SHIFT IN SIZE-AT-AGE OF THE STRAIT OF GEORGIA POPULATION OF PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*)

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ABSTRACT

The Strait of Georgia Pacific hake (*Merluccius productus*) population is a resident population, distinct from the migratory offshore coastal stock. Spawning occurs in the south central strait with peak spawning from February through April. Biological samples were obtained for this main spawning stock during the peak spawning season, from 1981–2005. Size-at-age for mature fish, ages 4 and 5 years, exhibited a dramatic step-wise decline evident in 1994 and 1995 respectively. The fish from year-classes 1990 to 2001 were smaller in size than previous year-classes. While the size-at-age of Pacific hake has declined since 1990, the abundance of Pacific hake has increased as a result of improved year-class success. We propose that the larval survival rate for Pacific hake improved in the 1990s as a result of increased overlap of first-feeding larvae with calanoid copepods presence. As a result, subsequent density–dependent mechanisms resulted in increased competition for Pacific hake resources and reduced growth.

INTRODUCTION

The Strait of Georgia is a semi-enclosed marine basin between the mainland of British Columbia and Vancouver Island, Canada (fig. 1). It is connected to the Pacific Ocean by two narrow passages: Johnstone Strait in the north; Juan de Fuca Strait in the south. The Strait of Georgia's average depth is 155 m, but deep basins of up to 420 m occur in the central portion. The two narrow passages affect the circulation of the Strait of Georgia with outflowing low-salinity, higher-temperature surface waters and inflowing nutrient-rich deep water from
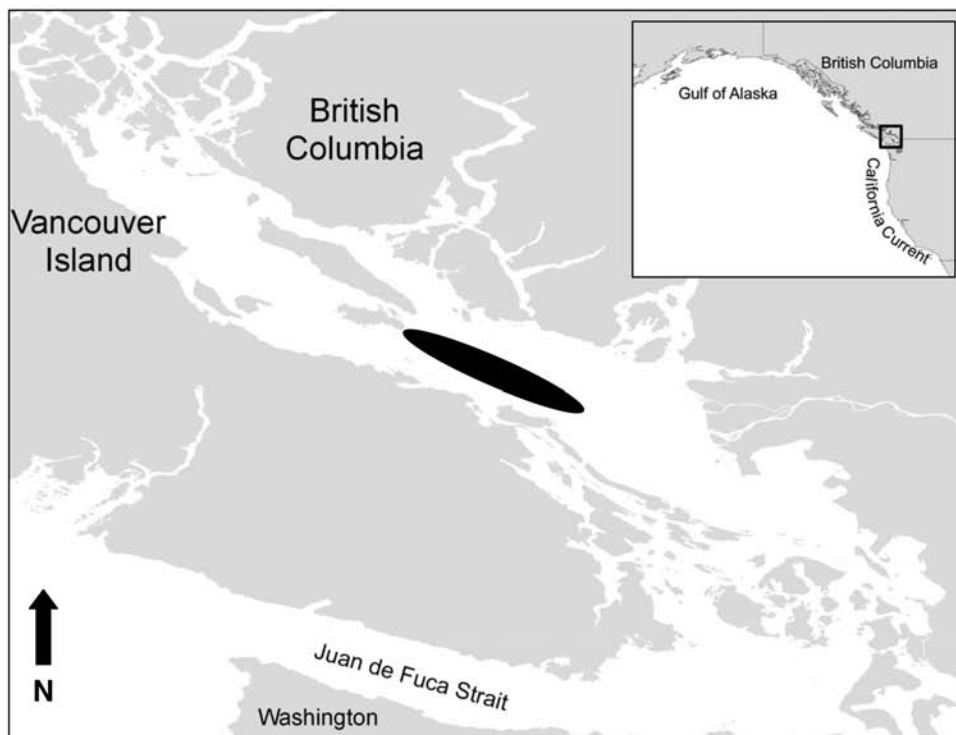

Figure 1. The Strait of Georgia is a semi-enclosed basin between Vancouver Island and mainland British Columbia. It is connected to the Pacific Ocean by Johnstone Strait to the north (not shown) and the Juan de Fuca Strait to the south. Pacific hake (*Merluccius productus*) spawn in the central basin of the Strait of Georgia from January to March (denoted by black oblong). Inset shows location of Strait of Georgia off the west coast of North America.
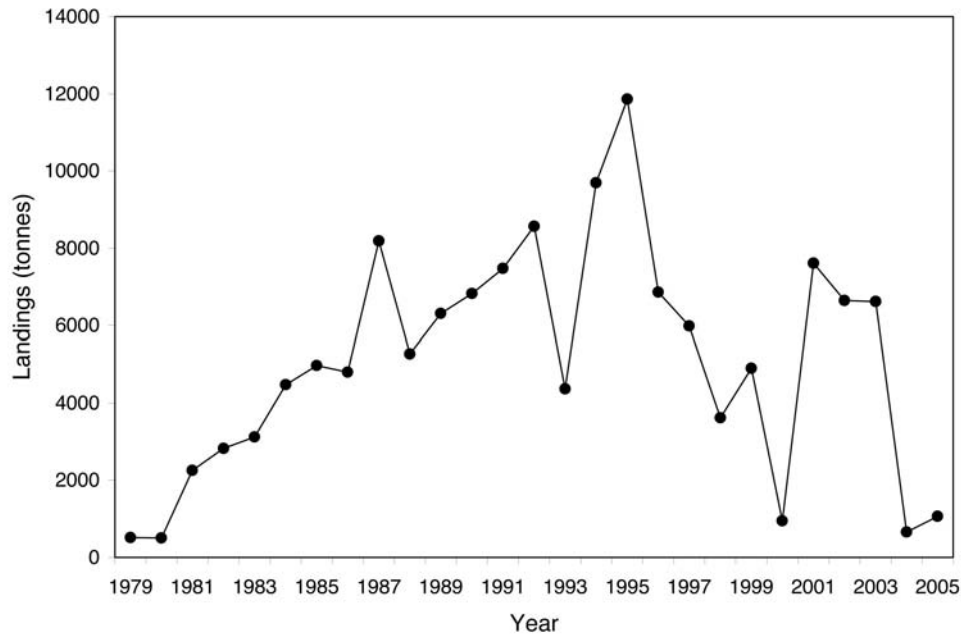
Figure 2.   The annual landings (tonnes) of Pacific hake (*Merluccius productus*) captured in the Strait of Georgia.

offshore. The surface waters are mainly influenced by freshwater input from the Fraser River, which has minimal discharge through the winter months, increasing discharge in March, and maximum discharge in June. The freshwater discharge, together with tides and winds, influences the overall circulation, mixing, and stratification (Thomson 1994). When the surface water exits the Strait it is replaced by nutrient-rich deep water (Harrison et al. 1994). Wind mixing entrains this nutrient-rich deep water into surface waters. When Fraser River discharge is low, wind mixing is more effective and nutrient entrainment improves, thereby increasing primary productivity (St. John et al. 1993; Harrison et al. 1994; Yin et al. 1997a and b).

The Pacific hake (*Merluccius productus*) population that inhabits the Strait of Georgia is a resident stock distinct from the larger coastal population. Otolith morphology (McFarlane and Beamish 1985) and parasite analyses (Kabata and Whitaker 1981) indicate that the Strait of Georgia population is distinct from the migratory offshore coastal stocks. This population is the most abundant resident fish species in the Strait of Georgia (McFarlane and Beamish 1985). Strait of Georgia Pacific hake feed primarily on euphausiids, but small pelagics such as Pacific herring (*Clupea harengus*), bathylagids, and eulachon (*Thaleichthys pacificus*) are also important components of their diet. Overall the growth rate of Pacific hake in the Strait of Georgia is slower and the maximum size is lower than for the migratory, offshore stocks (Beamish and McFarlane 1985; McFarlane and Beamish 1985). For the Strait of Georgia stock, age at 50% maturity is 3, and age at 100% maturity is 5, compared to coastal Pacific hake which are 100% mature by age 4 (Dorn and Saunders 1997).

The Strait of Georgia population was recognized only recently to be of ecological and commercial importance. The large resident population of Pacific hake was discovered in 1974 (Westrheim 1974) and several research surveys were conducted from 1975–79 to investigate the biology and distribution of this stock. Initial studies included several surveys throughout the year, but by 1981 surveys that collected biological and abundance data focused only on the spawning aggregate in the central basin. A commercial fishery was initiated in 1979 and was well established by 1981 (fig. 2). Since 1981, annual landings have ranged from 655 tons (in 2004) to 11,860 tons (in 1995), with a mean of approximately 5,400 tons (fig. 2). The fishery occurs during the spawning season and targets the central basin spawning aggregate.

In our study, we used biological data collected from both research surveys and from the commercial fishery to examine the changes in the size-at-age of resident Pacific hake in the Strait of Georgia. We relate observed changes in size–at–age to noted changes in the Strait of Georgia ecosystem through a conceptual mechanism of Pacific hake population dynamics.

METHODS

Biological samples were collected from mid–water trawl research surveys or from commercial trawl samples from 1981 to 2005 (tab. 1). All samples were collected in late-February or March, during the peak spawning season, from the central basin in the southern Strait of Georgia (fig. 1). Trawls were conducted at depths greater

TABLE 1
Sampling period, type of sample (commercial or research survey), the range of depths (m) that trawls were conducted, and number of samples for Pacific hake in the Strait of Georgia used in this study. Years with sample sizes below the minimum number required to detect significant differences in mean fork length (cm) as determined by power analyses are denoted with an asterisk.

Year	Sampling period	Type	Depth range (m)	Age 4	Age 5
				Number of samples	
1981	20 Feb.–29 March	Research	135–295	40	28
1982	19 Jan.–26 April	Commercial	130–200	73	54
1983	12–13 Feb.	Research	200–250	65	61
1984	26 March	Research	240	12	28
1985	24–25 March	Research	230–245	24	18
1986	31 March–1 April	Commercial	110–230	25	21
1987	4–23 March	Commercial	155–185	53	19
1988	21–27 March	Research	110–160	144	77
1989	28 Feb.–17 March	Commercial	220	1*	6*
1990	14 March–7 May	Commercial	110	12	19
1991					
1992	27 Feb.–19 March	Research/Commercial	(170)	3*	10*
1993	16 March–20 April	Research/Commercial	(160–275)	13	17
1994	3 Feb.–12 March	Commercial	185–330	34	11
1995	16 Jan.–12 April	Research/Commercial	(190)	21	14
1996	8 Feb.–7 May	Commercial	150–400	176	144
1997	26 Feb.–4 March	Research	175–275	25	84
1998	18–27 March	Research	130–365	30	23
1999	16 Feb.–12 April	Research/Commercial	(180–345)	78	28
2000	2–19 April	Research	135–310	14	48
2001	23 Jan.–27 March	Research/Commercial	(175)	29	5*
2002	14 Feb.–21 March	Research	180–280	689	43
2003					
2004	4–5 March	Research	180–300	81	40
2005	28 Feb.	Research	340	11	3*
Total				1653	801

than or equal to 110 m, which corresponds to depths at which mature females are found (McFarlane et al. 1981). Fork length (cm), weight (g), and sex were recorded for each fish, and otoliths were collected for age estimation. We used data for female Pacific hake only.

For a subsample of fish, stage of maturity was determined. Fish with small, pink, and semi-transparent ovaries—with or without yolk-less ova—were classified as immature. Fish with enlarged ovaries, blood vessels on ovaries, and yellow or translucent ova were classified as mature. Fish that had spawned that season (i.e., were spent) contained bloodshot purple ovaries with some translucent ova, and were also classified as mature.

Ages were estimated from otoliths using the break and burn method (Chilton and Beamish 1982) which has been validated for ages up to 12 for Pacific hake in the Strait of Georgia (McFarlane and Beamish 1985). Since samples were taken from spawning aggregates, we wanted to ensure that the size data that we used for analysis represented the ranges of sizes for each age-class by year. To minimize bias that might be introduced by size differential maturation, we selected fish from the first two age-classes after the estimated age at 50% maturity, i.e., ages 4 and 5.

We used ANOVA to test for significant differences in mean size-at-age between years. Power analyses were performed to calculate the proportions of years in which the number of fish sampled was sufficient to detect a target difference between means (Sokal and Rohlf 1981). The median of all calculated differences in mean fork length (cm) for each age-class was used as a target difference. Power analyses were based on a power of 0.80 as recommended by Peterman (1990) for fisheries science. Years with insufficient samples were removed from subsequent analyses. We used *post hoc* Bonferroni-adjusted comparison of means to look at sequential groupings of years and time-series plots to identify the period of overall change in mean size-at-age.

We used the maturity stage data to estimate the maturity proportion by age and by fork-length intervals (10 cm) pooled across groups of years identified in the size-at-age analyses. Logistic equations were fit to the proportions-at-age and proportions-by-size interval data to estimate age and size at 50% maturity.

Hydroacoustic surveys were conducted in February or March in 1981, 1988, 1996, and 1997 to estimate the spawning biomass (tonnes) of Pacific hake (Kieser et al. 1999). During these surveys, mid-water trawls provided biological samples in the two layers of Pacific hake detected hydroacoustically: shallow layer (<110 m; juvenile Pacific hake) and deep layer (>110; adult Pacific hake). We used the biomass estimates (tonnes) for the
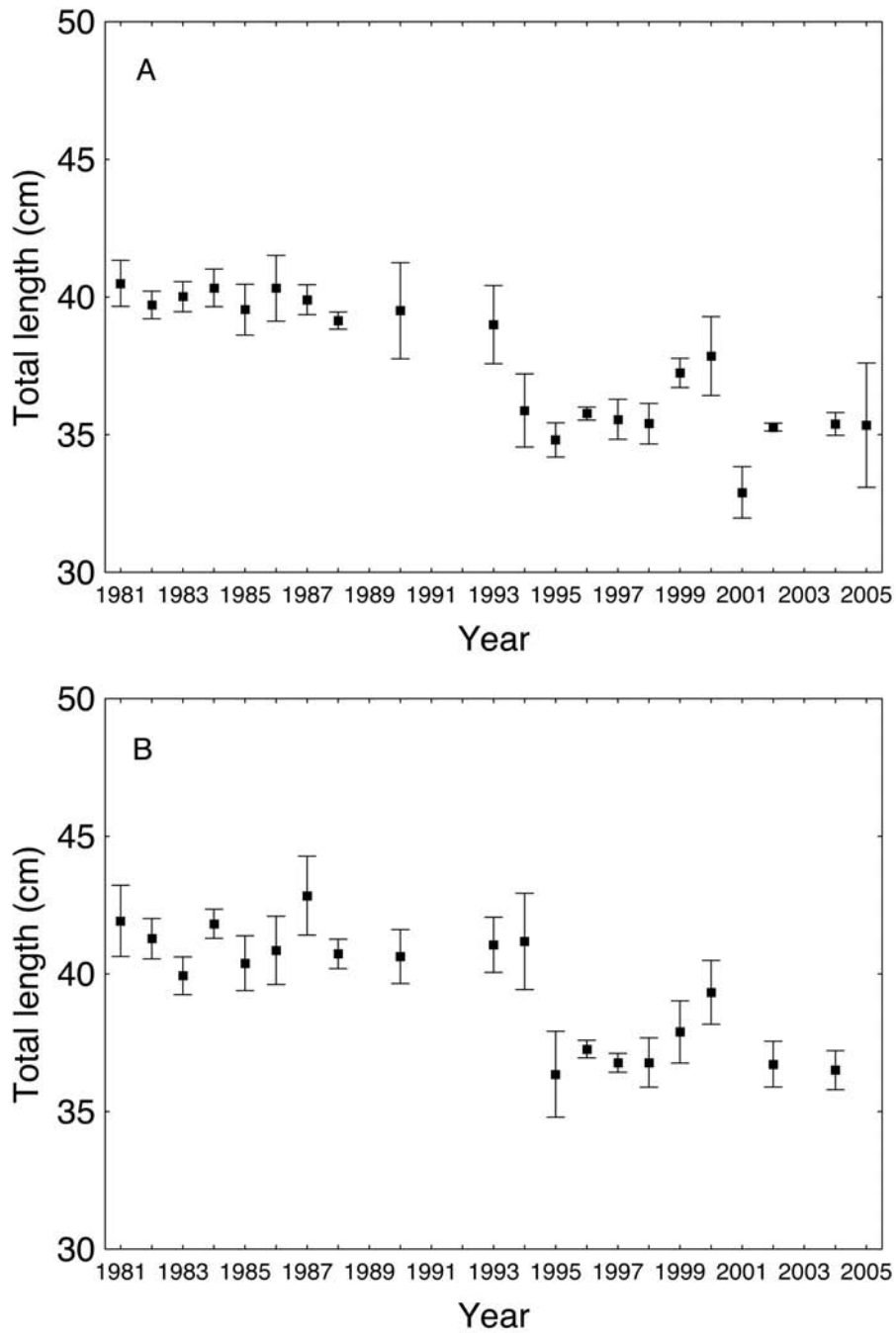
Figure 3.   Annual mean fork length (cm) for female Pacific hake (*Merluccius productus*) in the Strait of Georgia: A) age 4; and B) age 5.

deep layer provided in Kieser et al. (1999) and the corresponding age composition and weight-at-age data to estimate the abundance of age-4 and -5 Pacific hake (numbers of fish).

RESULTS

Plots of size-at-age exhibit a striking and persistent change in mean fork length in 1994 and 1995 for age-4 and -5 female Pacific hake, respectively (fig. 3).

ANOVA analysis found significant differences in annual mean fork length for both age-classes, and Bonferonni adjusted comparisons confirm the time-series plots. For age-4 and age-5 fish, the mean fork lengths in 1994 and 1995, respectively, were significantly lower than the mean fork lengths in all years prior. This decrease in mean fork length was persistent in subsequent years. For age-4 fish, the mean fork lengths in 1995 through 2000 and 2002 through 2005 were not significantly different from mean
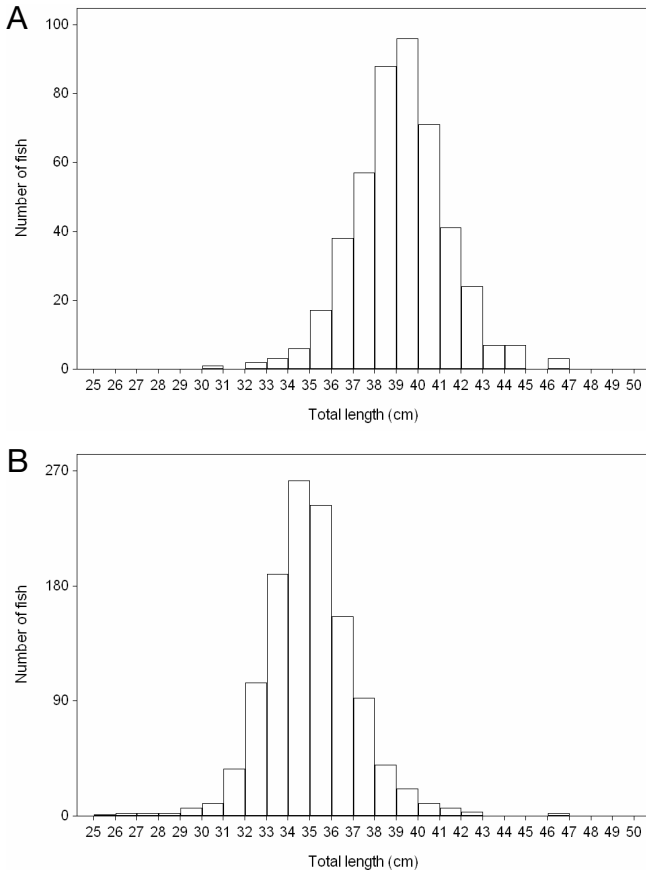
Figure 4.   Fork length frequency plots of female Pacific hake (*Merluccius productus*) age 5 A) from 1981–93; and B) from 1994–2005, by intervals of 1 cm.
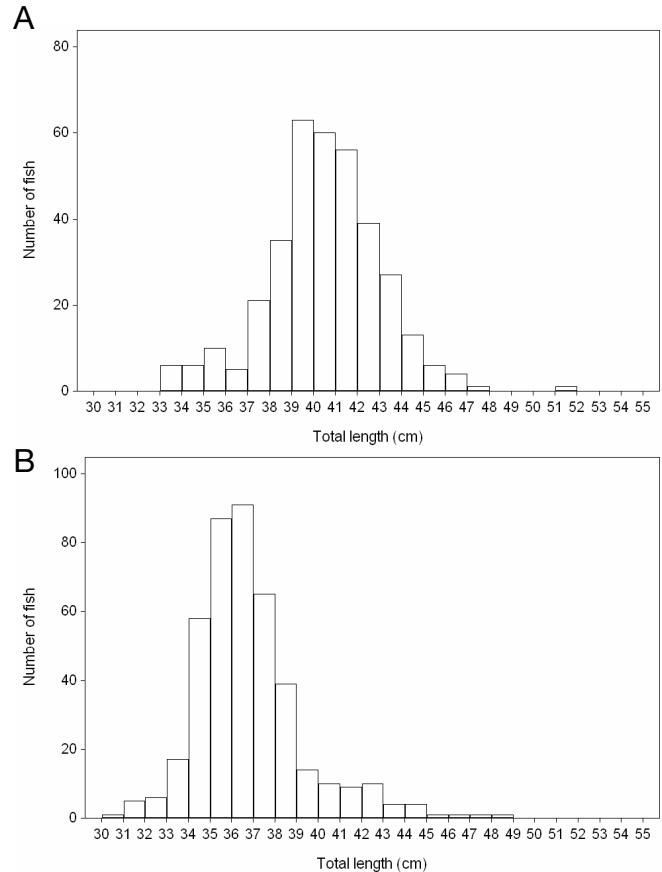

Figure 5.   Fork length frequency plots of female Pacific hake (*Merluccius productus*) age 5 A) from 1981–94; and B) from 1995–2004, by intervals of 1 cm.

fork lengths in 1994. The mean fork length in 2001 was significantly lower than in 1994. For age-5 fish, mean lengths from 1995–2004 were only significantly different (higher) from 1994 in 2000.

Overall, the mean fork length of age-4 female Pacific hake decreased by 4.2 cm from 1981–93 ($n = 461$) to 1994–2005 ($n = 1188$) (fig. 4). A similar decrease (3.7 cm) was observed for age-5 fish from 1981–94 ($n = 342$) to 1996–2004 ($n = 435$) (fig. 5). Mean weight of age-4 female Pacific hake decreased significantly (*t* test: $t_{(2),0,05,266} = 8.66$; $p < 0.001$) between 1981–93 (mean weight = 396 g; $n = 79$) and 1994–2005 (mean weight = 298 g; $n = 189$). Mean weight for age-5 fish also decreased significantly (*t* test: $t_{(2),0,05,269} = 7.35$; $p < 0.001$) between the period 1981–94 (mean weight = 450 g; $n = 40$) and 1995–2004 (mean weight = 328 g; $n = 231$).

Based on the observed changes in annual mean size noted above, we partitioned the maturity data for the periods 1981–88 and 1995–2004 in order to detect corresponding changes in size-at-maturity or age-at-maturity. No maturity data were available for 1989 or 2005. From 1981–88, 50% of the female Pacific hake examined ($n = 2933$) were mature at sizes between 30–35 cm

(fig. 6A). From 1995–2004 this proportion corresponded to a size interval of 25–30 cm (fig. 6B) for the female Pacific hake examined ($n = 5075$). For data with corresponding age estimates, the age at 50% maturity was age 3 for both of the periods, 1981–88 ($n = 2548$) and 1995–2004 ($n = 2456$).

There was an overall decline in the deep layer (adult) estimated biomass based on hydroacoustic surveys for 1981 and 1988 to 1996 and 1997 (tab. 2). However, the relative abundance of age-4 and -5 Pacific hake, estimated from the biomass data along with the proportion of age-4 and -5 fish and their associated mean weights, increased from the 1981 and 1988 surveys (mean abundance = 39.1 millions of fish) to 1996 and 1997 surveys (mean abundance = 72 millions of fish) (tab. 2).

DISCUSSION

Our analyses indicated that the size-at-age of Pacific hake in the Strait of Georgia dramatically declined in the 1990s. This decline in size was first apparent in the 1990 year-class and has persisted to date. Concurrently, there has been a corresponding decline in the weight-at-age of Pacific hake for these year-classes. We can re-
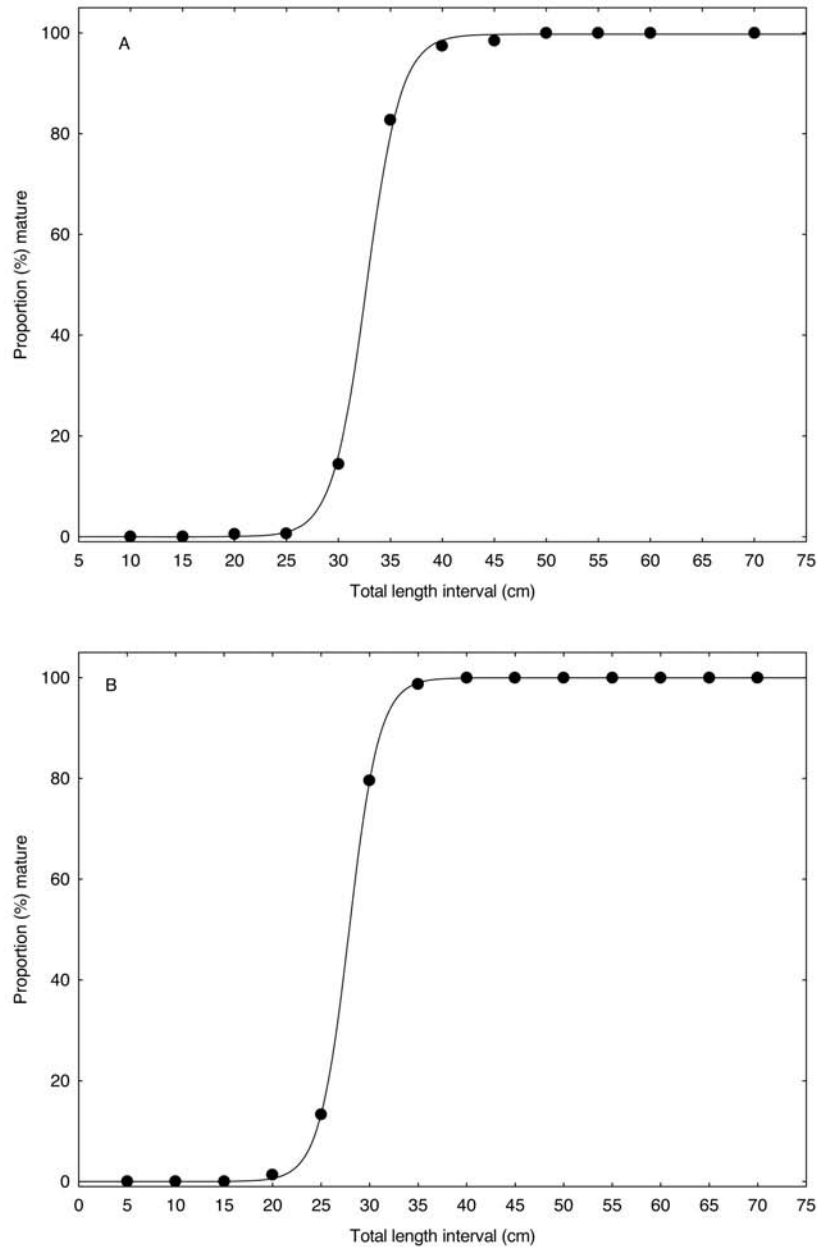
Figure 6.   Proportion (%) of female Pacific hake (*Merluccius productus*) sampled from A) 1981–88, and B) 1995–2004 that were sexually mature.

TABLE 2

Deep-layer biomass estimates (tonnes) for Pacific hake based on hydroacoustic surveys conducted in February or March (from Kieser et al. 1999). The proportion (%) of age-4 and age-5 Pacific hake (*Merluccius productus*) and mean weights (g) respectively are based on biological samples obtained from mid-water trawls through the deep layer conducted during the hydroacoustic surveys. Estimated abundance (millions of fish) of age-4 and -5 Pacific hake based on biomass estimates, proportion of fish, and mean weight data.

Date of survey	Biomass estimate (tonnes)	Proportion of fish (%)		Mean weight (g)		Abundance estimate (millions of fish)
		Age 4	Age 5	Age 4	Age 5	
9–20 February 1981	65,921	14	6	416	444	31.1
18–28 March 1988	55,415	24	12	416	440	47.1
20 February–5 March 1996	55,702	24	25	281	313	92.1
17–28 February 1997	43,326	11	24	270	304	51.9

port that the detected change in size-at-age is not due to a change in age-estimation methods, i.e., it is not a function of age underestimation. When the change in size-at-age was first detected in the mid-1990s, a review of the age-estimation method was made to ensure consistent application of methodology.

The 1989 regime shift observed in the North Pacific (Hare and Mantua 2000; McFarlane et al. 2000) had a regional impact on the Strait of Georgia ecosystem in 1990 (Beamish and McFarlane 1999). The spring freshet of the Fraser River started earlier, as measured by April discharge, and the sea-surface temperatures increased (Beamish and McFarlane 1999). Bornhold (2000) reported that the timing of the copepod reproduction cycle was approximately one week earlier in the 1990s than the 1980s. In the 1990s, year-class success of some species, such as lingcod (*Ophiodon elongatus*), was poor (King, 2001) as was the productivity of Pacific salmon species, such as coho salmon (*Onchorhynchus kisutch*), pink salmon (*O. gorbuscha*), and sockeye salmon (*O. nerka*) (Beamish, et al. 2004; Bradford and Irvine 2000). However, the productivity improved for some species, such as Pacific herring (*Clupea harengus*), which matched historic high spawning abundances in the 1990s (Schweigert 2004). While the overall biomass of Pacific hake in the Strait of Georgia declined (Keiser et al. 1999), our estimates indicated that the relative abundance actually increased.

Beamish and McFarlane (1999) proposed that Pacific hake abundance is regulated by: (1) year-class success dependent on the timing of the copepod reproduction cycle, and (2) juvenile survival dependent on cannibalism by adult Pacific hake. These two mechanisms would work in opposite direction. For example, improved year-class success would translate into increased juvenile and adult abundance, which would subsequently translate into increased predation on juveniles and decreased juvenile abundance. We propose that the Strait of Georgia ecosystem response to the 1989 regime shift resulted in improved year-class success for Pacific hake. The dramatic shift in size-at-age for 4-year-olds in 1994 and by 5-year-olds in 1995 suggests that the change in size-at-age is driven by a year-class effect beginning in 1990 and not by the reduction of adult cannibalism beginning in 1994 (e.g., increased fishing mortality on adult Pacific hake). The annual landings did peak in 1994 and 1995 (fig. 2), however, for this increase in fishing mortality on spawning Pacific hake to translate into reduced cannibalism on juvenile Pacific hake, the subsequent effect on size-at-age would not be evident in age-4 fish until 1998. In addition, when this fishing pressure was released (i.e., reduced landings in 1996 through 2000, fig. 2) an increase in size-at-age was not observed.

The improved year-class and subsequent increase in relative abundance resulted in a density-dependent re-

duction in growth and subsequent smaller size-at-age for year-classes since 1990. The sustained decrease that we observed in size-at-age for year-classes since 1990, coupled with the observed changes in Strait of Georgia spring conditions (i.e., timing of the spring freshet and copepod reproduction cycle) suggests that Pacific hake abundance since the 1989 regime shift has been predominately regulated by year-class success. There is no indication that subsequent cannibalism on juveniles has been a major component for regulating Pacific hake during this period. Pacific hake less than 40 cm in fork length feed predominately on euphausiids and not on fish species (Tanasichuk et al. 1991). This implies that for the smaller Pacific hake in the Strait of Georgia, cannibalism may have been eliminated from their behavior during the 1990s.

If the change in size-at-age of Pacific hake reflects ecosystem changes in the Strait of Georgia with cascading effects on year-class success, then it is important to note that, unlike the 1989 regime shift discussed here, the 1998 regime shift observed for the North Pacific (King 2005) has not affected (in either abundance or size-at-age) Pacific hake in the Strait of Georgia. Not all ecosystems of the North Pacific have responded to the 1998 regime shift (King 2005), and we see no evidence of an impact in the Strait of Georgia Pacific hake population.

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