Regime Shifts, Ecosystem Change and Sardines off the West Coast of Canada

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(summarized from McFarlane and Beamish, 2000)

The Pacific sardine (*Sardinops sagax*) fishery was the largest in British Columbia from the mid – 1920s to the mid – 1940s. From 1925 to 1946 catches of sardines ranged from approximately 5 to 80,000t and averaged approximately 40,000t annually. The collapse of this fishery in 1947 was historically described as an example of over-fishing (Hillbourn & Walters, 1992). However, more recent information has led to the recognition that fishing may have affected the rates of population change, but the collapse in 1947 and subsequent reappearance in 1992 of sardines is a function of climate and ocean change. The change in sardine dynamics in 1947 is now seen as synchronous with the 1947 regime shift (Minobe, 1997; Francis & Hare, 1994; Beamish et al., 1999). The reappearance in 1992 is proposed to be related to the now accepted 1989 regime shift (Beamish et al., 1999; McFarlane et al., 2000; Hare & Mantua 2000). The observation that the 1977 regime shift did not reverse the conditions (for sardines) that occurred after 1947 is possibly evidence of the multidimensional nature of the impact of regime changes on the organization of ecosystems.

It was also believed that a genetically distinct northern migratory stock had been over-fished to a biomass too small to rebuild, leaving little prospect for the recovery of the fishery off the British Columbia coast (Murphy, 1966; MacCall, 1979). In this study we describe the reappearance of sardines off British Columbia in relation to climate and ocean conditions and compare current biology with descriptions published during the 1940s.

Biological Data

Midwater trawl research cruises have been conducted annually off the west coast of Vancouver Island since the early 1970s. Biological data were collected from sardine during all research trawling operations since they reappeared in catches in 1992. Fork length, sex and maturity were recorded for all sardine sampled. Paired otoliths were collected for age determinations from fish from selected sets, according to the procedures described in Beamish and McFarlane (2000).

No sardines were captured in nearly 1500 reasearch trawl sets conducted off the west coast of Vancouver island between 1977 and 1992 (DFO Groundfish database). From 1992 to 1995 small numbers of sardines were captured in both commercial and research catches of Pacific hake (*Merluccius productus*) (Fig. 1). The catches in the hake fishery have continued through 1999, but are not an indication of sardine abundance as hake are fished at depths below the concentrations of sardines (McFarlane & Beamish, 1999). Since 1995 catches in an experimental fishery have increased from 200t to over 1200t in 1999 (Fig. 1). The sex ratio of

50% male and 50% female sardines in the catch in the 1990s was similar to that determined during the 1930s (45% male) (Table 1). The average length of fish captured during the summer in 1992 (244mm) and 1993 (262mm) was similar to the average length from 1936 to 1940 (258mm) (Fig. 2). From 1997 to 1999 the average length (230mm) was smaller than previously reported (Fig. 3). Similarly, the average age of sardine in 1997, 1998 and 1999 (4.1 years) was younger than that in the 1930s (6.2 years) and 1940s (4.6 years) (Table 2; Fig. 4), and the range of ages was smaller (Fig. 4).

Sardine in spawning condition were sampled off southern Vancouver Island in July 1997, and large numbers of young of the year (x = 10mm) were captured in the same area in February, 1998, juvenile sardines were a common component of the fish community in Vancouver Island surface waters, outnumbering catches of 1997 year class herring (*Clupea harengus*) 2 to 1. These young sardines have remained off the coast and have been captured throughout British Columbia waters including the Strait of Georgia, northern Hecate Strait and Alaska. Sardines remained abundant and spawned off the west coast of Vancouver Island in 1998.

Stomach contents for sardine from selected sets during cruises in 1997, 1998 and 1999 were identified to lowest taxonomic group possible and volume (cc) estimated for each prey item.

During 1997 and 1998 sardines fed mainly on phytoplankton (diatoms, *Coscinodiscus* spp.) and zooplankton (copepods and euphausiids), similar to the diet in the late 1920s (Fig. 5). During 1999, a major portion of the diet was composed of surface water tunicates (*Oikopleura* spp.) as well as diatoms, copepods and euphausiids.

Abundance of sardines off the west coast of Vancouver Island was estimated using the volume fished in each of 6 regions from the northern part of Vancouver Island (region 1) to the southern part (region 6) (Fig. 6). Tracklines were predetermined to ensure maximum coverage within the limited cruise time available. Only sets which fished the top 30m of the water column were used as 99% of sardines were captured in the top 30m (McFarlane & Beamish, 1999). Swept volume for each set was determined according to the procedures described by Beamish et al. (2000).

The minimum estimated abundance of sardines in coastal waters off the west coast of Vancouver Island was 85, 993t in 1997 and 72, 080t in 1999 (Table 3). These assume a catchability of 1, and do not include sardines occupying large inlets along the west coast of Vancouver Island, or large concentrations just outside of the survey area on the northern tip of Vancouver Island. From 1992 until 1996 most sardine were captured off the west coast of Vancouver Island. Sardines were captured in Queen Charlotte Sound and Dixon Entrance in 1997 and 1998, and some were captured in waters off south – east Alaska in 1998 (Fig. 7). During 1999, no research fishing for sardines was conducted in waters north of Queen Charlotte Sound

Climate data

The Aleutian Low Pressure Index (ALPI), Pacific Circulation Index (PCI), and Atmospheric Forcing Index (AFI) were obtained from the Pacific Biological Station website (http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/english/ clm_indx1.htm). For a detailed description of these indices see McFarlane et al., 2000. The Pacific Interdecadal Oscillation Index (PDO) (Martua et al., 1997) was obtained via the website (http://ipbc.washington.edu/staff/home/html/decadal/ post1977). The Southern Oscillation index (SOI), commonly associated with El Niño events was obtained via the website (http://www.ios.bc.ca/ios/osap/projects/ elnino/s_osc.txt) (Fig. 8). In general, the intensity and position of the Aleutian Low determines atmospheric circulation patterns. Atmospheric circulation patterns drive oceanic circulation, which determines amount of ekman pumping and spatial distribution of sea surface temperatures. The three climate – ocean indices (ALPI, PCI, PDO) were combined to form the Atmospheric Forcing Index (AFI) using principal component analysis based on their concentration matrix (McFarlane et al., 2000) (Fig. 9). The first principal component scores positive for an intense Aleutian Low, above average frequency of south-westerly and westerly atmospheric circulation, and a general cooling in the central north Pacific and warming in the coastal areas. The composite index scores negative for a weak Aleutian Low, a decrease in south-westerly and westerly circulation, and a warming trend in the central north Pacific and cooling along the coast. Decadal scale patterns in sea surface temperatures along the south west coast of Vancouver Island since 1935 have not been synchronous with larger scale climate/ocean index patterns, nor with ecosystem changes seen in fish and plankton, such as periods of sardine population fluctuation (Fig. 10).

Other recent changes in the ecosystem occupied by sardines

A number of other indications of ecosystem change have been reported (McFarlane et al., 2000; Hare & Mantua, 2000). Like sardines, salmon population abundance patterns have reflected ecosystem change (Fig. 11). Decadal scale trends have also been evident in other fish species, such as Pacific Hake, Pacific Mackerel, Sablefish, Pacific Cod and English Sole (Francis, 1983; Saunders & McFarlane, 1998; McFarlane et al., 2000; King et al., 2000; Fargo, 1998) (Fig. 12, 13 & 14).

Zooplankton sampling off southern Vancouver Island has been conducted frequently since 1979, and exists as a reasonably consistent time series since 1985. Zooplankton populations have undergone chages in distribution and composition since 1989, such as a shift to a more southerly copepod fauna, and increases in the biomass of the two major euphausiid species (Mackas et al., 2000) (Fig. 15).

The reappearance of sardines off the west coast of Canada in 1992, and their spawning patterns in 1997 and 1998 represent a change in their behaviour. Although we do not understand fully the mechanisms that are responsible for the fluctuations in sardine abundance, it is clear that ocean conditions affect distribution and survival. Neither overfishing nor sea – surface temperature fluctuations alone can account for the large increases and decreases in sardine abundance recorded during the last century. It does seem evident, however, that the appearance and disappearance of sardines off of Canada's west coast corresponded with periods of regime shifts. Recent changes we have seen in sardine distribution, abundance and spawning (and the same changes in other fish) appear consistent with a major shift in the dynamics of the ecosystem in waters off British Columbia at the time of the 1989 regime shift. Kawasaki and Omori (1986) recognised that there was a synchrony in the trends of abundance of sardine populations off Japan, California and Chile, supported the theory that large fluctuations in sardine populations are a consequence of changes in ocean habitat around the north Pacific ocean. A key to understanding why large fluctuations in sardine abundance occur may be by understanding why they have shifted their range northward. We also hypothesize that during the 1989 regime shift phytoplankton (particularly diatom) abundance and composition was affected by an altered nutrient supply, as was observed in the Black Sea after the damming of the Danube River (Humborg et al., 1997). However, it is difficult to observe these changes in waters off the west coast of Vancouver Island as the recycling of nutrients and phytoplankton masks variations in this system (Parsons et al., 1977).

In the past, changes in fish population abundance have usually been linked to fishing effects; however, in order to understand how to manage sardine stocks we must understand how they are regulated naturally. The history of sardine behavior is an example of the effects that climate/ocean changes can have on abundance, and a reminder that ecosystem changes need to be regarded as distinct organizations, rather than cycles or oscillations. In addition, population dynamics of other species, such as coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon may also respond to changes in a manner specific to the new organization. Climate related fluctuations need to be recognized in any legislation requiring expenditures and management actions.

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Figure Captions

Figure 1. Catches of Pacific sardine in Canadian waters. (A) catches from 1920 – 1999. (B) combined research and fishery catches, 1992 – 1999.

Figure 2. Length frequency of Pacific sardine (A) Summer 1997; (B) February – April 1998; (C) Summer 1998. Note the abundance of 7 and 8 month old sardines in the winter.

Figure 3. Length frequency of Pacific sardine captured in Canadian waters, 1929 – 1933, 1992, 1993, and 1997 – 1999.

Figure 4. Age frequency of Pacific sardine captured in Canadian waters, 1940 –1942 and 1997 – 1999.

Figure 5. Stomach contents of Pacific sardine captured in Canadian waters from 1927 – 1930 and 1997 – 1999.

Figure 6. The west coast of Vancouver Island, divided into the six regions used to estimate abundance. Tracklines were occupied during July and August, 1997 and 1999.

Figure 7. Distribution of Pacific sardine in Canadian waters from 1992 to 1999.

Figure 8. Index of Southern Oscillation, 1950 – 1999.

Figure 9. Indices of climate change (A) Aleutian Low Pressure Index (ALPI); (B) Pacific Circulation Index (PCI); (C) Pacific Interdecadal Oscillation Index (PDO); (D) Atmospheric Forcing Index (AFI), a composite of A, B and C.

Figure 10. Sea surface temperature anomalies off south west Vancouver Island, 1935 – 1999. Black bar indicates presence of sardine in Canadian waters.

Figure 11. Total catch of Pacific salmon (pink, sockeye, chum, coho and chinook) 1970 – 1999.

Figure 12. Changes in distribution and spawning area of Pacific hake during the 1990s, illustrating (A) increased northward movement in Canadian waters; (B) a change in spawning area during the 1990s.

Figure 13. Distribution of Pacific mackerel from 1992 to 1999.

Figure 14. Indices of relative year class strength of (A) sablefish (1960 – 1996); (B) Pacific cod (1960 – 1998); and (C) English sole (1960 – 1996).

Figure 15. Annual average log scale anomalies of biomass of major southern Vancouver Island zooplankton taxa.

Table 1. Sex ratio of Pacific sardine captured from 1936 to 1940[a] and from 1992 to 1999.

year	% male	n	year	% male	n
1936	48.0		1992	51.8	2023
1937	45.0		1993	53.9	193
1938	45.0		1997	47.0	4067
1939	50.0		1998	48.9	1005
1940	51.0		1999	46.9	3942

a) Data from 1936 – 1939 from Clemens (e.g. Clemens 1936).
Data from 1940 from Foerster (1940)

Table 2. Average age of Pacific sardine captured in Canadian waters from 1935 to 1939[a], from 1940 to 1945[a] and from 1992 to 1999.

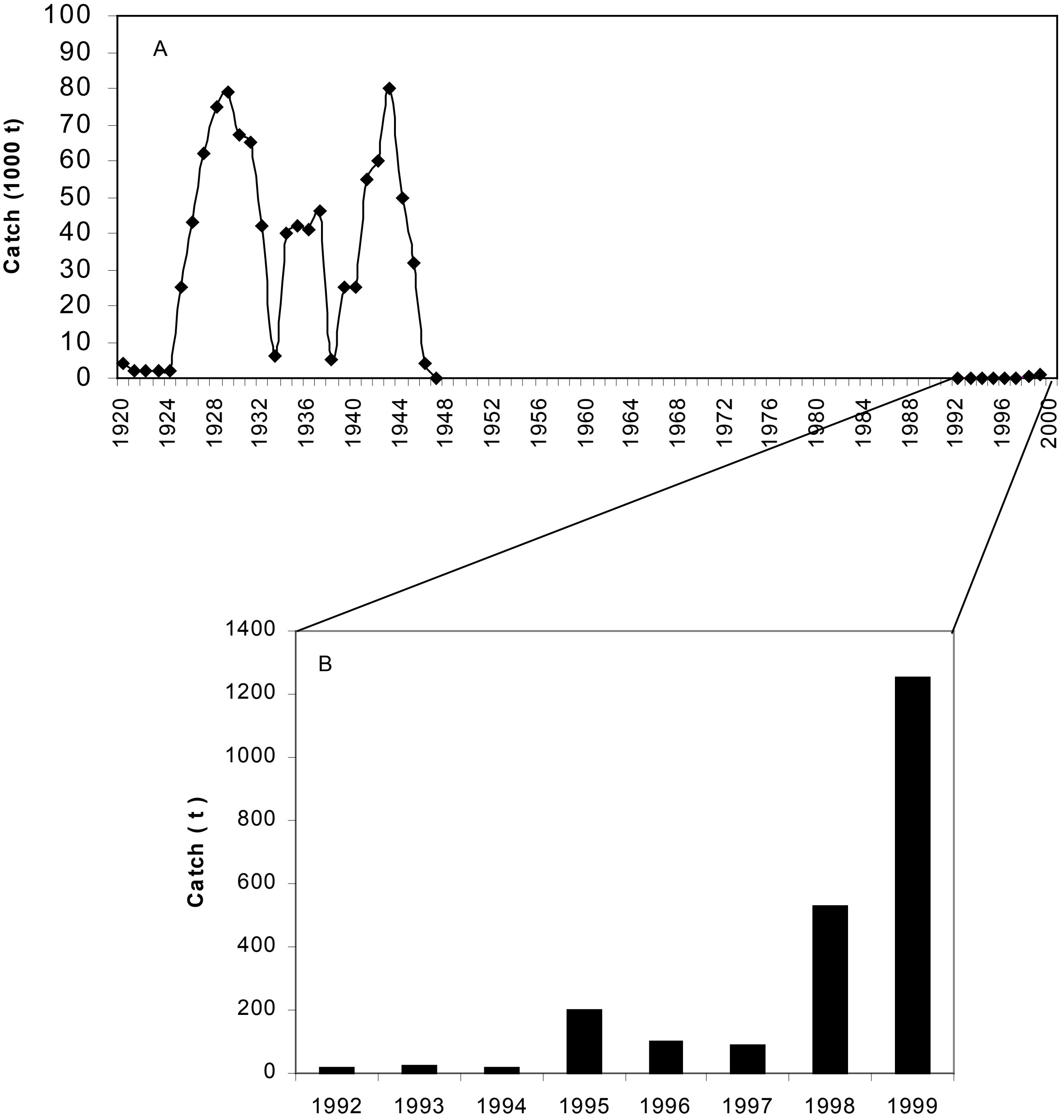
year	average age (years)	n	year	average age (years)	n	year	average age (years)	n
1935	7.5		1940	5.15		1997	4.02	96
1936	4.6		1941	3.96		1998	3.93	142
1937	6.7		1942	3.66		1999	4.23	136
1938	6.5		1943	4.65				
1939	5.69		1944	4.77				
			1945	5.16				

a) Ages from 1935 to 1945 from Marr (1960).

Table 3. Biomass of Pacific sardine (t) off the west coast of Vancouver Island, 1997 and 1999.

Year	Area[a]	Total Vol (km^3)	Mean Swept Vol (km^3)	Swept Vol (±) 95% CI	Average # fish/set	Average weight (kg)/fish	Total numbers	Biomass (t): 95% C.I.		
								Min.	Avg.	Max.
1997	1	91.02	0.00468	0.0013838	36	0.165	707580	90	117	166
	2	66.6	0.00341	0.0007695	4386	0.165	57153884	11080	14144	19549
	3	119.7	0.00292	0.0011891	537	0.165	41930677	2459	3637	6976
	4	83.85	0.00320	0.0010563	10585	0.165	185113128	31837	45730	81132
	5	71.76	0.00256	0.0005061	1537	0.165	42896895	5934	7106	8856
	6	127.65	0.00200	0.0002673	1450	0.165	270325085	12764	15260	18969
								64165	85993	135648
1999	2	66.6	0.00271	0.000496	1161	0.165	28575758	3985	4715	5772
	3	119.7	0.00215	0.00005	828	0.165	46187276	7274	7621	7828
	4	83.85	0.00223	0.0008278	228	0.165	8591544	1048	1418	2326
	5	71.76	0.00192	0.0006377	375	0.165	14030575	1738	2315	3466
	6	127.65	0.00192	0.0004952	5115	0.165	339467563	44587	56012	75311
								58787	72080	94704

a) See Figure 6.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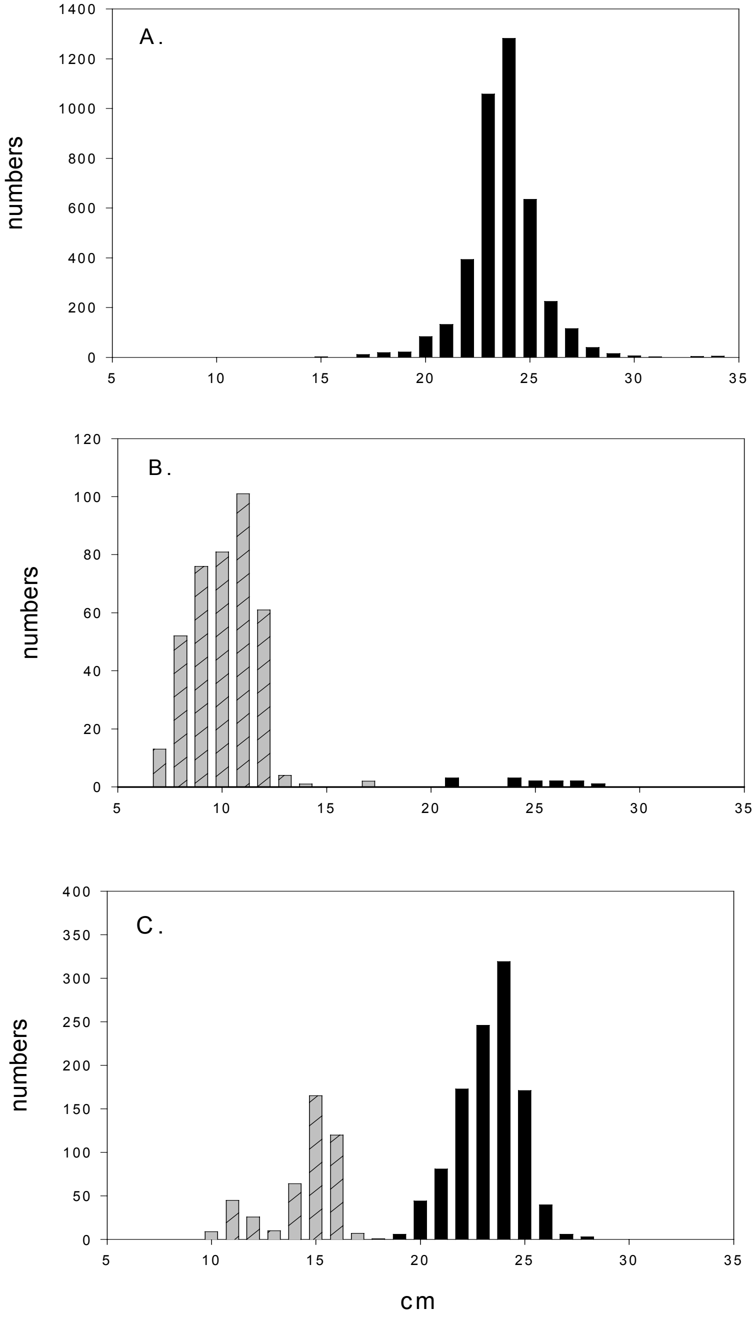
Catch (1000 t)
0
10
20
30
40
50
60
70
80
90
100
1920
1924
1928
1932
1936
1940
1944
1948
1952
1956
1960
1964
1968
1972
1976
1980
1984
1988
1992
1996
2000
B
Catch (t)
0
200
400
600
800
1000
1200
1400
1992
1993
1994
1995
1996
1997
1998
1999

Figure 1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numbers
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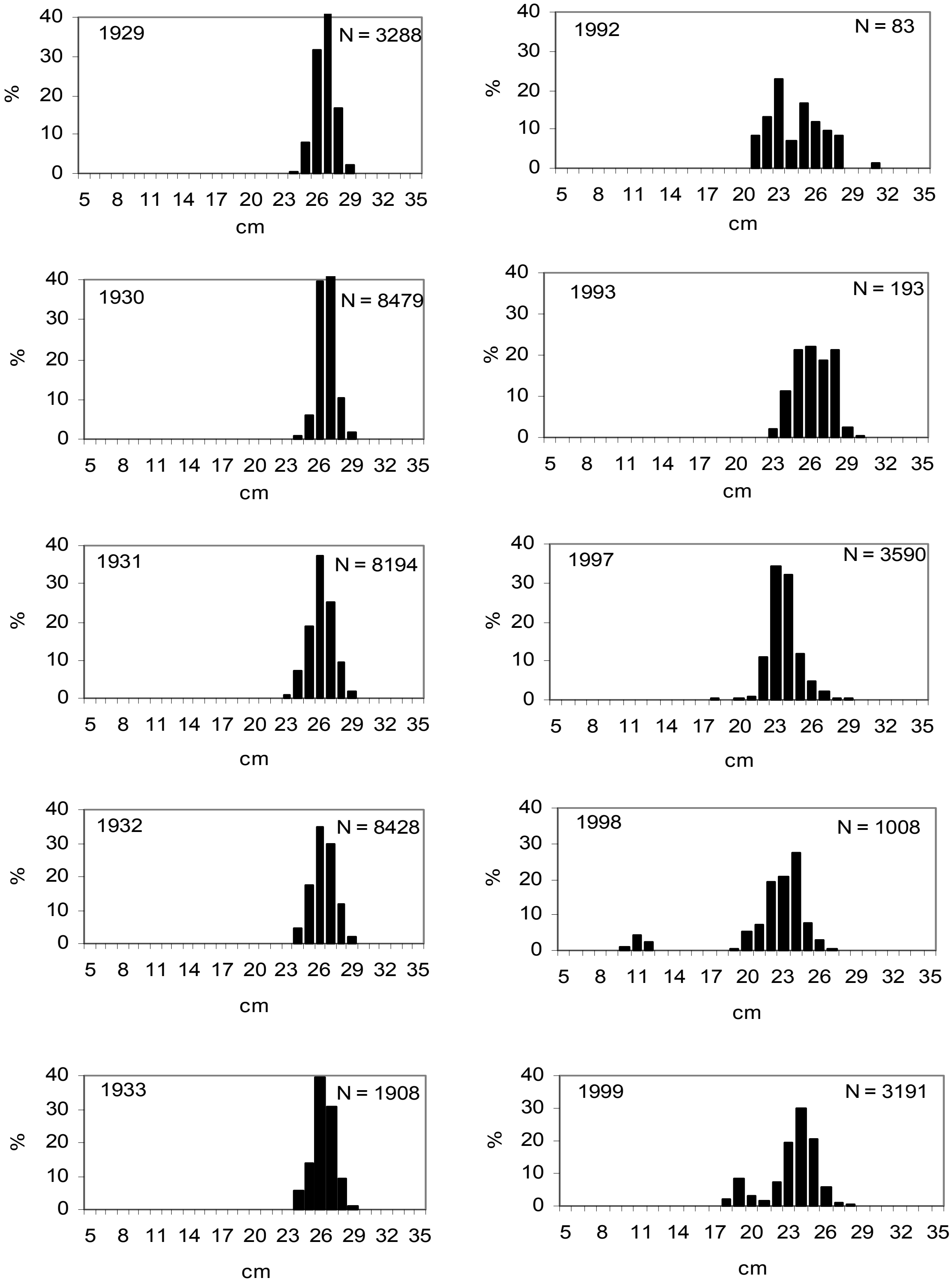
1200
1000
800
600
400
200
0
5
10
15
20
25
30
35
B.
numbers
120
100
80
60
40
20
0
5
10
15
20
25
30
35
C.
numbers
400
350
300
250
200
150
100
50
0
5
10
15
20
25
30
35
cm

Figure 2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N = 3288
1930
N = 8479
1931
N = 8194
1932
N = 8428
1933
N = 1908
1992
N = 83
1993
N = 193
1997
N = 3590
1998
N = 1008
1999
N = 3191
%
0
10
20
30
40
cm
5
8
11
14
17
20
23
26
29
32
35

Figure 3

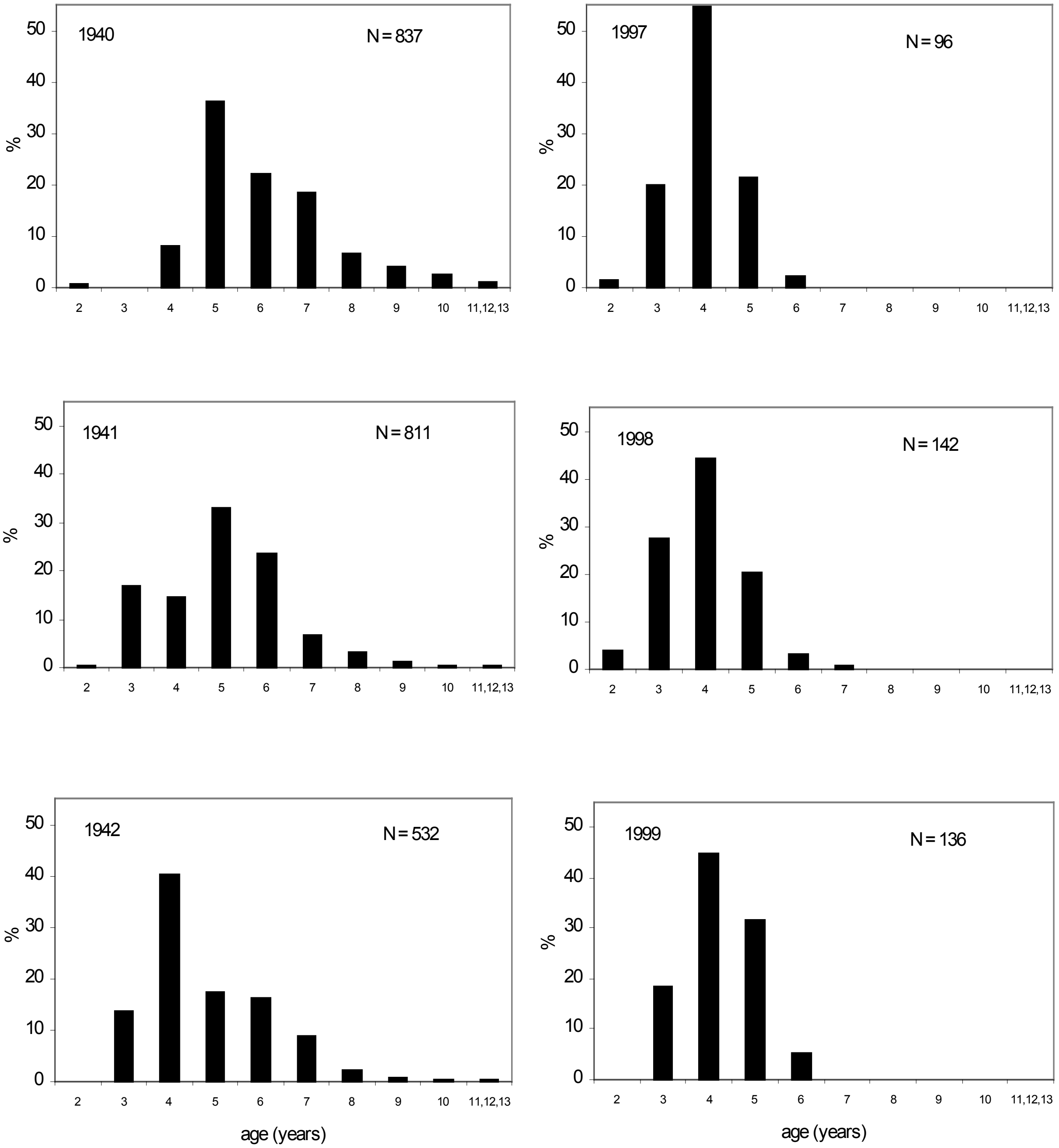

1940
N = 837
1997
N = 96
1941
N = 811
1998
N = 142
1942
N = 532
1999
N = 136
%
0
10
20
30
40
50
2
3
4
5
6
7
8
9
10
11,12,13
age (years)

Figure 4

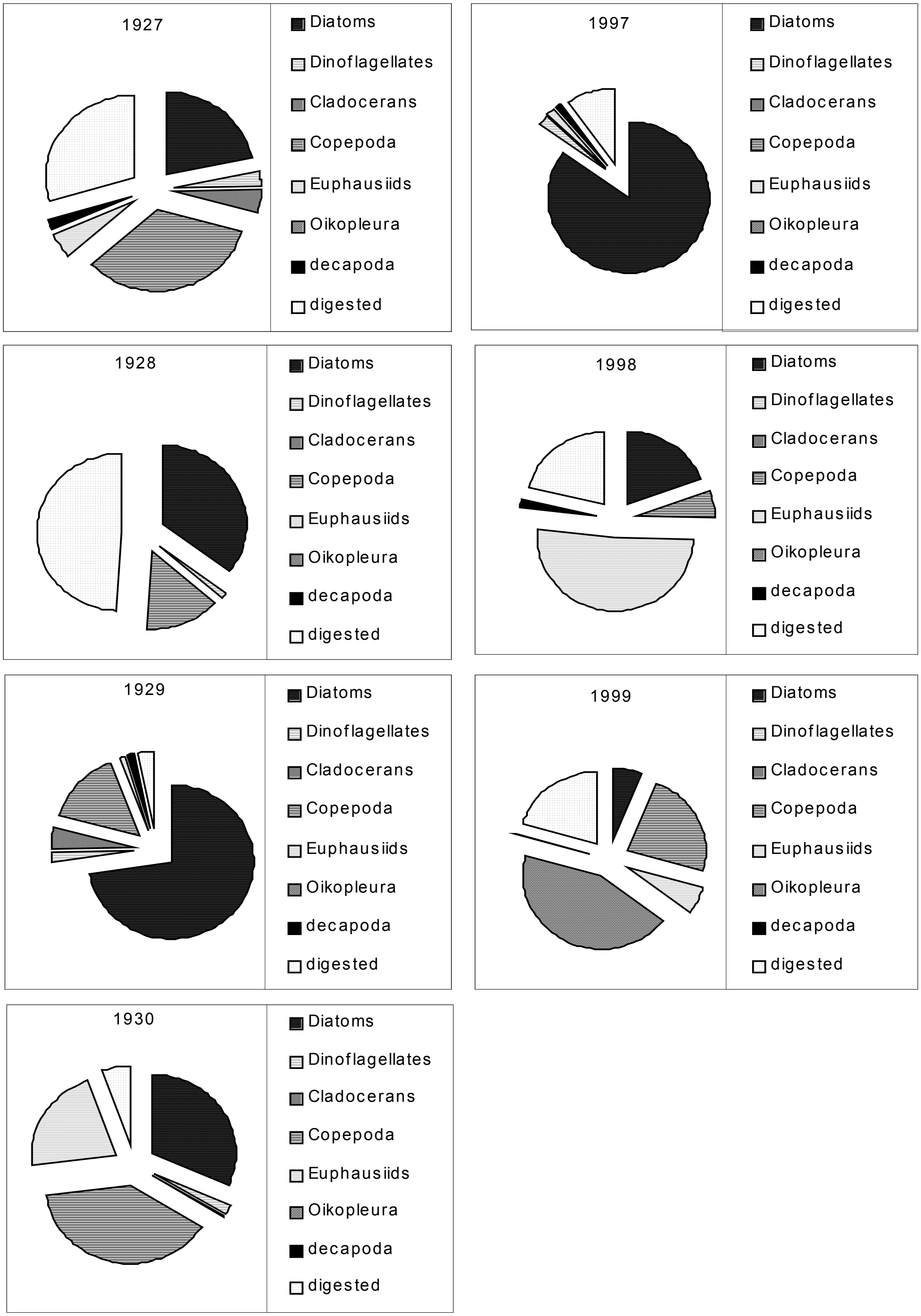
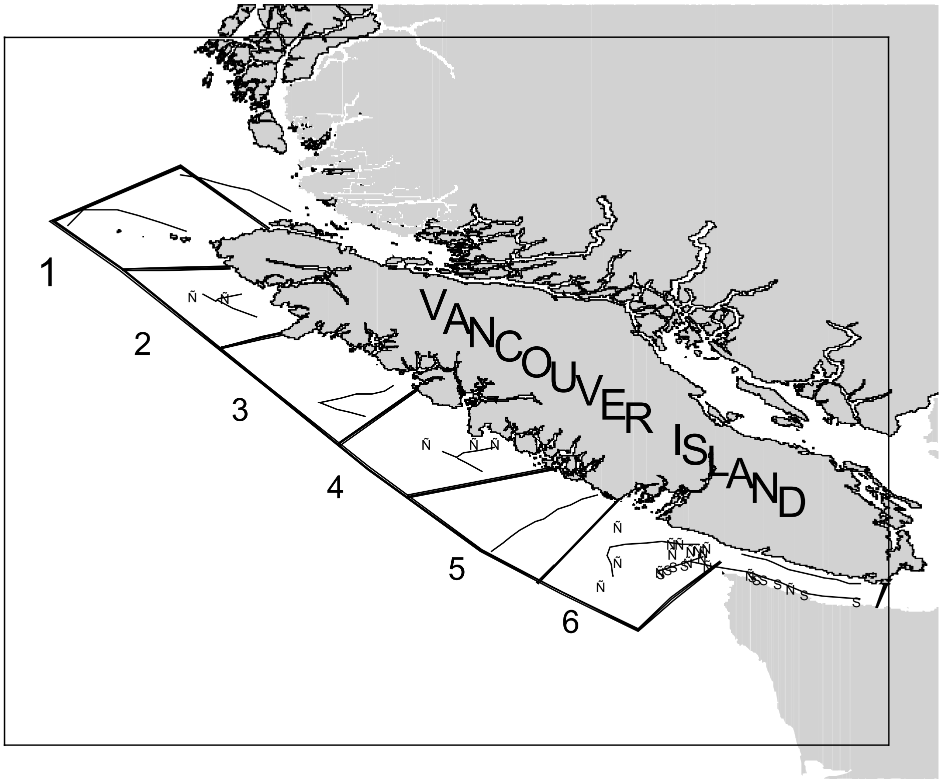

1927
Diatoms
Dinoflagellates
Cladocerans
Copepoda
Euphausiids
Oikopleura
decapoda
digested
1997
Diatoms
Dinoflagellates
Cladocerans
Copepoda
Euphausiids
Oikopleura
decapoda
digested
1928
Diatoms
Dinoflagellates
Cladocerans
Copepoda
Euphausiids
Oikopleura
decapoda
digested
1998
Diatoms
Dinoflagellates
Cladocerans
Copepoda
Euphausiids
Oikopleura
decapoda
digested
1929
Diatoms
Dinoflagellates
Cladocerans
Copepoda
Euphausiids
Oikopleura
decapoda
digested
1999
Diatoms
Dinoflagellates
Cladocerans
Copepoda
Euphausiids
Oikopleura
decapoda
digested
1930
Diatoms
Dinoflagellates
Cladocerans
Copepoda
Euphausiids
Oikopleura
decapoda
digested

Figure 5



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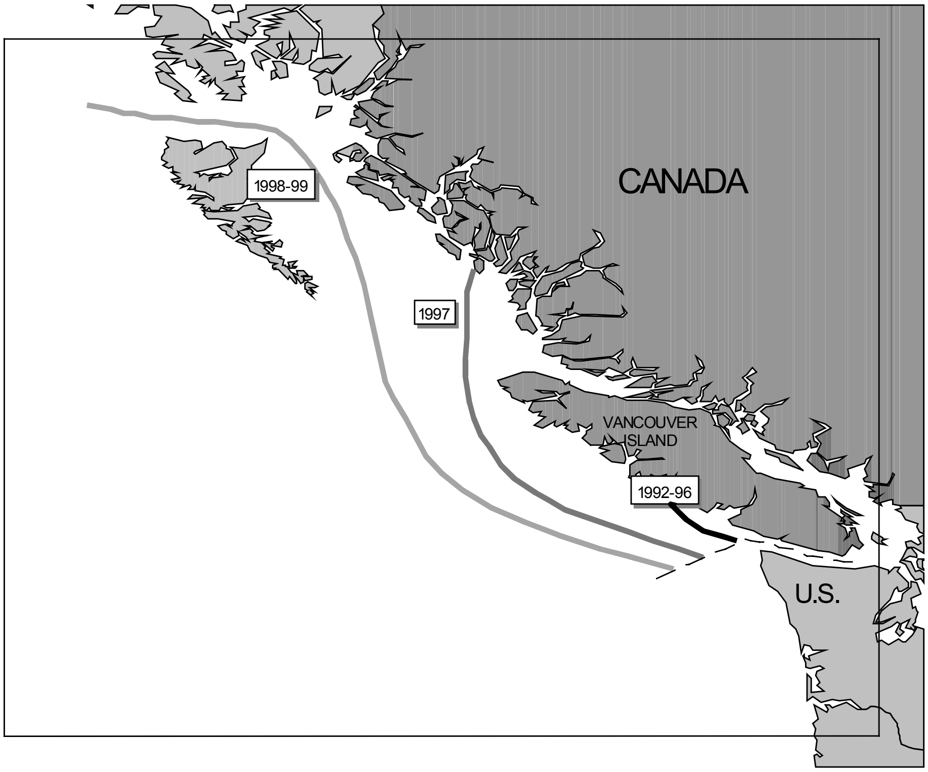

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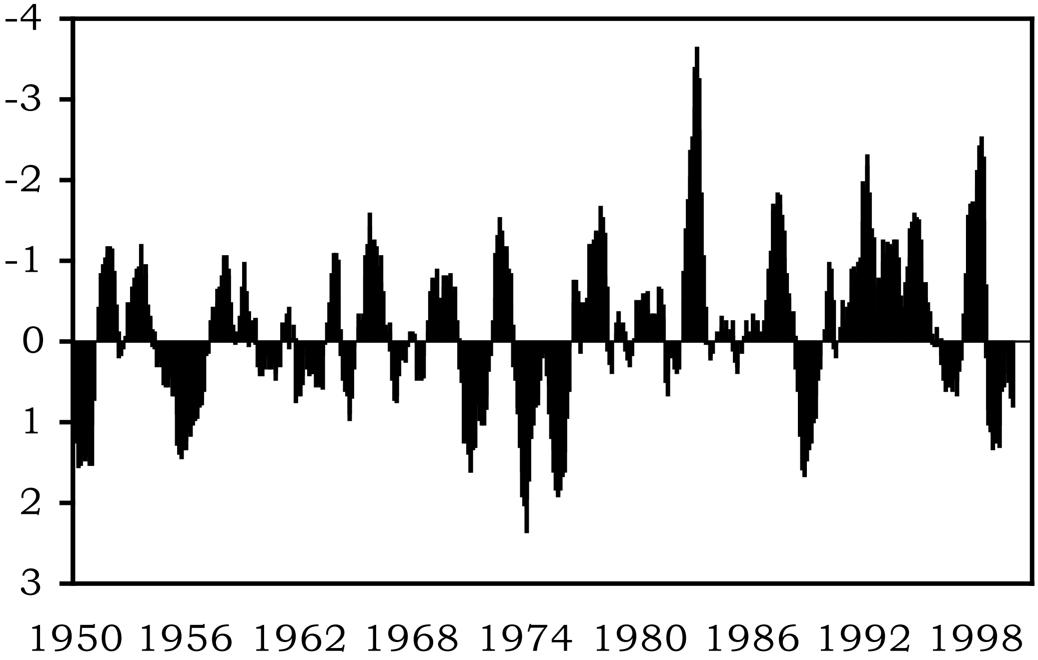

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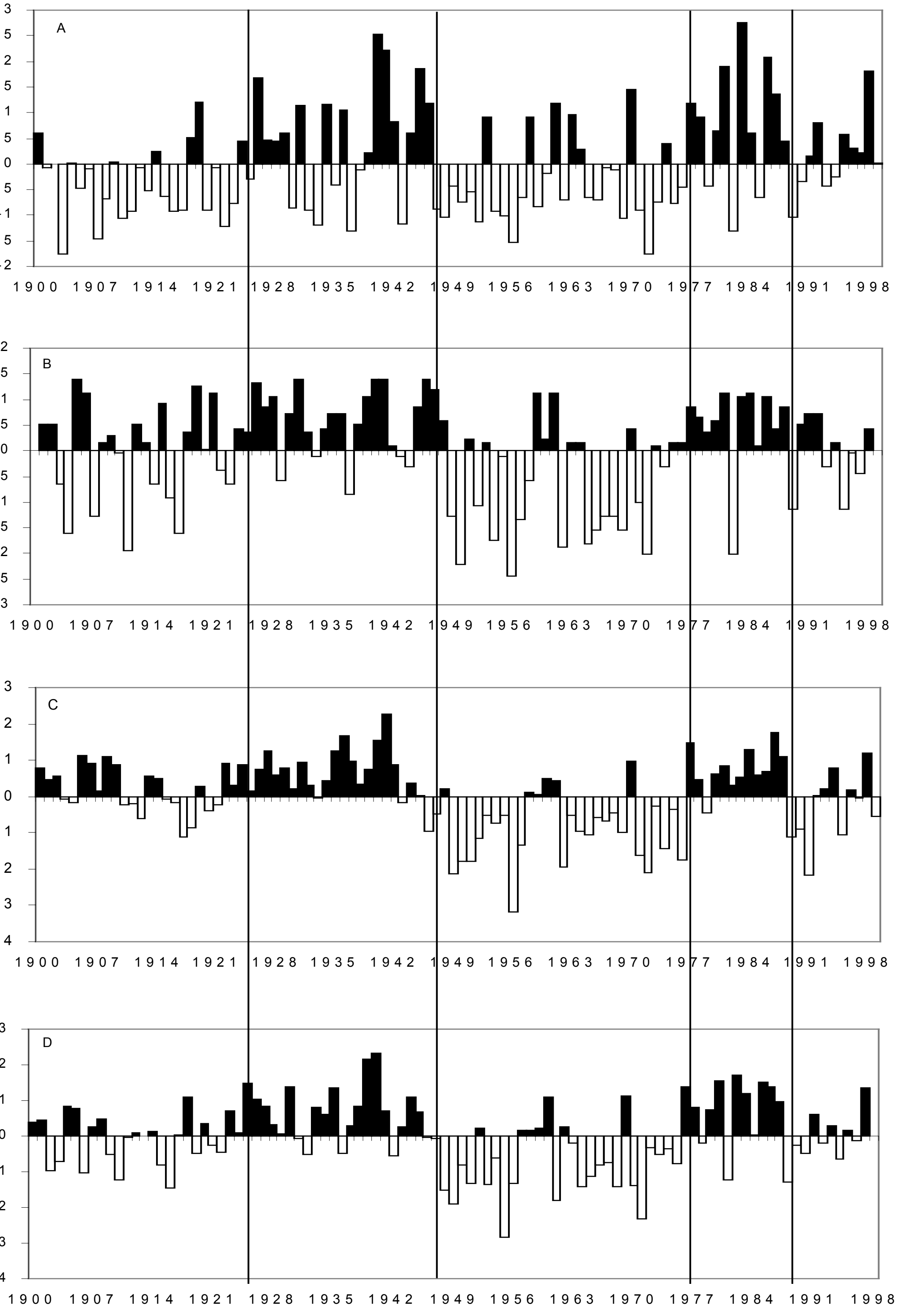
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3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
1900 1907 1914 1921 1928 1935 1942 1949 1956 1963 1970 1977 1984 1991 1998
B
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
1900 1907 1914 1921 1928 1935 1942 1949 1956 1963 1970 1977 1984 1991 1998
C
3
2
1
0
-1
-2
-3
-4
1900 1907 1914 1921 1928 1935 1942 1949 1956 1963 1970 1977 1984 1991 1998
D
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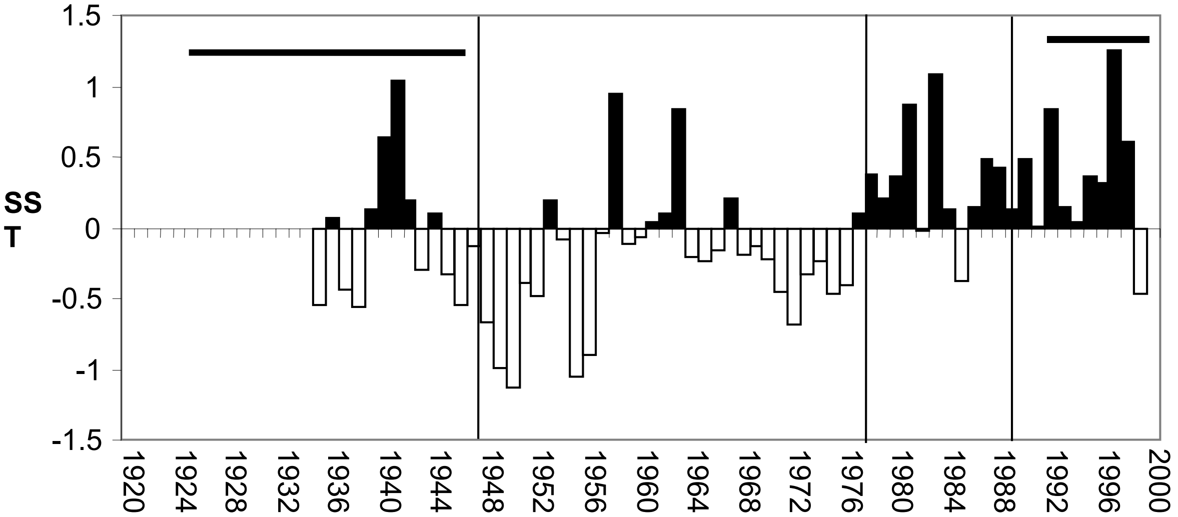
2
1
0
-1
-2
-3
-4
1900 1907 1914 1921 1928 1935 1942 1949 1956 1963 1970 1977 1984 1991 1998

Figure 9



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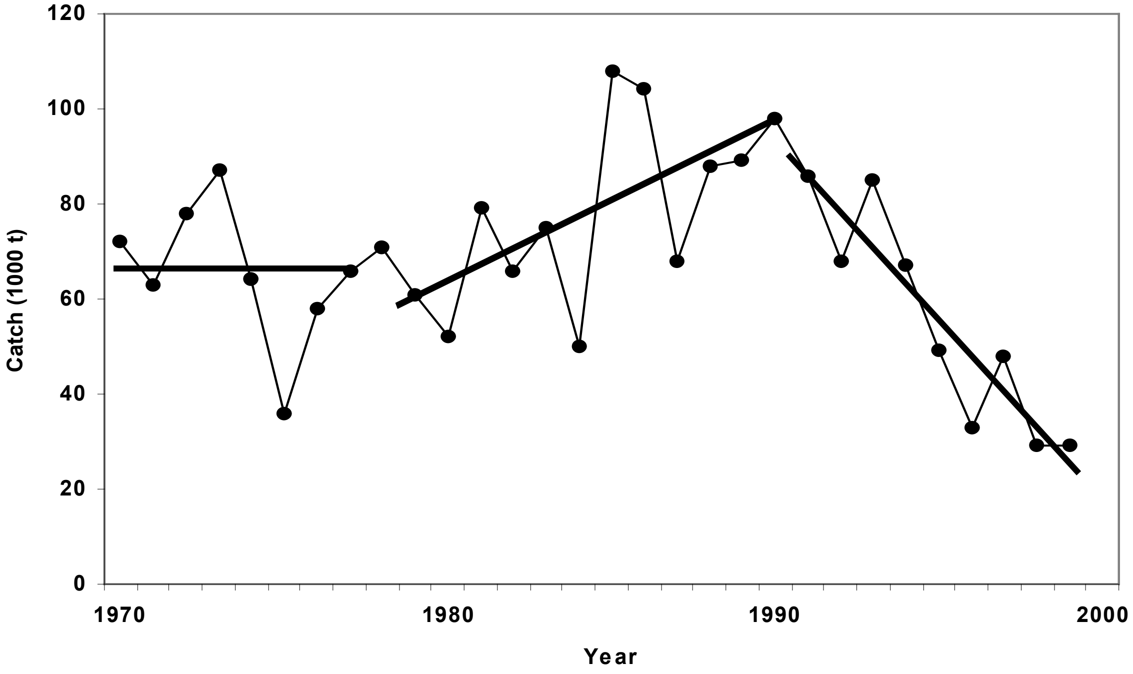


Figure 11

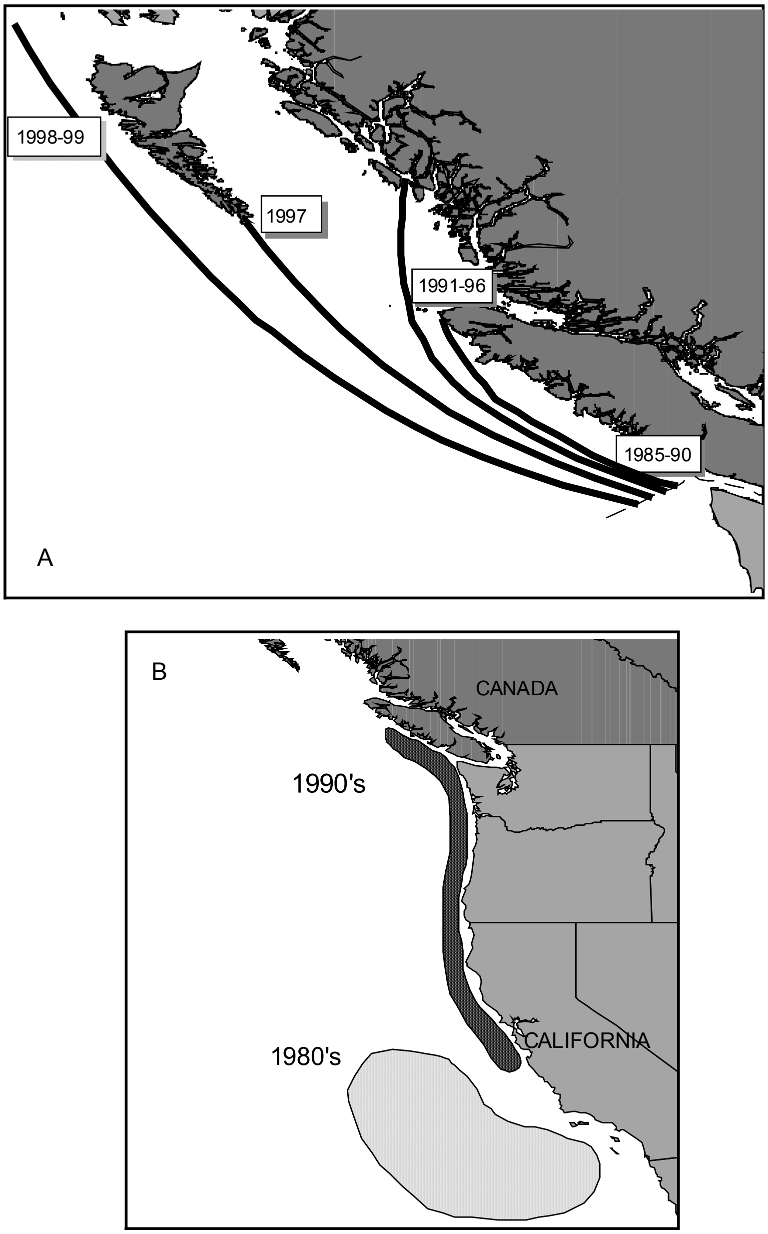


Fig. 12

Figure 12

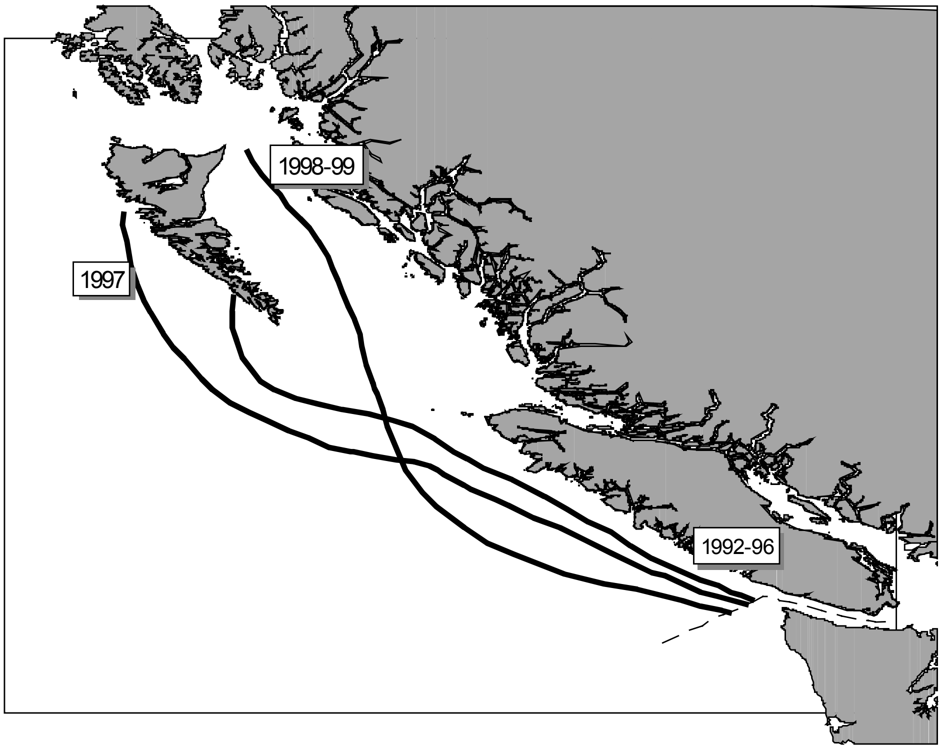
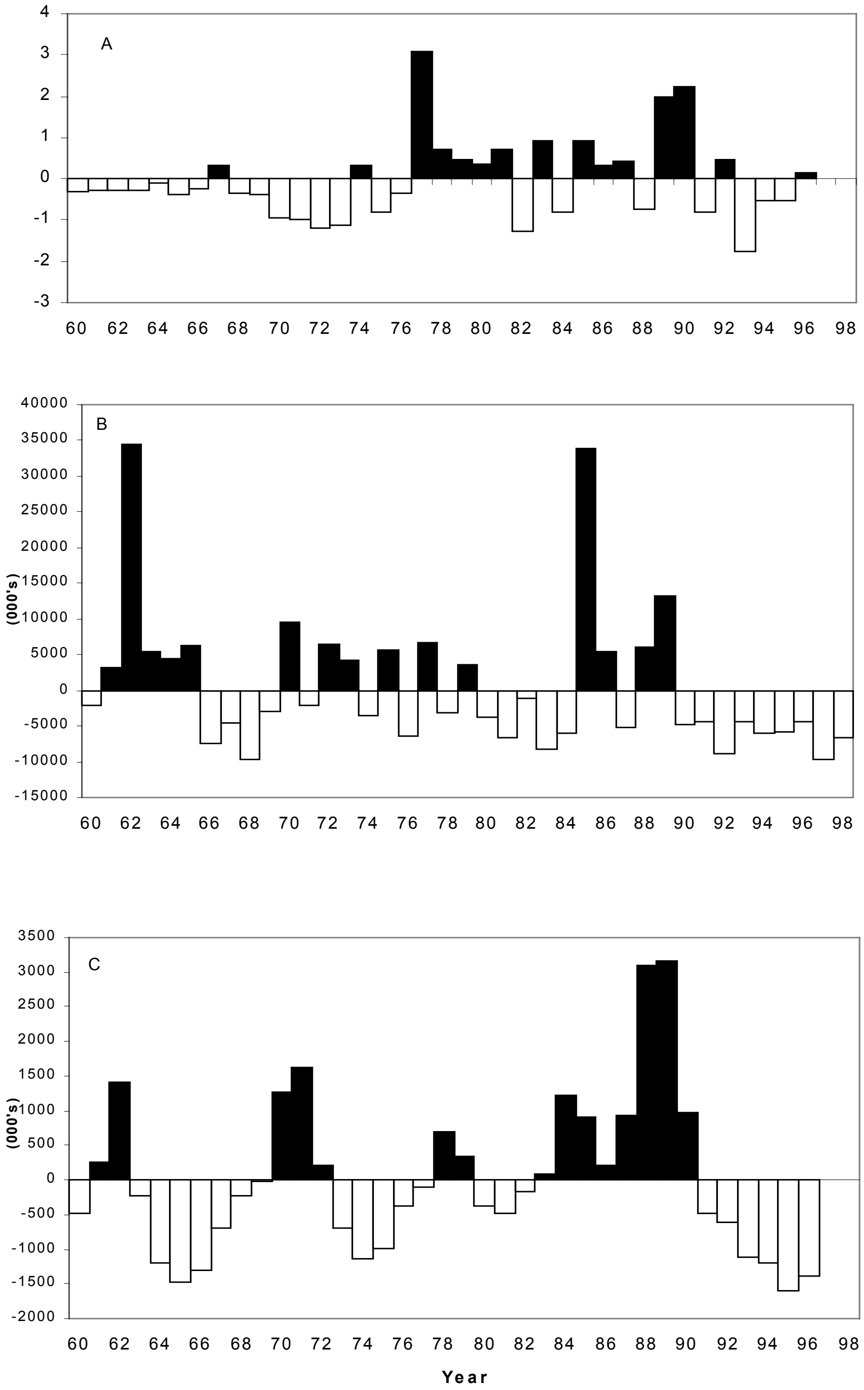


Figure 13



A
4
3
2
1
0
-1
-2
-3
60 62 64 66 68 70 72 74 76 78 80 82 84 86 88 90 92 94 96 98
B
(000's)
40000
35000
30000
25000
20000
15000
10000
5000
0
-5000
-10000
-15000
60 62 64 66 68 70 72 74 76 78 80 82 84 86 88 90 92 94 96 98
C
(000's)
3500
3000
2500
2000
1500
1000
500
0
-500
-1000
-1500
-2000
60 62 64 66 68 70 72 74 76 78 80 82 84 86 88 90 92 94 96 98
Year

Figure 14

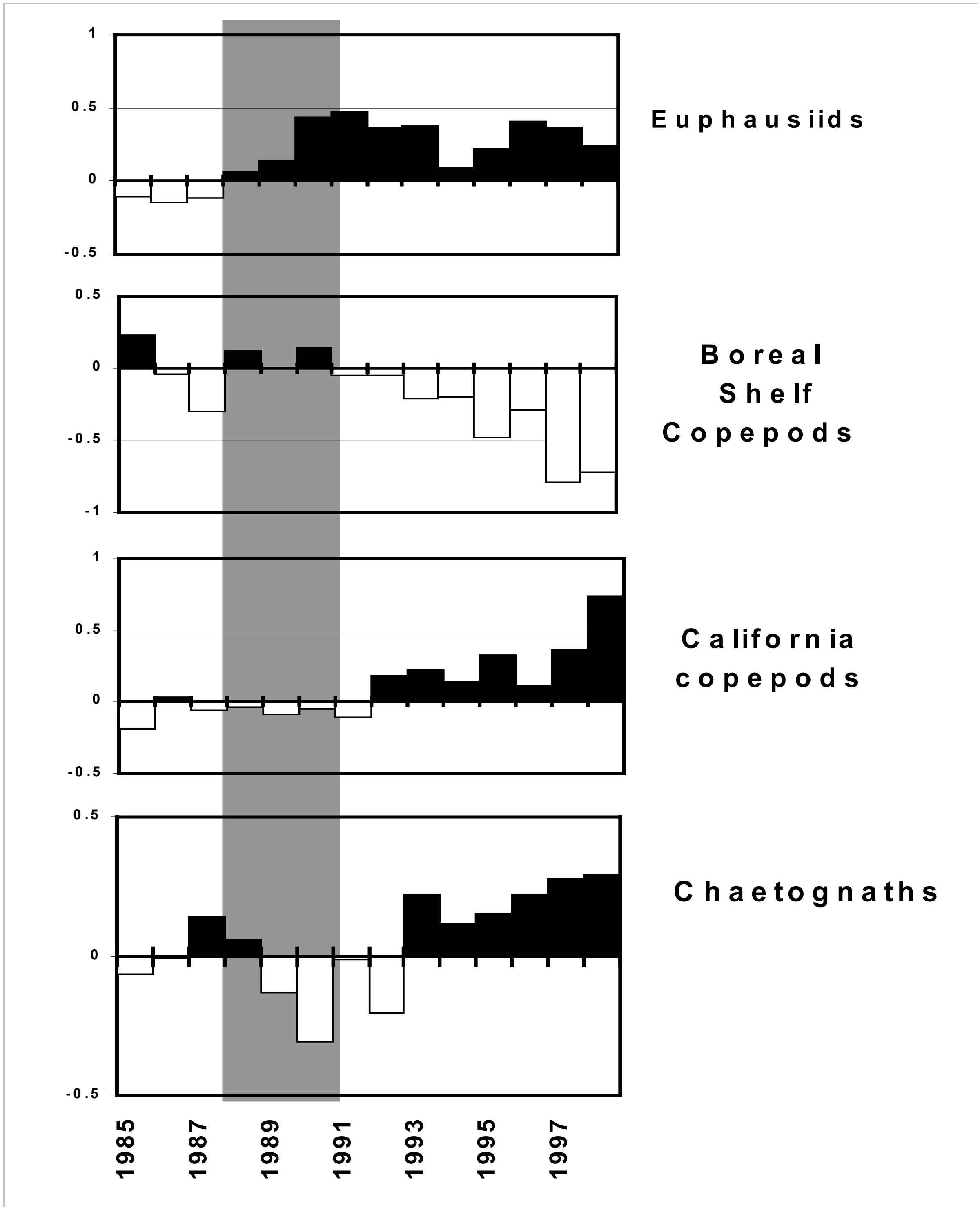

1
0.5
0
-0.5
Euphausiids
0.5
0
-0.5
-1
Boreal Shelf Copepods
1
0.5
0
-0.5
California copepods
0.5
0
-0.5
Chaetognaths
1985
1987
1989
1991
1993
1995
1997

Figure 15

Ecosystem Consequences and Sardine Population - Zooplankton Effects

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On the interannual time scale (1950-1984), changes in biomass of macrozooplankton are correlated from San Francisco to mid-Baja California; hence, data from the Southern California Bight (SCB) sector can be taken as representative. On the interdecadal time scale (1950-1998), biomass of macrozooplankton in the SCB has decreased, and the water is warmer; unlike the effects of El Niño, however, these trends were not accompanied by a reduction in the California Current's geostrophic transport, nor by an increase in salinity. Hence, what provided food for the expansion of the sardine? Biomass of macrozooplankton in the Alaska Gyre has increased during these decades, but too far north to "cause" the sardine expansion. In the SCB sector, euphausiids (an important food source for sardines) have not decreased in proportion to the total macrozooplankton, nor have the smaller types of zooplankton. Hence, better definition of what constitutes sardine "food" for various life stages and in various environmental regimes is needed, as are more general use of measured of physiological health and growth.

Of Sardines and Seabirds

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Although seabirds are often overlooked by scientists, fishers, and fishery managers as significant marine predators, in fact, many species feed exclusively on finfish, including the juveniles of many important commercial species (e.g., rockfish, salmon), as well as on the adults of commercially important baitfish (e.g., anchovy, herring). The degree to which seabirds impact fishery stocks thus depends on the abundance of each piscivorous seabird species and their diet (also expressible more generally as daily energetic demand). Because many piscivorous seabirds take forage fish, the re-emergence of sardines (*Sardinops sagax*) over anchovies within the California Current System (CCS) may create both trickle down and trickle up change in nearshore systems.

Seabirds are marine birds foraging primarily to exclusively in the marine environment. Many species spend the majority of their lives on the ocean, returning to land only to breed. Seabirds are generally long-lived (20-70 years, depending on the species), and display many life history traits common to mammals: sexual maturity is delayed several years, annual reproductive output is low (from a maximum of 3 chicks in the gulls and terns, to a minimum of one chick every other year in some albatross), juvenile survivorship is low, and adult survivorship is usually high (90+ percent annually). Because of the tradeoff between long life and low fecundity, seabird populations are vulnerable to decline if adult survivorship decreases by as little as 3-5%. Many seabirds are natally philopatric – returning to their place of birth to breed. This latter trait has the potential to create somewhat closed populations, if environmental conditions remain favorable at the colony site.

Within the CCS, seabirds are found both breeding and as non-breeders. This latter category includes young individuals (prebreeders), individuals which have elected to skip breeding in any given year, and species which breed elsewhere, but spend time foraging in the CCS (Table 1). In total, 16 primarily piscivorous seabird species (excluding minor gull species) are found within the nearshore CCS (defined herein as from the shoreline out to 2000 meters of depth). For this analysis, we divide the CCS into political regions (British Columbia, Washington, Oregon, and California), and further subdivide California into north and south (subdividing the State at Pt. Conception). Although oceanographic regions may be more biologically appropriate, data are most often reported by state.

There are several patterns of note. First, several species occur during the summer, but are not found in substantial numbers in the winter (e.g., pelicans, shearwaters, albatross), and vice versa. The latter two species breed outside of the CCS (southern hemisphere and Hawaii, respectively). Kittiwakes and fulmars (the Alaska breeders) are only found in the CCS during the winter.

Second, some species exhibit a cline in distribution (e.g., pelicans are found in the south, but not in the north; murres are found predominantly in the middle of the CCS). Third, some species appear to have an erratic distribution and abundance pattern (e.g., rhinoceros auklets). This latter pattern may be more indicative of data quality, than biological reality, and reflects the fact that the smaller, burrow nesters are harder to adequately sample both during the breeding season and on the water in the winter.

Abundance, although useful, does not adequately represent seabird pressure on forage fish resources, because piscivorous seabirds range widely in mass from black-legged kittiwakres (.04 kg) to black-footed albatross and brown pelicans (3.0 kg). Figure 1A shows annualized biomass (metric tons) for all species combined. Using standard field and laboratory-derived measurements, as well as occasional allometric standardization equations, it is possible to calculate a second parameter – energy demand (billions of Kcal; Figure 1B). In total in the CCS, we estimate 3606 metric tons of seabirds annually demand 431 billion kilocalories of fish. Note that these estimates only include adult birds, and do not include the chicks produced within the breeding season. Thus, these values are conservative. Because the nearshore environment differs greatly in size among the political regions of the CCS, we have also divided seabird biomass and energy demand by region size, to produce annual estimates per kilometer squared (Figure 2A & B).

Energy demand can be translated into biomass of forage fish using literature-derived values for forage fish energy content (in kcal/g). Thus, if seabird diet is known, total biomass for each fish species consumed can be calculated. Results of such a calculation are shown for common murres (*Uria aalge*), by region, based on gut contents from birds collected at sea and observation of fish brought back to chicks (Figure 3). Of course, during the breeding season, murres and other CCS breeders do not range evenly over the nearshore, but are found clustered adjacent to the colony. Assuming murres have a foraging range of 30 km, prey consumption for the largest colonies may be 5-15 times higher than the estimates given in Figure 3.

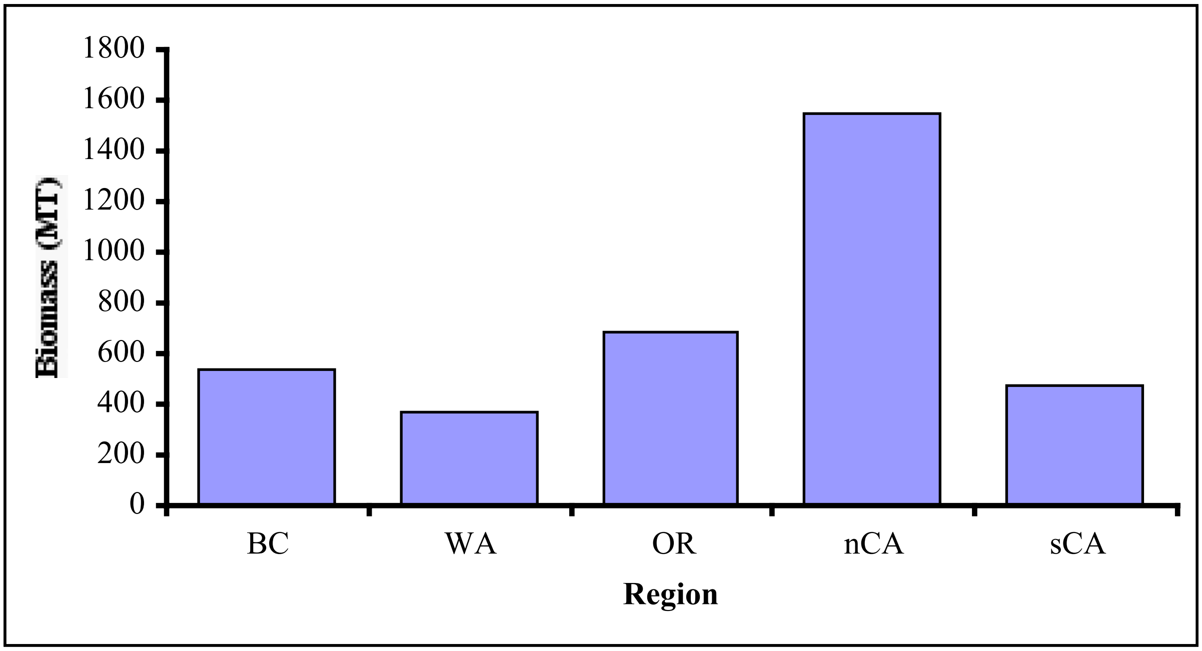
Will sardines be affected by seabird energy demands? We conservatively estimate total seabird biomass in the nearshore CCS at 3,600 metric tons. Excluding chicks, these birds require 431 billion kilocalories each year. Thus, depending on which prey species are consumed, seabirds eat 220-300 thousand metric tons of fish annually. Because sardines are a high energy content fish (2.08 kcal/g), second only to eulachon (*Thaleichthys pacificus*) and well above anchovy (*Engraulis mordax*; .094 kcal/g), they should be a preferred food resource for any predator. If all seabird demand was satisfied by sardines, seabirds would consume 0.21MMT, or approximately 13% of the 1999 total age1+ population estimate (1.58MMT). This is approximately twice as much as the fishery landed in 1999.

However, there are several reality caveats. First, sardines should be highly desirable as food, especially as food for chicks because adults must transfer fish back to the colony. Thus, low value fish such as Pacific cod (Gadus macrocephalus, 0.94 kcal/g) would require many more trips to satisfy the energy demands of the chick(s). Second, because sardines have a higher energy value than anchovies, there may be additional predation pressure on sardines. At the same time, the ecosystem may produce a lower biomass of sardines, if trophic energy is conserved. In other words, a kilogram of anchovies is worth only 0.76 kg of sardines, if the currency is energy rather than biomass. Third, adult sardines are large enough to escape seabird predation, potentially falling prey to only the largest species of gulls, cormorants, pelicans, and albatross. However, these seabird species make up a minor proportion of the total seabird biomass (15 %). Thus, seabird predation on sardines may actually be less than that on anchovies (per fish biomass) during the previous half of the cycle. In this case, the replacement of sardines by anchovies may negatively affect seabirds by effectively removing a food source. Finally, because all seabirds can take juvenile sardines, seabird predation may have the greatest effect on the early life history stages. Since the last cycle of sardine dominance, seabird populations throughout the CCS, particularly breeding seabirds which must target smaller fishes to feed their chicks, have grown substantially. Whether this route of trophic interaction significantly affects sardines, for instance by depressing the re-initiation of sardine predominance, is not known.

Table 1. Summer and winter population estimates for seabird taxa in the CCS, by region. Data are taken from a variety of published sources and represent an amalgam of at sea and on colony counts and estimates from the 1970s through the 1990s. Data quality vary greatly across regions.

	BC	WA	OR	nCA	sCA
Summer					
Murres	13000	15000	1068000	527000	0
Rhinos	1078500	91200	1500	2600	0
Gulls	86900	59900	25500	50700	41900
Cormorants	19900	9800	81500	81000	44000
Puffins	116900	4500	7500	0	0
Terns	0	0	24000	0	0
Pelicans	0	0	0	0	17900
Shearwaters	114000	415000	55700	2161700	107500
Albatross	14100	4400	3300	20100	600
Winter					
Murres	33700	94500	97800	296400	0
Gulls	31100	35900	22400	227700	838700
Rhinos	25500	1000	1400	149900	0
Kittiwakes	0	28000	12500	103800	42100
Fulmars	9400	68300	7600	23000	85500
Cormorants	7500	5700	5000	8400	0

Figure 1A & B. Annual total biomass and total energy demand by region for all species listed in Table 1 combined.



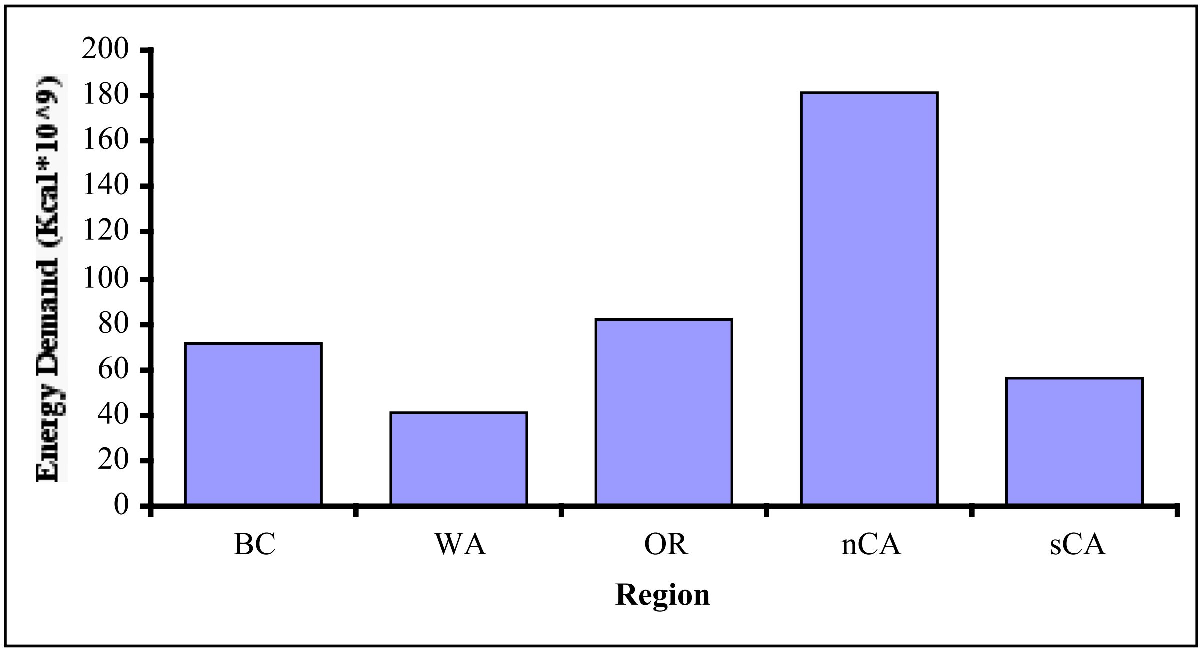


Figure 2A & B. Annual biomass and energy demand per km^2, by region.

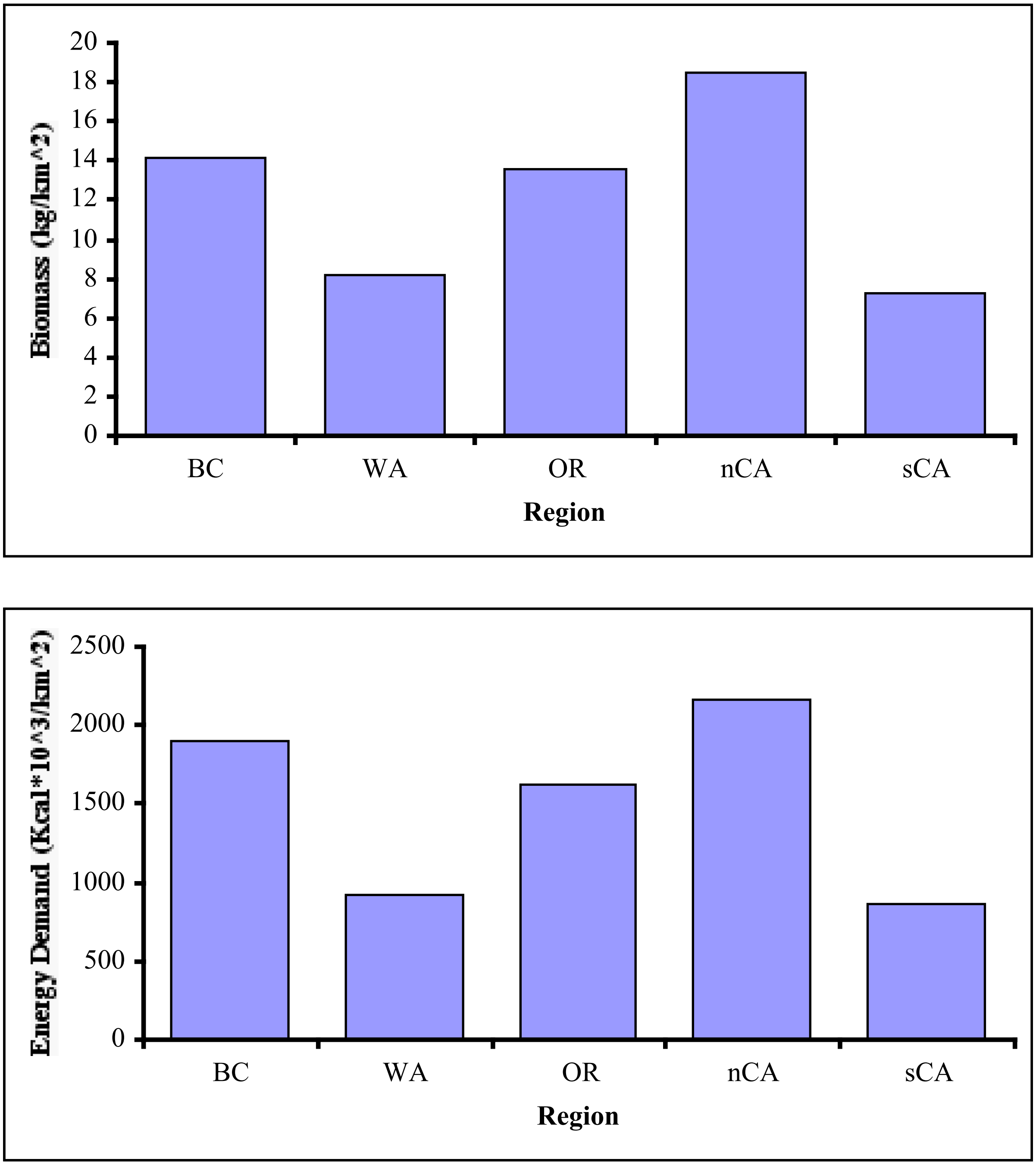
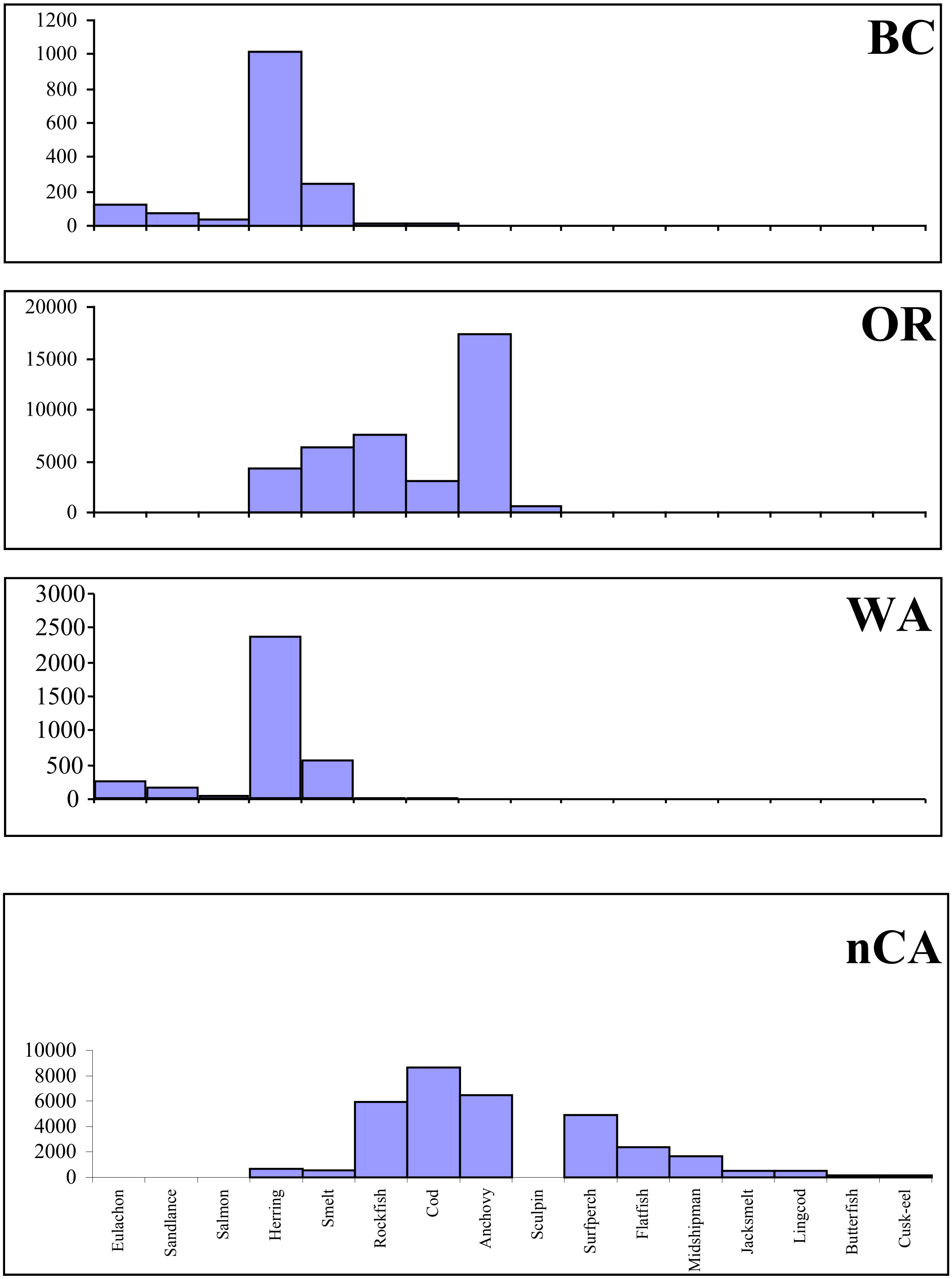


Figure 3. Annual prey consumption in MT of common murres, by region.



Large-and Long-Term Natural Variability of Small Pelagic Fishes in the California Current

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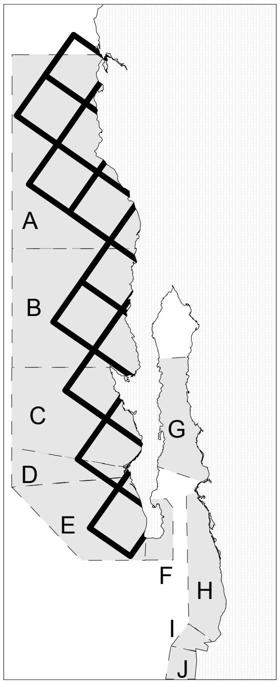
A number of recent studies have suggested that ocean-climate interactions can drastically change the productivity of small pelagic fish populations in different current systems, with seemingly parallel variations in the biomass of phytoplankton, zooplankton, and other fish.

Sardinops and *Engraulis* populations, occurring in most of both eastern and western boundary currents seem to be very sensitive to climate-driven interdecadal regime shifts in the systems, and have been associated to long-term changes in distribution. When their population level within a current system is high they dominate its entire neritic zone. Alternatively, when their population level is low their distribution is greatly reduced and they are at times totally absent from certain areas. That spatial processes is known as expansion-contraction.

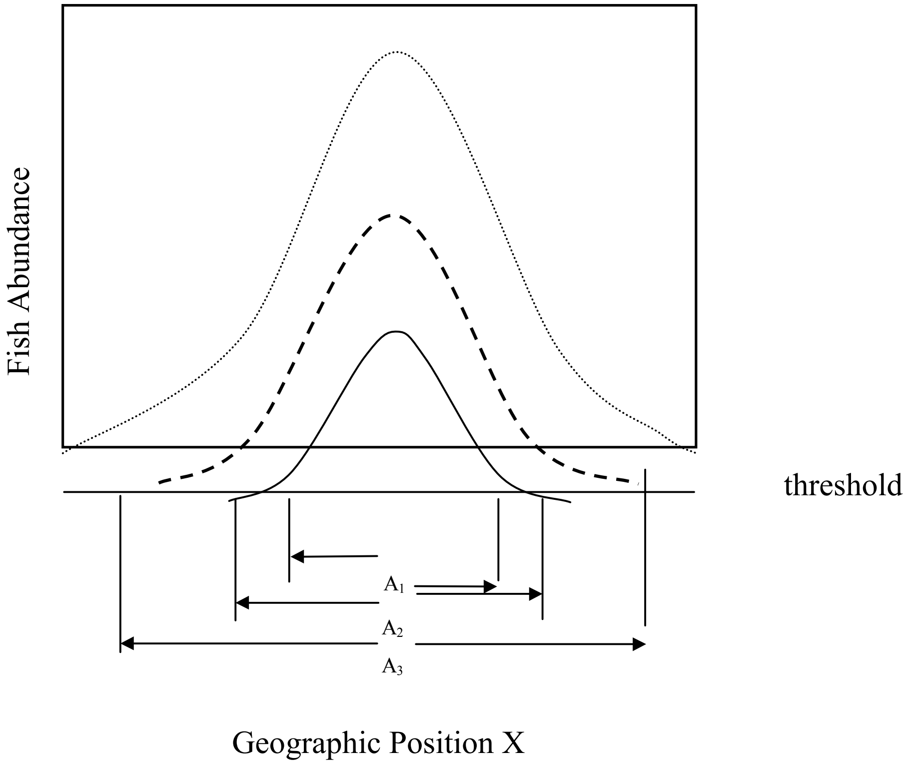
Live-bait boats fishing for tuna in the California Current use as bait available clupeoid fishes caught in the vicinity of tuna fishing grounds. The wide distribution of this fleet during a 50-year period is analyzed on yearly and decadal basis for the area ranging from the California coastline in the north to Cabo Corrientes in the south, including the Gulf of California.

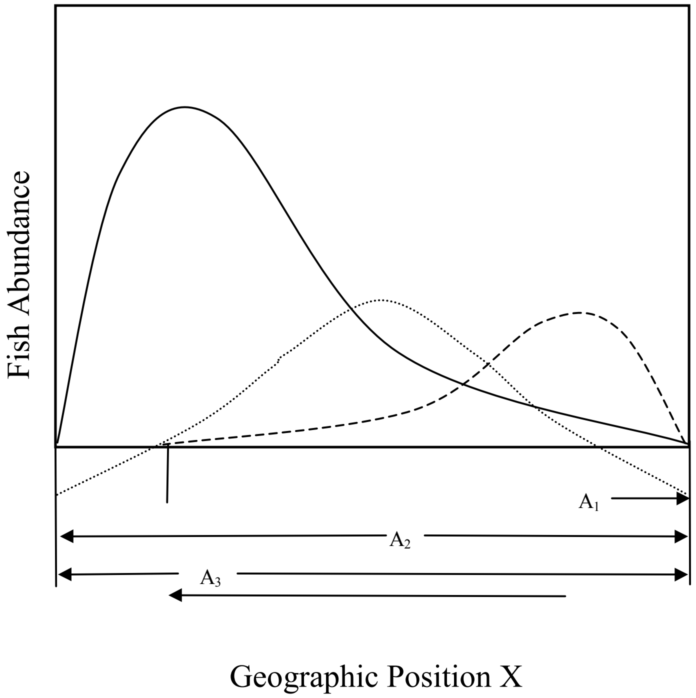
The CPUE pattern for live-bait species, used as a proxy of abundance, suggests that when *Sardinops caeruleus* population increases its geographic range, the bulk of its biomass and the center of distribution is in the north. Prior to the 1960s, when the population was reducing its range, the center of distribution and bulk of abundance shifted from north to south and massively entered the Gulf of California during the cold 1960s.This population movement maybe gave rise to a new fishery inside the Gulf of California.The spatial process described here is different to that of homogeneous spread resulting from simple expansion-contraction.

A spatial pattern of *Engraulis mordax* abundance alongshore is inferred assuming that sardine abundance is deletereous to anchovy populations. Anchovy colonized and increased its abundance where sardine population level was low or absent.

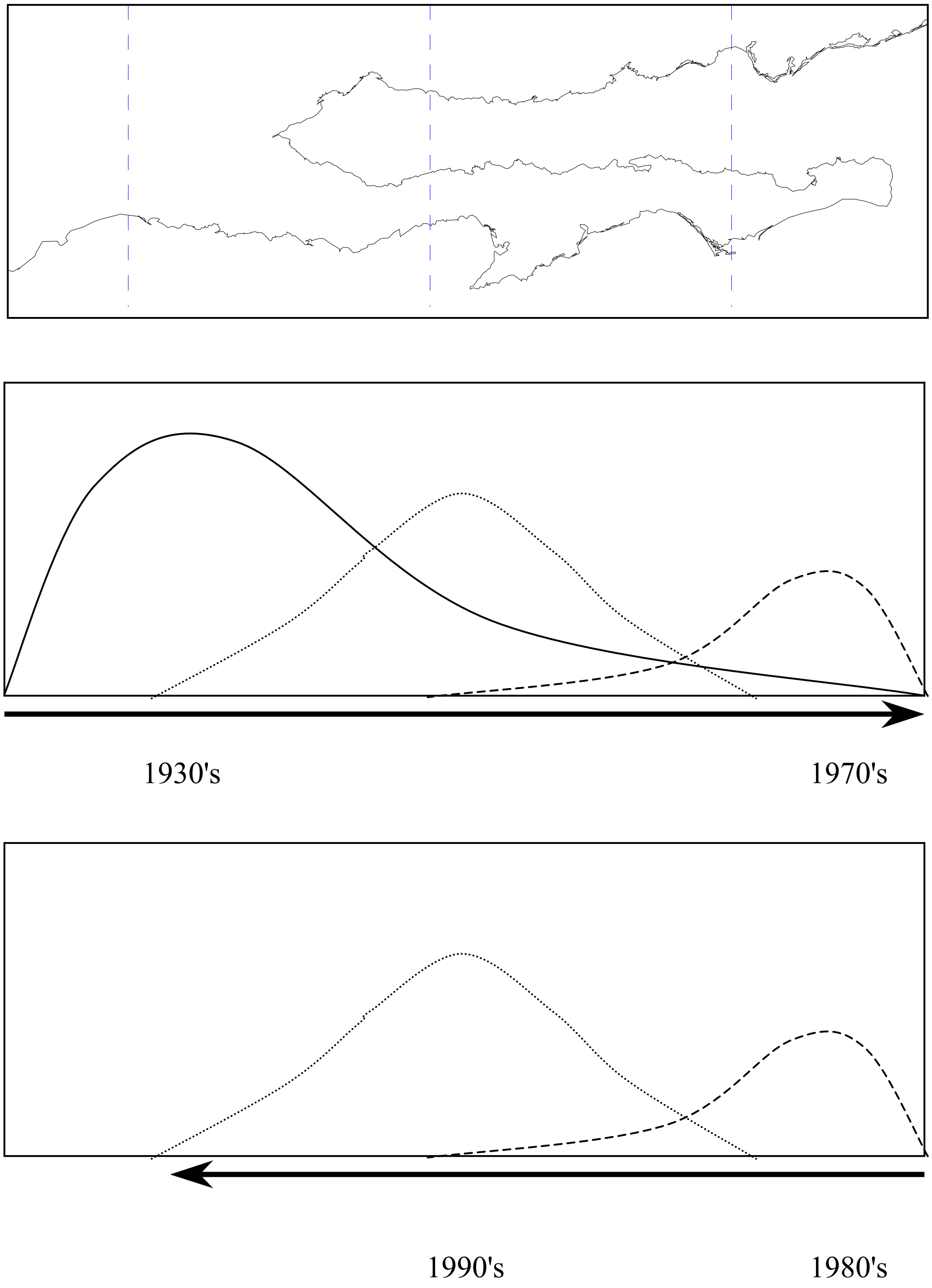


Live-bait fishery areas off California, Baja California and Gulf of California (after Alverson and Shimada 1957), including squares of 2 X 2 degrees from which time-series of SST were obtained from COADS database.





Simplified diagram illustrating the differences between an homogeneous spread resulting from simple expansion-contraction and the spatial process described here for *Sardinops caeruleus.*



Schematic diagram illustrating the large- and long-term sardine population movement. When sardine abundance population increased its geographic range, the bulk of its biomass and the center of distribution was in the north. When the population was reducing its range, the center of distribution and bulk of abundance shifted from north to south. Currently, the abundance of sardine in the California Current System is increasing its range. If the trend of this movement continues our hypothesis predicts an increase in sardine abundance off California and decreasing off Magdalena Bay.

Effects of Foraging Strategy on Catches of Northern Bluefin Tuna (Thunnus thynnus) in the Eastern Pacific

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CICIMAR-IPN, La Paz, Mexico

Northern bluefin tuna, *Thunnus thynnus*, apparently spawns only in the western Pacific and a portion of the juveniles migrate to the eastern Pacific. During the past decade, catches in the eastern Pacific have declined. One possible cause for this, proposed by Dr Polovina at Honolulu Laboratory SWFSC-NMFS, is a reduction in the proportion of bluefin that migrate out of the western Pacific since 1977. This period of reduced bluefin migration coincides with one during which a prey of bluefin, the Japanese sardine *Sardinops melanosticta*, was abundant off Japan. Polovina's hypothesis points out that during years when sardines are abundant off Japan, a higher proportion of bluefin stay in the western Pacific, as compared to years during which sardines are scarce.

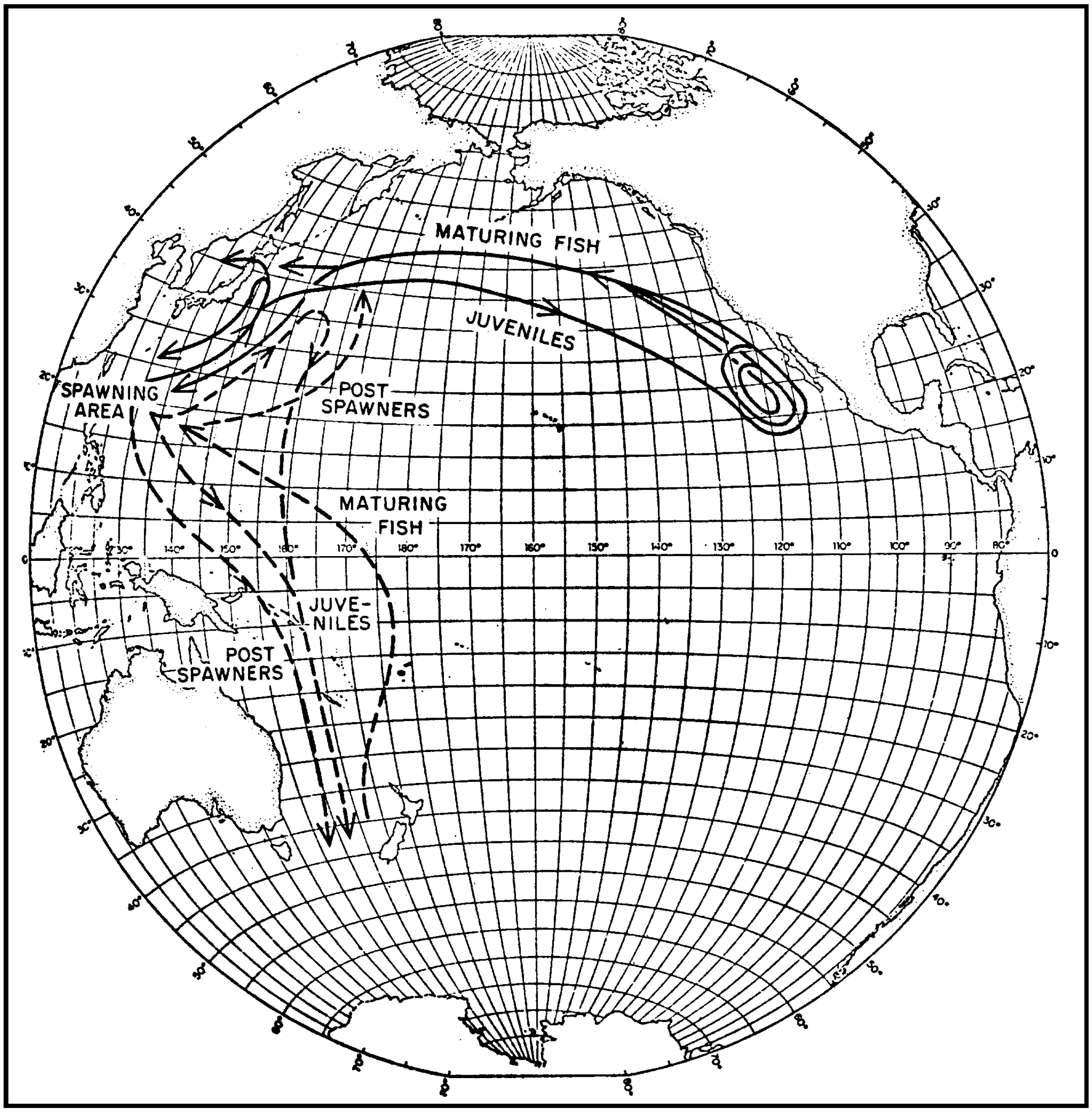
Why does northern bluefin tuna go so far as off the Baja California peninsula, Mexico?

The Pacific or California sardine *Sardinops caeruleus* is distributed along the California Current; it is a similar prey for northern bluefin tuna. We are currently undartaking studies of both spatial and temporal distribution of California sardine using catch records of live-bait by boats fishing for tuna along the California, Baja California, and Gulf of California coasts during a 50-year period (1931-79). The results will shed light on the question of why northern bluefin tuna reaching the eastern Pacific are caught mostly off Baja California.

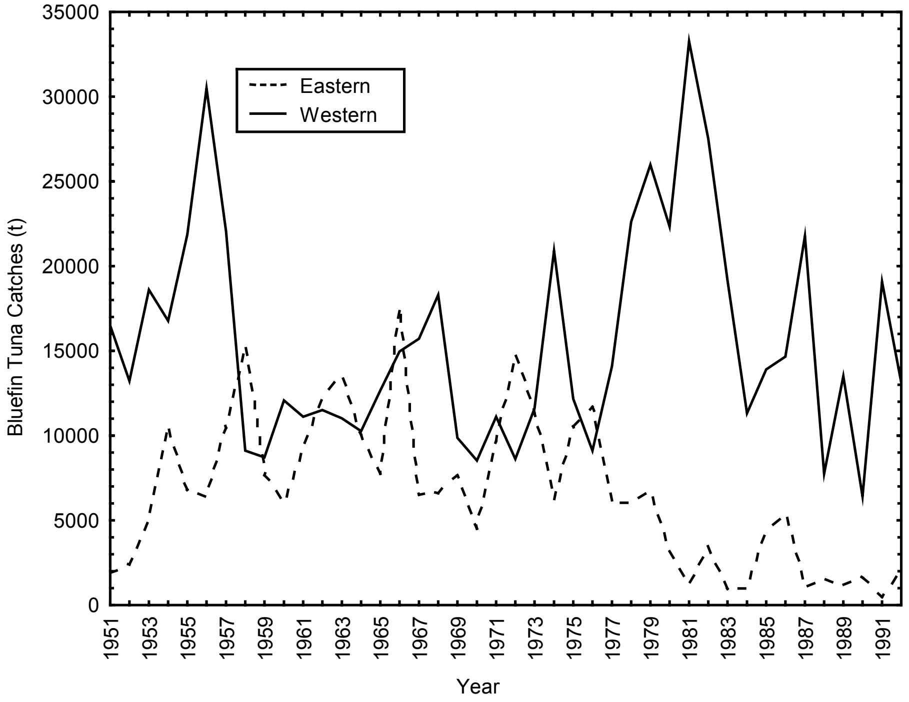
The spatial and temporal results of this sardine studies agrees with already published papers. California sardines were abundant off California during the 1930´s, with catches plummeting during the 1940´s without recovery until the end of the period. Lagging about a decade, they were abundant south of the Mexico-USA international border to Punta Eugenia during the 1940´s, collapsing during the 1950´s. In the Punta Eugenia to Cabo San Lázaro subarea, California sardine has always been present during the 50 year series, showing some variations in abundance along with cold-warm periods. These features agree with the formerly published hypothesis of a resident California sardine population in this area.

A permanent population of California sardine off Baja California is an alternative source of food always available to northern bluefin tuna when Japanese sardine abundance diminish. If the Japanese sardine is abundant, a higher proportion of bluefin stay in the western Pacific compared to those years when sardines are scarce, when bluefin migration increases towards the eastern Pacific looking for California sardine.

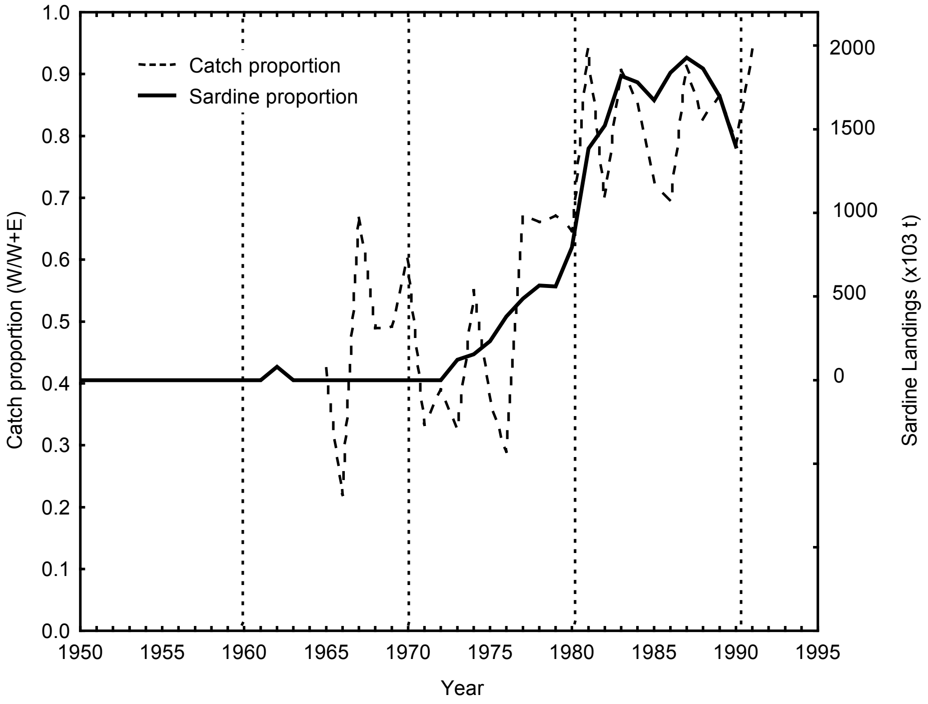
Tuna, as any other animal, seeks to achieve a maximum net energy gain to maximize its lifetime reproductive success, or fitness. The total energy consumed as food minus the energy costs of obtaining it (e.g. staying in the western Pacific or migrating to the eastern Pacific) is the net energy gain. The way in which bluefin tuna is achieving a long-term maximum net energy gain has resulted in such a foraging strategy.



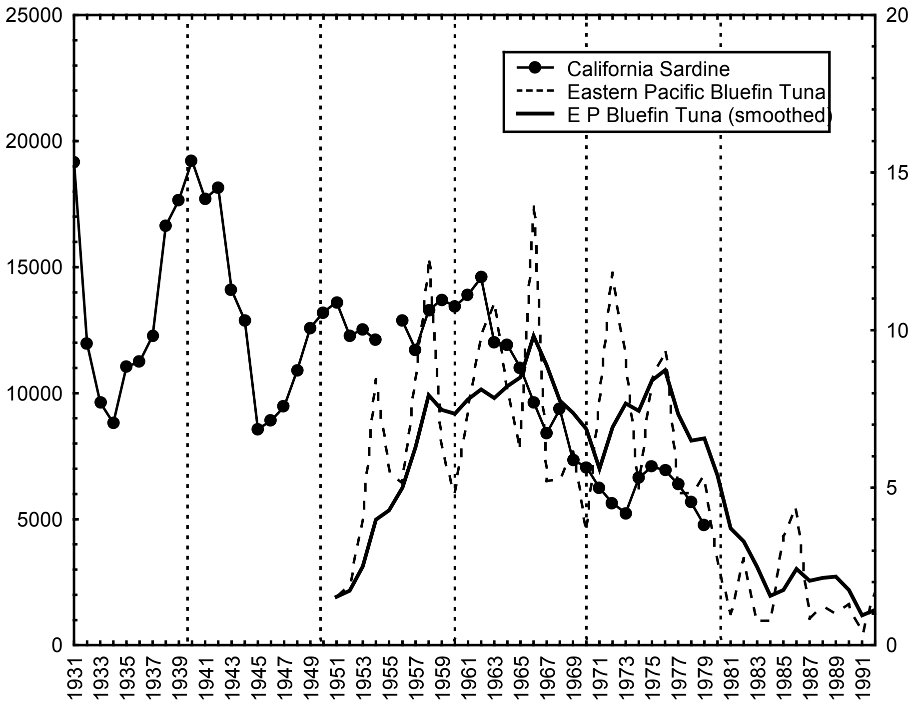
A model for northern bluefin migration in the Pacific Ocean (taken from Bayliff 1980)



Landings of northern Pacific bluefin tuna (short tons) from the western and eastern Pacific Ocean 1951-1992 (Taken from Polovina, 1996)



Proportion of age 1-4 northern Pacific bluefin caught in the western Pacific relative to combined eastern and western Pacific catches overlaid with north Pacific landings of sardine (Taken from Polovina, 1996)



Pacific bluefin tuna caught in the eastern Pacific overlaid with California sardine CPUE in the California Current

Towards an Ecosystem Management Plan for the Northern California Current: The Role of Coastal Pelagic Species

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In recognition of the need for a broader approach to fisheries management, the 1996 Sustainable Fisheries Act established an advisory panel of experts to develop recommendations to expand the application of ecosystem principals in fishery conservation and management activities. Among the recommendations of that panel's report were that the regional Fisheries Management Councils develop demonstration Fisheries Ecosystem Plans (FEP's) for the ecological systems under their jurisdictions, in the interest of advancing the ability to quantitatively employ the holistic objectives of ecosystem management principals (EPAP 1999).

Among the key elements that should be included in such plans were : delineating the geographic extent of the ecosystems that occur within Council authority, including characterization of the biological, chemical and physical dynamics of those ecosystems; developing conceptual models of the food webs in those systems; calculating total removals (including incidental mortality) and showing how these removals related to standing biomass, production, optimum yield, natural mortality and trophic structure. Using the Northern California Current as a test case, we intend to develop some of these elements of a draft FEP.

One of the most significant human effects on marine ecosystems is the alteration of biotic communities by fishing activities, which are often directed at the middle or near the tops of food webs. Actual structural changes to trophic webs could occur in heavily fished marine ecosystems (Apollonio, 1994; Parsons, 1993), thus the ecological effects of fishing could be substantially greater and more complex than the reductions in the biomass of the target species themselves. Both contemporary process-oriented research and paleo studies have clearly demonstrated that the productivity and abundance of populations in the Northern California Current are associated with large scale variability in various physical properties. However, this does not necessarily preclude alterations or perturbations to the ecosystem resulting from biological removals.

The NCCE has a lengthy history of exploitation; beginning with the depletion of marine mammal populations in the 19th century and the sequential development of major fisheries for salmon, sardine and herring, groundfish, shellfish and hake over the past 150 years. Currently the cumulative removals from the system approach five hundred thousand metric tons per year. Because the potential consequences of these removals are uncertain, one of our goals is to refine our understanding of how trophic structure could change depending both upon the magnitude of the removals and the climatic regime under which those removals occurred.

In terms of defining the system, Bottom et al (1993) divided the California Current Ecosystem into two major subregions north and south of Cape Mendocino, CA, and suggested that the northern region (or the northern California Current Ecosystem, NCCE) is an appropriate ecological unit for regional resource management. As a first step in evaluating both the consequences of fishery removals and the potential varying states of the system in response to climate forcing, we have constructed a simplified numerical model of the NCCE food web using Ecopath software to amass critical food habit and other trophic data. The general assumption in this approach is that over an appropriate period of time (perhaps a decade, or decades which have been identified as regimes) a mass-balance model can be generated to represent basic trophic interactions between the major components (species or species assemblages) of an ecosystem. Balanced models are a framework for summarizing information over trophic levels and comparing the trophic structure, flux rates and construction of food webs both within and between ecosystems.

The basic Ecopath interactions were constructed by Polivina (1984), and developed into an interactive software package by Christenson and Pauly (1992). The model is essentially little more than a series of linear equations, where the production of each component is equal to its withdrawals by other components in the system (predation mortality, natural mortality and flow to detritus) and removals from the system due to fishing mortality or migration (for details, see also www.ecopath.org). There are quite significant and very real constraints in attempting to construct any mass balance model which purports to represent the steady state of any system, particularly a transition environment best characterized by the enormous level of physical and biological variability on broad spatial and temporal scales. Amongst the major constraints include the lack of abundance or production data for a vast majority of species assemblages, uncertainty over key biological rates, and the inability to account for the disconnect between population stability and recruitment processes. Perhaps most troubling would be the high degree of aggregation of parameters over species (and populations), age and size classes, and spatial structure.

Despite these limitations, a mass balance approach is a useful starting point for evaluating the amount of energy transferred through a system, and may be an effective tool for comparing different states of the ecosystem over time. As mentioned previously, systems may be affected both by climate variability and change (bottom up forcing) and by fishing pressure (top down forcing). As an example of the applications of this approach, Trites et al. (1999) used the Ecopath model to develop two snapshots of the structure of the Bering Sea ecosystem in 1950 and 1980, to assess the hypothesis that major changes in ecosystem structure were driven by the harvest of major predators (notably baleen whales) in the mid-20th century. Similarly, Jarre-Teichmann and Christensen (1998) developed a series of Ecopath models for Eastern Boundary Current Ecosystems to compare differences in productivity, primary production requirements and energy transfer efficiencies in upwelling ecosystems. In all these models forage fish such as capelin, anchovy and sardine are critical links in the transfer of energy and biomass from producers and consumers to higher trophic levels. Accounting for the estimated consumption and energy transfer of forage fish has also proven to be among the most significant challenges in modeling large-scale changes in ecosystem structure and efficiency.

We believe that there are numerous ways in which a successful mass balance approach may help both managers and researchers understand the magnitude and consequences of changes in the trophic structure in the NCCE. Such an approach may also offer insights regarding the effects of the historical removal of species and populations from the NCCE system over the last 200 years, to assess whether top-down forcing could be a significant factor in maintaining stability in trophic structure. Similarly, the model might also be used to compare climate regimes, and could be useful in accounting for changes in productivity and/or transport of nutrients and plankton which may be necessary to account for large-scale changes in biomass or fisheries production. A model may also be useful to assess the extent to which the high biomass levels of pelagic species estimated by paleo studies to have occurred in the early 20th century, such as sardine and hake, are in balance with concurrent estimates of zooplankton production. Ultimately, we hope to reveal insights as to how the potential interactions of fishing and physical forcing alter both ecological structure and stability, and in doing so further the search for new directions in sustainable fisheries management.

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Sardines in the Ecosystem of the Pacific Northwest

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The Pacific sardine (*Sardinops sagax*) has been one of the most dominant pelagic fishes in the California Current system over the last several millennia and its abundance has fluctuated greatly over time (Baumgartner et al. 1992). During peak abundance periods, this population is capable of supporting major fisheries. The main population and fishery is centered in central and southern California, but during periods of high abundance and warmer ocean temperatures, some portion of the population resides off Oregon, Washington, and British Columbia, with some schools or individuals making it as far north as southern Alaska (Hart 1973, Wing et al. MS). At these times, commercial fisheries develop for sardines, or pilchards as they are called locally, in the Pacific Northwest (PNW) and off British Columbia. In order to effectively manage a fish stock, it is necessary to acquire some basic biological parameters on the stock; however, we are generally lacking any such information on sardines in the PNW.

Sardines were first landed commercially in Oregon during the 1935-36 fishing season and a year later in Washington, well after the commencement of fisheries in both California and British Columbia (Chapman 1936, Schaeffer et al. 1951). Fish were landed in Gray's Harbor, Washington, Astoria and Coos Bay, Oregon, and were generally rendered to oil and fishmeal. Following the collapse of the fishery in the late 1940s, there have been few reports of sardine captures in the PNW. Reid (1960) reported the catch of a single male in Winchester Bay, Oregon in August of 1957. In purse seine surveys off the coast of Oregon and Washington from 1979-1985, five sardines were caught between June and September of 1984, all off central Oregon (Brodeur and Pearcy 1986, Pearcy and Schoener 1987). Ermakov and Stepanenko (1996) also reported that some sardines were caught in the PNW in the 1980s. These sporadic occurrences are apparently connected to warm ocean conditions and anomalous northward advection associated with El Niño (Pearcy and Schoener 1987). These warm years were generally followed by cool years that may have inhibited the growth of the northern sardine population.

Beginning in 1992, sardines increased dramatically in the PNW as first reported by Hargreaves et al. (1994), again apparently in response to 1992-93 El Niño. This time, however, they continued to increase and even reproduce in the PNW up to the present time (Bentley et al. 1996, McFarlane and Beamish 1999, Busby et al. MS). This change followed an apparent regime shift and coincided with a dramatic increase in overall pelagic fish biomass off the PNW (Emmett and Brodeur 2000). Using a variety of data sources, we describe biological characteristics such as the distribution, life history and ecological relations of sardines during this recent population increase.

Results

Egg and larval distribution related to environment – The National Marine Fisheries Service (NMFS) conducted ichthyoplankton surveys off the coast of Oregon and Washington for five years (1994-1998) sampling a similar grid of stations every July. The sampling consisted of a vertical tow with a CalVET net to a maximum depth of 70 m (Bentley et al. 1996). Sardine eggs were distributed over a substantial proportion of the study area and extending well offshore (Fig. 1). In some cases (e.g. 1995) the entire range of the distribution was probably not effectively sampled. Eggs were generally distributed between the 14^o and 16^o C isotherms, except in 1995 and 1997 when these isotherms were pushed close to shore (Fig. 1). The distribution of sardine larvae was similar to that of the eggs, although they were slightly farther offshore in most cases (Fig. 2).

Adult distribution and size – To describe the adult distribution of sardines, we used three different data sources more fully described in Emmett and Brodeur (in press). It should be noted that none of these surveys were specifically targeting sardines and the distribution of sampling effort was mostly at predetermined station locations.

The first comes from the NMFS West Coast triennial groundfish bottom trawl surveys that began in 1979 (data courtesy of Mark Wilkins, AFSC, Seattle). We examined catches only from the U.S.-Canada border south to 42^o N, although many sardines were caught outside this region. Sardines were first caught beginning in the 1992 summer survey, with the highest catches mainly around the Columbia River (Fig. 3). Sardines were distributed mainly over the middle and outer shelf regions. In the 1995 survey, sardines appeared to be more spread out occurring both farther to the south and more inshore compared to 1992, although the overall abundance was lower. In 1998, catches were lower still and occurred predominantly in the vicinity of the Columbia River (Fig. 3). Biomass caught in this survey has shown a steady decline in both the U.S. Vancouver and Columbia statistical regions since 1992 (Fig. 5). Several age-classes are apparently represented in these catches in 1998 (Fig. 4). There is a progression of the dominant size mode from south to north, with a second smaller group appearing off northern Washington.

During the summer and fall of 1998 and 1999, NMFS conducted near-surface surveys for juvenile salmon along transects off the Washington and Oregon coasts (Emmett and Brodeur 2000). Sardines were collected in all five surveys although the catch varied greatly (Fig. 6). They were widely caught during the May, 1998 cruise from Gray's Harbor south to the Central Oregon Coast. The next three surveys caught relatively few sardines but by the September cruise, they again occurred in very high numbers, but at stations mainly north of the Columbia River (Fig. 6). The size distribution in 1998 was generally very broad compared to the 1998 triennial survey (Fig. 7). In 1999, however, there was a narrow range of individuals represented, although there were relatively few fish caught in May and June.

The last survey examined was a series of biweekly cruises in the area of the Columbia River plume in spring and summer of 1998 and 1999 (Emmett et al. MS). These generally used the same trawl as the salmon surveys but were targeting predators so they mainly fished at night. Sardines ranked third in abundance in 1998 but was the dominant species caught in 1999, making up more than a third of the total catch. No sardines were caught in April or May but were caught rather consistently beginning in June through August (Fig. 8).

Food habits -- Collection of Pacific sardines from research trawls off of La Push (LP transect) and Willapa Bay (WB transect), Washington, during September 1999, has allowed for an initial investigation into the trophic role of sardines in this region. Immediately after collection, stomachs were preserved by either freezing or placing in 10% buffered formalin. Five sardine stomachs were analyzed from each station. The two anterior-most compartments were used in the analysis. Contents were removed and washed through a series of 500, 200 and 100µm sieves to separate phytoplankton from animal contents for volumetric measurement. Volume was measured by settling contents in a volumetric test tube for approximately 24 h.

Phytoplankton and marine-snow like material made up between 50 and 70% of the volume of total contents (Table 1). All stages of copepods (*Acartia* spp., *Paracalanus* spp. and *Pseudocalanus mimus*), euphausiid eggs, and the appendicularian, *Oikopleura* spp., were the primary animal prey items. Copepodites, copepod nauplii, and euphausiid eggs were found in higher abundance from offshore stomachs, while the appendicularian, *Oikopleura* spp., was generally found more frequently in nearshore stomachs (Table 1).

Table 1. Average percent phytoplankton and average number of animals per sardine stomach.

STATION	Phyto plankton (%)	Copepod (adult)	Copepod (cope podite)	Copepod (nauplii)	Copepod (egg)	Euphausiid (egg)	Appendicularian *Oikopleura*
WB 14	71	2	28	62	32	106	27
WB 19	62	27	38	101	17	189	14
LP 09	53	44	18	22	21	< 1	15
LP 22	63	15	33	70	3	55	12

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Figure Legends

Figure 1. Distribution of sardine eggs from NMFS 1994-1998 Ichthyoplankton surveys off Oregon and Washington. Also shown are isotherms at 3 m depth.

Figure 2. Distribution of sardine larvae from NMFS 1994-1998 Ichthyoplankton surveys off Oregon and Washington. Also shown are isotherms at 3 m depth.

Figure 3. Distribution of sardines from NMFS 1992, 1995, and 1998 triennial surveys off Oregon and Washington. Also shown is the 200 m depth contour.

Figure 4. Size distribution of sardines collected in the NMFS 1998 triennial trawl survey by degree of latitude.

Figure 5. Estimated minimum biomass of sardines off the U.S. Vancouver and Columbia Statistical regions. Numbers on graph are the coefficient of variation for the biomass. These are considered minimum since the trawl was mainly on the bottom and may not have sampled the full population of sardines which was mainly in midwater.

Figure 6. Distribution of sardines from NMFS 1998 and 1999 surface trawl surveys off Oregon and Washington. The + signs indicate locations of each trawl.

Figure 7. Size distribution of sardines collected in the 1998 and 1999 surface trawl survey by cruise.

Figure 8. Catch of sardines from the 1998 and 1999 NMFS predator surveys off the Columbia River by cruise date.