mature males, 21% reproductive females and 10% post-reproductive females. Discrepancies between the sex- and age-structure of the study populations and those of a stable population can be largely attributed to the selective cropping of pods prior to the start of the study. Simulations indicate that the population could sustain a maximum non-selective harvest of 2.84%; or maximum selective harvests of 4.70% of juveniles or 8.43% of adults, which represented total population harvest levels of 1.89% and 3.17% respectively. Sensitivity analyses reveal that populations are robust to changes in mortality rates, particularly adult mortality rates, which implies that density dependence is expressed primarily through changes in reproductive parameters. It is predicted that (1) a stationary population at carrying capacity will comprise 37% juveniles, 20% mature males, 14% reproductive females and 29% post-reproductive females; and (2) in a stationary population, females surviving to the end of their 14.0 year reproductive lifespan will produce an average of 2.0 calves.

CONTENTS

1. INTRODUCTION

Our current understanding of the life history and population dynamics of cetaceans has been deduced largely from data collected from carcasses. However, this traditional approach has provided little insight into the life history of killer whales, *Orcinus orca* (IWC, 1982) for a number of reasons. First, relatively few specimens have been examined because the species has not been intensively exploited. Second, the commercial catches analyzed were size– or sex-selective and therefore not representative of the actual population (Nishiwaki and Handa, 1958; Jonsgård and Lyshoel, 1970; Christensen, 1982; 1984). Third, killer whales cannot be accurately aged beyond about age 20 years from teeth (IWC, 1980; Yochem, Myrick, Cornell and Arnell, 1987; Myrick, Yochem and Cornell, 1988).

The development of photo-identification techniques has offered a second approach for assessing the life history and population dynamics of cetaceans. Photo-identification studies of killer whales have been underway in coastal waters off British Columbia and Washington State since the early 1970s (Balcomb, Boran and Heimlich, 1982; Bigg, 1982). This has provided a unique perspective of the life history and population dynamics of this species (Bigg, 1982). All members of the two communities of the resident form of killer whale inhabiting this area, both of which are closed to immigration and emigration, have been identified and monitored annually since 1973–74. Genealogical trees have also been constructed for each community (Bigg, Olesiuk, Ellis, Ford and Balcomb, 1990), which can be used to age individuals. Thus, the study has provided a complete record of the number of viable births, deaths and total size of the two communities as well as information on the age, growth, maturity and calving histories of their constituent individuals.

In this report, we describe the life history of the resident form of killer whale in coastal waters off British Columbia and Washington State. The analysis was based on demographic changes observed in the two resident populations during 1973–87. The life history parameters were used to develop an age– and sex-structured population model. We assessed the validity of the model by how well it emulated the observed demographic changes in the study population. The model was subsequently used to: (1) derive population parameters; (2) estimate sustainable harvests; (3) assess the impact of a live-capture fishery conducted prior to the study on local stocks; and (4) examine the sensitivity of the population to changes in life history parameters so as to identify likely mechanisms of population regulation. Finally, the life history and population parameters of killer whales were compared to those of other cetaceans, particularly pilot whales (*Globicephala* spp.).

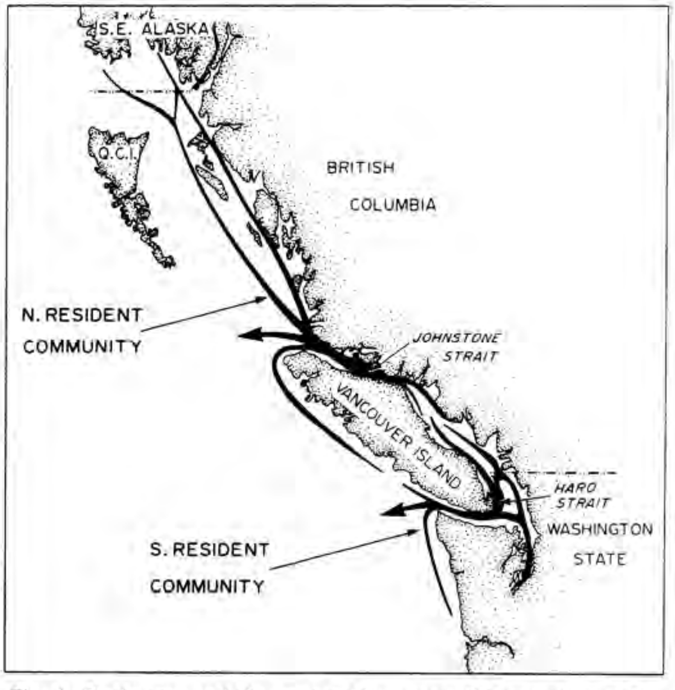

Fig. 1. Study area and the geographic ranges of the southern and northern resident communities and core areas (Johnstone and Haro Straits).

2. STUDY POPULATION

2.1 Data collection

Data collection procedures were described in detail in Bigg *et al.* (1990) and are thus only outlined briefly here.

The study was based on repeated observations of individual whales, all of which could be recognized from the distinctive features of their dorsal fin and saddle patch. Each individual was assigned an alpha-numeric code. A single letter designated its pod and a two-digit number its identity within the pod. The identities of all individuals and their pods are given in Appendix Tables A and B in Bigg *et al.* (1990).

The study was conducted in coastal waters of British Columbia and Washington State (Fig. 1) during 1973–87. The basic sampling unit was an encounter, during which the total number and identity of all individuals present was recorded along with information on their sex and relative size. Whales were encountered throughout the study area and in all months of the year, but the majority of encounters occurred during July-September when the whales congregated in core areas such as Johnstone and Haro Straits. Thus, the encounters essentially represented an annual summer census of the population.

2.2 Sympatric forms

Two distinct forms of killer whale inhabited the study area (Bigg Ford and Ellis, 1985; Bigg, Ellis, Ford and Balcomb, 1987). The two forms, known as residents and transients, differed in morphological appearance and behaviour (Bigg *et al.*, 1985; 1987; Baird and Stacey, 1988; Heimlich-Boran, J.R., 1988; Morton, 1990). The two forms were sympatric, but appeared to be socially isolated as whales of one form were never observed to associate with whales of the other form. The resident form, which constituted 75% of all the individuals identified in the study area, was the most abundant form.

2.3 Resident communities

The resident killer whales inhabiting coastal waters off British Columbia and Washington comprise two geographic communities: the northern and the southern resident communities (Bigg, 1982; Bigg *et al.*, 1990).

Pods from each community were observed in the study area in all months of the year, which indicated that the communities were non-migratory. Pods belonging to one community only occasionally ventured into the range of the other and, although pods within each community often associated with each other, pods never associated with pods outside their community. The two communities were therefore geographically isolated from one another.

Interchange of individuals between the northern and southern communities has not been observed (Bigg *et al.*, 1990). Furthermore, photo-identification studies in southeast Alaska and Prince William Sound indicated that pods belonging to the northern community did not venture north of southern southeast Alaska and that the Alaskan resident pods did not venture into British Columbia (Leatherwood, Balcomb, Matkin and Ellis, 1984). Indeed, Bigg *et al.* (1990) concluded that resident whales of both sexes remained in their natal pod throughout life. Thus, each community was considered to be a separate population that was closed to immigration and emigration.

2.3.1 Northern resident community

The northern resident community ranged through coastal waters of northern British Columbia south to the mid-latitudes of Vancouver Island (Fig. 1). Northern residents were encountered on 660 occasions, during which a total of 16 pods was identified (Bigg *et al.*, 1990). Excluding animals born during the study, all members of the 16 pods had been identified by the 1979 field season (Fig. 2). Indeed, all but the smallest pod (W01), which comprised four individuals, had been identified by 1975. Despite intensive sampling effort (see Bigg *et al.*, 1990), no new pods belonging to this community have been discovered since 1979.

Not all of the northern pods were encountered every year. On average, pods were seen in 81.7% of the years between the years they were first and last encountered (Table 1). In most cases, a pod not seen in a particular year was seen the following year. However, in seven instances pods were not seen for two consecutive years and in one instance a pod was not seen for three consecutive years.

The smallest pod (W01) varied in size from 3–4 individuals during the study and the largest pod (G01) varied in size from 17–24 individuals (Table 1). The mean size of all pods over the course of the study was 9.7 animals. Between the first complete census of all the northern pods in 1979 and the last complete census of all pods in 1986, the community increased from 140 to 171 individuals, which represented a mean annual rate of increase of 2.90%. Using those pods that were censused as an index of changes in pod size, we projected the total size of the northern community prior to and following the last complete census of all pods. Assuming that the censused pods were representative of all pods, we estimated the total size of the community in a given year, N_t, by:

$$N_t = N_{t\pm1} \cdot n_t / n_{t\pm1} \qquad (1)$$

where n_t and $n_{t\pm1}$ represent the total number of animals in the censused pods in years t and t±1 respectively and $N_{t\pm1}$ the estimated or known total size of the community in the preceding or proceeding year. A log-linear regression fitted to these estimates indicated that the northern community was increasing at a relatively constant finite rate of 2.62% ($r^2=0.964$; $P<0.01$) between 1973–87 (Fig. 3).

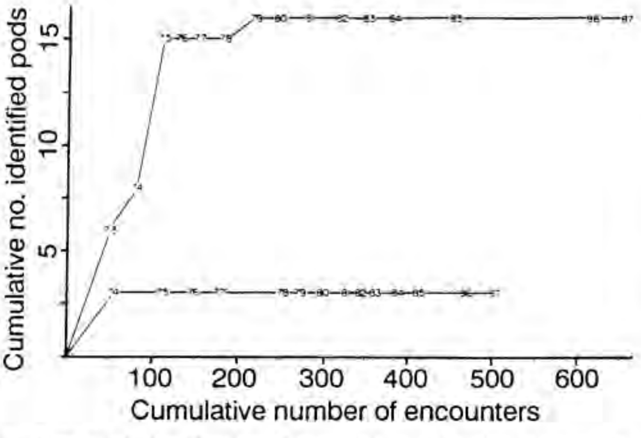

Fig. 2. Rate of identification of new pods as a function of year and cumulative number of encounters in the southern community (lower) and northern community (upper).

2.3.2 Southern resident community

The southern resident community ranged through the coastal waters of Washington State and southern British Columbia (Fig. 1). The southern residents were encountered on 502 occasions, during which a total of three pods were identified (Bigg *et al.*, 1990). All members of the three pods, excluding those born during the study, were identified by the end of the first southern field season in 1974 (Fig. 2). Despite intensive sampling effort (see Bigg *et al.*, 1990), no new pods belonging to this community have been discovered since 1974. The three southern community pods were encountered every year since 1974. The smallest pod (K01) varied in size from 14–17 individuals and the largest pod (L01) varied from 39–49 individuals (Table 2). The mean size of all pods over the course of the study was 26.0 individuals.

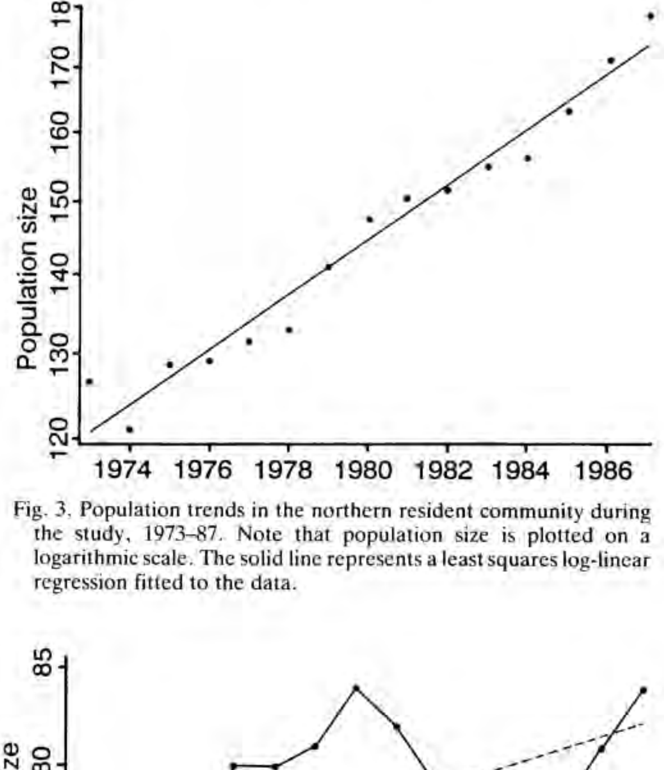

Fig. 3. Population trends in the northern resident community during the study, 1973–87. Note that population size is plotted on a logarithmic scale. The solid line represents a least squares log-linear regression fitted to the data.

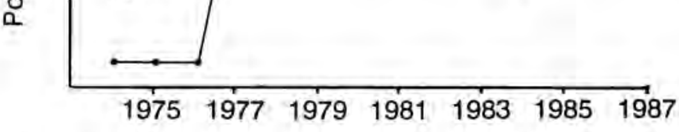

Fig. 4. Population trends in the southern resident community during the study, 1974–87. Note that population size is plotted on a logarithmic scale. The dashed line represents a least squares log-linear regression fitted to the data.

Table 1

Summary of the number of encounters, births, deaths, and size of the 16 northern resident pods during the study.
Asterisks denote the first and last complete census of the pod. Births and deaths are given in the year they were first observed.
For example, a death reported for 1984 occurred sometime between the 1983 and 1984 field seasons.

Pod:		<1973:	73:	74:	75:	76:	77:	78:	79:	80:	81:	82:	83:	84:	85:	86:	87:	Total:
A01	Encounters:	2	26*	8	9	10	0	19	26	1	19	23	17	18	29	108	16	331
	Births:	-	1	0	2	0	1	0	0	0	1	1	0	1	0	0	0	7
	Deaths:	-	-	0	1	1	0	0	0	1	0	0	0	1	0	0	0	4
	Size:	-	13	13	14	13	14	14	14	13	14	15	15	15	15	15	15	+2
A04	Encounters:	0	6*	3	5	7	3	10	15	8	13	16	7	8	16	40	8*	165
	Births:	-	1	1	0	0	0	1	0	0	0	0	3	0	1	0	1	8
	Deaths:	-	-	1	0	0	0	0	0	0	0	0	0	2	1	0	1	5
	Size:	-	5	5	5	5	5	6	6	6	6	6	9	7	7	7	7	+2
A05	Encounters:	4	15*	12	20	8	12	13	23	14	22	18	7	10	32	92	15*	317
	Births:	-	0	1	0	0	1	0	1	1	1	0	0	0	0	1	0	6
	Deaths:	-	-	1	0	0	0	1	0	0	1	0	0	0	0	0	0	3
	Size:	-	10	10	10	10	11	10	11	12	12	12	12	12	12	13	13	+3
B01	Encounters:	2	22*	7	0	1	6	4	3	9	7	11	5	1	2	28	1*	109
	Births:	-	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	4
	Deaths:	-	-	1	0	0	0	0	0	0	0	0	1	0	0	1	0	3
	Size:	-	8	7	7	7	7	7	8	8	8	8	7	8	8	7	8	0
C01	Encounters:	2	4*	3	2	0	4	5	0	5	1	7	5	10	6	65	11*	130
	Births:	-	0	0	1	0	0	0	1	0	0	0	0	0	2	0	0	4
	Deaths:	-	-	0	0	0	0	0	0	0	1[1]	1[2]	0	0	1	0	2	5
	Size:	-	9	9	10	10	10	10	11	11	10	9	9	9	10	10	8	-1
D01	Encounters:	0	5*	1	6	0	0	5	0	10	2	3	1	7	5	44	8*	97
	Births:	-	0	0	1	0	0	1	0	0	0	1	0	1	0	0	3	7
	Deaths:	-	-	0	0	0	0	0	0	0	0	1	1	0	1	0	0	3
	Size:	-	8	8	9	9	9	10	10	10	10	10	9	10	9	9	12	+4
G01	Encounters:	0	3	3*	5	1	7	5	0	3	4	8	9	5	9	15	5*	82
	Births:	-	-	0	1	1	0	0	1	1	1	1	0	1	0	2	1	10
	Deaths:	-	-	-	0	0	0	0	1[3]	0	0	1	0	0	0	0	0	2
	Size:	-	-	16	17	18	18	18	18	19	20	20	20	21	21	23	24	+8
G12	Encounters:	1	1	3*	4	1	2	0	0	1	2	1	0	0	4	2*	0[7]	22
	Births:	-	-	1	0	0	1	1	0	0	1	0	0	0	2	1	≥1	8
	Deaths:	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	≥0	0
	Size:	-	-	4	4	4	5	6	6	6	7	7	7	7	9	10	-	+7
H01	Encounters:	1	1	4	5*	0	2	4	3	1	3	8	0	2	6	32	2*	74
	Births:	-	-	-	1	0	0	0	0	0	1	0	0	0	0	1	0	3
	Deaths:	-	-	-	-	0	0	0	0	0	0	0	1	0	0	0	0	1
	Size:	-	-	-	6	6	6	6	6	6	7	7	6	6	6	7	7	+1
I01	Encounters:	0	1	0	2*	1	1	0	6	3	0	3	0	0	0	2*	0	19
	Births:	-	-	-	0	0	0	0	0	1	0	0	1	0	0	1	-	3
	Deaths:	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0
	Size:	-	-	-	4	4	4	4	4	5	5	5	6	6	6	7	-	+3
I02	Encounters:	0	0	0	2*	0	1	0	5	4	2	4	2	2	4	11	1*	38
	Births:	-	-	-	0	0	0	0	0	1	0	0	0	0	0	0	1	2
	Deaths:	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0
	Size:	-	-	-	6	6	6	6	6	7	7	7	7	7	7	8	+2	
I11	Encounters:	2	2	2	4*	0	0	6	0	3	4	5	6	0	3	14	3*	54
	Births:	-	-	-	0	0	0	0	1	2	0	0	2	0	2	1	0	8
	Deaths:	-	-	-	-	1[4]	0	0	0	0	0	0	0	0	0	0	0	1
	Size:	-	-	-	7	6	6	6	7	9	9	9	11	11	13	14	14	+7
I18	Encounters:	0	0	0	2*	0	1	0	2	2	1	3	0	0	3	4*	0	18
	Births:	-	-	-	1	1	0	0	2	1	0	0	2	0	0	2	-	9
	Deaths:	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0
	Size:	-	-	-	5	6	6	6	8	9	9	9	11	11	11	13	-	+8
I31	Encounters:	1	0	0	4*	0	0	2	0	0	4	4	4	2	5	24	6*	56
	Births:	-	-	-	0	0	0	0	0	1	0	0	0	0	2	0	0	3
	Deaths:	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0
	Size:	-	-	-	4	4	4	4	4	5	5	5	5	5	7	7	7	+3
R01	Encounters:	0	0	0	2*	0	1	0	2	0	2	1	2	4	8	6	4*	32
	Births:	-	-	-	1	0	0	0	2	0	0	1	0	1	1	0	2	8
	Deaths:	-	-	-	-	2[5,6]	0	0	0	0	0	0	1	0	0	0	1	4
	Size:	-	-	-	17	15	15	15	17	17	17	18	17	18	19	19	20	+3
W01	Encounters:	0	0	0	0	0	0	0	1*	0	3	7	5	1	3	2	2*	24
	Births:	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0
	Deaths:	-	-	-	-	-	-	-	-	0	0	0	0	1	0	0	0	1
	Size:	-	-	-	-	-	-	-	4	4	4	4	4	3	3	3	3	-1
	Encounters:	11	39	31	34	14	26	29	39*	27	34	38	32	31	72	161*	42	660
	Births:	-	≥3	≥3	≥8	≥2	≥3	≥3	9	8	5	4	8	5	10	9	≥10	≥90
	Deaths:	-	-	≥4[7]	≥1	≥4	≥0	≥1	1	1	2	3	4	4	3	1	≥4	≥33
	Size:	-	-	-	-	-	-	-	140	147	150	151	155	156	163	171	-	-

[1,2,3,4,5,6] Exact year of death unknown. [1] Died between 1981-82. [2] Died between 1982-83. [3] Died between 1979-81. [4] Died between 1976-79. [5] One died between 1976-81. [6] Based on encounter of a portion of the pod. [7] Includes one individual that died before its pod was identified.

Between 1974 and 1987, the southern community increased in size from 71 to 84 individuals, which represented a mean annual rate of increase of 1.30% (Fig. 4). A log-linear regression indicated that the overall rate of increase was significantly greater than zero ($r^2=0.319$; $P<0.05$), but the rate of increase was not nearly as constant as that of the northern community. This was likely because: (1) the southern community, being about half the size of the northern community, was more sensitive to the stochastic nature of births and deaths; and (2) the sex- and age-structure of the southern community had been distorted by selective cropping prior to the start of the study (Sections 2.4.2 and 4.3.3).

2.4 History of exploitation

2.4.1 Historical kills

Prior to this century, killer whale populations in coastal waters off British Columbia and Washington State were probably in an unexploited state. Aboriginal utilization of killer whales appear to have been negligible. Although marine mammals were a common component of the fauna excavated at anthropological sites in the Pacific Northwest, only one killer whale has been identified (R. Wigen, University of Victoria, Victoria, British Columbia, pers. comm.). Their scarcity may have been due to the special mythological significance of killer whales in local aboriginal cultures (Cavanagh-Ford, 1984; Tanami, 1984). The journals of the early explorers of the west coast of Canada made no reference to the exploitation of killer whales.

Killer whales were never the target of commercial whalers in British Columbia or Washington State, but were occasionally taken incidentally to other species. The only documented commercial kill was a photograph of an adult male being processed at a local whaling station in 1955 (Pike and MacAskie, 1969).

Prior to about 1970, killer whales were viewed locally as a nuisance as it was believed they preyed on commercial fish stocks and posed a potential hazard to small vessels. During the 1940s, the Royal Canadian Air Force used killer whales for targets in practice bombings (Carl, 1946), but no records were maintained on the magnitude or location of potential kills. In 1960, the Canadian Department of Fisheries installed a machine gun in the Strait of Georgia in an attempt to cull populations, but no whales were sighted while the station was operational (Pacific Biological Station, unpubl. data). Nevertheless, substantial numbers of killer whales may have been killed opportunistically by fishermen, fisheries personnel and sportsmen during this era. Bullet wounds were evident in up to 25% of the animals taken from the study area during the live-capture fishery (Keyes, *in* Hoyt, 1981). Shooting by fishermen was cited as the most likely cause of abnormally high mortality in a particular pod of killer whales in Prince William Sound, Alaska, that recently learned to remove cod from longlines (Matkin, Ellis, von Ziegessar and Steiner, 1986).

Since the early 1970s, local attitudes toward killer whales have changed dramatically. Recent surveys of the attitudes of commercial fishermen in British Columbia showed that few (11.3%) considered killer whales more than a minor problem (Olesiuk, unpubl. data). Killer whales have been protected in Canadian waters by the Fisheries Act since 1970 and in USA waters by the Marine Mammal Protection Act since 1972. However, several permits have been issued for the capture of specimens in Canada since the species was protected (Section 2.4.2).

2.4.2 Live-capture fishery

Between 1962 and 1977, a total of 68 killer whales were removed from the coastal waters of British Columbia and Washington State during a live-capture fishery, for exhibition in aquaria (Bigg and Wolman, 1975). Bigg (1982) identified the pods for 53 of the 68 (78%) animals taken. Of these, 48 (90.6%) were of the resident form. Since residents were the most abundant form in the study area, most if not all of the 15 remaining animals were probably also of the resident form. All but one of the 15 were captured within the range of the southern community. We therefore estimated that 63 (93%) of the animals cropped were residents and that the majority of residents (76%) were taken from the southern community.

Table 2

Summary of the number of encounters, births, deaths, and size of the three southern resident pods during the study. Asterisks denote first and last complete census of the pod. Births and deaths are given in the year they were first observed.

Pod:		<1973:	73:	74:	75:	76:	77:	78:	79:	80:	81:	82:	83:	84:	85:	86:	87:	Total:
J01	Encounters:	5	0	25*	40	20	17	62	14	21	20	10	9	9	11	31	17*	311
	Births:	-	-	1	0	1	1	1	1	0	1	1	0	0	1	0	1	9
	Deaths:	-	-	-	0	0	0	0	0	0	1	1	0	1	0	2	0	5
	Size:	-	-	15	15	16	17	18	19	19	19	19	19	18	19	17	18	+3
K01	Encounters:	3	1	17*	25	2	8	40	6	8	8	9	7	19	16	37	14*	240
	Births:	-	-	1	0	0	1	0	0	0	0	0	0	0	1	2	1	6
	Deaths:	-	-	-	1	1	0	0	0	0	0	1	1	0	1	0	0	5
	Size:	-	-	17	16	15	16	16	16	16	16	15	14	14	14	16	17	0
L01	Encounters:	4	1	12*	21	16	14	31	3	9	14	8	9	9	11	20	16*	198
	Births:	-	-	3	1	0	6	1	1	3	0	0	0	3	3	5	2	28
	Deaths:	-	-	-	0	0	0	1	1	0	2	2	2	3	1	2	1	15
	Size:	-	-	39	40	40	46	46	46	49	47	45	43	43	45	48	49	+10
	Encounters:	10	2	43*	58	37	30	75	19	26	29	16	16	27	25	57	32*	502
	Births:	-	-	5	1	1	9[1]	2	2	3	1	1	0	3	5	7	4	44
	Deaths:	-	-	-	1	1	0	2[1]	1	0	3	4	3	4	2	4	1	26
	Size:	-	-	71	71	71	80	80	81	84	82	79	76	75	78	81	84	+13

[1] Includes one individual that died before its pod was identified.

In order to assess the impact of the live-capture fishery on each community, the approximate age-composition of the harvest was reconstructed based on the sex and size of the cropped animals (Table 3). Females and males both measured about 2.3m in length at birth (Section 3.2) and in captivity grew at a rate of about 0.35 $m.yr^{-1}$ (Bigg, 1982). Whales less than 3.5m in length were thus considered less than 4 years of age. Field observations of known-aged females (Bigg, unpubl. data) indicated that females approached adult-size by about 10 years of age. Given that females matured at about 4.6–4.9m (Christensen, 1982; 1984; IWC, 1982), we estimated that females measuring 3.5–4.5m were 4–10 years of age whereas those measuring more than 4.5m were older than 10 years of age. Field observations of known-aged males (Bigg, unpubl. data) indicated that males approached adult-female size by about 8 years of age and continued to grow until they were sexually mature at about 6m in length (Bigg, 1982) and 15 years of age (Section 3.3.2). Therefore, we estimated that males measuring 3.5–4.5m were 4–8 years of age, males 4.5–6m were 9–15 years of age, and males longer than 6m were older than 15 years of age.

Table 3

Summary of the number of killer whales captured or killed by pod, date, length (in metres) and sex (M, F, ?) during the live-capture fishery in British Columbia and Washington State (modified from Bigg, 1982).

			Physically immature						Mature			
			≤3.5m			3.5-4.5			4.5-6	≥4.5	≥6	
Pod/Area	Caught	N	M	F	?	M	F	?	M	F	M	?
S. Resident												
J01,K01,or L01	Jul 64	1	-	-	-	-	-	-	1	-	-	-
J01,K01,or L01	Oct 65	2	-	-	-	-	1	-	-	1	-	-
K01	Feb 67	8	1	2		2	1	-	-	1	1	-
J01,L01	Oct 68	5	-	-	-	3	-	-	2	-	-	-
J01,K01,or L01	Aug 70	11	2	-	2	3	2		1	1	-	-
L01	Aug 71	3	-	1	-	1	1	-	-	-	-	-
J01	Mar 72	1	1	-	-	-	-	-	-	-	-	-
K01	Aug 73	1	-	-	-	-	-	-	-	1	-	-
L01	Aug 73	2	-	-	-	-	-	-	1	1	-	-
Total		*34*	*4*	*3*	*2*	*9*	*5*	-	*5*	*5*	*1*	-
N. Resident												
C01	Jun 65	1	-	-	-	-	-	-	-	-	1	-
I11	Jul 67	1	-	-	-	1	-					
A(A05)	Apr 68	6	1	-	-	-	1	-	1	3	-	-
A05	Dec 69	6	-	2	-	2	1	-	1	-	-	-
Total		*14*	*1*	*2*	-	*3*	*2*	-	*2*	*3*	*1*	-
Transient												
M01	Mar 70	3	-	-	-	-	2	-	-	1	-	-
Q01	Aug 75	2	-	-	-	1	1	-	-	-	-	-
Total		*5*	-	-	-	*1*	*3*	-	-	*1*	-	-
S. Vancouver I[1]	Sep 62	2	-	-	-	-	-	-	-	-	2	-
S. Vancouver I[1]	Jul 66	1	1	-	-	-	-	-	-	-	-	-
S. Vancouver I[1]	Feb 68	2	-	-	-	1	-	-	-	1	-	-
S. Vancouver I[1]	Apr 69	2	-	-	-	-	-	-	-	1	1	-
S. Vancouver I[1]	Oct 69	1	-	-	-	-	-	-	-	-	-	1
S. Vancouver I[1]	Feb 70	1	-	-	-	-	-	1	-	-	-	-
S. Vancouver I[1]	Aug 70	1	-	1	-	-	-	-	-	-	-	-
S. Vancouver I[1]	Aug 77	1	-	1	-	-	-	-	-	-	-	-
Washington[1]	Nov 71	2	-	-	-	2	-	-	-	-	-	-
Washington[1]	Mar 73	1	-	-	-	-	-	-	-	1	-	-
Total		*14*	*1*	*2*	-	*3*	-	*1*	-	*3*	*3*	*1*
NE Vancouver I[2]	Jul 68	1	-	-	-	1	-	-	-	-	-	-
Grand Total		*68*	*6*	*7*	*2*	*17*	*10*	*1*	*7*	*12*	*5*	*1*

[1] Assume belonged to southern resident community.
[2] Assume belonged to northern resident community.

The above criteria indicated that the live-capture fishery was selective for physically immature animals, which accounted for 73% (46 of 63) of the total take of resident whales (Table 3). The take was also biased toward males, which represented 68% (40 of 59) of the cropped residents of known sex.

3. LIFE HISTORY

Life history parameters were estimated from demographic events observed between the first and last census of each pod (Tables 1 and 2). Where possible, life history parameters were derived separately and compared for cropped and uncropped pods to ascertain whether cropping had any discernible effect. Pods were classified as cropped if more than one individual was known to have been removed during the live-capture fishery. Since all three of the southern community pods, but only one of the northern community pods (A05) had been cropped, comparing cropped and uncropped pods was essentially equivalent to comparing the southern and northern communities.

3.1 Age determination and longevity

3.1.1 Juveniles

Calves born during the study were aged in reference to the year they were born. Since births generally occurred in October-March (Section 3.2) and most encounters were in July-September (Fig. 2 in Bigg *et al.*, 1990), animals were assumed to have been censused at their pivotal ages (i.e. the midpoint between birthdays). For example, an individual born between the 1973 and 1974 field seasons was assigned an age of 0.5 years in 1974, 1.5 years in 1975, etc. Ages estimated in this manner were thus considered accurate to within ±0.5 years.

Some calves born during the study in the northern pods that were not encountered every year may not have been seen in the year they were born. In cases where the mothers of new calves had not been seen in the preceding year(s), the calves were aged based on their body-size when first seen relative to that of known-aged juveniles. We judged that eight of the calves born during the study were first seen at 1.5 years of age and four each at 2.5 years and 3.5 years of age. Similarly, calves judged to have been born 1–3 years prior to the first encounter with their pod were aged based on their body-size when first seen. In cases where it was judged that a calf may have been born in either of two years, the birth was amortized over the period in question. For example, a calf that may have been born between either the 1973 and 1974 or the 1974 and 1975 field seasons was tallied as half a 1.5 year old and half a 2.5 year old in the 1976 census. Ages estimated in this manner were thus considered accurate to within ±1 year. Individuals aged by the above two methods are subsequently referred to as known-aged animals.

Most older juveniles were aged in reference to the year they matured, but four were aged based on their body-size when first seen. One individual (W05) that had not matured by the end of the study was judged to have been aged 5.5 years when first seen in 1979 and a female (K40) that remained barren during the study was judged to have been aged 9.5 years when first seen. In addition, two females (A24 and R04), judged to have been aged 5.5 and 10.5 years at the start of the study, were aged based on their body-size in photographs taken prior to the start of the study. One additional individual (B04) that died and was recovered within a few days of first being encountered was aged at 11.5 years based on the number of dentinal annuli. These age estimates were considered accurate to within about ±2 years.

3.1.2 Adult females

With the above noted exceptions, females that were large juveniles when first encountered were aged in reference to the year they gave birth to their first viable offspring. Viable offspring were defined as those that survived to at least 0.5 years of age. Age at first birth was established based on the ages at which known-aged females gave birth to their first viable calf (Section 3.3.1). The probability of a female being aged x in the year it gave birth to its first viable calf was estimated as:

$$\Pr(\text{Age}=x + 0.5) = r_{(x)} \qquad (2)$$

where $r_{(x)}$ represents the proportion of known-aged females that first gave birth at age x (Table 6). The correction of 0.5 accounted for the fact that animals were censused at their pivotal ages. Age point estimates, X, were obtained from the age probability density function (2) by:

$$X = \sum_{x=12.5}^{18.5} x \cdot \Pr(\text{Age}=x) \qquad (3)$$

Since females typically gave birth to their first viable offspring between 12 and 18 years of age (Section 3.3.1), the point estimates were considered accurate to within ±3 years.

An extension of the above method was applied to females that were adult-sized when first seen and gave birth to their first known offspring during the study or had given birth prior to the start of the study. The calving histories of the latter were determined from the genealogical trees given in Bigg *et al.* (1990). If it was assumed that a female's oldest known offspring represented her first born, the year she first gave birth could be established from the age of her oldest offspring, and subsequently her age using equations (2) and (3). However, this tended to underestimate ages because females may have lost their first viable progeny prior to the start of the study.

We corrected for this bias by incorporating a probabilistic adjustment for calf loss in equation (2):

$$\Pr(\text{Age} = [x + \text{CI}.N] + 0.5) = r_{(x)} \cdot \Pr(L = N) \qquad (4)$$

where CI denotes the mean calving interval, 5.32 years (Section 3.4.2), and $\Pr(L = N)$ the probability that a female lost her first N offspring prior to the start of the study. For example, a female that lost her first offspring was assumed to have given birth to her first calf 5.32 years prior to the birth of her oldest known offspring, a female that lost her first two offspring was assumed to have given birth 10.64 years prior to the birth of her oldest known offspring, etc. Age point estimates corresponding to the age probability density function (4) were obtained using equation (3).

The probabilities of a female losing her first N progeny were calculated sequentially as follows:

$$\Pr(L \geq N) = 1 - \{\text{SURV}(\text{CI} + [Y_o - Y_f])\} \quad \text{for } N = 1 \qquad (5)$$

$$\Pr(L \geq N) = \Pr(L \geq N-1) \cdot \{1 - \text{SURV}(N \cdot \text{CI} + [Y_o - Y_f])\} \quad \text{for } 1<N \leq M \qquad (6)$$

$$\Pr(L = N) = 1 - \Pr(L \geq 1) \quad \text{for } N=0 \qquad (7)$$

$$\Pr(L = N) = \Pr(L \geq N) - \Pr(L \geq N + 1) \quad \text{for } 0<N<M \qquad (8)$$

$$\Pr(L = N) = \Pr(L \geq N) \quad \text{for } N=M \qquad (9)$$

where Y_o denotes the estimated year of birth of the oldest known offspring, Y_f the year the female and its offspring were first encountered and M the maximum number of calves that could have been lost. Maximum calf loss, M, was set at five viable calves, the approximate number born during the reproductive lifespan (Section 3.5.3). Since $\Pr(L = N)$ diminished rapidly with N, this constraint had little effect on the age estimates. Given that the sex ratio was equal at birth (Section 3.6.3), the proportion of viable offspring that survived to age x, SURV(x), was:

$$\text{SURV}(x) = [\prod_{0.5}^{x} \text{SV}_{f(x)} + \prod_{0.5}^{x} \text{SV}_{m(x)}]/2 \qquad (10)$$

where $\text{SV}_{f(x)}$ and $\text{SV}_{m(x)}$ represent the age-specific female and male survival rates respectively (Section 3.6).

The magnitude of the correction for the loss of offspring varied as a function of Y_o-Y_f, the age of a female's oldest offspring in the year she was first seen. Oldest progeny ranged in age from 1.5 to an estimated 40.2 years, which corresponded to corrections of 0.9 to 9.7 years. Accordingly, the accuracy of the age point estimates, nominally calculated as the minimum age interval over which the age probability density function (4) summed to 0.8, ranged from ±3 years for females aged 20 when first seen, to ±4 years for females aged 35 when first seen, to ±8 years for females aged 50 when first seen.

The above ageing procedure involved four assumptions: (1) age at first birth had remained constant; (2) the genealogical trees given in Bigg *et al.* (1990) were accurate; (3) calving intervals had remained constant; and (4) survival rates had remained constant. The validity of the first assumption could not be directly evaluated because known-aged females only began to give birth late in the study. Consequently, the age estimates were subject to biases of the same magnitude as any shift that might have occurred in the mean age at first birth. However, considering that the age-structure of the study population conformed with that of a stable population (Section 4.3), and that the stable age-structure was sensitive to shifts in age at first birth (Section 4.4.1), it was unlikely this parameter had changed appreciably in recent years.

Inaccuracies in the genealogical trees derived in Bigg *et al.* (1990) were probably not an important source of bias. Eighteen (29.5%) of the age estimates were based on positive lineages, 30 (49.2%) on highly probable lineages and 13 (21.3%) on probable lineages. There were few sources of errors in the lineages at the positive and highly probable level of certainty (Bigg *et al.*, 1990). Moreover, most females had several similarly aged offspring so that a single incorrect lineage would have had little effect on the age estimates. Of the 13 females aged on the basis of probable lineages with their oldest offspring, 12 (92.3%) had at least one younger offspring, the age of which was an average of 7.6 years less than that of the oldest offspring. It should also be noted that the potential biases in the ages based on the probable lineages were of little consequence in the population model, as 11 of the 13 females were post-reproductive.

With respect to the final two assumptions, there was no way of independently estimating calving intervals and mortality rates prior to the start of the study. However, the net apparent fecundity rate, which represents the net product of fecundity and mortality, appeared to have been constant since at least 1955 (Section 3.5.4). This implied that both calving intervals and survival rates were constant, or that changes in one were balanced by reciprocal changes in the other. In either case, the ages of females born after 1940, which included essentially all reproductive females, would have been unbiased.

Some discretion was used in applying the above ageing procedure to females in cropped pods. Because these females may have had progeny cropped, equation (10) tended to overestimate the survival rate of their progeny and hence underestimate their age. Since there was no way of establishing which females had progeny cropped, the ageing procedure was applied only to females: (1) that had at least four identified offspring; or (2) for which the birth dates of their identified offspring spanned at least 20 years. As females typically gave birth to about five calves over a 25 year reproductive lifespan (Section 3.5), individuals satisfying these criteria were unlikely to have had their first offspring cropped.

The females in cropped pods that failed to satisfy either of the above criteria were aged by one of two alternative methods. First, females that became post-reproductive just prior to or during the study were aged in reference to the year of birth of their last viable calf. Females were defined as post-reproductive when they had not calved for at least 10 years. The year of birth of post-reproductive females was estimated by subtracting 39, the mean age of females at last birth (Section 3.5.3), from the year of birth of their last offspring. Since only 10% of females were post-reproductive by 29 years of age and 90% were post-reproductive by 48 years of age (Section 3.5.3), ages estimated in this manner were considered accurate to within ±10 years.

Second, the females in cropped pods that failed to meet either of the above criteria fell into two categories: (1) those that were reproductive during the study; and (2) those that gave birth to their last identified calf more than five years prior to the start of the study. There was no way of knowing whether the former were in the early stage of their reproductive lifespan and would give birth again in coming years, or were in their late stage but had their oldest progeny cropped. Similarly, there was no way of knowing whether the latter had been post-reproductive for a long time or had become post-reproductive just prior to the start of the study but had their youngest progeny cropped. Females in both categories were aged based on the mean birth date of their identified offspring, which we assumed coincided with the midpoint of their reproductive lifespan. Females typically gave birth to 50% of their calves by 24 years of age and had a mean reproductive lifespan of 25 years (Section 3.5.3). The accuracy of these age estimates varied depending on the number and span between the offspring used to calculate the mean birth date. For example, an estimate based on the mean birth date of one offspring was only accurate to within ±12 years whereas an estimate based on two offspring born over a 15 year period was probably accurate to within about ±5 years.

3.1.3 Adult males

Males that were large juveniles when first encountered were aged in reference to the year they attained sexual maturity. Age at onset of sexual maturity was established based on the rate of development of the dorsal fin (a secondary sexual characteristic) of known-aged males (Section 3.3.2). Assuming that age at maturity had remained constant, the probability that a male was aged x in the year it became sexually mature was:

$$\Pr(\text{Age}{=}x) = r_{m(x)} \qquad (11)$$

where $r_{m(x)}$ represented the proportion of known-aged males that attained sexual maturity at age x (Table 7). Age point estimates, X, were obtained from the age probability density function (11) by:

$$X = \sum_{x=10.5}^{17.5} x \cdot \Pr(\text{Age} = x) \qquad (12)$$

which coincided with the mean age at onset of sexual maturity. Since most males attained sexual maturity between 11.5 and 17.5 years of age, the point estimates were considered accurate to within ±3 years.

Development of the male dorsal fin continued for about six years following the onset of sexual maturity, at which point males were referred to as physically mature (Section 3.3.2). Males that were sexually, but not physically, mature when first seen were aged in reference to the year they attained physical maturity. The probability that a male was aged x in the year it attained physical maturity was:

$$\Pr(\text{Age} = x + 6) = r_{m(x)} \qquad (13)$$

and the corresponding point estimate, which coincided with the mean age at physical maturity, was obtained by equation (12). Since complete development of the fin actually required 4–8 years (Section 3.3.2), ages estimated in this manner were considered accurate to within ±5 years.

We had no way of accurately ageing males that were physically mature when first encountered. Thus, their minimum ages were estimated by assuming that they had attained physical maturity in the year they were first seen. In some cases, the minimum ages of males were based on photographs taken prior to the start of the study. Minimum ages were denoted as X+.

3.1.4 Longevity

The point estimated ages of all individuals are given in Appendix Tables A and B in Bigg *et al.* (1990). The superscripts accompanying the age estimates in the Appendix Tables correspond to the ageing methods summarized in Table 4, and therefore indicate the accuracy of the age estimates. Although the age point estimates, particularly for older individuals, were subject to considerable inaccuracies (Table 4), these inaccuracies tended to negate one another at the population level. For example, while the ages of females that matured atypically early and/or whose progeny exhibited above average survival were overestimated, the ages of females that matured atypically late and/or whose progeny exhibited below average survival were underestimated. In effect, the inaccuracies at the individual level represented imprecision at the population level. This imprecision was accounted for in subsequent age-specific analyses by: (1) utilizing the probability density functions rather than the point estimates; or (2) grouping data into age categories, the width of which reflected the accuracy of the age estimates.

The ages of all females that were mature when the study began or matured during the study are shown in Fig. 5. Approximately half of the females attained ages of 35 years or greater during the study. Eight females (3 in uncropped and 5 in cropped pods), six of which were still alive in 1987, attained ages of greater than 60 years. The two oldest females were estimated to have been 76.5 and 77.5 years of age when last seen in 1987. Thus, maximum longevity of females likely extended to at least 80 years. The age probability density functions (4) for the oldest females indicated that several were possibly as old as 90 years of age (see also Section 4.2.6).

Table 4

Summary of the ageing methods used and the nominal accuracy of the age estimates. The letters denoting the basis of age estimate correspond with the superscripts accompanying the age estimates given in Appendix Tables A and B (Bigg *et al.*, 1990).

	Cropped			Uncropped			
Basis of age estimate	?	M	F	?	M	F	Acc.
(A) Year of birth known	34	8	7	48	6	7	±0.5
(B) Year of birth estimated based on its size	1	3	3	27	1	3	±0.5
	1	3	7	1	6	4	±1
	0	0	1	0	2	2	±2
(C) Year of first calf known	-	-	4	-	-	9	±3
(D) Year of first calf estimated from age of oldest known calf	-	-	11	-	-	37	±3-10
(E) Year of last calf known	-	-	8	-	-	-	±10
(F) Mean birth date of all calves	-	-	17	-	-	-	±5-12
(G) Year of sexual maturity known	-	8	-	-	19	-	±3
(H) Year of physical maturity known	-	5	-	-	5	-	±5
(I) Physically mature when first encountered	-	5	-	-	19	-	min.

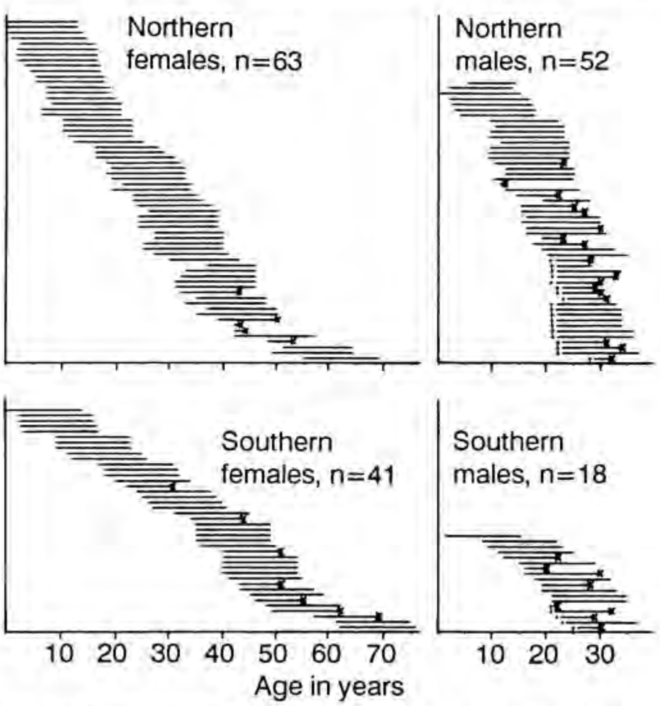

Fig. 5. Age point estimates for all mature individuals during the study in (a) the southern community and (b) the northern community. The Xs denote deaths and +s minimum ages.

Maximum longevity of males could not be directly established as only the minimum ages of the oldest males were ascertained. Nevertheless, it appeared that males were not as long-lived as females. Even if all minimum aged males are included, less than 25% of mature males attained ages of 35 years compared with 50% of mature females (Fig. 5). However, at least seven males, and possibly as many as 32, attained ages of 35 years or greater during the study. Maximum longevity of males therefore likely extended beyond 40 years. Life tables suggested that male longevity was likely on the order of 50-60 years (Section 4.2.6).

Our age estimates were considerably greater than those previously estimated from teeth. Mitchell (1975) reviewed earlier literature and noted that the oldest recorded killer whale, a female, was estimated to have been 25 years of age based on the counts of dentinal growth layer groups (GLGs) (Caldwell and Brown, 1964). Participants at the IWC Ageing Workshop (IWC, 1980) counted up to 29 GLGs in both the dentine and cementum in the killer whale teeth examined. Mitchell and Baker (1980), using a combination of dentinal and cemental GLGs, reported 35 GLGs in a reputedly very old male, known to locals of Twofold Bay, Australia, as 'Old Tom'. Christensen (1982; 1984) counted a maximum of 34 and 32 dentinal GLGs in a sample of 68 females and 53 males respectively collected off Norway.

The discrepancy between our age estimates and those based on dental laminations can probably be attributed to the poor definition of GLGs in older specimens. IWC (1980) concluded that killer whale age estimates based on dentinal layers were both inaccurate and imprecise. Myrick *et al.* (1988) examined labelled killer whale teeth with known histories and concluded that dentinal GLGs beyond about 20 years of age were too poorly defined to count and that cementum deposits were too thin to count.

Our estimates of the longevity of killer whales were of the same magnitude as the theoretical longevity of 72–81 years predicted for killer whales from intra-specific allometric relationships (Sacher, 1980). The longevity of killer whales was also comparable to that of pilot whales (*Globicephala* spp.). Based on cemental GLGs, Kasuya and Marsh (1984) found maximum ages of 63 and 46 years respectively for female and male short-finned pilot whales (*G. macrorhynchus*) taken off Japan. Similarly, maximum ages of up to 56.5 and 35.5 years were reported for female and male long-finned pilot whales (*G. melas*) taken off Newfoundland (Kasuya, Sergeant and Tanaka, 1988).

3.2 Calving and mating seasons

Information on the seasonality of calving in the study area was compiled from three sources: (1) observed births; (2) neonate strandings; and (3) the appearance of newborn calves between consecutive encounters.

We have never witnessed an animal giving birth in the wild. However, Jacobsen (1980), studying the northern community, observed the birth of a calf on 20 September 1980. Emery (1960) also gave an account of the birth of a set of twins in March 1949, off eastern Vancouver Island. In addition, a new born calf measuring 257cm was taken in the live-capture fishery in February 1967 (Wolman, National Marine Mammal Laboratory, Seattle, Wash., pers. comm.) and another calf was born in February to a female being held during the live-capture fishery (Newby, formerly University of Washington, Seattle, Wash., pers. comm.).

The timing of neonate strandings also provided information on the seasonality of calving. Carl (1946) reported a stranded calf found on 28 September 1944. In addition, eight stranded calves were recovered from the study area during 1973–87 (Table 5). Six of these, measuring 218 to 250cm in length, had umbilical stubs indicating they were neonates. Since the remaining three calves fell within the same length range, they were also considered neonates.

The dates of birth of the majority of calves born during the study were not known other than they were born sometime between summer field seasons. In some cases, however, newborn calves appeared between closely spaced consecutive encounters and the interval over which it was born could be delineated. The exact month of birth was established for four calves and the birth of eight others

Table 5

Information on neonate strandings recovered in the study area.

Date	Location	Form	Sex	Lcm	Condn	Umb.	Breathed	Source
28.09.44	Cherry Pt		F	246	fresh		stillborn?	1
	Lasqueti I.	T	M	244	fresh		stillborn?	2
09.05.76	Long Bch	R	M	250	fresh	yes		2
05.11.76	Radar Bch		M	226	fresh	yes		2
31.03.78	Oyster Bay		M	225	1-2 mo		yes	2
04.10.78	Victoria		M	221	3 wks	yes		3
15.11.83	Seattle		F	218	fresh	yes	yes	4
07.10.86	Tsawassen	R	M	226	fresh	yes	yes	2
13.11.87	Ucluelet	R	M	245	fresh	yes	yes	2

Key: T=Transient; R=Resident; L=Length; Condn=Condition; Umb.=Umbilicus; Y=yes. Sources:- 1=Carl, 1946; 2=Pacific Biological Station; 3=R. Baird pers. comm.; 4=T. Gornall pers. comm.

could be assigned to one of several months. The latter births were amortized over the interval in question. For example, a calf that was born between 1 December and 15 January was tallied as 0.67 births in December and 0.33 births in January.

Each source of data indicated that calving was diffusely seasonal with most births occurring between fall and spring (Fig. 6). The bimodal appearance of the frequency distribution was probably an artifact: the paucity of mid-winter births was attributable to a reduced sampling effort and the relative frequency of the study births during the study in fall months was undoubtedly exaggerated as this represented the end of the field season.

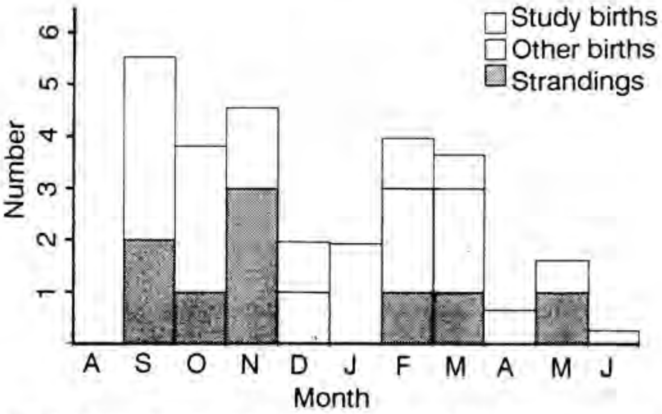

Fig. 6. Seasonality of calving in the study area. Data sources were: (1) the appearance of neonates between consecutive encounters during the study; (2) other observations of births; and (3) the timing of neonate strandings (see Section 3.2).

Using all three sources of data, the mean birth date was calculated as 16 December. In view of the aforementioned biases, the birth dates based on the appearance of calves between encounters were excluded and the mean birth date recalculated as 1 January. We considered the latter mean date more accurate and defined the calving season as the six months centered on this date, namely October-March. This period accounted for 70% of all births shown in Fig. 6. Assuming that the gestation period was 514.5 days (Walker, Cornell, Dahl, Czekala, Dargen, Joseph, Hsueh and Lasley, 1988), we estimated that mating occurred in May-October, with a mean date of conception in late-July or early-August.

Additional observations also suggested a winter calving season. Pike and MacAskie (1969) noted that very small calves were most prevalent in waters off British Columbia in winter and early spring, which they took to indicate a winter peak in parturition. A neonate with attached umbilicus stranded in Astoria, Oregon on 9 March 1987 (D. Duffield, Portland State University, Oregon, pers. comm.) and a 1–2 month old calf (260cm in length with most teeth erupted) was found stranded in California on 21 April 1985 (Heyning, 1988). Lengths of foetuses collected off Japan indicated a peak in mating during May-July and a probable gestation period of 16 months (Nishiwaki and Handa, 1958), which implied a September-November calving season. The available data therefore suggested that the reproductive cycle was synchronized throughout the North Pacific.

It is unclear to what extent the reproductive cycle varies in other regions. Term-size foetuses were prevalent in the Antarctic catches taken in January-March (Anderson, 1982), which suggested a peak in parturition in about January-April (i.e. late austral summer). The bimodal length frequency of the Antarctic foetuses also indicated a gestation period of greater than 12 months. The Norwegian data were ambiguous (see also Anderson, 1982). Based on foetal lengths, Christensen (1982; 1984) calculated that conceptions peaked during September-January, but was unable to ascertain the gestation period. Applying a gestation period of 514.5 days (Walker *et al.*, 1988) to the Norwegian data suggests a February-June calving season, but the few term-sized foetuses collected were taken in August-November. The seasonality of calf sightings in British and Irish waters suggested calves were born mainly between November-February (Evans, 1988).

3.3 Age at maturity

3.3.1 Females

In the cetacean literature, female age at maturity has been variously measured as the age at first ovulation, age at first pregnancy or the age at first parturition. We defined sexual maturity as the age at which females gave birth to their first viable calf (i.e. calves that survived to at least 0.5 years of age). The analysis was restricted to viable calves because many neonates likely died prior to age 0.5 years before being identified (Section 3.6.2). Moreover, since the age of the first viable birth represented the age at which females first contributed to recruitment, this was the most pertinent parameter in the population model.

Age at first birth was established based on the ages at which known-aged females gave birth to their first viable calves. In a few cases where the ages of females were only known to within ±1 year, data were amortized over the two-year period. For example, a female born during either the 1972 or 1973 calving seasons was tallied as half a 14 and half a 15 year old during the 1987 calving season.

Fourteen known-aged females gave birth to their first viable calves during the study. Of the 24 known-aged females monitored to 11 years of age, none had given birth. Conversely, 4 of 5 females monitored to 16 years of age, the maximum age attained by known-aged females, had given birth. Thus, females typically gave birth to their first viable calf between 12 and 16 years of age.

DeMaster (1984) reviewed various procedures for estimating the mean age at maturity. The simplest method was to calculate the mean of the ages at which females matured. The mean of the ages at which the six known-aged females in cropped pods first gave birth was

Table 6

Rate and mean of maturation (i.e. birth of first viable calf) of known-aged females in cropped and uncropped pods combined. Computations and notation follow DeMaster (1978).

x	$n_{(x)}$	$y_{(x)}$	$z_{(x)}$	$r_{(x)}$	$x\,r_{(x)}$
10	25.0	0	0	0	0
11	24.0	0	0	0	0
12	24.0	3.0	0.125	0.125	1.500
13	19.0	4.0	0.211	0.086	1.118
14	15.0	6.0	0.400	0.189	2.646
15	11.5	7.5	0.652	0.252	3.780
16	5.0	4.0	0.800	0.148	2.368
17	-	-	0.900^1	0.100	1.700
18	-	-	1.000^1	0.100	1.800

$\overline{X}$ mean age at first birth $[\Sigma\, x\, r_{(x)}]$ =14.91

x age

$n_{(x)}$ total number of known-aged females

$y_{(x)}$ number of females that had given birth to viable calves

$z_{(x)}$ proportion of females mature at age x $[y_{(x)}/n_{(x)}]$

$r_{(x)}$ proportion of females maturing at age x $[z_{(x)}-z_{(x-1)}]$

[1] Assumed that one known-aged female (G29) that had not given birth at age 16.5-17.5 years would give birth at age 17.5-18.5 years.

14.33 years (SE=0.432) and the mean for the eight females in uncropped pods was 13.19 years (SE=0.357). The means were not significantly different (t=2.043; P=0.076) so data were pooled for subsequent analyses. Although these means provided a valid comparison between cropped and uncropped pods, they tended to underestimate the true mean age at first birth. This bias was due to the decline in the sample-size of known-aged females with age (Table 6), such that females that matured at an early age were more likely to have matured during the study than those that matured at an older age.

The age by which 50% of the females were mature has often been reported as the mean age at maturity. In fact, this represents the median age at maturity and coincides with the mean only when the maturation curve is symmetric. The median age of first birth was interpolated as 14.40 years (14.64 and 13.77 years in cropped and uncropped pods; Fig. 7). Kasuya's (in DeMaster, 1984) small sample summation method gave similar values: 14.43 years overall (14.51 and 14.03 years in cropped and uncropped pods). Since the medians were based on the proportion of females mature at a given age, they were not subject to the aforementioned sample biases.

The bias introduced by diminishing sample sizes with age can be avoided by using DeMaster's (1978) method to estimate mean age at maturity. We should note that that method was more appropriate in the present case than DeMaster's (1981) method specifically designed to estimate the mean age at first birth. This was because we knew the complete calving histories of all known-aged females, which in essence satisfied DeMaster's (1978) assumption that 'animals that have not ovulated at age x have not ovulated before age x...[and] ... animals that have ovulated at age x will ovulate every year thereafter'.

Since DeMaster's (1978) method required that the sample span the entire indeterminate period, we had to assume that the one known-aged female (G29) that had not given birth by age 16.5-17.5 years would have done so in the following year.[1] Although this tended to underestimate the true mean, the bias increased by only 0.2 years for each additional year the animal remained barren. The overall mean age at first birth was calculated as 14.91 years (Table 6). The mean ages at first birth were similar in cropped and uncropped pods, 15.00 and 14.57 years respectively, but could not be formally compared due to the interdependence of the observations (i.e. the status of the same individual over several years was used in the analysis). These estimates were considered the most accurate indicator of mean age at first birth.

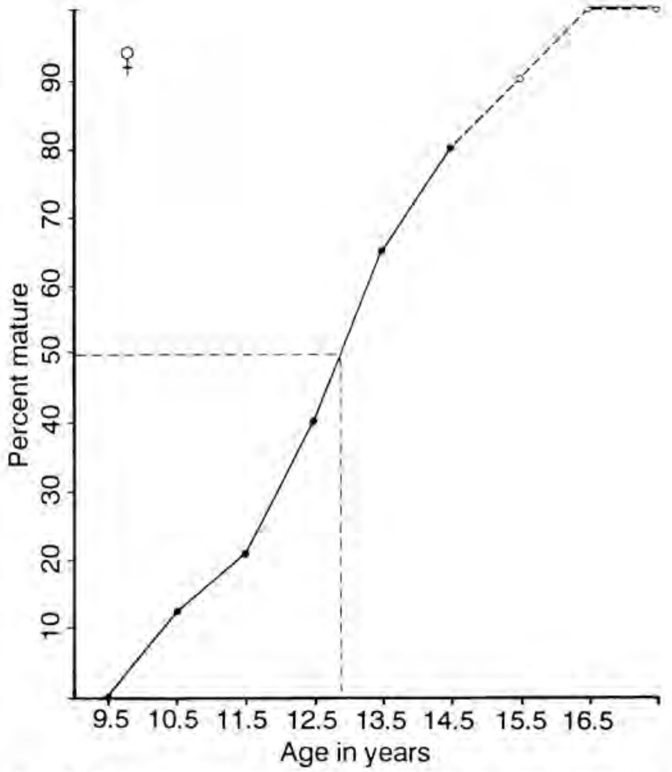

Fig. 7. Rate of maturation ($MAT_{f(x)}$) of known-aged females in cropped and uncropped pods combined based on age at birth of the first viable calf. Note that the data are plotted at the pivotal ages at which calves were considered viable.

Assuming that the gestation period was 514.5 days (Walker *et al.*, 1988), we estimated that the first viable calf was conceived at 10.6–16.6 (mean=13.5) years of age. However, because neonate mortality was high (Section 3.6.2), the first conception may have occurred at a somewhat younger age. For example, if we assume that mortality in the first six months was 43% for all calves (Section 3.6.2) and the calving interval at 15 years of age was 4.3 years (equation (24)), the mean age at first birth of a calf, viable or non-viable, would be 13.1 years, and the mean age of conception 11.7 years. Considering that pubescent females may ovulate several times before conceiving (IWC, 1982), females may ovulate at an even earlier age.

Collections in the Antarctic indicate that females first became pregnant at about 16ft (4.9m) in length (IWC, 1982). Similarly, Christensen (1982; 1984) found that females off Norway first became pregnant at 15–16ft (4.6–4.9m) in length and suggested that this corresponded to 6–8 years of age. However, no data collaborating age and reproductive condition were provided. Christensen's (1982; 1984) growth curves indicated that females measuring 15–16ft in length actually ranged in age from 5 to 22 years (mean=15.0 years).

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[1] Data collected subsequently indicated that G29 did give birth in the following year, 1988.

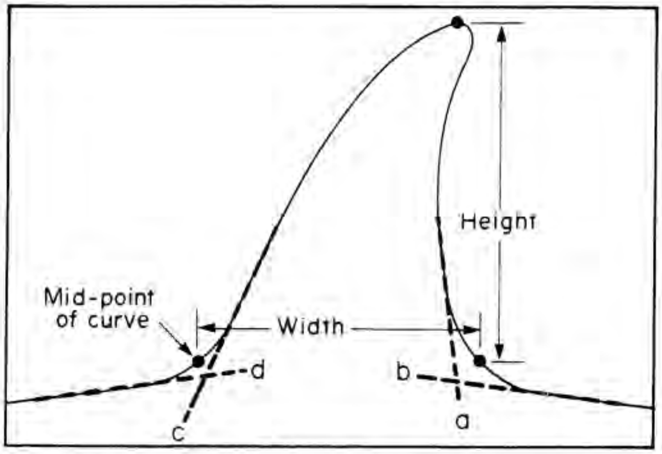

Fig. 8. Schematic of killer whale dorsal fin showing measurements used to derive height to width ratios (HWRs).

Age of maturation of female killer whales was slightly greater than in short-finned pilot whales (*G. macrorhynchus*), which first ovulate at 7–12 years of age (Kasuya and Marsh, 1984). Long-finned pilot whales (*G. melas*) first conceive at about 6–7 years of age (Sergeant, 1962; Kasuya, Sergeant and Tanaka, 1988).

3.3.2 Males

Mature male killer whales can be distinguished from mature females and juveniles by their tall dorsal fins. The adult male dorsal fin attains a height of about 1.5m compared to 0.9m in females (Bigg, 1982). The age at maturity of males was assessed based on the height to width ratio (HWR) of this secondary sexual characteristic (Fig. 8).

Fig. 9 shows the pattern of growth of the dorsal fin HWR for eight known-aged animals of each sex. Representative HWRs for each individual in a particular year were obtained by averaging 5–10 measurements (Fig. 8) from photographs in which parallax error appeared to be minimal.

The growth of the female dorsal fin was asymptotic with age, X, and could be described by a von Bertalanffy curve:

$$HWR = A \cdot \{1-1/3\ e^{(-K.[X-I])}\}^3 \qquad (14)$$

with an asymptote, A, of 1.219 (SE=0.007), K of 0.182 (SE=0.008) and I of –7.658 (SE=0.269). The mean HWR for 15 older reproductive and post-reproductive females ranged from 1.11–1.34 with a mean of 1.182 (SE=0.019), which was not significantly different ($P>0.10$) from the asymptote of the von Bertalanffy curve. Thus, growth of the female dorsal fin ceased or became isometric at about 10 years of age. The HWR of females never exceeded 1.40.

The growth of the male dorsal fin followed a different pattern (Fig. 9). The increase in HWR with age was initially rapid but slowed by about 4–7 years of age. Growth during this phase could be described by a von Bertalanffy curve with A=1.157 (SE=0.012), K=0.760 (SE=0.160) and I=–2.346 (SE=0.466). However, between 8 and 15 years of age, HWR increased linearly with age, X:

$$HWR = 1.014 + 0.027 \cdot X \ (P<0.001,\ r^2=0.95) \qquad (15)$$

By 10.5 to 17.5 years of age, the HWR surpassed 1.40, at which point males could be readily distinguished from juveniles and adult females. We thus defined the year in which the HWR attained a value of 1.40 as the onset of sexual maturity. Being a secondary sexual characteristic, the development of the dorsal fin probably coincided with the onset of spermatogenesis. However, since the male dorsal fin actually began to develop 2–3 years prior to becoming distinguishable from female and juvenile fins, some sperm production probably occurred several years prior to that which we defined as the onset of sexual maturity.

After attaining an HWR of 1.40, growth of the male dorsal fin continued but was asymptotic (Fig. 10) and conformed to a von Bertalanffy curve with A=1.743 (SE=0.030), K=0.318 (SE=0.051) and I=-4.728 (SE=0.671). The mean HWR of ten randomly selected older males exhibiting stable HWRs ranged from 1.63 to 1.83 with a mean of 1.72 (SE=0.023), which was not significantly different from the asymptote of the growth curve ($P>0.50$). Thus, by about six years following the onset of sexual maturity (HWR=1.40) the increase in the dorsal fin HWR was 90% complete and was not discernible from that of older males. At that point, males were referred to as physically mature.

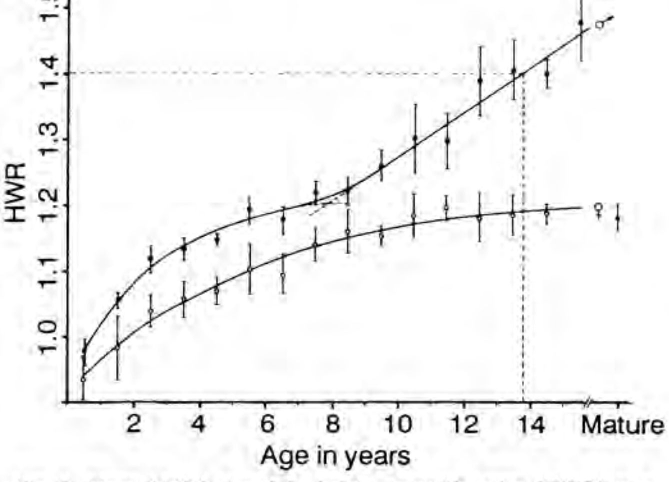

Fig. 9. Mean (±SE) dorsal fin height to width ratios (HWR) as a function of age for 8 known-aged animals of each sex: females (bottom) and males (top). The trend lines represent a linear regression and von Bertalanffy curve, both fitted by least squares criterion. The triangle represents the mean (±SE) for 15 older reproductive and post-reproductive females.

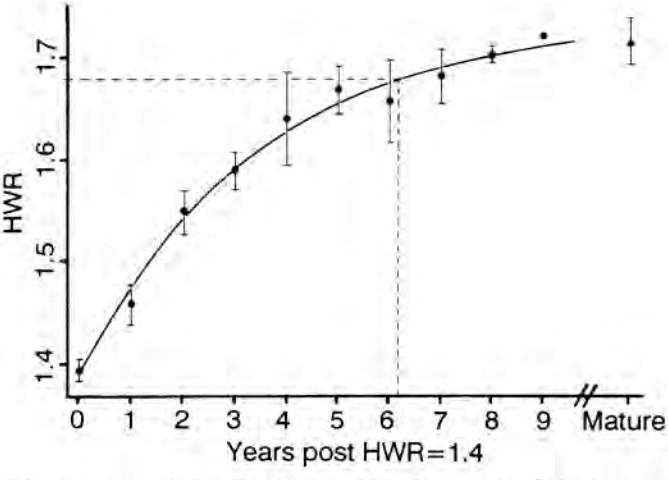

Fig. 10. Mean (±SE) dorsal fin height to width ratios (HWR) as a function of the number of years following the onset of sexual maturity (i.e. the first year the HWR attained 1.40). The triangle represents the mean (±SE) for 10 older physically mature males.

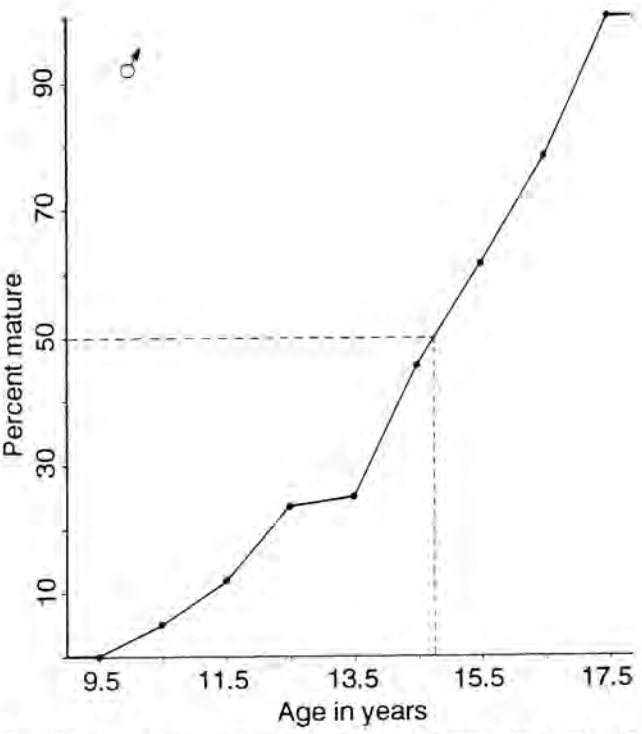

Fig. 11. Rate of maturation ($MAT_{m(x)}$) of known-aged males in cropped and uncropped pods combined based on the first year that the HWR attained 1.40.

The mean and median ages at sexual maturity of males were calculated in the same manner as the age at first birth of females (Section 3.3.1). Because only one known-aged male matured (at age 14.5 years) in cropped pods, data for cropped and uncropped pods were pooled. Known-aged males attained sexual maturity between 10.5 and 17.5 years of age and 50% had matured by 14.78 years of age (Fig. 11). A nearly identical value, 14.62 years, was obtained using Kasuya's (DeMaster, 1978) small sample procedure. Using DeMaster's (1978) method, the mean age at onset of sexual maturity was estimated at 15.00 years (Table 7). Since the dorsal fin continued to develop for an additional 6 years, the mean age at physical maturity was estimated at 21.00 years.

Jonsgård and Lyshoel (1970) examined the testes of three killer whales taken off Norway and suggested that spermatogenesis first occurred at about 19ft (5.8m) in length. Based on changes in testes weight, Mikhalev, Ivashin, Savusin and Zelenya (1981) reported that males taken in the Southern Hemisphere matured at 21ft (6.4m) in length whereas Bigg (1982), noting that the sharpest increase in testis weight occurred between 18 (5.5m) and 19–20ft (5.8–6.1m), interpreted the data as indicating maturity at 19–20ft. According to Christensen's (1982, 1984) growth curve, males measuring 19–20ft were generally aged 15–18 years (mean=19.8 years; range 13–32 years).

In comparison, Kasuya and Marsh (1984) found that the testes of short-finned pilot whales (*G. macrorhynchus*) were typically functional by 15.8 years of age. However, they also noted that testis weight continued to increase to about 25 years of age and thus postulated that males attained social maturity many years after functional maturity.

Table 7

Rate and mean of age of maturation (i.e. first year HWR ≥ 1.40 of known-aged males in cropped and uncropped pods combined. Calculations and notation as per Table 6.

x	$n_{(x)}$	$y_{(x)}$	$z_{(x)}$	$r_{(x)}$	$x.r_{(x)}$
9.5	23.0	0	0	0	0
10.5	21.0	1.0	0.048	0.048	0.504
11.5	17.0	2.0	0.118	0.070	0.805
12.5	17.0	4.0	0.235	0.117	1.463
13.5	14.0	3.5	0.250	0.015	0.203
14.5	11.0	5.0	0.455	0.205	2.973
15.5	6.5	4.0	0.615	0.160	2.480
16.5	4.5	3.5	0.778	0.163	2.690
17.5	0.5	0.5	1.000	0.222	3.885
					$\overline{X}=15.00$

3.4 Gross reproductive rates

Reproductive terminology has not been used consistently in the literature. We defined the fecundity rate as the proportion of mature females that gave birth to viable calves each year; the fertility rate as proportion of mature females that gave birth to either viable or non-viable calves each year; and the pregnancy rate as the proportion of mature females pregnant at a specified time. We focused on fecundity, as it represented the net contribution to recruitment and was therefore the most pertinent parameter in the population model.

3.4.1 Multiplets

A total of 134 calves were born during the study. Except for two sets of twins (one in both cropped and uncropped pods), females gave birth to single calves. This represented a twinning frequency of 1.5% (SE=1.06%). In the first set, one died between 1.5 and 2.5 years of age whereas its sibling was still alive when last seen at age 3.5 in 1987; and in the second set, both were still alive when last seen at age 7.5 years in 1987. Emery (1960) also described the birth of a set of twins in a shallow lagoon off eastern Vancouver Island in 1949.

These observations apparently represent the first of viable multiplets in cetaceans (IWC, 1984). *In utero* multiplet frequencies ranging from 0.57% to 2.3% have been reported in baleen whales, but it was assumed that mature delivery of these would have been unlikely (IWC, 1984). Gambell (1972) reported *in utero* twinning frequencies of about 0.5% in sperm whales. Multiplets have not been observed in long-term field studies of *Tursiops* or *Stenella* (Scott and Wells *in* IWC, 1984). Similarly, Kasuya and Marsh (1984) reported single foetuses in all of the 141 short-finned pilot whale (*G. macrorhynchus*) pregnancies examined. The twinning frequency in killer whales was similar to the 1–2% average reported for humans (Benirschke *in* IWC, 1984).

3.4.2 Calving intervals

The interval between successive births provided one measure of the rate of calf production. The intervals between 77 viable births (28 in cropped and 49 in uncropped pods) were established. These included the intervals between all viable calves born during the study as well as several intervals between calves born 1–2 years prior to the start of the study and calves born early in the study. The latter intervals were included because the gestation period was 514.5 days (Walker *et al.* 1988), so that females could not have given birth to viable calves that died in the intervening years.

Calving intervals ranged from 2–12 (mean=5.86) years in cropped pods and 2–10 (mean=5.02) years in uncropped pods (Fig. 12). The difference between the means was marginally significant (ANOVA; F=2.87, P=0.095) and was largely attributable to the two 12-year intervals in the cropped pods. Data were therefore pooled giving an overall mean calving interval of 5.32 years (SE=0.241). When the two 0-year intervals are included to account for the two sets of twins, the mean calving interval was 5.19 years (SE=0.253).

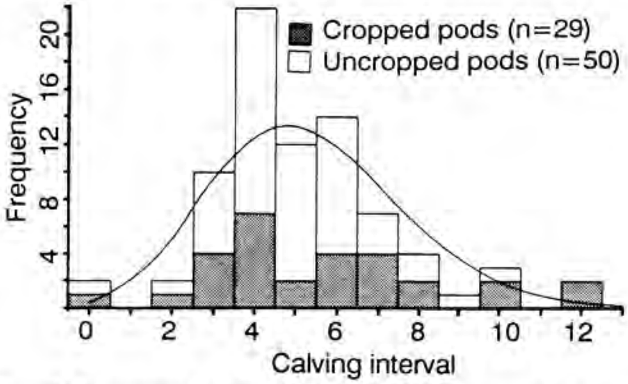

Fig. 12. Frequency distribution of calving intervals recorded during the study. The two zero-intervals represent the birth of twins. The trend line represents a Poisson distribution.

The relative frequencies of the calving intervals followed a Poisson distribution (chi-squared=12.5; P=0.160), which implied that females gave birth at random intervals rather than conforming to a fixed calving schedule.

3.4.3 Fecundity rates

One measure of the fecundity rate of females that calved during the study, $\mathrm{FEC_c}$ is:

$$\mathrm{FEC_c}' = \mathrm{CI}^{-1} \qquad (16)$$

where CI represents the mean calving interval (including the 0– year intervals for twins). This gave fecundity rates of 0.177 and 0.203 for cropped and uncropped pods respectively and an overall fecundity rate of 0.193. However, $\mathrm{FEC_c}'$ underestimates the true fecundity of reproductive females. Females are defined as being reproductive between the birth of their first and last calves. The bias in $\mathrm{FEC_c}'$ arises because, by definition, females give birth in both the first and last year of their reproductive lifespan (RL) such that the number of calves born is one greater than the number of calving intervals. Thus, an unbiased estimate of $\mathrm{FEC_c}$ is:

$$\mathrm{FEC_c} = (\mathrm{RL}\cdot\mathrm{CI}^{-1} + 1)/\mathrm{RL} \qquad (17)$$

For an RL value of 25.5 years (Section 3.4.4), $\mathrm{FEC_c}$ was estimated at 0.216 in cropped pods, 0.242 in uncropped pods and 0.232 overall.

Alternatively, the fecundity rate of all mature females, $\mathrm{FEC_t}$, is given by:

$$\mathrm{FEC_t} = \sum_{i=1}^{n} \mathrm{NC_i} \,/ \sum_{i=1}^{n} \mathrm{NY_i} \qquad (18)$$

where $\mathrm{NC_i}$ is the total number of calves born to the ith mature female during the study, $\mathrm{NY_i}$ the total number of years the ith mature female was monitored and n the total number of mature females in the population. Mature females are defined as those that had given birth to viable calves. The variance of $\mathrm{FEC_t}$ is:

$$\mathrm{Var(FEC_t)} = \mathrm{FEC_t}\,(1 - \mathrm{FEC_t}) \sum_{i=1}^{n} \mathrm{NY_i}^{-1} \qquad (19)$$

The 46 mature females in cropped pods were monitored for a combined total of 520 years (mean=11.3 years) during which they gave birth to 50 viable calves. This represents a fecundity rate of 0.096 (SE=0.0129). The 56 mature females in uncropped pods were monitored for a combined total of 544 years (mean=9.7 years) during which they were known to have given birth to 84 viable calves. An additional 1.2 viable calves in uncropped pods were estimated to have died prior to being identified (Section 3.6.3). This represents a fecundity rate of 0.157 (SE=0.0155). Fecundity rates in cropped and uncropped pods were significantly different (P<0.01). Also, both were considered significantly lower than their respective $\mathrm{FEC_c}$s. Although $\mathrm{FEC_t}$ and $\mathrm{FEC_c}$ could not be formally compared, the $\mathrm{FEC_t}$ values were significantly lower than the respective $\mathrm{FEC_c}'$ values (P<0.01), and the latter were lower than the corresponding $\mathrm{FEC_c}$s.

The disparity between $\mathrm{FEC_c}$ and $\mathrm{FEC_t}$ resulted because not all mature females were equally productive. Indeed, there were a number of mature females in both cropped and uncropped pods that did not give birth during the study and others that gave birth to their last calf early in the study. We attribute this to reproductive senescence. With one exception (K40 – a female that had not given birth by 20.5–24.5 years of age), all of the young mature females were productive (Section 3.5.3). Conversely, the unproductive females tended to be the oldest females and all had older progeny, indicating that they had been productive in the past.

The fecundity rates of reproductive females, $\mathrm{FEC_r}$, were calculated using equation (18) by excluding all post-reproductive females. Post-reproductive females were classified as mature females that had not given birth for at least 10 years. This gave $\mathrm{FEC_r}$s of 0.198 (SE=0.0251) and 0.224 (SE=0.0215) for cropped and uncropped pods, respectively. These values were not significantly different (P>0.50), so data were pooled giving an overall $\mathrm{FEC_r}$ of 0.214 (SE=0.0164). The $\mathrm{FEC_r}$s were similar and not significantly different (P>0.30) than the corresponding $\mathrm{FEC_c}$s. The $\mathrm{FEC_c}$ values were about 8–10% greater than the $\mathrm{FEC_r}$s, as the former tended to overestimate fecundity because shorter calving intervals were more likely to have been completed during the study than longer calving intervals. We therefore consider the overall $\mathrm{FEC_r}$ of 0.214 as the most accurate measure of the fecundity rate of reproductive females.

The disparity of the $\mathrm{FEC_t}$s between cropped and uncropped pods could be attributed to differences in the ratios of reproductive to post-reproductive females. In uncropped pods, a weighted mean of 66.1% of mature females were reproductive – remarkably close to the 66.9% expected in a stable population (Section 4.2.6). In contrast, only 45.7% of the mature females in cropped pods were reproductive. This anomaly is discussed in Section 4.3.3. Based on the overall $\mathrm{FEC_r}$ of 0.214, and assuming that 66.9% of mature females were reproductive, the $\mathrm{FEC_t}$ for a stable population was estimated at 0.143, which does not differ significantly from the observed value of 0.154 in uncropped pods (P>0.40).

3.4.4 Reproductive lifespan

The reproductive lifespan is defined as the span between the onset of sexual maturity and onset of reproductive senescence (i.e. the interval between the birth of the first and last viable calf). This parameter could not be estimated directly because a number of females that gave birth prior to the start of the study were still reproductive at the end of the study, which indicated that the reproductive lifespan exceeded the 15 year duration of our study.

The youngest female that gave birth was 12.0 years of age and the oldest was estimated to have been 41.7 years of age (several females greater than 40 years of age gave birth). This implies that the reproductive lifespan spanned up to 30 years. The maximum number of calves presumed to have been born to females provided another measure of the length of the reproductive lifespan. Nine females had five offspring and one had six (Bigg *et al.*, 1990). Given a mean calving interval of 5.32 years (Section 3.4.2), this suggests that the reproductive lifespan is on the order of 21–27 years.

An estimate of the mean reproductive lifespan, RL, is given by:

$$RL = NC/FEC_r \qquad (20)$$

where NC denotes the mean number of calves born to a female over her RL. NC cannot be directly estimated because RL exceeded the duration of our study. However, if it is assumed that the reproductive females in uncropped pods were randomly distributed at various stages of their RL, they would, on average, have given birth to about half their total progeny. NC can thus be estimated by doubling the mean number of offspring born to females, including those born prior to start of the study (Bigg *et al.*, 1990). Females in cropped pods were excluded from the analysis since they may have had progeny removed prior to the start of the study.

The 45 reproductive females in uncropped pods had a mean of 2.73 offspring, which gave an NC of 5.47. On the one hand, this is an underestimate because (1) some progeny may have died prior to the start of the study; and (2) the age-composition of females in an increasing population would be skewed toward younger females (Section 4.2.7). On the other hand, it is an overestimate because fecundity tended to decline with age such that more than half of progeny would be born by the midpoint of the reproductive lifespan (Section 3.5.2). Assuming these biases cancel, the mean RL is estimated to be 25.5 years.

A more precise estimate of RL is obtained and reproductive senescence discussed in greater detail in Section 3.5.3.

3.4.5 Fertility and pregnancy rates

Because some calves die at birth or shortly thereafter, fertility rates, FER, tend to be greater than fecundity rates, FEC:

$$FER = FEC / 1\text{-}MR_n \qquad (21)$$

depending on the magnitude of neonate mortality, MR_n. Neonate mortality is defined as that occurring before 0.5 years of age. Although precise estimates could not be obtained, the available data indicate that MR_n is of the order of 43% (Section 3.6.2). Substituting this value and the overall FEC_r estimate of 0.214 (Section 3.4.3) in equation (21), the fertility rate for reproductive females, FER_r, is 0.375. Similarly, the fertility rate of all mature females, FER_t, is 0.251.

Ignoring *in utero* mortality, the mean annual pregnancy rate, MAPR, is:

$$MAPR = FER \cdot G / 365.25 \qquad (22)$$

where G is the gestation period measured in days. Walker *et al.* (1988) measured the average gestation period for two captive killer whales at 514.5 days (16.9 months). We considered these direct measurements more reliable than the crude 12–16 month estimates based on foetal-length data (Christensen, 1982; 1984; Nishiwaki and Handa, 1958). This gives a $MAPR_r$ of 0.528 for reproductive females and a $MAPR_t$ of 0.354 for all mature females.

Due to the seasonality of calving, pregnancy rates fluctuate about the MAPR throughout the year. The proportion of females pregnant in month m, $MPR_{(m)}$, can be calculated as:

$$PR_{(m)} = MAPR \sum_{i=m}^{m+17} NB_i \Big/ \sum_{i=m}^{m+12} NB_i \qquad (23)$$

where NB_i denotes the proportion of births that occurred in the ith month, with $NB_i = NB_{i-12}$ for $i > 12$. Note that the gestation period has been rounded to 17 months. Based on the NB_is shown in Fig. 6 (excluding the study births had a negligible effect), the $MPR_{r(m)}$ for reproductive females varied from 0.409 at the end of the calving season in April to 0.614 just prior to the start of the calving season in September, which corresponds to $MPR_{t(m)}$s for all mature females of 0.274 and 0.411 (Fig. 13). The April maximum and September minimum represent 77% and 116% of the MAPR, which indicates that monthly pregnancy rates can vary by a factor of 1.5 depending on season.

Fig. 13. Seasonal variation in the estimated monthly pregnancy rates ($MPR_{(m)}$) (solid line) and the mean annual pregnancy rate (MAPR)(dashed line) for reproductive females (right scale) and all mature females (left scale).

The estimated $MAPR_t$ of 0.354 falls within the broad range of published pregnancy rates for mature killer whales. Pregnancy rates of 0.275 were reported for mature females collected in the Southern Hemisphere mainly during December-March in 1961–79 (Mikhalev *et al.*, 1981) and 0.334 for mature females collected in the Antarctic during January-March in 1979/80 (Anderson, 1982). These rates represent 78% and 94% of our $MAPR_t$ or, perhaps more appropriately (Section 3.2), 67% and 81% of our pre-calving estimate of 0.411. Christensen (1984) reported that 0.432 of mature females of known status were pregnant based on an examination of ovaries collected off Norway from 1978–80 – 122% of our $MAPR_t$. In contrast, foetuses were reported in only 0.148 of the females measuring ≥16ft (4.9m) collected annually off Norway from 1938–67 (Jonsgård and Lyshoel, 1970; modified from Bigg, 1982) – only 42% of our $MAPR_t$. However, the data given in Christensen's (1982) Appendix Tables indicated that 47% of foetuses had been overlooked by the Norweigian whalers.

Fertility rates (i.e. pregnancy rates adjusted for the gestation period) have been widely used as a measure of recruitment rates in cetacean population assessments. The foregoing analysis indicates that, for killer whales, fertility rates grossly overestimates recruitment due to the high incidence of neonate mortality. Since there is some evidence that neonate mortality may also be appreciable in other species (Section 3.6.2), fertility rates may generally overestimate recruitment. Fortunately, the net bias introduced by neglecting neonate mortality may not be serious, because fecundity and juvenile survival rates are often estimated jointly by balancing the population. There would, however, be a tendency to overestimate fecundity and underestimate juvenile survivorship. For example, Kasuya and Marsh (1984) dismissed the high neonate mortality indicated by their data, but subsequently had to inflate juvenile mortality rates to balance the population. Moreover, if neonate mortality is depensatory density dependent changes in fecundity rates may not necessarily be reflected by changes in pregnancy rates.

3.5 Age-specific reproductive rates

3.5.1 Calving intervals

Age-specific changes in the fecundity of reproductive females should be reflected by variations in calving intervals with age. Fig. 14 shows the calving intervals, CI_i, derived in Section 3.4.2, plotted as a function of the estimated ages of mothers at the midpoint of the interval, $MAGE_i$. Despite the large degree of scatter, CIs tend to increase with MAGE in both cropped and uncropped pods. The regressions were marginally significant for cropped pods ($r^2=0.118$; $P=0.073$) and highly significant for uncropped pods ($r^2=0.115$; $P=0.007$). Since the regressions were not significantly different ($P>0.50$), data were pooled giving an overall regression of:

$$CI_{(MAGE)} = 3.045 + 0.086 \cdot MAGE \qquad (24)$$

$$(r^2=0.077;\ P=0.014)$$

Although the regression indicates that the fecundity rates declined with age, it accounts for only 7.7% of the total variation in calving intervals and is thus of little predictive value and does not indicate whether the relationship was in fact linear.

3.5.2 Fecundity rates

Age-specific fecundity rates can be calculated analogous to equation (18) on a probabilistic age basis. The fecundity rate at age x, $FEC_{(x)}$, is:

$$FEC_{(x)} = \sum_{i=1}^{n} PC_{i(x)} \Big/ \sum_{i=1}^{n} PY_{i(x)} \qquad (25)$$

where $PC_{i(x)}$ denotes the probability that the ith female was aged x in each of the years she calved during the study, $PY_{i(x)}$ the probability that the ith female was aged x in each year she was monitored and n the number of mature females. The probabilities of being a given age were obtained from the age probability density functions (2) and (4). The analysis was based on all mature females in uncropped pods and females in cropped pods that were not aged on the basis of the mean birth date of their calves or the birth date of their last calf. The other females in cropped pods were excluded because age-specific reproductive parameters had been used in the derivation of their ages. The calculated $FEC_{(x)}$ values in uncropped pods were multiplied by a correction factor of 1.014 to account for the estimated 1.2 viable calves that died prior to being seen (Section 3.6.3). As in Section 3.4.3, fecundity rates were calculated for both reproductive females, $FEC_{r(x)}$, and for all mature females, $FEC_{t(x)}$.

Changes in the fecundity of reproductive females, $FEC_{r(x)}$, with age are shown in Fig. 15. Since only mature females were included in the analysis, and mature females were defined as those that had given birth to viable calves, the $FEC_{r(x)}$ values between ages 12.5 and 19.5 years warrant comment. The fecundity rate of females aged 12.5 was 1.0, as this represents the earliest age at which females gave birth, such that all females classified as mature gave birth. Fecundity rates subsequently declined to age 17.5 years as the proportion of females that matured increased, but few had given birth to a second calf. In essence, this segment of the fecundity curve represents the reciprocal of the maturation curve (Fig. 7). The secondary peak at ages 18.5–19.5 represents females that were giving birth to their second calves. By 20.5 years of age, the above patterns were obscured.

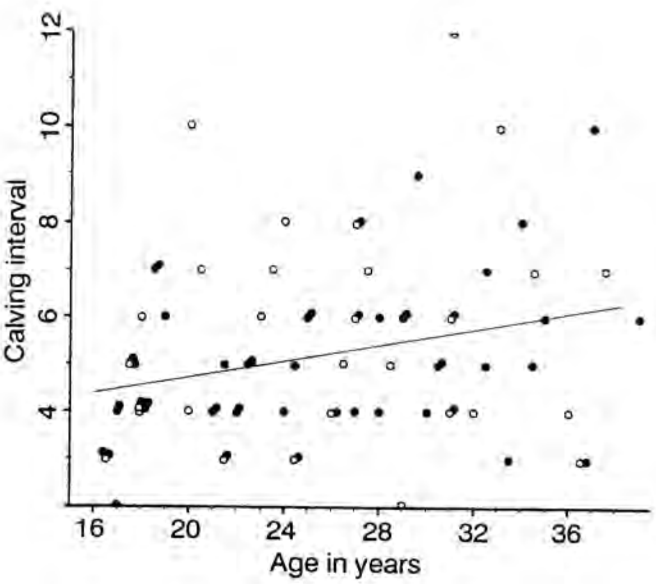

Fig. 14. Calving intervals (CI) in cropped (○) and uncropped (●) pods as a function of the estimated age of the mother at the midpoint of the calving interval (MAGE). The trend line represents a least squares linear regression fitted to pooled data.

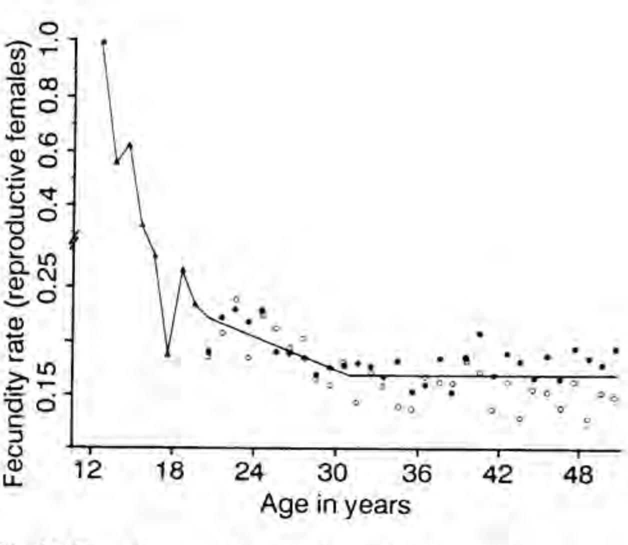

Fig. 15. Fecundity rates for reproductive females ($FEC_{r(x)}$) in both cropped (○) and uncropped (●) pods as a function of age. The trend lines represent a least squares regression fitted to pooled data for females aged 20.5–29.5 years and the mean weighted fecundity rate of females aged ≥30.5 years.

Beyond 20.5 years of age, $FEC_{r(x)}$ declined with age in both cropped ($P=0.049$) and uncropped pods ($P=0.011$), but the declines were non-linear (Fig. 15). A series of piecewise regressions (Neter and Wasserman, 1974), indicated that inflections occurred between 29.5 and 30.5 years of age. Separate regressions, with each datum weighted according to its total $PY_{(x)}$, were therefore fitted to ages 20.5 through 29.5 years and to ages greater than 29.5 years. The former regressions were significant for females in both cropped ($r^2=0.365$; $P=0.049$) and uncropped pods ($r^2=0.523$; $P=0.012$), but the regressions were not significantly different from each other ($P>0.40$). Data were therefore pooled, giving an overall regression of:

$$FEC_{r(x)} = 0.318 - 0.00487 \cdot X \quad \text{for } 20.5 \leq X \leq 29.5 \quad (26)$$
$$(r^2=0.516;\ P=0.013)$$

Beyond 30.5 years of age, there was no evidence of a further change in $FEC_{r(x)}$ with age in either cropped ($r^2=0.103$; $P=0.156$), or uncropped pods ($r^2=0.101$; $P=0.161$), or when data were pooled ($r^2=0.016$; $P=0.586$). Representative fecundity rates for females aged 30.5 years or greater were therefore calculated as the weighted mean $FEC_{r(x)}$. The means for cropped pods and uncropped pods were not significantly different ($F=0.307$; $P>0.50$), so data were pooled giving an overall weighted mean $FEC_{r(x)}$ of 0.162. It should be noted that the probabilities of reproductive females being aged greater than about 40 years were very small. Thus, the differences between the $FEC_{r(x)}$ of the oldest females in cropped and uncropped pods apparent in Fig. 15 were unimportant and had little effect in the ANOVA.

Age-specific fecundity rates for all mature females, $FEC_{t(x)}$, were calculated in the same manner (Fig. 16). For ages 12.5 through 19.5 years, $FEC_{r(x)}$ and $FEC_{t(x)}$ coincided because all of the mature females were reproductive. Beyond 20.5 years of age, $FEC_{(x)t}$ declined linearly with age for females in both cropped ($r^2=0.930$; $P<0.01$) and uncropped pods ($r^2=0.971$, $P<0.01$). The regressions were not significantly different ($P>0.50$), so data were pooled giving an overall regression of:

$$FEC_{t(x)} = 0.367 - 0.00714 \cdot X \quad \text{for } 20.5 \leq X \leq 60.5 \quad (27)$$
$$(r^2=0.971,\ P<0.01)$$

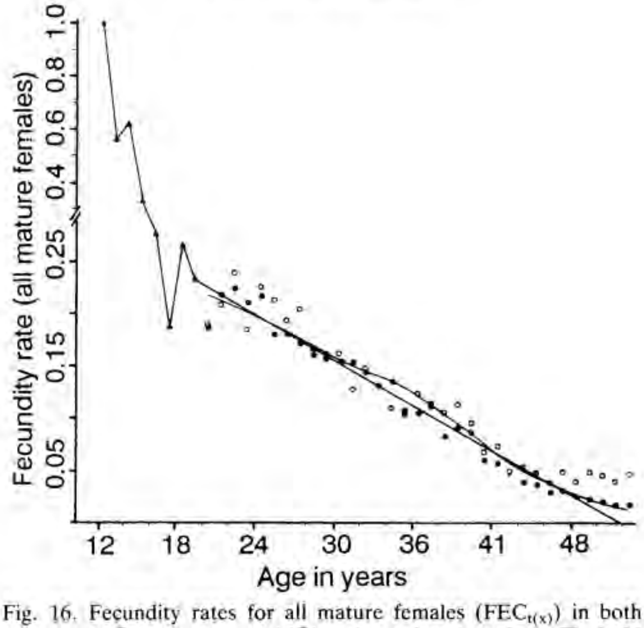

Fig. 16. Fecundity rates for all mature females ($FEC_{t(x)}$) in both cropped (○) and uncropped (●) pods as a function of age. The bold trend line represents a least squares linear regression fitted to pooled data and the thin trend line the product of $FEC_{r(x)}$ and $PR_{(x)}$.

3.5.3 Reproductive senescence and lifespan

As discussed in Section 3.4.3, there was evidence of reproductive senescence in older females. This explains why $FEC_{r(x)}$ remained constant beyond age 30.5 years whereas $FEC_{t(x)}$ declined linearly with age. Indeed, the ratio of these two parameters provides an estimate of the proportion of females that were post-reproductive at a given age, $PR'_{(x)}$:

$$PR'_{(x)} = 1 - (FEC_{t(x)}/FEC_{r(x)}) \quad (28)$$

where $FEC_{t(x)}$ and $FEC_{r(x)}$ represent the weighted mean of values for cropped and uncropped pods.

The $PR'_{(x)}$ estimates indicates that the rate of onset of reproductive senescence is symmetrical (Fig. 17) and can be described by a logistic equation:

$$PR_{(x)} = (e^{-K(X-I)} + 1)^{-1} \quad (29)$$

with rate, K, of 0.217 (SE=0.006) and inflection, I, of 40.098 (SE=0.128). The poor fit of the right tail of the logistic curve is probably an artifact of the recursive ageing method used, such that the age probability density functions had long right-hand tails. Since the vast majority of these older females were post-reproductive, the poor fit is of little consequence. For example, the cumulative difference between the $PR'_{(x)}$s and $PR_{(x)}$s for ages 48–62 years translates to a total of only 0.081 calves.

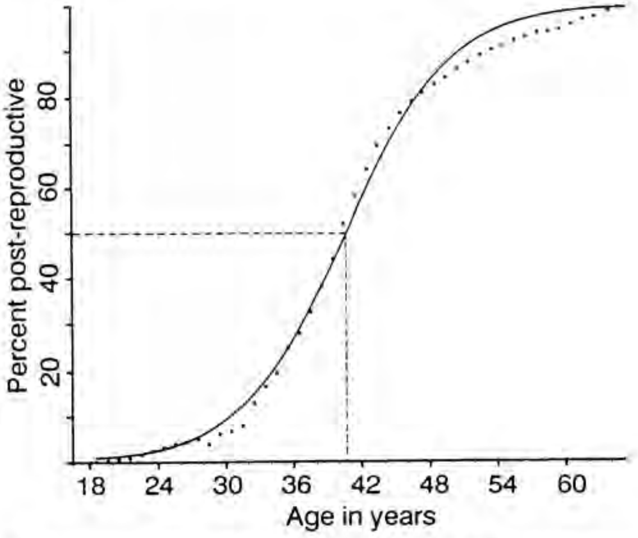

Fig. 17. Rate of onset of reproductive senescence ($PR_{(x)}$) of females in cropped and uncropped pods combined. The trend line represents a logistic equation fitted to pooled data using least squares criterion.

The estimated mean age of onset of post-reproduction is 40.1 years, which indicates that females typically gave birth to their last viable calf at 39.1 years of age. Given that the estimated mean age at first birth was 14.9 years (Table 6), the mean reproductive lifespan is 25.2 years – similar to the 25.5 years estimated in Section 3.4.4.

The mean cumulative number of viable calves produced by females at a given age can be calculated in two ways: (1) from the cumulative sum of the product of the $MAT_{f(x)}$, $FEC_{r(x)}$ and $PR_{(x)}$ shown in Figs 7, 15 and 17; and (2) from the cumulative sum of the product of the $MAT_{f(x)}$ and $FEC_{t(x)}$ shown in Figs 7 and 16. The two methods gave nearly identical results, never deviating from one another by more than 1.5%, and indicate that females that survived to the end of their reproductive lifespan produced an estimated 5.38 and 5.32 viable calves, respectively. In both

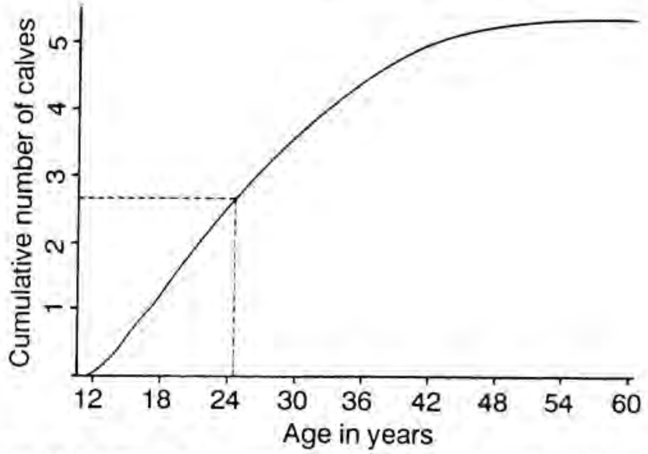

Fig. 18. Estimated mean cumulative number of viable calves that were produced by females at a given age. The two methods used to calculate this statistic (see text) gave results that were graphically indistinguishable from one another.

cases, 50% of the calves were born by 24.5 years of age (Fig. 18). These estimates agree with the maximum number of offspring assigned to mothers in genealogical trees in Bigg *et al.* (1990): 9 females had 5 offspring and 1 female had 6 offspring. The number of calves produced by females subsequent to 35 years of age was estimated at 0.95 calves; subsequent to 40 years of age at 0.45 calves; and subsequent to age 45 years at 0.13 calves.

Reproductive senescence has not been previously reported for killer whales. However, the age-specific reproductive rates of killer whales are in many ways similar to those in short-finned pilot whales (Kasuya and Marsh, 1984). In the latter species, reproductive senescence was first evident at age 28–32 years and, although female longevity extended to 63 years, all females were post-reproductive by age 40 years. However, the two species differ in one respect. In short-finned pilot whales, the estimated calving intervals increased progressively with age whereas in killer whales there was no evidence of a further decline in the fecundity of reproductive females after age 30.5 (Fig. 15). This difference may have been an artifact of the more conservative criteria used by Kasuya and Marsh (1984) to identify post-reproductive females. Some of the older females which they classified as resting or lactating may actually have been post-reproductive (Marsh and Kasuya, 1986), such that the calving intervals of older females would have been overestimated. Interestingly, Kasuya *et al.* (1988) found little evidence of reproductive senescence in long-finned pilot whales (*G. melas*).

3.5.4 Temporal changes in fecundity

To determine whether fecundity rates varied during the course of the study, the expected annual number of births in the tth year, B_t, was calculated:

$$B_t = \sum_{i=1}^{n} (PY_{ti(x)} \cdot FEC_{r(x)} [1 - PR_{(x)}]) \qquad (30)$$

where $PY_{ti(x)}$ denotes the probability the ith female was aged x in the tth year as per equation (25). The deviations between B_t and the actual number of calves born each year (Tables 1 and 2) showed no temporal trend in either cropped ($r^2=0.061$; $P>0.50$) or uncropped ($r^2=0.003$; $P>0.50$) pods, which indicates that fecundity rates had remained relatively constant throughout the study.

An index of fecundity, termed the net apparent fecundity rate, was also calculated for the 20 years preceding the study (1955–74) based on the age-composition of the populations at the start of the study. The net apparent fecundity represents the number of progeny born to females during 1955–74 that survived to the start of the study. The ages of all females alive at the start of the study during 1955–74 was reconstructed by subtracting the appropriate number of years from their estimated ages at the start of the study. Using equation (30), we calculated the expected number of calves born to these females during 1955–74 and then used equation (10) to calculate the number of their calves that should have survived to the start of the study. The expected number of offspring born during 1955–74 was then compared to the observed number that survived to the start of the study based on the age-composition of the population in 1974. The analysis could only be extended as far back as 1955, because the minimum-aged adult males (Section 3.1.3) could have been born anytime prior to 1955.

The net apparent fecundity rate in uncropped pods during 1955–74 was 90.6% of its expected value (Table 8). Not surprisingly, the number of calves born in cropped pods during 1955–74 that survived to the start of the study was far below (48.6%) the number expected because many had been cropped prior to the start of the study. A correction was calculated to account for cropping. The number of cropped calves that were born during 1955–74 was estimated from the age-composition of the harvest

Table 8

Net apparent fecundity rates for the period 1955-74 (see Section 3.5.4 for details).
Key. For cropped pods: - Observed=estimated number of calves born during interval that survived to start of study; Cropped=estimated number of calves born during interval that were cropped; Rate=estimated proportion of calves born during interval that were cropped; Other=estimated number of calves born during interval to females that were cropped; Corrected=estimated number of calves born to females alive at the start of the study; (i.e. Observed and Cropped – (Rate x Other)).

Period	Uncropped pods		Cropped pods					
	Observed no.calves	Expected no.calves	Observed no.calves	No.Calves cropped	Cropping rate	Other calves	Corrected no.calves	Expected no.calves
1971-74	18	17.97	20	0.80	0.04	1.19	20.75	16.91
1967-70	8	15.53	0	9.90	1.00	3.54	6.36	16.14
1963-66	14	12.68	7	16.67	0.70	5.02	20.16	14.17
1959-62	5	9.33	3	12.33	0.80	4.52	11.71	13.26
1955-58	12	7.43	6	5.22	0.47	3.91	9.38	13.11
Total	57	62.94	36	44.92			68.36	74.13

(Section 2.3.2). Using equation (30), we estimated the number of these calves that would have been offspring of the mature females that had been cropped and, based on the overall cropping rates (Table 8), subtracted the estimated number of their offspring that would also have been cropped. The corrected net apparent fecundity rate for cropped pods was 92.2% of its expected value (Table 8).

The overall net apparent fecundity rate during 1955–74 for cropped and uncropped pods combined was 91.5% of its expected value. This implies that fecundity rates during this period were 91.5% of their current values or that juvenile mortality rates were 1.05 times their current values. Since these rates were within the 95% confidence limits of the current parameter estimates, we conclude that both fecundity and juvenile mortality rates have remained relatively constant between 1955 and 1987.

3.6 Survival and mortality rates

3.6.1 Methods

As discussed at the beginning of Section 2.3 and in Bigg *et al.* (1990), there is no evidence of dispersal of individuals from their natal pods. Thus, animals have been assumed to have died when they disappeared from their pods.

The finite annual survival rate at age x, $SV_{(x)}$, was estimated from the proportion of animals aged x in year t, $L_{x,t}$ that survived to age x+1 in year t+1, $L_{x+1,t+1}$:

$$SV_{(x)} = L_{x+1,t+1} / L_{x,t} \qquad (31)$$

This is analogous to the animal-year method used by Bigg (1982) except that data for the last year individuals were seen were not included in the denominator because the status of these individuals in year t+1 was not yet known. The finite annual mortality rates, $MR_{(x)}$, were estimated by:

$$MR_{(x)} = D_{x,t} / L_{x,t} = 1 - SV_{(x)} \qquad (32)$$

where $D_{x,t}$ represents the total number of animals that died between age x and x+1 during the interval t to t+1:

$$D_{x,t} = L_{x,t} - L_{x+1,t+1} \qquad (33)$$

The variances of $SV_{(x)}$ and $MR_{(x)}$, reciprocal binomial variates, were given by:

$$\mathrm{Var}(SV_{(x)}) = \mathrm{Var}(MR_{(x)}) = SV_{(x)}\, MR_{(x)}\, L_{x,t}^{-1} \qquad (34)$$

It should be noted that these mortality rate estimates are unique for cetaceans in that they were derived horizontally based on the fate of individuals over time. To our knowledge, previous cetacean mortality rates have all been derived vertically from, for example, the age-composition of catches. Horizontal estimates are preferable in that nothing need be assumed about the status or age-structure of the population whereas vertical estimates are valid only if the population is stationary, or is stable and the population growth rate is known. The biases introduced in vertical analyses by failure of these assumptions are discussed further in Section 4.2.7. Horizontal estimates are also statistically preferable in that they are uncorrelated:

$$\mathrm{Cov}(SV_{(x)},SV_{(y)})=\mathrm{Cov}(MR_{(x)},MR_{(y)})=0 \quad \text{for } x\neq y \qquad (35)$$

(Seber, 1982) whereas vertical estimates generally exhibit serial correlations.

3.6.2 Neonates

Neonate mortality is defined as that which occurred between birth and 0.5 years of age, including stillbirths. Because pods were usually censused during the non-calving season, most calves were first identified at age 0.5 years of age. Consequently, neonate mortality can not be estimated in the same manner as other age-classes. Fortunately, an estimate of this parameter is not required in the population model as neonate mortality is absorbed into the fecundity rate, which we defined as the rate of birth of viable calves. Nevertheless, as there is evidence that neonate mortality was appreciable, we have attempted to obtain objective, albeit crude, estimates of its magnitude.

The first estimate was based on the number of neonate strandings recovered in the southern portion of the study area. A total of eight neonate carcasses were recovered from the study area during 1973–87 (Table 5). No neonate carcasses were recovered from the northern portion of the study area, almost certainly because the northern portion was much less accessible and less densely populated by people. Preliminary analyses of the DNA of four of the neonates indicated that 3 (75%) were of the resident form and 1 (25%) was of the transient form (R. Hoelzel, University of Cambridge, Cambridge, England, pers. comm.). Based on this proportion, six of the eight neonates recovered were assumed to have been of the resident form. Although all the neonates were found within the range of the southern community, three were situated on the west coast of Vancouver Island near the boundary of the two resident communities. The southern resident community commonly occur in this area while the northern resident community rarely occur there. We have therefore assumed that two of the three neonates belonged to the southern community and one to the northern community. Thus, five of the neonates were estimated to have originated from the southern resident community.

During the study, a total of 44 viable calves was born in the southern community. If we assume that all the neonates that died were recovered, the neonate mortality rate was 10% (5/44+5). In reality, however, the strandings probably represent only a small fraction of the total number of neonate deaths. For example, only 3 of the 26 (11.5%) whales that died in older age-classes in the southern community during the study were recovered. Applying this recovery rate to the neonate strandings gives a more realistic neonate mortality rate of 50% (i.e.[5/0.115]/[44 +(5/0.115)]).

The second estimate was based on the survival rates of the 15 newborn calves first encountered during winter prior to 0.5 years of age. Of these, three had died prior to the next field season at which time they would have had a mean age of 0.5 years. This represents a mortality rate of 20%, but is an underestimate as it does not account for stillbirths or mortality between birth and the first encounter. Two adjustments have been made to account for these biases. First, it was assumed that the 15 calves were born at the midpoint of the interval over which they were known to have been born (i.e. the interval between the last encounter the calf was not present and the first encounter it was present). Mortality rates were recalculated for the fraction of the interval between the estimated birth date and 1 July (i.e. mean age 0.5 years) that the calf had been monitored. Second, it was assumed that 20% of neonate deaths were stillbirths (Table 5). This gives a corrected neonate mortality rate of 37%.

Averaging the 50% and 37% estimates results in a provisional estimate of neonate mortality of approximately 43%. This is of course based on an extremely small sample size and the confidence limits associated with the estimates are too large to be of any practical value. However, Bain (1990) independently estimated that neonate mortality in the northern community was 42% based on the distribution of calving intervals.

There are few estimates of the magnitude of neonate mortality for other cetaceans. It could be argued that data given in Kasuya and Marsh (1984) for short-finned pilot whales indicated high neonate mortality. In their sample, pregnant females outnumbered calves aged 16 months or less (i.e. the gestation period) by 60 to 20, implying a neonate mortality rate of at least 67% between birth and 16 months of age. Kasuya and Marsh (1984, p.292–3) however rejected such a high mortality rate and concluded that pregnant females were under-represented in the sample. There was also evidence of high neonate mortality in other cetaceans. Sergeant (1962) calculated that mortality in the first year of long-finned pilot whales (*G. melas*) was 35%. Captive *Tursiops truncatus* exhibited 32% mortality between 0–6 months of age and 17% mortality between 6–12 months of age (Sweeney, 1977). First-year mortality in gray whales (*Eschrichtius robustus*) was estimated at 35–36% (Swartz and Jones, 1983; Sumich and Harvey, 1986).

3.6.3 Juveniles

Since both males and females mature at about 15 years of age (Section 3.3), juvenile mortality is defined as that which occurred between 0.5 and 15.5 years of age.

Juvenile mortality rates were estimated based on the 61 individuals that were juvenile when first encountered as well as the 134 calves born during the study. To smooth irregularities and improve sample sizes, data were grouped into the following age-categories: 0.5, 1.5–2.5, 3.5-5.5, 6.5–9.5, and 10.5–14.5 years. The progressively larger intervals were selected to take advantage of the greater numbers of younger individuals, and because age-related changes in mortality rates were likely to be most pronounced in early life.

Several minor adjustments to the data were necessary. Where ages were only known to within ±1 or ±2 years, data were amortized over the possible age range. Similarly, the death of one animal that had died sometime during a 6-year period was amortized over this interval. Lastly, because calves born in the northern community were not all seen in the year they were born (Section 3.1.1), a correction had to be made to account for viable calves that may have died prior to being identified. The correction was calculated by applying the survival rates for calves seen every year since their birth to the 16 calves that were older than 0.5 years of age when first encountered. It was estimated that 0.30 viable calves had died prior to age 1.5 years before being identified, 0.27 prior to age 2.5 years and 0.61 prior to age 3.5 years. These deaths were partitioned among each of the age categories according to the distribution of the deaths at known ages.

Juvenile mortality rates tended to be higher in cropped pods. However, a weighted ANOVA of $Z = \arcsin \cdot X^{0.5}$ transformed mortality rates (Snedecor and Cochran, 1980) blocked by the age categories indicated that the differences were not significant (F=0.77; P=0.431). Data for cropped and uncropped pods were thus pooled. The weighted overall mean juvenile mortality rate was 0.018, but mortality rates declined with age (Table 9). Net survival from 0.5 to 15.5 years of age was calculated ($^{14.5}_{0.5}\pi\, SV_{(x)}$) at 77.9%. In comparison, the survival rate of the 34 individuals that were born early in study to the end of the study, at which time they were aged 10.5–14.5 years, was 76.5% (81.3% and 72.2% in uncropped and cropped pods, respectively). Although this did not provide a completely independent test, because the 34 animals were used in the calculation of mortality rates, these individuals accounted for only 25% of the total sample.

Table 9

Finite annual survival and mortality rates for juveniles in cropped and uncropped pods combined.

Age group	$L_{(x)}$	$L_{(x+1)}$	$D_{(x)}$	$SV_{(x)}$	$MR_{(x)}$	SE
0.5	116.2	111.5	4.7	0.960	0.040	0.0183
1.5-2.5	221.9	216.3	5.6	0.975	0.025	0.0105
3.5-5.5	296.5	290.0	6.5	0.978	0.022	0.0085
6.5-9.5	338.2	332.8	5.3	0.984	0.016	0.0068
10.5-14.5	364.0	362.0	2.0	0.995	0.005	0.0039
Total	1336.8	1312.6	24.2	0.982	0.018	0.0036

The sex of most juveniles was unknown, so mortality rates could not be calculated separately by sex. However, assuming that the sex ratio was equal at birth, differences in female and male mortality rates would be reflected by a skewed sex ratio at the onset of maturity. The sex ratios of animals that matured during the study, as well as of adolescents aged 10.5–20.5 years, were not significantly skewed (chi-squared values of 0.397 and 0.140; $P \geq 0.50$) (Table 10), which suggests that female and male juvenile mortality rates are equivalent.

To determine whether juvenile mortality rates varied over the course of the study, the expected number of juvenile deaths in 2-year intervals was calculated based on the age distribution of juveniles during each interval and the mean mortality rates (Table 9). A chi-squared test indicated that the distribution of the observed and expected deaths were not significantly different (chi-squared=3.71; P=0.72). Moreover, the residuals showed no consistent temporal trend ($r^2=0.041$; $P>0.50$), which indicates that juvenile mortality rates had remained constant during 1973–87. Furthermore, the constancy of the net apparent fecundity rates during 1955–74 (Section 3.5.4) suggests that juvenile mortality rates had remained constant since at least 1955.

3.6.4 Mature males

The survival and mortality rates of mature males were estimated based on the 90 males that attained ages of 15.5 years or greater during the study. As was the case for juveniles, ages known to ±1 or ±2 years and one death that occurred sometime during a four year period were amortized. Data were grouped into three five-year age-categories: 15.5–19.5, 20.5–24.5, and 25.5–29.5 years; and an age-category that included all males aged greater than 30.5 years. Minimum-aged male aged 21.5+ to 29.5+ were excluded from the age-specific analysis as they could not be assigned to their correct age-category.

A weighted ANOVA of $Z = \arcsin X^{0.5}$ transformed mortality rates, blocked by the above age-categories, indicated that male mortality rates in cropped and uncropped pods were not significantly different (F=3.22; P=0.181). Data for cropped and uncropped pods were therefore pooled. Mature males exhibited an overall weighted mean mortality rate of 0.039, but mortality rates increased with age (Table 11). The mortality rate increased from 0.008 for males aged 15.5–19.5, which did not differ significantly from the mortality rate of juveniles aged

Table 10

Numbers (and proportion) of animals that (1) matured; or (2) were aged 10.5-20.5 years during the study [of each sex]. Chi-squared tests indicated that none of the ratios differed significantly from parity ($P \geq 0.45$).

	Cropped pods		Uncropped pods		Combined	
	Males	Females	Males	Females	Males	Females
(1) Matured	7 (0.41)	10 (0.59)	22 (0.48)	24 (0.52)	29 (0.46)	34 (0.54)
(2) Aged 10-20	23 (0.51)	22 (0.49)	36 (0.52)	33 (0.48)	59 (0.52)	55 (0.48)

Table 11

Finite annual survival and mortality rates for mature males in cropped and uncropped pods combined.

Age group	$L_{(x)}$	$L_{(x+1)}$	$D_{(x)}$	$SV_{(x)}$	$MR_{(x)}$	SE
15.5-19.5	152.50	151.25	1.25	0.992	0.008	0.0073
20.5-24.5	165.50	159.75	5.75	0.965	0.035	0.0142
25.5-29.5	79.00	75.00	4.00	0.949	0.051	0.0247
30.5+	85.00	79.00	6.00	0.929	0.071	0.0278
21.5+-29.5+ [1]	162.00	154.00	8.00	0.951	0.049	0.0170
Total	644.00	619.00	25.00	0.961	0.039	0.0076

[1] Excluded from age-specific analysis because could not be assigned to proper age-group.

10.5–14.5 years (P>0.50), to 0.071 for males aged 30.5+ years (Table 11). The exclusion of males aged 20.5+ – 29.5+ years from the analysis, which accounted for 25% of the total sample, probably had little effect. Their mortality rate was 0.049 which, as might be expected, was only slightly greater than the rate of 0.048 for non-minimum aged males greater than 20.5 years of age.

Temporal patterns in mature male mortality rates were investigated in the same manner as juveniles. The expected and observed numbers of deaths in two-year intervals were not significantly different (chi-square=6.60; P>0.40) and the residuals showed no discernible temporal trend ($r^2=0.075$; P>0.50), which indicates that male mortality rates were constant throughout the study.

3.6.5 Reproductive females

Reproductive females were classified as females aged 15.5 years or greater that had given birth within the past 10 years. Several of the females meeting these criteria may actually have been post-reproductive as there was no way of knowing whether those that gave birth late in the study would subsequently give birth. Data were grouped into four ten-year age-categories: 15.5–24.5, 25.5–34.5, 35.5–44.5 and 45.5–54.5 years.

Reproductive females exhibited extremely low mortality. During the study, only 1 of 32 reproductive females died in cropped pods and only 2 of 41 died in uncropped pods. These rates were not significantly different (P>0.50), so data were pooled giving an overall weighted mean mortality rate of 0.0048 (Table 12). The reproductive females that died tended to be older individuals which suggests that mortality rates increased slightly with age (Table 12). Indeed, two of the females died at an estimated age of 38.5 years and thus may have actually been post-reproductive ($PR_{(38.5)}=0.41$; Section 3.5.3). There were no apparent biases to account for these low mortality rates and they could not be attributed to small sample sizes. Our sample was equivalent to three deaths among 62 females monitored for 10 years.

Table 12

Finite annual survival and mortality rates for mature females in cropped and uncropped pods combined.

Age group	$L_{(x)}$	$L_{(x+1)}$	$D_{(x)}$	$SV_{(x)}$	$MR_{(x)}$	SE
Reproductive females						
15.5-24.5	242.0	242.0	0.0	1.0000	0.0000	-
25.5-34.5	262.0	261.0	1.0	0.9962	0.0038	0.00381
35.5-44.5	118.0	116.0	2.0	0.9831	0.0169	0.01188
45.5-54.5	1.0	1.0	0.0	1.0000	0.0000	-
Total	623.0	620.0	3.0	0.9952	0.0048	0.00277
Post-reproductive females						
15.5-24.5	1.0	1.0	0.0	1.0000	0.0000	-
25.5-34.5	19.0	19.0	0.0	1.0000	0.0000	-
35.5-44.5	158.0	157.0	1.0	0.9937	0.0063	0.00631
45.5-54.5	159.0	155.0	4.0	0.9748	0.0252	0.01242
55.5-64.5	61.0	59.0	2.0	0.9672	0.0328	0.02280
≥ 65.5	29.0	27.0	2.0	0.9310	0.0690	0.04705
Total	427.0	418.0	9.0	0.9789	0.0211	0.00695
All mature females						
15.5-24.5	243.0	243.0	0.0	1.0000	0.0000	-
25.5-34.5	281.0	280.0	1.0	0.9964	0.0036	0.00355
35.5-44.5	276.0	273.0	3.0	0.9891	0.0109	0.00624
45.5-54.5	160.0	156.0	4.0	0.9750	0.0250	0.01234
55.5-64.5	61.0	59.0	2.0	0.9672	0.0328	0.02280
≥ 65.5	29.0	27.0	2.0	0.9310	0.0690	0.04705
Total	1050.0	1038.0	12.0	0.9886	0.0114	0.00328

3.6.6 Post-reproductive females

Post-reproductive females were operationally defined as mature females that had not given birth for at least 10 years. Since only 2.6% of calving intervals were greater than 10 years (Fig. 12), these females were unlikely to give birth subsequently. The population contained 37 post-reproductive females. There were insufficient numbers of post-reproductive females to compare cropped and uncropped pods, so data were pooled. Data were grouped into five ten-year age-categories: 15.5–24.5, 25.5–34.5, 35.5–44.5, 45.5–54.5, and 55.5–64.5 years; and a category that included all those aged greater than 65.5 years.

Mortality rates for post-reproductive females were extremely low prior to age 44.5, but increased with age (Table 12). A comparison of reproductive and post-reproductive females aged 25.5–34.5 and 35.5–44.5 years, the only age-categories with sufficient overlap, showed no significant differences (P>0.50). Data were therefore combined and mortality rates re-calculated for all mature females (Table 12).

There was no obvious temporal pattern in the mortality rates of mature females but the paucity of deaths precluded a formal analysis.

Both female and male killer whale mortality rates (Fig. 19) conformed with the typical mammalian U-shaped pattern (Caughley, 1966). These mortality rates represent the first age-specific rates for killer whales. DeMaster and

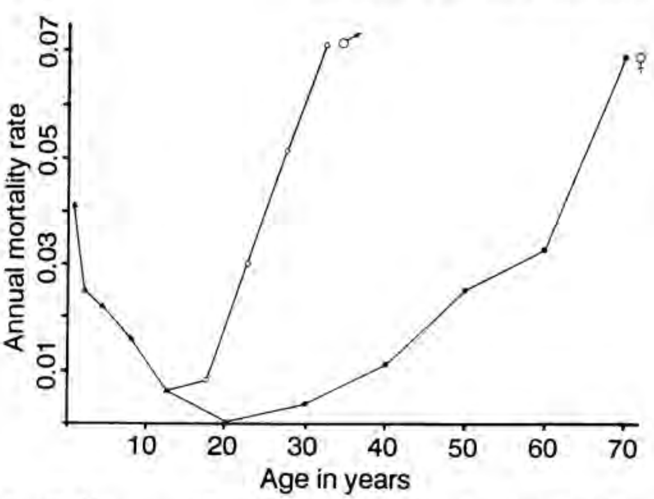

Fig. 19. Mean annual finite mortality rates ($MR_{(x)}$) as a function of age for juveniles of both sexes (triangles), mature males (○), and mature females (●). Mortality rates were plotted at the midpoint of the age-intervals over which they applied.

Drevenak (1989) estimated annual mortality rates for captive killer whales at 0.04 for females and 0.12 for males, whereas Duffield and Miller (1988) reported annual rates of 0.089 for both captive males and females. Based on the age-composition of short-finned pilot whales taken in drive fisheries, Kasuya and Marsh (1984) calculated annual mortality rates of 0.0251 for females aged 18–47 years and 0.0393 for males aged 9–30 years, with sharp increases in mortality at older ages in both sexes. However, considering these animals would have been recruited following a period of heavy exploitation, these vertically derived rates may have been overestimates (see Section 4.2.7).

3.7 Status of the study populations

Since life history parameters often vary in a density-dependent fashion, it is important that the parameters be viewed in the context of the status of the population from which they were derived. Several observations lead us to conclude that both the northern and southern communities were at levels sufficiently below carrying capacity that density-dependent effects were not evident.

The status of the northern community was assessed on the basis of its population growth curve (Fig. 3). During the study, the size of the community increased by a factor of 1.4. Indeed, the sex– and age-structure of the population indicated that it had nearly doubled in size since 1960 (Section 4.3.2). If the northern community was approaching its carrying capacity, its population growth rate should have declined as density increased during the study. The trajectory of the northern community growth curve was evaluated with a step-wise second-order polynomial:

$$\ln N_t = [a + b\,t] + [c\,t^2] \qquad (36)$$

where N_t denotes the size of the community in year t. The first-order term was forced into the regression and the improvement by adding the second-order term assessed. The procedure was in essence a derivative of DeMaster, Goodman, DeLong and Stewart's (1982) Dynamic Response Assessment (see also Boveng, 1988). The first term described an exponentially increasing population while the second term allowed for compensatory changes in the population growth rate. The analysis indicated that the growth trajectory was nearly exponential ($r^2=0.964$ for b; $P<0.001$) and the growth rate had not declined during the study (partial r^2 for $c = 0.001$; $P>0.50$). This conclusion was also supported by the absence of perceptible temporal trends in the life history parameters during the study.

The status of the southern community could not be assessed in the same manner because its sex- and age-structure had been distorted by the live-capture fishery (Section 4.3.3). However, the fact that the live-capture fishery had reduced the southern commumitity to 70% of its original size and the community had not recovered to its original size (Section 4.3.3) indicated that it was also below carrying capacity. This was also supported by the similarity of the life history parameters for the southern and northern communities.

In an earlier assessment, Bigg (1982) had suggested that cropping may have affected several life history parameters. Our revised view can be attributed to the fact that smaller sample sizes were available in 1982 and that new knowledge has been acquired since then which has permitted an improved assessment (e.g. accounting for age-related effects and distinguishing between reproductive and post-reproductive females). Furthermore, a re-analysis of the data in Bigg's (1982) Tables 5–9 using chi-squared tests indicates that none of the differences reported between cropped and uncropped pods are statistically significant ($P>0.50$).

In large mammals, density dependent changes in life history parameters are generally most pronounced at population levels just below carrying capacity (Fowler, 1984; 1987). Since density dependent effects may not be apparent until populations are very close to their carrying capacity, it has not been possible to ascertain how far below carrying capacity the study populations are.

4. POPULATION DYNAMICS

4.1 Population projections

4.1.1 The model

The life history parameters were incorporated into a population model that described changes in the sex– and age-structure of a population with time. The model was discrete and projected populations in annual increments from one census period to the next. The number of animals of sex s (f=female and m=male) and pivotal age x at time t was denoted as $n_{s(x)t}$. We assumed that mortality was constant throughout the year, that births occurred as a pulse at the mid-point between censuses, and that the sex ratio was equal at birth.

The number of viable calves of each sex recruited during the interval t to t+1 was calculated from the number of reproductive females that survived to the next calving season, t+0.5, and the age-specific fecundity rates:

$$n_{s(0.5)t+1} = \sum_{x=0.5}^{90.5} n_{f(x)t}\, F_{(x)} \qquad (37)$$

where:

$$F_{(x)}=0.5.SV_{f(x)}^{0.5}\cdot[(MAT_{f(x+0.5)}-PR_{(x+1)})\ FEC_{r(x+1)}] \qquad (38)$$

with $SV_{f(x)}$ as per Tables 9 and 12, $MAT_{f(x)}$ as shown in Fig. 7, $FEC_{r(x)}$ as shown in Fig. 15, and $PR_{(x)}$ as shown in Fig. 17. The number of animals of sex s that survived to age x+1 at time t+1 was calculated from the age-specific survival rates:

$$n_{s(x+1)t+1} = n_{s(x)t}\cdot SV_{s(x)} \qquad (39)$$

where $SV_{s(x)}$ was as per Tables 9, 11 and 12. Maximum longevity was set at 60.5 years for males and 90.5 years for females (i.e. $SV_{s(max)}=0$ with max=60.5 for m and 90.5 for f). These specific limits (see Section 4.2.6) were of little consequence in the model because such old animals constituted only a negligible proportion of the total population.

Lewis (1942) and Leslie (1945) developed matrix models that greatly simplified the above computations. Although the models were originally designed for juvenile and reproductive females, they can be extended to include post-reproductive females and males (Usher, 1972). If $\mathbf{n}_t$ is defined as a column vector of the sex– and age-structure of the population at time t and **M** a transition matrix as follows:

$$\mathbf{n}_t = \begin{array}{l} n_{m(0.5),t} \\ n_{f(0.5),t} \\ n_{m(1.5),t} \\ n_{f(1.5),t} \\ \cdot \\ \cdot \\ n_{m(60.5),t} \\ m_{f(60.5),t} \\ m_{f(61.5),t} \\ \cdot \\ n_{f(90.5),t} \end{array} \quad \mathbf{M} = \begin{array}{cccccccccc} 0 & F_{(0.5)} & 0 & F_{(1.5)} & \cdots & 0 & F_{(60.5)} & \cdots & 0 & F_{(90.5)} \\ 0 & F_{(0.5)} & 0 & F_{(1.5)} & \cdots & 0 & F_{(60.5)} & \cdots & 0 & F_{(90.5)} \\ SV_{m(0.5)} & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ 0 & SV_{f(0.5)} & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdots & \cdot & \cdot & \cdots & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdots & \cdot & \cdot & \cdots & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdots & SV_{m(60.5)} & 0 & \cdots & & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdots & 0 & SV_{f(60.5)} & \cdots & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdots & \cdot & \cdot & \cdots & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdots & \cdot & \cdot & \cdots & \cdot & \cdot \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & SV_{f(90.5)} & 0 \end{array}$$

the sex– and age-structure of the population at time t+1, $\mathbf{n}_{t+1}$, can be obtained by:

$$\mathbf{n}_{t+1} = \mathbf{M} \cdot \mathbf{n}_t \tag{40}$$

or, more generally, the sex– and age-structure at time t+z, $\mathbf{n}_{t+z}$, by:

$$\mathbf{n}_{t+z} = \mathbf{M}^z \cdot \mathbf{n}_t \tag{41}$$

On the condition that the life history parameters remain fixed, a population will ultimately attain a stable sex– and age-distribution and will increase or decrease at a constant rate. The stable sex– and age-structure, $\mathbf{n}_s$, can be calculated by:

$$\mathbf{n}_s = \mathbf{M}^z \cdot \mathbf{n}_i \tag{42}$$

where the initial sex– and age-structure, $\mathbf{n}_i$, is irrelevant so long as z is sufficiently large. The stable rate of increase or decrease, λ, is thus:

$$\lambda = \Sigma \mathbf{n}_{s+1} / \Sigma \mathbf{n}_s \tag{43}$$

where the summation refers to all elements within the vectors. Alternatively, λ and $\mathbf{n}_s$ can be obtained by computing the dominant eigenvalue and eigenvector of the transition matrix, **M**. The stable population is described in Section 4.2.

For long-lived species such as cetaceans, matrix models have often been simplified by grouping age-classes into stages. However, the stage models are unrealistic and can be misleading, even in cases where the life history parameters are uniform for the age-classes grouped. Suppose, for example, that mortality rates were constant for all juveniles and they were grouped, and the stage model was then used to assess the effects of varying fecundity rates. In the stage model, juveniles would be treated uniformly and advanced to the next stage at the same rate. In reality, however, an increase in fecundity skews the juvenile component of the population toward younger age-classes such that a smaller proportion would advance to the next stage. These biases can only be avoided by setting the width of the stage-classes equal to the length of the projection increments.

4.1.2 Accuracy of the model

The population model embodies a number of simplified assumptions. Moreover, the raw data were grouped, pooled, smoothed and amortized to derive the transition probabilities of **M**.

The validity of the model was assessed by how well it emulated the demographic changes observed in the two communities over the course of the study. Column vectors, $\mathbf{P}_{jt}$, were created that gave the sex- and age-structure of each pod, j=1...19, in the year it was first encountered, t=0. Juveniles of unknown sex were partitioned equally among male and female sex-classes and ages only known to within ±1 or ±2 years were amortized. Minimum-aged males were amortized over their potential age-classes according to the relative frequencies of the age-classes in a stable population (Section 4.2.6). The initial sex- and age-structure of each pod was then projected for the number of years it had been monitored:

$$\mathbf{P}_{j,t+1} = \mathbf{M} \cdot \mathbf{P}_{jt} \tag{44}$$

At each iteration, the predicted numbers of births and deaths for each sex– and age-class were tabulated and categorized by sex and maturity status based on the estimated values of $MAT_{f(x)}$, $MAT_{m(x)}$ and $PR_{(x)}$ (Figs 7, 11 and 17).

In general, there is good agreement between the number of births and deaths predicted by the model and the number observed during the study (Table 13). The 122 observed viable births, plus the estimated 1.2 viable calves that died before being identified, was slightly less than the 130.2 predicted by the model. The discrepancy occurred mainly in the southern community and could be accounted for by two factors. First, the southern community contained a female (K40) that had remained barren to age 22.5 years whereas the model predicted a female would have produced 2.2 viable calves by that age. Second, the southern community contained nine females that had become post-reproductive early in the study, eight of these had been aged in reference to the year they gave birth to their last viable calf. None of the females subsequently gave birth, whereas the model assumed that females gradually became post-reproductive (Fig. 17) and gave birth to an estimated 0.45 calves subsequent to age 39.5 years (Fig. 18).

There was also a discrepancy in juvenile deaths. Although the overall predicted number of juvenile deaths of 26.0 was close to the 24.2 observed, there were more than expected in the southern community and fewer than expected in the northern community (Table 13). This was due to the slightly higher juvenile mortality rates in cropped pods. Since the mortality rates in cropped and uncropped pods were not significantly different (P=0.431), this discrepancy was likely due to chance.

Overall, the model satisfactorily emulated the demographic events observed during the study. It is worth noting that the population model had been derived independently and *a priori* to the above assessment of its validity.

4.2 Stable population (below carrying capacity)

In this Section, we describe the attributes of a stable population below its carrying capacity. In doing so, two classic constructs were used: life tables and Lotka's (1907a and b) population equations. Although the latter were originally derived in differential form, their finite approximations were used here. The approximations are

Table 13

Comparison of the number of births and deaths predicted by the model (and actual number observed) during the study subsequent to the first year each pod was censused.

Period	New[1] ind	Births	Deaths: Juvenile	Male	Reprod. F	Post. F	Total	Net change	Popn size
Northern Community									
1973-74	54	2.73 (2)	0.44 (3)	0.64 (0)	0.05 (1)	0.07 (0)	1.20 (4)	+1.52 (-2)	55.52 (52)
1974-75	20	3.89 (5)	0.63 (0)	0.75 (0)	0.07 (0)	0.11 (1)	1.56 (1)	+2.33 (+4)	77.86 (76)
1975-76	49	5.92 (2)	1.14 (2)	1.27 (2)	0.11 (0)	0.14 (0)	2.66 (4)	+3.26 (-2)	130.11 (123)
1976-77	0	5.77 (3)	1.19 (0)	1.27 (0)	0.12 (0)	0.18 (0)	2.76 (0)	+3.01 (+3)	133.13 (126)
1977-78	0	6.04 (3)	1.20 (0)	1.26 (0)	0.14 (0)	0.19 (1)	2.79 (1)	+3.25 (+2)	136.39 (128)
1978-79	0	5.84 (9)	1.24 (0)	1.32 (1)	0.13 (0)	0.19 (0)	2.88 (1)	+2.96 (+8)	139.34 (136)
1979-80	4	6.39 (8)	1.31 (0)	1.35 (1)	0.13 (0)	0.23 (0)	3.02 (1)	+3.37 (+7)	146.69 (147)
1980-81	0	6.45 (5)	1.32 (1)	1.32 (1)	0.14 (0)	0.24 (0)	3.02 (2)	+3.43 (+3)	150.12 (150)
1981-82	0	6.55 (4)	1.33 (0)	1.33 (2)	0.14 (0)	0.24 (1)	3.04 (3)	+3.51 (+1)	153.62 (151)
1982-83	0	6.85 (8)	1.36 (0)	1.34 (4)	0.13 (0)	0.25 (0)	3.08 (4)	+3.77 (+4)	157.40 (155)
1983-84	0	7.07 (5)	1.39 (2)	1.43 (1)	0.15 (1)	0.27 (0)	3.24 (4)	+3.83 (+1)	161.21 (156)
1984-85	0	7.19 (10)	1.40 (0)	1.47 (3)	0.17 (0)	0.31 (0)	3.35 (3)	+3.84 (+7)	165.04 (163)
1985-86	0	7.60 (9)	1.43 (0)	1.49 (1)	0.17 (0)	0.34 (0)	3.43 (1)	+4.17 (+8)	169.23 (171)
1986-87[2]	0	6.31 (10)	1.18 (3)	1.46 (1)	0.13 (0)	0.36 (0)	3.13 (4)	+3.18 (+5)	147.82 (146)
Total		84.60(84.2)[3]	16.58(12.2)[3]	17.70 (17)	1.76 (2)	3.12 (3)	39.16(34.2)[3]	+45.41(+49)	
Southern Community									
1974-75	71	3.63 (1)	0.62 (0)	0.43 (1)	0.12 (0)	0.24 (0)	1.41 (1)	+2.23 (0)	73.23 (71)
1975-76	0	3.58 (1)	0.62 (1)	0.50 (0)	0.11 (0)	0.25 (0)	1.48 (1)	+2.10 (0)	75.33 (71)
1976-77	0	3.45 (9)	0.66 (0)	0.50 (0)	0.11 (0)	0.27 (0)	1.54 (0)	+1.90 (+9)	77.23 (80)
1977-78	0	3.69 (2)	0.70 (1)	0.48 (1)	0.10 (0)	0.31 (0)	1.59 (2)	+2.10 (0)	79.33 (80)
1978-79	0	3.44 (2)	0.73 (0)	0.51 (1)	0.10 (0)	0.35 (0)	1.69 (1)	+1.75 (+1)	81.08 (81)
1979-80	0	3.58 (3)	0.75 (0)	0.54 (0)	0.11 (0)	0.40 (0)	1.80 (0)	+1.78 (+3)	82.86 (84)
1980-81	0	3.33 (1)	0.78 (2)	0.54 (1)	0.09 (0)	0.40 (0)	1.81 (3)	+1.52 (-2)	84.38 (82)
1981-82	0	3.26 (1)	0.79 (3)	0.53 (0)	0.09 (0)	0.42 (1)	1.83 (4)	+1.43 (-3)	85.81 (79)
1982-83	0	2.90 (0)	0.77 (0)	0.53 (1)	0.09 (1)	0.44 (1)	1.83 (3)	+1.07 (-3)	86.88 (76)
1983-84	0	3.25 (3)	0.74 (2)	0.57 (1)	0.08 (0)	0.44 (1)	1.84 (4)	+1.41 (-1)	88.29 (75)
1984-85	0	3.49 (5)	0.74 (0)	0.56 (1)	0.10 (0)	0.48 (1)	1.88 (2)	+1.61 (+3)	89.90 (78)
1985-86	0	3.72 (7)	0.75 (3)	0.59 (0)	0.10 (0)	0.48 (1)	1.92 (4)	+1.80 (+3)	91.70 (81)
1986-87	0	4.29 (4)	0.76 (0)	0.59 (0)	0.09 (0)	0.49 (1)	1.93 (1)	+2.36 (+3)	94.06 (84)
Total	-	45.60 (39)	9.40 (12)	6.86 (7)	1.30 (1)	4.99 (6)	22.54 (26)	+23.06(+13)	-
Combined		130.20(123.2)[3]	25.98(24.2)[3]	24.56 (24)	3.06 (3)	8.11 (9)	61.70(60.2)[3]	+68.47(+62)	

[1] Number of individuals in pods that were first identified that year. [2] Based on census of some pods within community (see Table 1).
[3] Expected value includes an estimated 1.2 juveniles that died before being identified.

valid because reproduction is seasonal and the age-intervals adopted were small relative to the total lifespan (Cole, 1954).

4.2.1 *Life tables*

Life tables were constructed for a cohort of 1,000 killer whales of each sex, s. The number of whales in the cohort that survived to age x, $L_{s(x)}$, was calculated as:

$$L_{s(x+1)} = 1000 \prod_{0.5}^{x} SV_{s(x)} \qquad (45)$$

where values for $SV_{s(x)}$ were given in Tables 9, 11 and 12. As in the matrix model, the $L_{s(x)}$ series were truncated at 60.5 years for males and 90.5 years for females (Section 4.2.6). The number of animals dying between ages x and x+1 was given by:

$$d_{s(x)} = L_{s(x)} - L_{s(x+1)} \qquad (46)$$

such that the age-specific finite annual mortality rates, $q_{s(x)}$, were:

$$q_{s(x)} = d_{s(x)}/L_{s(x)} \qquad (47)$$

It was assumed that mortality was constant throughout the year. The number of animals that survived to the midpoint between censuses (i.e. the next calving season), $l_{s(x+0.5)}$, was:

$$\begin{aligned} l_{s(x+0.5)} &= \text{antilog}[(\ln L_{s(x)} + \ln L_{s(x+1)})/2] \\ &= SV_{s(x)}^{0.5} \cdot L_{s(x)} \end{aligned} \qquad (48)$$

except for the last age-classes, for which $l_{s(x+0.5)}$ was set at $0.5L_{s(x)}$. For females, the number of viable calves of each sex produced at age x was calculated from:

$$m_{(x)} = 0.5[MAT_{f(x)}\,(1 - PR_{(x)})\,FEC_{r(x)}] \qquad (49)$$

which was merely a re-parameterization of the $F_{(x)}$ in equation (38). In the matrix model, production of viable calves was calculated as $\Sigma L_{f(x)} F_{(x)}$ whereas in the life table it was calculated as $\Sigma l_{f(x)}\, m_{(x)}$, which gave identical results.

The female and male life tables are given in Tables 14 and 15 respectively. The fate of cohorts over time is shown graphically in Fig. 20, which indicates that 78.1% of females survived to mean age at first birth and 71.1% to mean age at onset of post-reproduction. Integrating the $L_{f(x)}$s within each category indicates that females are, on average, juvenile for 23.7% of their lives, reproductive for 39.8% and post-reproductive for 36.5%. For males, 78.1% survived to mean age at sexual maturity and 73.4% to mean age at physical maturity. On average, males are juvenile for 42.7% of their lives, sexually but not physically mature for 15.7% and physically mature for 41.5% of their lives.

4.2.2 *Life expectancy*

The cumulative number of years lived by the cohort subsequent to age x, $T_{s(x)}$, was:

$$T_{s(x)} = \sum_{x}^{max} l_{s(x)} \qquad (50)$$

Table 14

Condensed female life table for a stable population below carrying capacity. Parameters are described in Section 4.2.

x	$L_{(x)}$	$d_{(x)}$	$q_{(x)}$	$l_{(x+0.5)}$	$e_{(x)}$	$m_{(x)}$	$P_{(x)}$
0.5	1000.0	40.5	0.0405	979.6	50.1	0.0000	1000.0
1.5	959.6	24.2	0.0252	947.4	51.2	0.0000	932.3
2.5	935.3	23.6	0.0252	923.5	51.5	0.0000	883.0
3.5	911.7	20.0	0.0219	901.7	51.9	0.0000	836.2
4.5	891.7	19.6	0.0219	881.9	52.0	0.0000	794.7
5.5	872.2	19.1	0.0219	862.6	52.2	0.0000	755.2
6.5	853.1	13.4	0.0157	846.4	52.3	0.0000	717.7
7.5	839.7	13.2	0.0157	833.1	52.1	0.0000	686.3
8.5	826.6	13.0	0.0157	820.1	52.0	0.0000	656.4
9.5	813.6	12.8	0.0157	807.2	51.8	0.0000	627.8
10.5	800.9	4.4	0.0055	798.6	51.6	0.0000	600.4
11.5	796.5	4.4	0.0055	794.3	50.9	0.0625	580.1
12.5	792.1	4.4	0.0055	789.9	50.2	0.0591	560.6
13.5	787.7	4.3	0.0055	785.6	49.4	0.1235	541.6
14.5	783.4	4.3	0.0055	781.2	48.7	0.1059	523.4
15.5	779.1	0.0	0.0000	779.1	48.0	0.1103	505.7
16.5	779.1	0.0	0.0000	779.1	47.0	0.0834	491.4
17.5	779.1	0.0	0.0000	779.1	46.0	0.1317	477.4
18.5	779.1	0.0	0.0000	779.1	45.0	0.1156	463.8
19.5	779.1	0.0	0.0000	779.1	44.0	0.1089	450.7
20.5	779.1	0.0	0.0000	779.1	43.0	0.1061	437.9
25.5	779.1	2.8	0.0036	777.7	38.0	0.0913	379.1
30.5	765.3	2.7	0.0036	764.0	33.6	0.0745	322.5
35.5	751.8	8.2	0.0109	747.7	29.2	0.0601	274.3
40.5	711.8	7.7	0.0109	707.9	25.7	0.0383	224.8
45.5	674.0	16.9	0.0250	665.5	22.0	0.0185	184.3
50.5	593.8	14.9	0.0250	586.4	19.6	0.0073	140.6
55.5	523.2	17.2	0.0328	514.6	16.9	0.0026	107.3
60.5	442.9	14.5	0.0328	435.6	14.5	0.0009	78.6
65.5	374.9	25.9	0.0690	361.7	11.7	0.0000	57.6
70.5	262.3	18.1	0.0690	253.1	10.8	0.0000	34.9
75.5	183.5	12.7	0.0690	177.0	9.4	0.0000	21.1
80.5	128.4	8.9	0.0690	123.8	7.4	0.0000	12.8
85.5	89.8	6.2	0.0690	86.6	4.6	0.0000	7.8
90.5	62.8	62.8	1.0000	31.4	0.5	0.0000	4.7

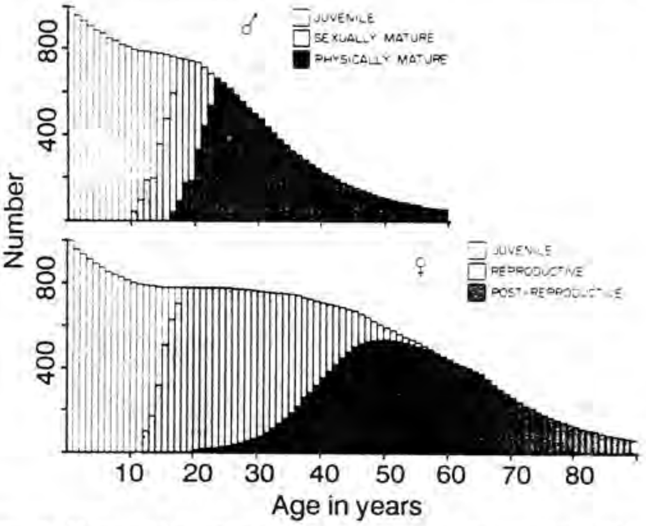

Fig. 20. Horizontal perspective of the sex- and age-structure of a male (top) and female (bottom) cohort in a stable population below carrying capacity. This figure shows the change in size of a cohort of each sex followed over time as it ages (see Sections 4.2.1 and 4.2.7 for details).

from which can be calculated the future life expectancy at age x, $e_{s(x)}$:

$$e_{s(x)} = T_{s(x)} / L_{s(x)} \tag{51}$$

Table 15

Condensed male life table for a stable population below carrying capacity. Parameters are described in Section 4.2.

x	$L_{(x)}$	$d_{(x)}$	$q_{(x)}$	$l_{(x+0.5)}$	$e_{(x)}$	$P_{(x)}$
0.5	1000.0	40.5	0.0405	979.6	28.7	1000.0
1.5	959.6	24.2	0.0252	947.4	28.8	932.3
2.5	935.3	23.6	0.0252	923.5	28.6	883.0
3.5	911.7	20.0	0.0219	901.7	28.3	836.2
4.5	891.7	19.6	0.0219	881.9	27.9	794.7
5.5	872.2	19.1	0.0219	862.6	27.5	755.2
6.5	853.1	13.4	0.0157	846.4	27.1	717.7
7.5	839.7	13.2	0.0157	833.1	26.6	686.3
8.5	826.6	13.0	0.0157	820.1	26.0	656.4
9.5	813.6	12.8	0.0157	807.2	25.4	627.8
10.5	800.9	4.4	0.0055	798.6	24.8	600.4
11.5	796.5	4.4	0.0055	794.3	23.9	580.1
12.5	792.1	4.4	0.0055	789.9	23.0	560.6
13.5	787.7	4.3	0.0055	785.6	22.2	541.6
14.5	783.4	4.3	0.0055	781.2	21.3	523.4
15.5	779.1	6.4	0.0082	775.9	20.4	505.7
16.5	772.7	6.3	0.0082	769.5	19.6	487.3
17.5	766.4	6.3	0.0082	763.2	18.7	469.6
18.5	760.1	6.2	0.0082	757.0	17.9	452.5
19.5	753.9	6.2	0.0082	750.8	17.0	436.1
20.5	747.7	26.0	0.0347	734.6	16.2	420.2
25.5	626.5	31.7	0.0506	610.4	13.8	304.9
30.5	483.2	34.1	0.0706	465.8	12.2	203.6
35.5	335.1	23.7	0.0706	323.0	11.6	122.2
40.5	232.4	16.4	0.0706	224.0	10.6	73.4
45.5	161.2	11.4	0.0706	155.4	9.3	44.1
50.5	111.8	7.9	0.0706	107.7	7.3	26.5
55.5	77.5	5.5	0.0706	74.7	4.5	15.9
60.5	53.8	53.8	1.0000	26.8	0.5	9.5

The mean life expectancy of viable calves aged 0.5 years was 50.1 years for females and 28.7 years for males (Tables 14 and 15). The life expectancy of females increased slightly to 52.3 years by age 6.5 years because females that survived their first few vulnerable years did not experience appreciable mortality until the end of their reproductive lifespan. In contrast, the life expectancy of males declined with age subsequent to 1.5 years because those that survive their first few vulnerable years face relatively higher mortality at the onset of physical maturity.

The above life expectancies were calculated at pivotal ages. Due to the high incidence of neonate mortality, life expectancy at birth is considerably less than that at 0.5 years. Based on the neonate mortality estimate of 43% (Section 3.6.2), such that $l_0=1{,}000/(1-0.43)$, and transposing the $L_{(x)}$ and $l_{(x)}$ series in equations (50) and (51), the life expectancy at birth was calculated to be 28.9 and 16.6 years for females and males, respectively.

4.2.3 Stable (intrinsic) rate of increase

The stable rate of increase, r, was obtained iteratively using Lotka's (1907) first equation:

$$\sum_{x=0.5}^{90.5} e^{-rx} l_{(x)} m_{(x)} = 1 \tag{52}$$

which gave r=0.0288. It should be noted that the $L_{(x)}$ and $l_{(x)}$ series were rescaled to an initial cohort of 1 for computations involving Lotka's equations. The corresponding finite growth rate, λ, was:

$$\lambda = e^{r} = 1.0292 \tag{53}$$

which indicates that the stable population increased at a rate of 2.92% per annum. An identical value was obtained using equation (43). This rate of increase applied to all sex- and age-classes in the population. At this rate, populations would double in size every 24.1 years.

The study population was below its carrying capacity and increasing exponentially (Section 3.7), so λ represents the maximum or intrinsic rate of increase for killer whales within the study area.

4.2.4 Reproductive potential and generation time

The net reproductive rate at age x, $R_{(x)}$, was calculated by:

$$R_{(x)} = \sum_{x}^{90.5} l_{(x)} m_{(x)} \qquad (54)$$

which represents the expected number of viable progeny of both sexes produced by females subsequent to a given age. The reproductive rate increased from 4.08 at 0.5 years of age to 5.03 at 11.5 years (Fig. 21) as the proportion of females that survived to reproduce increased. The reproductive rate at age 11.5 years was 93.5% of the 5.38 calves that were produced by females that survived to the end of their reproductive lifespan (Section 3.5.3) because reproductive females exhibited extremely low mortality rates. The reproductive rate declined beyond 13.5 years of age, not so much because of mortality, but almost entirely because females had expended their reproductive potential.

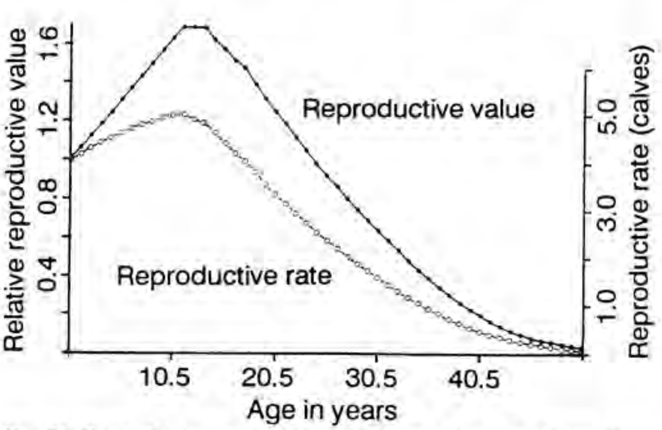

Fig. 21. Reproductive potential of females as a function of age. The reproductive rate ($R_{(x)}$) (bottom) represents the mean number of progeny produced by an individual subsequent to age x. The reproductive value ($RV_{(x)}$) (top) represents the relative number of progeny produced by an age-class subsequent to age x.

A related statistic was the relative reproductive value, $RV_{(x)}$, of females (Fisher, 1929):

$$RV_{(x)} = e^{rx}/l_x \sum_{y=0.5}^{90.5} e^{-ry} l_y m_y \qquad (55)$$

which, expressed as a multiple of $RV_{(0.5)}$, provides an index of the relative reproductive value of each female age-class in the population. The relative reproductive values follow the same general pattern as the reproductive rates (Fig. 21) but the variations are more pronounced owing to the greater prevalence of younger age-classes in the population.

The mean generation time, G, was approximately equal to:

$$G = 0.5 \cdot \ln R_{(0.5)} / r = 24.8 \text{ years} \qquad (56)$$

which represents the mean interval between the birth date of a female and the mean of the birth date of her progeny. Because the generation time was less than the life expectancy of females, the population was comprised of overlapping generations. Considering that the mean life expectancy of females is about double (2.02 times) the mean generation time, it would be expected that approximately half of all offspring would have living grandmothers at birth. Indeed, the genealogical trees described in Bigg *et al.* (1990), which were constructed prior to the population assessment, indicated that 39 of the 80 (48.8%) offspring born in uncropped pods during the study had living grandmothers at birth.

4.2.5 Birth and death rates

The finite female birth rate, β_f, was obtained from Lotka's (1907) second equation:

$$1/\beta_f = \sum_{x=0.5}^{90.5} l_{(x)} e^{-r(x+1)} \qquad (57)$$

which gives $\beta_f = 0.04522$. This represents the mean number of viable female progeny born per annum per female, including both immature and mature females. Since an equal number of male progeny were born, and females constituted 56.4% of the stable population (Section 4.2.6), the total *per capita* birth rate, β_t, is 0.05103 progeny per animal per year.

The finite female death rate, δ_f, was estimated as:

$$\delta_f = \beta_f - (\lambda - 1) = 0.01599 \qquad (58)$$

which represents the number of female deaths per female per annum. Since the stable population comprised 56.4% females, the total *per capita* female death rate is 0.00902. Substituting the total *per capita* birth rate, β_t, into equation (58) gives a total *per capita* death rate, δ_t, of 0.02180. By subtraction, the male *per capita* death rate, δ_m, was estimated to be 0.01278 (0.02931 male deaths per male). Although equal numbers of males and females were born each year, fewer females died each year. However, this does not imply that the female segment of the population was increasing faster than the male segment. Both males and females increased at 2.92% per annum, but in absolute terms more females had to be added each year to maintain the skewed sex ratio.

The birth to death ratio perhaps provides the most meaningful comparison for populations with different generation times and longevity. In the stable killer whale population, births outnumbered deaths by a factor of 2.34:1 (2.83:1 for females and 2.00:1 for males). This is high for a marine mammal. In comparison, a harbour seal (*Phoca vitulina*) population increasing at its intrinsic rate of 12.5% per annum exhibited a birth to death ratio of only about 2:1 (Olesiuk, unpubl. data). Thus, while a net rate of increase of 2.92% appears modest, it represented an impressive rate of increase for such a long-lived species.

4.2.6 Stable sex– and age-structure

Populations are comprised of a series of cohorts that start life at different times. Unless populations are stationary (i.e. r=0 or λ=1), the initial size of the cohorts varies with time. As a result, the stable sex– and age-structure of the population differs from that of a cohort followed through time, the degree of difference being a function of the rate of population growth.

The stable sex– and age-structure, $P_{s(x)}$, was obtained using Lotka's (1907) third equation:

$$P_{s(x)} = \beta_s L_{s(x)} e^{-r(x+1)} \qquad (59)$$

This is identical to the structure given by equation (42).

The stable sex- and age-structure of the stable killer whale population is shown in Fig. 22. Integrating the $P_{(x)}$ and $P_{m(x)}$ indicates that the stable population comprised 56.4% females and 43.6% males. The sex ratios become more skewed with age. For example, 62.4% of mature animals are female. Overall, the stable population comprises 50.3% juveniles (50.5% female), 18.7% mature males (64.0% physically mature) and 31.0% mature females (69.2% were reproductive).

At this point, the rationale for truncating the $L_{s(x)}$ series at 60.5 years for males and 90.5 years for females can be explained. The truncation points represent the ages,

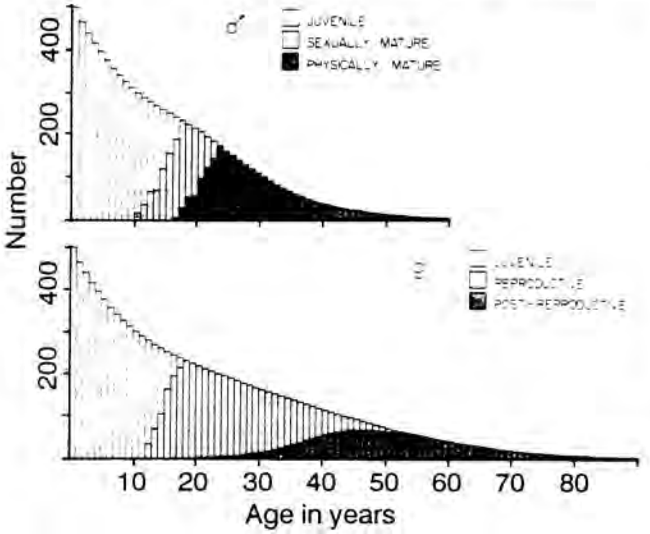

Fig. 22. Vertical perspective of the sex– and age-structure of males (top) and females (bottom) in a population below carrying capacity. The population is the same as that showed in Fig. 21 viewed from a different perspective. This figure shows the sex- and age-composition of the population (i.e. a series of cohorts recruited over a series of years) at any given point in time (see Sections 4.2.6 and 4.2.7 for details).

rounded to the nearest 10 years, by which the prevalence of the age-class in a stable population has diminished to less than 1% of the number of new recruits. Because older animals constituted only a small fraction of the total population, and all older females were post-reproductive, the exact truncation point is not critical. For example, females aged greater than 70.5 years comprised only 1.2% of the stable population whereas those aged greater than 81.5 years only 0.3%. These values are in accord with the direct estimates of female longevity (Section 3.1.4). Similarly, males aged older than 41.5 years comprised only 3.3% of the stable population and those greater than 51.5 years only 0.9%.

4.2.7 Horizontal versus vertical analysis

The preceding analyses provide two perspectives of the sex– and age-structure of the stable population. Fig. 20 gave a horizontal (longitudinal) perspective. This figure showed the fate of a particular cohort followed through time as it aged. The cohort declined in size with age (time) due to mortality. For example, the number of males aged 10.5 years was only 80.1% the number aged 0.5 years because only 80.1% of the cohort survived to age 10.5 years.

Fig. 22 gives a vertical (latitudinal) perspective of the stable population. This figure shows the sex– and age-structure of the population at a given point in time. The sizes of age-classes decline with age not only because of mortality, but also because of the increasing population. For example, the number of males in the 10.5 year age-class was only 60.0% of the number in the 0.5 year age-class because 80.1% of 10.5 year age-class had died since they were born into the population 10.5 years ago; and also because the population had grown in size such that the number of males recruited into the population 10.5 years ago was only 75.0% of the number recruited 0.5 years ago.

In most population assessments, horizontal data are unavailable and mortality and survival rates are inferred vertically from the age-composition of catches. As evident in Figs 20 and 22, this can lead to serious biases when the population is non-stationary. If the population growth rate is precisely known, the age-structure can be adjusted to account for these biases. However, in many cases, precise information on population trends are unavailable and stationarity is assumed.

Since both horizontal and vertical data are available for the study population, it provides an opportunity to evaluate the biases introduced by non-stationarity in vertical analyses. The magnitude of bias was assessed by analyzing the stable sex– and age-structure of the population as if the population was stationary. This was done by simply substituting the $P_{s(x)}$s for the $L_{s(x)}$s in the life table and recalculating the population parameters. The exercise can be considered realistic in that the population growth rate of 2.92% was probably too small to have been discernible using conventional censusing methods.

Mortality rates were overestimated in the vertical analysis because the decline in the size of the age-classes with age was not entirely due to deaths, but was also partly due to the fact that the initial size of cohorts was increasing with time. The magnitude of bias, expressed as a multiplier of the true mortality rate, was a function of the population growth rate, λ, and the true mortality rate, $MR_{(x)}$:

$$\text{Bias} = (1\text{-}[(1\text{-}MR_{(x)})/\lambda])/MR_{(x)} \qquad (60)$$

For example, for $MR_{(x)}=0.01777$ and $\lambda=1.0292$, the mean *per capita* death rate and finite rate of increase in the stable population (Sections 4.2.5 and 4.2.3), mortality rates are overestimated by a factor of 2.55. The degree of bias is greater for age-classes exhibiting low mortality, such as reproductive females, and less for age-classes exhibiting high mortality, such as juveniles.

The biased mortality rates substantially bias other population parameters (Table 16). However, the biased stable sex– and age-structure was, within computational error, identical to the unbiased stable sex– and age-structure of the population (Fig. 23). Thus, internal consistency checks would not have revealed that something was amiss.

The above exercise indicates that small departures from stationarity, likely too small to discern using traditional censusing methods, may introduce serious distortions in vertical population assessments. Such biases will occur whenever populations are below their carrying capacity, which would include populations that were being exploited or were recovering from exploitation. Indeed, the biases

Table 16

Biases in select population parameters resulting from non-stationarity (λ = 2.92%) in a vertical population analysis.

Life history parameter:	Stable:	Stationary:
Life expectancy:		
Male at age 0.5years	50.1 yrs	23.1 yrs
Female at age 0.5years	28.7 yrs	17.7 yrs
Survival:		
Both sexes to maturation (age15.5)	77.9%	50.6%
Female to post-reproduction (age 40.5)	71.2%	22.5%
Male to physical maturity (age 21.5)	72.2%	39.4%
Net reproductive rate		
(number of male and female calves)	4.08 calves	2.02 calves
Sex ratio (females:males)	1.30:1	1.29:1
Finite rates:		
Total death, *per capita*	0.02180	0.0488
Total birth, *per capita*	*0.05103*	*0.0495*
Population increase	2.92%	0.06%

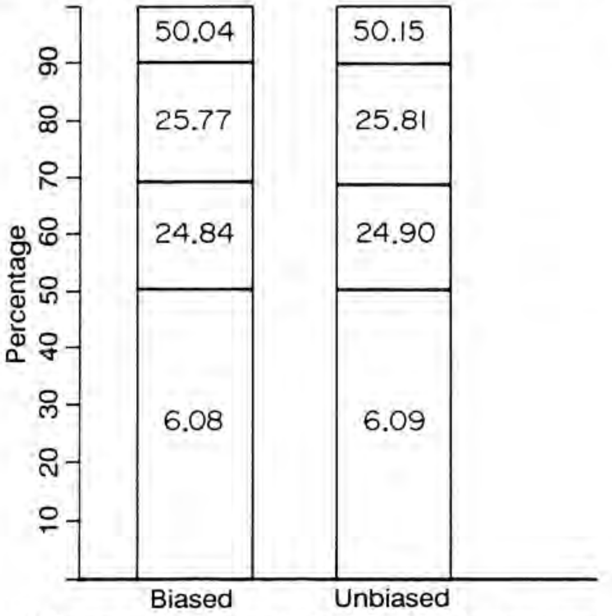

Fig. 23. Comparison of the actual (unbiased) sex– and age-structure in a stable population and the biased sex– and age-structure predicted by a vertical analysis assuming stationarity. The population is partitioned into, from bottom to top: juveniles, mature males, reproductive females and post-reproductive females. The numbers within each partition represent the mean age of animals in each category.

would persist in the older age-classes that had been recruited while the population was being exploited or recovering for considerable periods after the population had recovered. Since the implications of these biases are widely applicable to cetacean populations, future vertical population assessments should be subjected to sensitivity analyses to determine the effects of non-stationarity.

4.2.8 Sustainable harvests

Since the study populations were below carrying capacity and increasing exponentially at their intrinsic rate (Sections 3.7 and 4.2.3), the growth of the population represented the maximum surplus production that could be harvested on a sustained basis.

Assuming the harvest was taken just after the summer census and prior to the next calving season, we estimated the maximum sustainable non-selective harvest rate, HR_n, to be:

$$HR_n = (\lambda-1)/\lambda = 0.0284 \qquad (61)$$

which indicates that if 2.84% of each sex– and age-class was removed each year, the population would show no net change in size. The non-selective harvest would have no effect on the sex– and age-structure of the population.

In practice, fisheries are usually selective for particular sex– and/or age-classes. The impact of a selective harvesting regime can be assessed with the matrix projection model. Defining **H** as a matrix (of the same order as **M**) giving the rate of harvest of each sex– and age-class, $HR_{s(x)}$:

$$H = \begin{array}{llllll} HR_{m(0.5)} & 0 & 0 & 0 & \cdots\cdot & 0 \\ 0 & HR_{f(0.5)} & 0 & 0 & \cdots\cdot & 0 \\ 0 & 0 & HR_{m(1.5)} & 0 & \cdots\cdot & 0 \\ 0 & 0 & 0 & HR_{f(1.5)} & \cdots\cdot & 0 \\ . & . & . & . & \cdots\cdot & HR_{f(90.5)} \end{array}$$

the size and sex- and age-structure of the harvested population at time t+1, $\mathbf{n}_{t+1}$, can be obtained by:

$$\mathbf{n}_{t+1} = \mathbf{M}\cdot\mathbf{H}\cdot\mathbf{n}_t \qquad (62)$$

By projecting the harvested population for a sufficient period (equations (42) and (43)), the long-term impact of the harvesting regime on the rate of increase and structure of the population can be ascertained. Using this procedure, we iteratively established sustainable (i.e. $\lambda=1$) configurations of **H**.

Sustainable $HR_{s(x)}$s were derived for two types of fisheries: one that targeted exclusively juveniles aged 0.5 to 14.5 years, and one that targeted exclusively adults aged ≥15.5 years. In both cases, the fishery was assumed to be non-selective within these age ranges. The population was able to sustain the removal of 4.70% of juveniles each year. Since juveniles comprised 40.3% of the resulting stable population (Fig. 24), this represents a total population harvest level of 1.89%, of which half is female. Alternatively, the population was able to sustain the removal of 8.43% of adults each year. Since adults comprised 37.7% of the stable population (Fig. 24) this represents a total population harvest level of 3.17%. Due to the skewed adult sex ratio (Fig. 24), the harvest would comprise 54.7% females (88.8% reproductive).

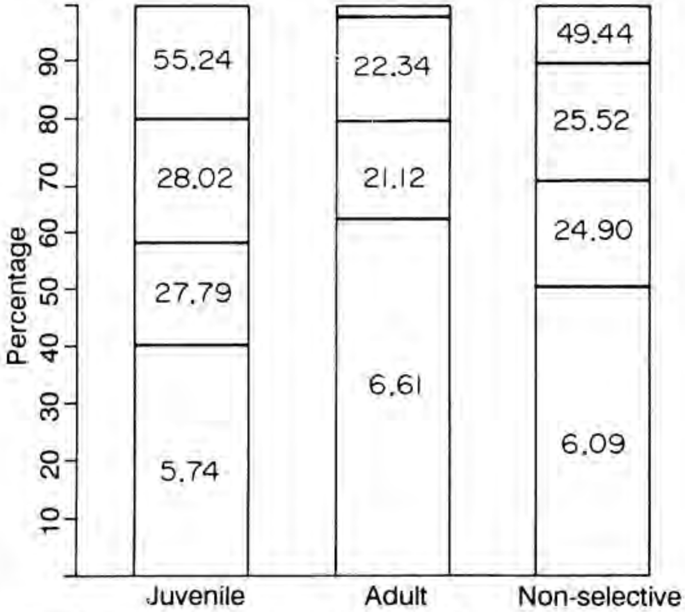

Fig. 24. Effect of sustainable juvenile, adult and non-selective harvests on the stable sex– and age-structure of a population. The population is partitioned into, from bottom to top: juveniles, mature males, reproductive females and post-reproductive females. The numbers within each partition represent the mean age of animals within each category.

This analysis indicates, rather surprisingly, that the population is more sensitive to removals of juveniles than mature animals. This is due to the high reproductive value of juveniles compared to mature females (Fig. 21). In general, the relative sensitivity of the population to the removal of an animal of a given age is directly proportional to the animal's reproductive rate; and the sensitivity of the population to the removal of a given age-class is directly proportional to the age-class's relative reproductive value (Fig. 21).

The harvests outlined in the preceding paragraph were limited only by the removal of females, as males made no direct contribution to recruitment. In many populations, particularly of polygamous species, harvest levels can be increased by targeting males. In our simplified model, the male harvests were limited only by the recruitment rate of males. For example, if all males in the stable population were harvested at birth, the sustainable harvest level would be equivalent to the male birth rate per female (Section 4.2.5), which represents a harvest level of 4.52% of the total population. Such a population would be completely devoid of males. Alternatively, removing all males as they attain sexual maturity results in a sustainable male harvest of 3.13% of the total population, which would be completely devoid of sexually mature males. Thus, the population is able to sustain only relatively small male harvests simply because their recruitment rates are so low.

All of the above harvesting rates probably overestimated the actual sustainable harvests because only the direct demographic contribution of animals was considered. Consequently, the removal of males and post-reproductive females had no effect because they made no direct contribution to recruitment. In reality, however, these animals likely make some social contribution. For example, at least some mature males are required for mating and post-reproductive females may play a role in the rearing of young, but these contributions cannot be quantified at present. Moreover, the removal of one animal may adversely affect the survival of other animals. For example, the death of females might also increase the likelihood of the death of their dependent offspring.

4.3 Stock assessment

The population model has provided a framework for examining the dynamics of the northern and southern communities during and prior to the study. Initially, we used the model to compare the observed sex– and age-structure of the two communities during the study to the predicted stable sex– and age-structure. This comparison serves two purposes. On the one hand, it provides an independent assessment of the validity of the population model. The assessment was in fact independent because the life history parameters were derived horizontally and were therefore in no way contingent upon the vertical sex– and age-structure of the study population. On the other hand, discrepancies between the observed and predicted sex– and age-structure provide insight into how departures from the model or stochastic events affect real populations. Secondly, the model was used to reconstruct population trends since 1960 to assess the impact of the live-capture fishery.

The above analyses are inseparable. The current sex– and age-structure could not have been evaluated without accounting for distortions that may have been introduced by selective cropping. Conversely, the reconstruction of the historic population was based on the current sex– and age-structure of the population.

4.3.1 Methods

The effect of cropping on the sex– and age-structure observed during the study was assessed by correcting the observed structure for cropping. The corrected sex– and age-structure in year t, $\mathbf{c}_t$, was obtained by projecting the sex– and age-structure of the harvest taken in each of i years in which there was a harvest to time t, $\mathbf{h}_{it}$, and adding it to the observed sex– and age-structure in year t,$\mathbf{a}_t$:

$$\mathbf{c}_t = \mathbf{a}_t + \sum_{i=1962}^{1977} \mathbf{h}_{it} \tag{63}$$

where $\mathbf{h}_{it}$ was obtained by:

$$\mathbf{h}_{it} = \mathbf{M}^{t-j} \cdot \mathbf{h}_{ij} \qquad \text{(with i=j)} \tag{64}$$

and where $\mathbf{a}_t$, $\mathbf{c}_t$ and $\mathbf{h}_{it}$ represent column vectors and **M** the transition matrix as defined in Section 4.1.1. For instance, the impact of the 1962 harvest on the sex– and age-structure in 1975 was determined by projecting the estimated sex– and age-structure of animals cropped in 1962 to 1975 (i.e. $\mathbf{h}_{62,75}=\mathbf{M}^{13}\mathbf{h}_{62,62}$) and adding it to the observed structure in 1975. The sex– and age-structure of the harvest in the year it was taken ($\mathbf{h}_{ij}$ with i=j) was estimated based on the sex and size of the cropped animals (Table 3). The four cropped animals of unknown sex were partitioned equally among females and males. Cropped animals were amortized over the age ranges corresponding to their size (Section 2.4.2) according to the relative frequencies of the age-classes in a stable population (Section 4.2.6). Since the cropped animals were predominately juveniles, the age estimates were reasonably precise.

To simplify comparison of the observed and corrected sex– and age-structures, animals were categorized as either juveniles, mature males, reproductive females or post-reproductive females. Since there was no way of knowing whether females that were reproductive late in the study would subsequently give birth, they were partitioned among reproductive and post-reproductive categories based on their estimated ages and the $PR_{(x)}$s (Fig. 17). The mean age of animals within each category was calculated as an index of its age composition.

The impact of the live-capture fishery on each community was assessed by projecting the size of each community back to 1960. Normally, the size and sex– and age-structure in year t-1 could have been obtained by multiplying the structure in year t by the inverse of the transition matrix, **M**. However, since the model had been extended to include males and post-reproductive females, it was not of Leslie form and $\mathbf{M}^{-1}$ was undefined. Alternatively, the number of animals in year t-1 in all but the oldest age-classes was estimated by:

$$n_{s(x-1)t-1} = n_{s(x)t}/SV_{s(x-1)} \tag{65}$$

and the number in the oldest age-class by:

$$n_{s(x)t-1} = \sum_{x=0.5}^{max} MAT_{s(x)} \cdot n_{s(x-1)t-1} \cdot PL_s \tag{66}$$

where values for $MAT_{f(x)}$ and $MAT_{m(x)}$ were given in Tables 6 and 7 and the PL_s denoted the proportion of the mature animals of sex s that died in the last age-class in a stable population (PL_f=0.036% and PL_m=0.122%).

4.3.2 Northern community

The observed and corrected sex– and age-structure of the northern community nearly coincide (Fig. 25a). The predicted rate of increase of the corrected population over the course of the study, calculated as per sections 2.3.1 and 2.3.2, is 2.65%, which is similar to the observed rate of 2.62% (Section 2.3.1). The absence of an appreciable cropping effect can be explained by the fact that relatively few animals (15) were cropped from the community and there was no pronounced bias toward either sex (7 females and 8 males).

The sex– and age-structure of the northern community generally conforms with that of a stable population (Fig. 25a). Overall, the weighted mean corrected population comprised slightly too few juveniles (47.0% observed vs 50.3% expected) and too many mature males (24.1% vs

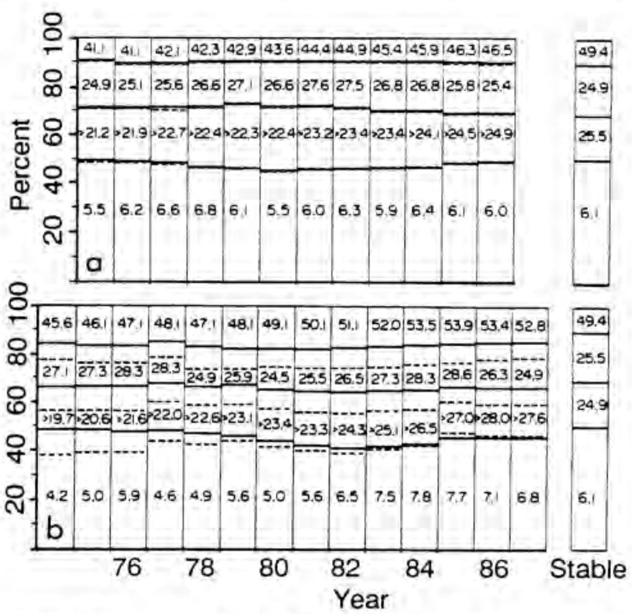

Fig. 25. The observed sex– and age– structure (solid lines) and the sex– and age-structure corrected for cropping (dashed lines) during the study in: a) the northern community; and b) the southern community. The observed and corrected populations are partitioned into, from bottom to top: juveniles, mature males, reproductive females and post-reproductive females. The numbers within each partition represent the observed mean ages of animals within each category.

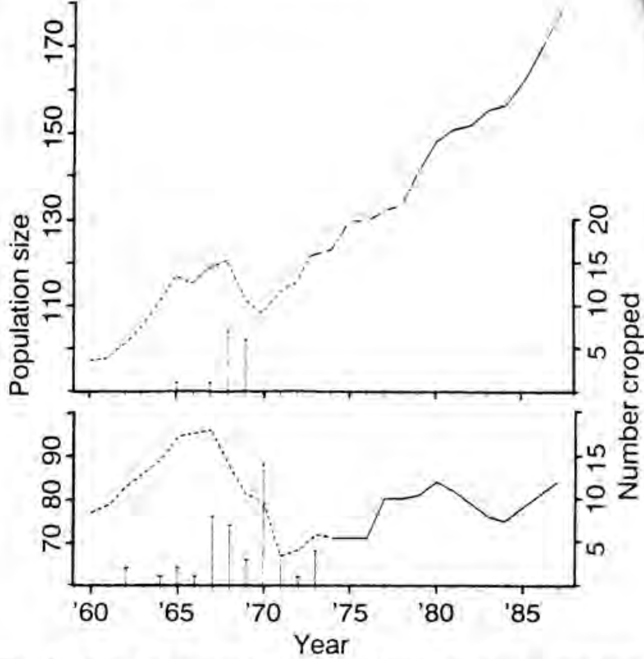

Fig. 26. Population trends during 1960–87 in: a) the northern community; and b) the southern community. Dashed lines indicate that the population trends were projected with the matrix model; solid lines indicate that the population trends were based on complete censuses of all pods in the community; and broken lines indicate that some pods were censused and the size of others projected. The vertical bars indicate the estimated number of animals removed from the community during the live-capture fishery.

18.7%) but roughly the expected number of reproductive (19.3% vs 20.8%) and post-reproductive females (9.6% vs 10.3%). The mean ages within each category are also similar to those expected in a stable population (Fig. 25a). Note that the mean minimum age of males converged on its expected value during the study as the errors inherent in the minimums diminished (e.g. a male aged 20+ years at the start of the study would have been aged 35+ years by the end of the study).

Fig. 25a also illustrates the subtle patterns that can arise due to the stochastic nature of the demographic events. Although essentially equal numbers of males and females matured during the study (22 males and 24 females), the majority of males (15 of 22) matured prior to 1981 and the majority of females (18 of 24) after 1981. As a result, during 1975–81 the sex ratio of mature animals became skewed toward males, recruitment rates declined and the proportion of juveniles decreased. Conversely, during 1982–86 more females than males matured and the above trend was reversed. By 1987, the population had returned to a stable sex– and age-structure. However, due to the 'bulge' in the number of mature males during the middle of the study (Fig. 25a), there were on average only 92.8% as many reproductive females as in a stable population. This largely explains why the observed rate of increase during the study of 2.65% was only 90.8% of the 2.92% expected in a stable population.

The back-projections indicate that, despite the removal of 15 animals during the live-capture fishery, the northern community has been increasing in size since at least 1960 (Fig. 26a). The high net apparent fecundity between 1955–74 (Table 8) and stable sex– and age-structure of the community supports this finding. The mean annual rate of increase during 1960–75 was estimated at 1.90%. However, during this period the community was harvested at a mean weighted rate of 0.83%. Thus, the total rate of production is about 2.73%, which represents 94% of the 2.92% expected rate for a stable population.

The growth of the northern community during the study could not be attributed to recovery from the live-capture fishery. It therefore implies that the population had been depleted prior to 1955–60, or that the carrying capacity has increased in recent years. With respect to depletion, it is possible that indiscriminate killing by fishermen and practice bombings (Section 2.4.1) exceeded the current non-selective sustainable kill of 5.1 animals *per annum* and depleted the population. Since it is not known what resources limit population size, nothing can be said at present concerning changes in carrying capacity.

4.3.3 Southern community

The assessment of the southern community was more complex than that of the northern community. Comparison of the observed and corrected sex-and age-structure of the community (Fig. 25b) indicates that the observed structure was distorted by selective cropping. Early in the study (1974–79), the observed population comprised too few juveniles (41.4% vs 50.1%) and these juveniles tended to be younger than expected (mean age 5.0 years vs 6.1 years) and their sex ratio was biased toward females (63.0% females vs 50.5%). The sex ratio of mature animals was also skewed toward females (2.4–2.6:1 vs 1.70:1).

These discrepancies can be largely attributed to selective cropping (Fig. 25b). Most importantly, juveniles (particularly males) and mature males were under-represented during the study because of the large number of immature males (23 males vs 12 females) that were cropped. The minimum mean age of males also increased during the study more rapidly than in the northern community because few males matured during the study (see also Table 10) due to the cropping of juvenile males.

When corrected for cropping, the 1974–79 sex- and age-structure of the southern community generally conforms to that of a stable population (47.9% vs 50.3% juveniles, 19.0% vs 18.7% mature males and 33.1% vs 31.0% mature females). Similarly the corrected sex composition of juveniles (49.1% females vs 50.5%) and the mature sex ratio (1.74:1 versus 1.70:1) were close to their expected values.

However, the discrepancy in the ratio of reproductive to post-reproductive females cannot be fully attributed to cropping. During 1974–79, only 42.9% of all mature females in the southern community were reproductive compared to the expected value of 66.9% in a stable population. Because few mature females were cropped, the corrected proportion of reproductive females, 50.1%, was also below the expected value. This aberration appears to have developed recently. During 1973–77, 9 of the 20 (45%) reproductive females in the community gave birth to their last viable calves. Thus, an estimated 65.6% of mature females were reproductive in 1972, which was close to the expected value of 66.9%.

Why so many females stopped calving over such a short period is unclear. During 1973–77, females stopped calving at a mean annual rate of 11.2%, which was about 4.5 times the steady-state rate of the onset of post-reproduction of 2.5% in a stable population. Unfortunately, the precise ages of the females in question could not be established because they likely had progeny cropped. In fact, eight of the nine were aged in reference to the year they last gave birth. One possible explanation is that the cropping of males had reduced the number of mature males in the community below a critical number for optimal productivity. During 1974–79, there were only 12–13 mature males in the community and only 10–11 of these were physically mature. Had the nine females in question remained reproductive, the mature male to reproductive female ratio would have declined to 0.57–0.65. However, because so many females stopped calving, the mature male to reproductive female ratio was maintained at 0.91, which was close to the 0.90 ratio in a stable population.

Whatever the underlying cause, the disproportionately low number of reproductive females at the start of the study resulted in lower productivity throughout the study. Moreover, the situation was further exacerbated by cropping. Because juvenile females were cropped prior to the study, fewer females matured than expected and the shortage of reproductive females persisted longer than it otherwise would have. During the study, a weighted mean of 52.3% of females were reproductive in the corrected population whereas only 43.2% were reproductive in the observed population. The observed value of 43.2% was only 65% of the expected value of 66.9% in a stable population. As a result, recruitment rates were low during the study such that the proportion of juveniles remained low and their mean age increased until about 1984, at which time females born after the live-capture fishery began to mature.

The back-projections (Fig. 26b) indicate that the southern community was increasing during 1960–65, which was prior to the live-capture fishery. However, the community could not sustain the large croppings during 1967–71 and by 1971 was reduced to 67 individuals, 70% of its 1967 peak size of 96 individuals. Overall, between 1960–74, the population showed little net change in size ($\lambda=0.994$). During this period, the community was cropped at a weighted mean rate of 4.10%, or about 1.44 times the non-selective sustainable take. The reason the community did not decline more sharply was that the cropped animals were mainly juveniles and males. As noted above, the impact of the removal of juvenile females was pro-rated over future years (i.e. had they not been cropped they would have been contributing to recruitment during the study). Also, the removal of males had no direct demographic impact on the population.

In summary, the recovery of the southern community from the live-capture fishery was hindered by several factors: (1) a disproportionate number of females became post-reproductive just prior to or early in the study – this may have been unrelated to the live-capture fishery, or been an indirect effect due to the reduction in the prevalence of mature males as a result of the fishery; (2) because of the cropping of juvenile females, fewer females than expected matured during the study to replace those that became post-reproductive; (3) one female (K40) remained unproductive to age 22.5 years; (4) juveniles experienced slightly higher mortality than expected (Section 4.1.2). The first three factors accounted for an estimated shortfall in recruitment of 4.1, 8.9 and 2.2 calves during the study, respectively. The fourth factor accounted for 2.6 more juvenile deaths than expected. If these figures are added to observed rate of increase of 1.30%, the net increase would have been 2.81%, or 96% of the expected rate of 2.92%.

4.4 Stationary population (at carrying capacity)

A population cannot continue to increase indefinitely and, as it approaches its carrying capacity, births and deaths must attain an equilibrium. A stable population that is neither increasing or decreasing in size is said to be stationary. Since we found no direct evidence of density dependence in the killer whale life history parameters (Section 3.7), we examined the sensitivity of the population to changes in each parameter. Based on the sensitivity analysis, we speculate as to how density dependence would most likely be expressed and how the sex- and age-structure would be affected by such changes.

4.4.1 Sensitivity analysis

Animal populations are regulated by changes in female birth and death rates which can be broadly categorized as follows:

(1) Birth rates	Parameter:
(i) Fecundity rates	$FEC_{r(x)}=FER_{r(x)} \cdot SV_{(0.5)}$
(ii) Age at first birth	$MAT_{f(x)}$
(iii) Age at onset of post-reproduction	$PR_{(x)}$
(2) Death rates	
(i) Juvenile mortality	$MR_{s(x)}$ for $0.5 \geq x \geq 14.5$
(ii) Adult mortality	$MR_{s(x)}$ for $x \geq 15.5$

Note that changes in fecundity may reflect either changes in the fertility (pregnancy) rate or the neonate survival rate. Since the effect of change in either of these parameters was identical (e.g. doubling the fertility rate was equivalent to doubling the neonate survival rate) only the sensitivity to net changes in fecundity was examined.

The relative sensitivity of the population to changes in each parameter was assessed with the matrix model by varying the transition probabilities in the projection matrix, **M**, and recalculating the stable rate of population growth, λ, and the stable sex- and age-structure, $\mathbf{n}_s$ using equations (43) and (42). Changes in fecundity and mortality rates were effected by simply multiplying the current estimates of the parameters by an appropriate factor. For example, the effect of a 2-fold increase in fecundity was assessed by multiplying the top two rows of the transition matrix, **M**, by 2. Because the mortality rates of females aged 15.5–24.5 years were below detectable limits (Table 12), the weighted mean mortality rate for ages 15.5–34.5 years was used. This tends to slightly exaggerate the sensitivity of the population to changes in adult mortality rates. Changes in $\mathrm{MAT}_{f(x)}$ and $\mathrm{PR}_{(x)}$ were effected by shifting the curves shown in Figs 7 and 17 by the appropriate number of years to the left or right.

The sensitivity analysis indicated that λ, was surprisingly insensitive to changes in life history parameters (Fig. 27). For example, a stationary population (λ=1) could only be obtained by either:

(1) reducing $\mathrm{FEC}_{r(x)}$ to 50% of the current values;
(2) increasing mean age at first birth from 15 to 30 years;
(3) decreasing mean age at last birth from 40 to 24 years;
(4) increasing juvenile mortality rates by a factor of 3.8; or
(5) increasing adult mortality rates by a factor of 50.

The stationary sex– and age-structures corresponding to each of the above changes are summarized in Fig. 28.

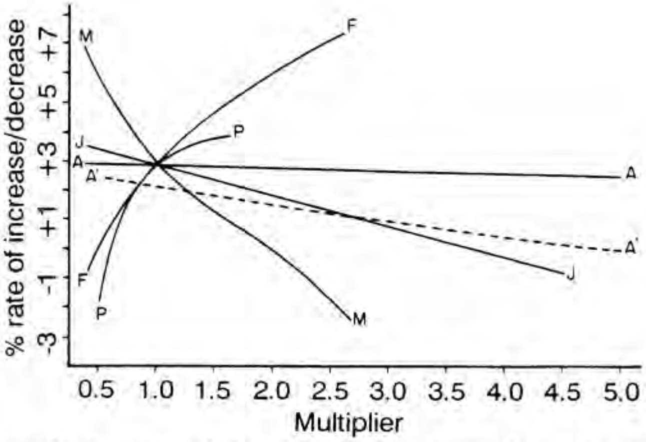

Fig. 27. Sensitivity of the population growth rate, λ, to relative changes in each life history parameter (F=fecundity rate; M=mean age at first birth; P=mean age at onset of reproductive senescence; J=juvenile mortality rate; A=adult mortality rate; and A'= adult mortality at 10-times the scale indicated on the horizontal axis). For example, the value of λ at 2.5 represents the finite rate of population growth resulting from a 2.5-fold increase in each parameter (solid lines) or a 25-fold increase in adult mortality rates (dashed line).

The population growth rate, λ, was generally more sensitive to changes in reproductive parameters (Fig. 27 – F, M and P) than mortality rates (Fig. 27 – J, A, and A′) The effects of changes in the reproductive parameters were non-linear. For example, increasing $\mathrm{FEC}_{r(x)}$ had less of an effect than decreasing $\mathrm{FEC}_{r(x)}$ (Fig. 27 – F). This was because a decrease in $\mathrm{FEC}_{r(x)}$ skewed the age-composition toward older mature animals (Fig. 28 – F) such that more animals were affected by the change. In contrast, the sensitivity of λ to changes in $\mathrm{MAT}_{f(x)}$ was more pronounced as $\mathrm{MAT}_{f(x)}$ was both increased and decreased (Fig. 27 – M). This was because a decrease in $\mathrm{MAT}_{f(x)}$ skewed the age-composition toward young animals such that progressively more were affected by the decrease. However, large increases in $\mathrm{MAT}_{f(x)}$ also had a pronounced effect because females began to become post-reproductive before they gave birth to their first viable calves (Fig. 28 – M). Decreasing $\mathrm{PR}_{(x)}$ had a far greater effect than increasing $\mathrm{PR}_{(x)}$ (Fig. 27 – P) for the same reasons outlined above for $\mathrm{FEC}_{r(x)}$ (Fig 28 – P).

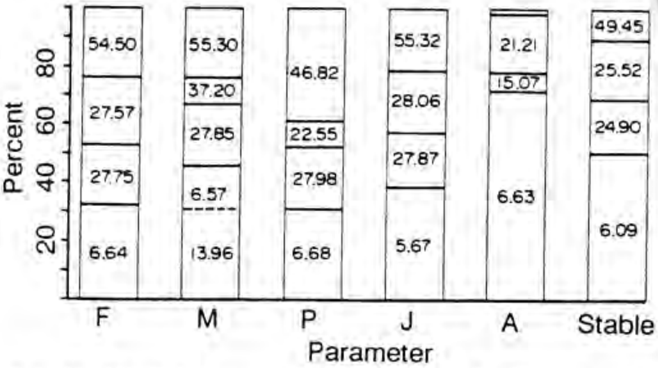

Fig. 28. The stable sex– and age– structure for the stationary populations (λ=1) corresponding to the change in each of the life history parameters required to balance the population. The populations are partitioned into, from bottom to top: juveniles, mature males, reproductive females and post-reproductive females. The numbers within each partition represent the mean age of animals within each category. Note that for M, only the mean age at maturation of females was adjusted; the disparate sex ratio of juveniles is indicated by the dashed line: females (bottom) and males (top).

The stationary sex– and age-structure resulting from a change in either of the reproductive parameters, or for that matter any combination of the reproductive parameters, is identical to that shown in Fig. 20. However, the ages at which females are categorized as juvenile, reproductive and post-reproductive differs depending on which of the reproductive parameters are varied. The age-structure is the same because mortality rates had not been altered so that the decline in cohort size with age was not affected. Also, by definition, the initial size of cohorts remains constant over time in a stationary population.

The population was less sensitive to changes in juvenile mortality rates than to changes in the reproductive parameters. The effect of a change in juvenile mortality rates was nearly linear and not as pronounced as might be expected (Fig. 27 – J). This was because an increase in juvenile mortality skewed the population toward older age-classes (Fig. 28 – J) so that fewer animals were affected by the change and vice versa. The sex– and age-structure of the stationary population resulting from a 3.8-fold increase in juvenile mortality was intermediate to those shown in Figs 20 and 22. The juvenile component of the stationary population resembled the latter whereas the mature component was identical to the former.

The population was extremely robust to changes in adult mortality rates (Fig. 27 – A and A'). The stationary population corresponding to a 50-fold increase in the adult mortality rate was grossly skewed toward juveniles and essentially devoid of post-reproductive females (Fig. 28 – A). The robustness could be attributed to the fact that reproductive females contributed most to recruitment early in their reproductive lifespan (i.e. they had to die early in their reproductive lifespan to have much of an effect) and the mortality rates of reproductive females were extremely low.

Contrary to the above, it has been widely cited that populations of large mammals are very sensitive to changes in adult mortality rates. This is in fact a misinterpretation of work by Eberhardt and Siniff (1977), Breiwick, Eberhardt and Braham (1984), Goodman (1984) and others that has actually shown that large-mammal populations are sensitive to changes in adult survival rates, which does not imply equal sensitivity to mortality rates. For example, female killer whales aged 15.5–34.5 years had a mean finite mortality rate of 0.0020 and survival rate of 0.9980. Thus, a 50-fold increase in mortality to 0.0992 represented less than a 10% reduction in the survival rate. Thus, like other large-mammal populations, killer whale populations are very insensitive to relative changes in mortality rates, but sensitive to relative changes in survival rates.

4.4.2 Stationary population parameters

The sensitivity analysis suggests that: (1) density dependence is more likely to be expressed through changes in reproductive rates rather than mortality rates, especially adult mortality rates; and (2) the magnitude of changes in any single life history parameter, with the exception of perhaps $\mathrm{FEC}_{r(x)}$, required to balance the population are unrealistic. Thus, density dependence is probably expressed by simultaneous changes in several life history parameters.

The most objective estimate of the sex– and age-structure of a stationary killer whale population was obtained by changing each life history parameter an equal relative amount. Iteratively, it was found that a 20% change in each parameter was required to balance the population. That is, $\mathrm{FEC}_{r(x)}$s were set at 80% of their estimated values, mean age at first birth was increased from 15 to 18 years, mean age at onset of post-reproduction was reduced from 40 to 32 years and mortality rates for all age-classes were set at 120% of their estimated values. The resulting stationary population comprised 36.6% juveniles (54.7% female and 45.3% male with mean ages of 8.1 and 6.5 years, respectively; the skewed ratio resulted because age of maturation of males was not adjusted), 19.8% males (mean age 26.6 years), 14.4% reproductive females (mean age 26.7 years) and 29.0% post-reproductive females (mean age 49.4 years). Selected population parameters for the stationary population are summarized in Table 17 and condensed life tables are given in Appendix 1.

The predicted stationary population probably provides a fairly accurate representation of an actual stationary population. This is because density dependence is likely to be expressed primarily through changes in reproductive parameters and the manner in which the reproductive parameters varied had no effect on the sex– and age-structure of the population. Moreover, an increase in juvenile mortality rates and a decrease in the reproductive rates has similar effects on the sex– and age-structure. Thus, serious inaccuracies will arise only if adult mortality plays a more important role in density dependence than we have predicted.

Table 17

Comparison of select population parameters for a stable population that is below carrying capacity and increasing at its intrinsic rate and population parameters for a stationary population at carrying capacity.

Life history parameter:	Stable:	Stationary:
Life expectancy:		
Male at age 0.5years	50.1 yrs	45.9 yrs
Female at age 0.5years	28.7 yrs	26.0 yrs
Survival:		
Both sexes to maturation (age)	77.9% (15.5)	74.1% (18.5)
Female to post-reproduction (age)	71.2% (40.5)	71.9% (32.5)
Male to physical maturity (age 21.5)	72.2%	67.6%
Net reproductive rate (number of male and female calves)	4.08 calves	2.00 calves
Sex ratio (females:males)	1.30:1	1.76:1
Finite rates:		
Total death, *per capita*	0.02180	0.02778
Total birth, *per capita*	0.05103	0.02772
Population increase	2.92%	0.01%

It is worth noting that the magnitude of changes in the life history parameters required to balance the population fall well outside the confidence limits of the parameter estimates in the present study. We therefore anticipate that continued monitoring of killer whales in the coastal waters of British Columbia and Washington State as they ultimately approach their carrying capacity will refine our understanding of the mechanisms of population regulation in this species.

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REFERENCES

Anderson, G.R.V. 1982. A re-examination of pregnancy rates and calf ratios in *Orcinus orca*. Appendix 5. Report of the Workshop on Identity, Structure and Vital Rates of Killer Whale Populations, Cambridge, England, June 23–25, 1981. *Rep. int. Whal. Commn* 32: 629–31.

Bain, D.E. 1990. Testing the validity of inferences drawn from photo-identification data, with special reference to the studies of the killer whales (*Orcinus orca*) in British Columbia. Paper SC/A88/ID33 (published in this volume).

Baird, R.W. and Stacey, P.J. 1988. Variation in saddle patch pigmentation in populations of killer whales (*Orcinus orca*) from British Columbia, Alaska and Washington State. *Can. J. Zool.* 66: 2582–5.

Balcomb, K.C. III, Boran, J.R. and Heimlich, S.L. 1982. Killer whales in greater Puget Sound. *Rep. int. Whal. Commn* 32: 681–6.

Bigg, M.A. and Wolman, A.A. 1975. Live-capture killer whale (*Orcinus orca*) fishery, British Columbia and Washington, 1962–73. *J. Fish. Res. Bd Can.* 32: 1213–21.

Bigg, M.A. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Rep. int. Whal. Commn* 32: 655–66.

Bigg, M.A., Ford, J.K.B. and Ellis, G.M. 1985. Two sympatric forms of killer whales off British Columbia and Washington. Abstract. Presented to the Sixth Conference on the Biology of Marine Mammals, Vancouver, Canada, November 1985 (unpublished).

Bigg, M.A., Ellis, G.M, Ford J.K.B. and Balcomb, K.C. 1987. *Killer Whales. A Study of Their Identification, Genealogy & Natural History in British Columbia and Washington State*. Phantom Press, Nanaimo, British Columbia 79pp.

Bigg, M.A., Olesiuk, P.F, Ellis, G.M., Ford, J.K.B. and Balcomb, K.C., III. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Paper SC/A88/ID39 (published in this volume).

Boveng, P. 1988. Status of Pacific harbor seal population on the U.S. west coast. Admin. Rep. LJ-88-06, Southwest Fish. Center, Natl. Mar. Fish. Serv. 43 pp.

Breiwick, J.M., Eberhardt, L.L and Braham, H.W. 1984. Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*). *Can. J. Fish. Aquat. Sci.* 41: 484–96.

Caldwell, D.K. and D.H. Brown. 1964. Tooth wear as a correlate of described feeding behavior by the killer whale, with notes on a captive specimen. *Bull. Southern Calif. Acad. Sci.*, 63: 128–40.

Carl, G.C. 1946. A school of killer whales stranded at Estevan Point, Vancouver Island. *Rept Prov. Museum Natural History and Anthrop.* pp. B21–8.

Caughley, G. 1966. Mortality patterns in mammals. *Ecology* 47: 906–18.

Cavanagh-Ford, D. 1984. Culture and nature on the Northwest Coast. *Waters (J. Vanc. Publ. Aquarium)* 7: 6–14.

Christensen, I. 1982. Killer whales in Norwegian coastal waters. *Rep. int. Whal. Commn* 32: 633–41.

Christensen, I. 1984. Growth and reproduction of killer whales, *Orcinus orca*, in Norwegian coastal waters. *Rep. int. Whal. Commn* (special issue 6): 253–8.

Cole, L.C. 1954. The population consequences of life history phenomena. *Quarterly Rev. Biol.* 29: 103–37.

DeMaster, D.P. 1978. Calculation of the average age of sexual maturity in marine mammals. *J. Fish. Res. Bd Can.* 35: 912–15.

DeMaster, D.P. 1981. Estimating the average age of first birth in marine mammals. *Can. J. Fish. Aquat. Sci.* 38: 237–9.

DeMaster, D.P. 1984. Review of techniques used to estimate the average age at attainment of sexual maturity in marine mammals. *Rep. int. Whal. Commn* (special issue 6): 175–9.

DeMaster, D.P. and Drevenak, J.K. 1988. Survivorship patterns in three species of captive cetaceans. *Mar. Mammal Sci.* 4: 297–311.

DeMaster, D.P., Miller, D.J., Goodman, D., DeLong, R.L. and Stewart, B.S. 1982. Assessment of California sea lion fishery interactions. *In*: Transactions of the 47th North American Wildlife and Natural Resource Conf., 1982. Wildlife Management Institute, Washington, D.C.

Duffield, D.A. and Miller, K.W. 1988. Demographic features of killer whales in oceanaria in the United States and Canada. *Rit. Fisk* 11:297–306.

Eberhardt, L.L. and Siniff, D.B. 1977. Population dynamics and marine mammal management policies. *J. Fish. Res. Bd Can.* 34: 183–90.

Emery, M. 1960. Mystery of Von Dunlop Lagoon. Did killer whales commit suicide? Victoria Daily Colonist, Victoria, British Columbia. 3 pp.

Evans, P.G.H. 1988. Killer whales (*Orcinus orca*) in British and Irish waters. *Rit. Fisk.* 11:42–54.

Fisher, R.A. 1929. *The Genetical Theory of Natural Selection, 2nd rev. ed.* Dover, New York.

Fowler, C.W. 1984. Density dependence in cetacean populations. *Rep. int. Whal. Commn* (special issue 6): 373–9.

Fowler, C.W. 1987. A review of density dependence in populations of large mammals. Chapter 10. *In*: H.H. Genoways (ed.). *Current Mammalogy, Vol. 1.* Plenum Publ.

Gambell, R. 1972. Sperm whales off Durban. *Discovery Rep.* 35: 199–358.

Goodman, D. Statistics of reproductive rate estimates, and their implication for population projection. *Rep. int. Whal. Commn* (special issue 6): 161–74.

Heimlich-Boran, J.R. 1988. Behavioural ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. *Can. J. Zool.* 66: 565–78.

Heyning, J.E. 1988. Presence of solid food in a young killer whale (*Orcinus orca*). *Mar. Mammal Sci.* 4: 68–71.

Hoyt, E. 1981. *The Whale Called Killer*. E.P. Dutton, New York.

International Whaling Commission. 1980. Report of the Workshop. *Rep. int. Whal. Commn* (special issue 3): 1–50.

International Whaling Commission. 1982. Report of the Workshop on Identity, Structure and Vital Rates of Killer Whale Populations, Cambridge, England. *Rep. int. Whal. Commn* 32: 617–31.

International Whaling Commission. 1984. Report of the Workshop. *Rep. int. Whal. Commn* (special issue 6): 1–24.

Jacobsen, J.K. 1980. The birth of a wild killer whale (*Orcinus orca*). Orca Symposium, the biology and behavior of the killer whale (*Orcinus orca*). Held at Kane Hall, Univ. Washington, 10–12 October 1980, Am. Cet. Soc. and College of Fisheries, Univ. of Washington, Washington. Abstract.

Jonsgård, A. and Lyshoel, P.B. 1970. A contribution to the knowledge of the biology of the killer whale *Orcinus orca* (L.). *Nytt magasin for Zoologi*: 41–8.

Kasuya, T. and Marsh, H. 1984. Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. *Rep. int. Whal. Commn* (special issue 6): 259–310.

Kasuya, T., Sergeant, D.E. and Tanaka, K. 1988. Re-examination of life history parameters of long-finned pilot whales in the Newfoundland waters. *Sci. Rep. Whales Res. Inst., Tokyo*, 39: 103–19.

Leatherwood, S., Balcomb, K.C., Matkin, C.O. and Ellis, G. 1984. Killer whales (*Orcinus orca*) of southern Alaska. Results of field research. Preliminary report. HSWRI Tech. Rept. No. 84–175. 59 pp.

Leslie, P.H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 35: 183–212.

Lewis, E.G. 1942. On the generation and growth of a population. *Sankhya* 6: 93–96.

Lotka, A.J. 1907a. Relation between birth rates and death rates. *Science* 26: 21–2

Lotka, A.J. 1907b. Studies on the mode of growth of material aggregates. *Amer. J. Sci.* 24: 119–216.

Marsh, H. and Kasuya, T. 1986. Evidence for reproductive senescence in female cetaceans. *Rep. int. Whal. Commn* (special issue 8): 57–74.

Matkin, C.O., Ellis, G., von Ziegesar, O., and Steiner, R. 1986. Killer whales and longline fisheries in Prince William Sound, Alaska. Report No. 40ABNF6 2262 to Northwest and Alaska Fisheries Center, National Marine Mammals Laboratory, Seattle, Wash. 15 pp.

Mikhalev, Y.A., Ivashin, M.V., Savusin V.P., and Zelenya, F.E. 1981. The distribution and biology of killer whales in the Southern Hemisphere. *Rep. int. Whal. Commn* 31: 551–66.

Mitchell, E.D.(ed.) 1975. Review of biology and fisheries for small cetaceans. *J. Fish. Res. Bd Can.* 32: 889–983.

Mitchell, E.D. and Baker, A.N. 1980. Age of reputedly old killer whale, *Orcinus orca*, 'Old Tom' from Eden, Twofold Bay, Australia. *Rep. int. Whal. Commn* (special issue 3): 143–54.

Morton, A.B. 1990. A quantitative comparison of behaviour in resident and transient killer whales of the central British Columbia coast. Paper SC/A88/P17 (published in this volume).

Myrick, A.C., Yochem, P.K., and Cornell, L.H. 1988. Toward calibrating dentinal layers in captive killer whales by use of tetracycline labels. *Rit. Fisk.* 11:285–96.

Neter, J. and Wasserman, W. 1984. *Applied Linear Statistical Models*. Richard D. Erwin, Inc., Illinois.

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

Pike, G.C. and MacAskie, I.B. 1969. Marine mammals of British Columbia. *Fish. Res. Bd Can. Bull.* 71. 54 pp.

Sacher, G.A. 1980. The constitutional basis for longevity in the Cetacea: Do the whales and terrestrial mammals obey the same laws? *Rep. int. Whal. Commn* (special issue 3): 209–14.

Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. 2nd Edn. Griffin, London. 645 pp.

Sergeant, D.E. 1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. *Fish. Res. Bd Can. Bull.* 132. 84 pp.

Snedecor, G.W. and Cochran, W.G. 1980. *Statistical Methods (7th edition)*. The Iowa State Univ. Press, Iowa.

Sumich, J.L. and Harvey, J.T. 1986. Juvenile mortality in gray whales (*Eschrichtius robustus*). *J. Mamm.* 67: 179–82.

Swartz, S.L. and Jones, M.L. 1983. Gray whale (*Eschrichtius robustus*) calf production and mortality in the winter range. *Rep. int. Whal. Commn* 34: 503–7.

Sweeney, J.C. 1977. Difficult births and neonatal health problems in small cetaceans. *In*: S.H. Ridgway and K. Benirschke (eds.). Breeding Dolphins: Present Status, Suggestions for the Future. U.S. Dept. Comm. N.T.I.S. PB-273 673 for Marine Mammal Commission, Washington. D.C. 308 pp.

Tanami, R. 1984. A killer whale legacy. *Waters (J. Vanc. Publ. Aquarium)* 7: 15–20.

Usher, M.B. 1972. Developments in the Leslie Matrix Model. pp 29–60 *In*: J.N.R. Jeffers (ed.). *Mathematical Models in Biology*. Blackwell, Oxford.

Walker, L.A., Cornell, L., Dahl, K.D., Czekala, N.M., Dargen, C.M., Joseph, B., Hsueh, A.J.W. and Lasley, B.L. 1988. Urinary concentrations of ovarian steroid hormone metabolites and bioactive follicle-stimulating hormone in killer whales (*Orcinus orca*) during ovarian cycles and pregnancy. *Biol. Reprod.* 39: 1013–20.

Appendix 1

Predicted condensed life tables for a stationary population at carrying capacity.

A. Females

x	$L_{(x)}$	$d_{(x)}$	$q_{(x)}$	$l_{(x+0.5)}$	$e_{(x)}$	$m_{(x)}$	$P_{(x)}$
0.5	1000.0	48.5	0.0485	975.4	45.9	0.0000	1000.0
1.5	951.5	28.8	0.0303	937.0	47.3	0.0000	951.4
2.5	922.7	27.9	0.0303	908.8	47.7	0.0000	922.6
3.5	894.7	23.5	0.0263	882.9	48.2	0.0000	894.6
4.5	871.2	22.9	0.0263	859.6	48.5	0.0000	871.0
5.5	848.3	22.3	0.0263	837.0	48.8	0.0000	848.0
6.5	825.9	15.5	0.0188	818.1	49.1	0.0000	825.7
7.5	810.4	15.2	0.0188	802.8	49.0	0.0000	810.1
8.5	795.2	15.0	0.0188	787.7	49.0	0.0000	794.8
9.5	780.2	14.7	0.0188	772.8	48.9	0.0000	779.8
10.5	765.5	5.1	0.0066	763.0	48.8	0.0000	765.1
11.5	760.5	5.0	0.0066	758.0	48.1	0.0000	760.0
12.5	755.5	5.0	0.0066	753.0	47.4	0.0000	755.0
13.5	750.5	5.0	0.0066	748.0	46.8	0.0000	750.0
14.5	745.6	5.0	0.0066	743.1	46.1	0.0000	745.0
15.5	740.6	0.0	0.0000	740.6	45.4	0.0489	740.0
16.5	740.6	0.0	0.0000	740.6	44.4	0.0460	740.0
17.5	740.6	0.0	0.0000	740.6	43.4	0.0955	739.9
18.5	740.6	0.0	0.0000	740.6	42.4	0.0813	739.9
19.5	740.6	0.0	0.0000	740.6	41.4	0.0838	739.9
20.5	740.6	0.0	0.0000	740.6	40.4	0.0626	739.8
25.5	740.6	3.2	0.0043	739.1	35.4	0.0694	739.6
30.5	725.0	3.1	0.0043	723.4	31.1	0.0456	723.7
35.5	709.6	9.3	0.0130	705.0	26.7	0.0236	708.2
40.5	664.5	8.7	0.0130	660.2	23.3	0.0104	663.0
45.5	622.3	18.7	0.0300	612.9	19.8	0.0039	620.7
50.5	534.4	16.0	0.0300	526.3	17.6	0.0014	532.9
55.5	458.9	18.1	0.0393	449.8	15.1	0.0005	457.5
60.5	375.5	14.8	0.0393	368.0	12.9	0.0000	374.2
65.5	307.2	25.4	0.0828	294.2	10.2	0.0000	306.1
70.5	199.4	16.5	0.0828	191.0	9.5	0.0000	198.7
75.5	129.5	10.7	0.0828	124.0	8.4	0.0000	129.0
80.5	84.1	7.0	0.0828	80.5	6.7	0.0000	83.7
85.5	54.6	4.5	0.0828	52.3	4.1	0.0000	54.3
90.5	35.4	35.4	1.0000	17.7	0.5	0.0000	35.3

B. Males

x	$L_{(x)}$	$d_{(x)}$	$q_{(x)}$	$l_{(x+0.5)}$	$e_{(x)}$	$P_{(x)}$
0.5	1000.0	48.5	0.0485	975.4	26.0	1000.0
1.5	951.5	28.8	0.0303	937.0	26.3	951.4
2.5	922.7	27.9	0.0303	908.6	26.1	922.6
3.5	894.7	23.5	0.0263	882.9	25.9	894.6
4.5	871.2	22.9	0.0263	859.6	25.5	871.0
5.5	848.3	22.3	0.0263	837.0	25.2	848.0
6.5	825.9	15.5	0.0188	818.1	24.9	825.7
7.5	810.4	15.2	0.0188	802.8	24.4	810.1
8.5	795.2	15.0	0.0188	787.7	23.8	794.8
9.5	780.2	14.7	0.0188	772.8	23.3	779.8
10.5	765.5	5.1	0.0066	763.0	22.7	765.1
11.5	760.5	5.0	0.0066	758.0	21.8	760.0
12.5	755.5	5.0	0.0066	753.0	21.0	755.0
13.5	750.5	5.0	0.0066	748.0	20.1	750.0
14.5	745.6	4.9	0.0066	743.1	19.3	745.0
15.5	740.6	7.3	0.0098	737.0	18.4	740.0
16.5	733.4	7.2	0.0098	729.7	17.6	732.7
17.5	726.1	7.1	0.0098	722.6	16.7	725.5
18.5	719.0	7.1	0.0098	715.5	15.9	718.3
19.5	711.9	7.0	0.0098	708.4	15.0	711.2
20.5	704.9	29.4	0.0417	690.1	14.2	704.1
25.5	569.7	34.6	0.0608	552.2	12.0	568.9
30.5	416.4	35.3	0.0847	398.4	10.5	415.7
35.5	267.5	22.7	0.0847	255.9	10.1	267.0
40.5	171.9	14.6	0.0847	164.4	9.4	171.5
45.5	110.4	9.4	0.0847	105.6	8.3	110.1
50.5	70.9	6.0	0.0847	67.9	6.6	70.7
55.5	45.6	3.9	0.0847	43.6	4.0	45.4
60.5	29.3	29.3	1.0000	14.6	0.5	29.2