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# Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean

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## Abstract

Large-scale shifts occurred in climatic and oceanic conditions in 1925, 1947, 1977, 1989 and possibly 1998. These shifts affected the mix and abundance of suites of coexisting species during each period of relative environmental stability—from primary producers to apex predators. However, the 1989 regime shift was not a simple reversal of the 1977 shift. The regime shifts occurred abruptly and were neither random variations nor simple reversals to the previous conditions. Timing of these anomalous environmental events in the North Pacific Ocean appears to be linked to physical and biological responses in other oceanic regions of the world. Changes in the atmospheric pressure can alter wind patterns that affect oceanic circulation and physical properties such as salinity and depth of the thermocline. This, in turn, affects primary and secondary production. Data from the North Pacific indicate that regime shifts can have opposite effects on species living in different domains, or can affect similar species living within a single domain in opposite ways. Climatic forcing appears to indirectly affect fish and marine mammal populations through changes in the distribution and abundance of their predators and prey. Effects of regime shifts on marine ecosystems are also manifested faster at lower trophic levels. Natural variability in the productivity of fish stocks in association with regime shifts indicates that new approaches to managing fisheries should incorporate climatic as well as fisheries effects.

**Keywords** climate, regimes, ecological impacts, North Pacific Ocean

## Introduction

The idea of 'locked in' trends in climatic, oceanic and biological systems was first introduced to fishery scientists by Isaacs (1975), who called these persistent trends *regimes*. Regimes have been defined as multi-year periods of linked recruitment patterns in fish populations or as stable conditions in physical data series (Beamish *et al.* 1999, 2000). Low frequency, high amplitude and sometimes abrupt changes in species abundance, community composition, and trophic organization that occur concurrently with physical changes in the climate system indicate a *regime shift* (McKinnell *et al.* 2001).

A number of physical changes were noted in the North Pacific Ocean in the late 1970s (Ebbesmeyer *et al.* 1991; Graham 1994). Sea surface temperatures cooled in the central Pacific and warmed along the west coast of North America (Miller *et al.* 1994), whereas the extent of sea-ice cover in the Bering Sea decreased (Manak and Mysak 1987). Changes were also observed in the surface wind stress (Trenberth 1991) that may have affected the ocean currents in the North Pacific. Other noted anomalies included changed atmospheric circulation throughout the troposphere (Trenberth 1990), and a deepening and eastward shift of the Aleutian low-pressure system (Trenberth 1990; Miller *et al.* 1994), which advected warm, moist air over Alaska and colder air over the North Pacific.

The large-scale climatic change observed in 1977 has been referred to as a regime shift, and does not appear to be the only occurrence of this phenomenon during the past century. There are indications of two previous shifts in 1925 and 1947 (Mantua *et al.* 1997; Minobe 1997), as well as a fourth shift in 1989 (Beamish *et al.* 1999; Overland *et al.* 1999), and a possible fifth shift around 1998 (e.g. McFarlane *et al.* 2000). Such natural shifts in ocean climate raise questions about the biological basis for managing sustainable fisheries (Beamish 1995), and are leading ecologists away from a single, steady-state view of ecosystems to one that recognizes that ecosystems fluctuate because of internal and external sources of variability (e.g. Steele 1996; Trites *et al.* 1999).

There are four commonly cited indices of climatic and oceanographic conditions for the Pacific Ocean. These include: (i) the Southern Oscillation Index (SOI), which describes the oscillation of air masses between the eastern and western tropical regions of the Pacific Ocean (Walker 1924; Trenberth and Hoar 1996), (ii) the Pacific Decadal Oscillation (PDO) which is defined as the first empirical orthogonal function of sea surface temperature in the North Pacific (Mantua *et al.* 1997), (iii) the Aleutian Low Pressure Index (ALPI) (Beamish and Bouillon 1993), and (iv) the North Pacific Index (NPI) (Trenberth and Hurrell 1995). Additional, but lesser known climate indices include (v) the Pacific Circulation Index (PCI) (King *et al.* 1998), (vi) the Northern Hemisphere Surface (land and ocean) Temperatures (NHST) (Jones 1994), (vii) the Length-Of-Day (LOD) which demonstrates changes in the earth's rotational speed (Stephenson and Morrison 1995), and (viii) the Atmospheric Forcing Index (AFI), which combines the ALPI, PDO, and PCI using principle components analysis (McFarlane *et al.* 2000).

Although the 1977 shift is apparent in all indices, it should be noted that not every regime shift is apparent in all eight indices. For example, the 1989 regime shift is not evident in the PDO (Beamish *et al.* 2000). Furthermore, some of the indices are inversely related, such as the ALPI (which measures the area of low pressure) and the NPI (which is an area weighted mean sea level pressure) (Trenberth and Hurrell 1995), and many of the indices appear to be dominated by the intensity of the Aleutian Low (McFarlane *et al.* 2000).

The ALPI is perhaps the best index of climate–ocean dynamics in the North Pacific (McFarlane *et al.* 2000) (Fig. 1). This is largely because the Aleutian Low is the dominant atmospheric pressure system in

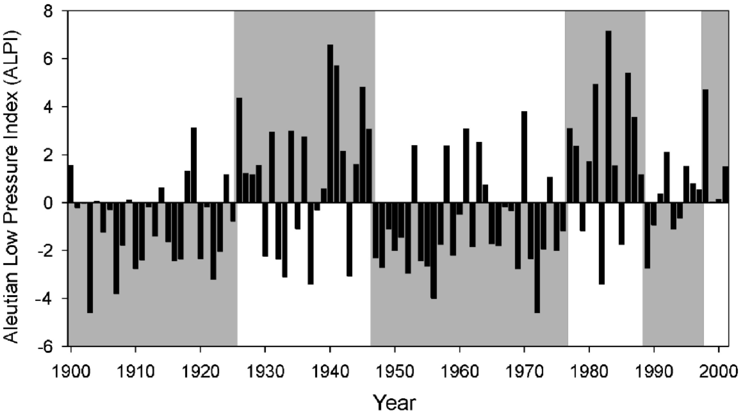

**Figure 1** The Aleutian Low Pressure Index (ALPI) from 1900 to 2001 modified from Beamish *et al.* (1997). The 1925–1946, 1947–1976, 1977–1988, 1989–1997 and 1998- regimes are highlighted.

the northeast Pacific during winter (September–January). It strengthens in the fall of each year and breaks down in the spring of the following year (Beamish and Bouillon 1995), and produces strong, cyclonic (counter-clockwise) winter winds. In early spring, the North Pacific High builds and dominates most of the North Pacific, resulting in weaker, anticyclonic summer winds.

ALPI is a measure of the geographical area of low surface pressure (<100.5 kPa) in the North Pacific Ocean (Beamish *et al.* 1997; 2000). Positive and negative ALPI values indicate whether or not the Aleutian Low was intense (large in size) compared to the long-term mean. In general, the ALPI was negative from 1947 to 1976 (i.e. the Aleutian Lows were smaller), and positive from 1977 to 1988 (reflecting a period of more intense Aleutian Lows) (Fig. 1). The intense period ended after 1989.

The following examines the biological responses of marine organisms (from primary producers through apex predators) to regime shifts in the Bering Sea and eastern North Pacific Ocean. We begin by describing the oceanographic effects of atmospheric variability over the northeast Pacific and other regions of the world as a basis for understanding the connection between changes in the atmosphere and the subsequent effects on marine organisms. We then consider the ecological impacts of atmospheric variability on phytoplankton, zooplankton, fish (small pelagics, groundfish, salmon, pollock and other northern species), marine mammals, and sea birds. We draw parallels between changes in the dynamics of marine organisms and changes in the Aleutian Low, using the ALPI as a proxy for a variety of climatic and oceanic processes. Our review extends the earlier analyses of Hayward (1997) and Francis *et al.* (1998), and summarizes the evidence that the 1989 regime shift was not a simple reversal of the 1977 shift.

## Global climate and regime shifts

In addition to the indices briefly described above for the North Pacific Ocean, a number of other indices have been derived for other regions of the world, such as the North Atlantic Oscillation Index (NAOI) (Walker and Bliss 1932; Hurrell 1995; Planque and Taylor 1998) and the Atmospheric Circulation Index (ACI) (Beamish *et al.* 1999) for the North Atlantic Ocean. Many of these indices exhibit similar, if not exact, timing of changes from one state to another, which is to be expected if climate and its variability are global phenomena. El Niño-Southern Oscillation (ENSO) events, for example, are connected to weather changes outside the Pacific Ocean that are linked by remote atmospheric associations or teleconnections (Mann and Lazier 1996). This means that changes in the position and intensity of atmospheric convection in one area will result in adjustments in pressure cells in adjacent areas and can lead to altered wind and ocean current patterns on a global scale.

The close correspondence in world-wide climate indices points to a yet undetermined common event (or energy source) as the cause of regime shifts (Beamish *et al.* 1999). One possibility is that regime shifts are caused by changes in the earth's nutation (wobbling motion of the earth's axis around the poles that involves varying attraction of the moon on the earth's equatorial bulge), which transfers energy to the sea system by a process known as forced oscillation (Yndestad 1999). Another possibility is that regime shifts are driven by changes in the earth's rotational speed, which redistributes angular momentum (energy) among the four shells of the earth—the core, mantle and crust, hydrosphere, and atmosphere—which all rotate at different speeds. Support for this idea comes from observations that the rotation speed of the solid earth appeared to increase around 1975, and decrease in the late 1980s (based on changes in LOD) (Beamish *et al.* 2000).

The majority of research into regime shifts has been conducted in the Pacific Ocean. However, there is increasing interest in understanding anomalous climate–ocean conditions in other systems, such as the Benguela upwelling ecosystem (Shannon *et al.* 1992) and the Atlantic basin, Labrador, Greenland, Iceland, western Europe and the Azores (Hurrell 1995; Beamish *et al.* 2000; Ottersen *et al.* 2001). The fact that many of the climate–ocean indices, as well as the global LOD, exhibit similar, if not exact, timing of changes from one state to another suggests that regime shifts are a global phenomenon. This, in turn, implies that the effects of decadal scale environmental variability should figure more prominently in fisheries research and management in all of the world's oceans.

## North Pacific oceanographic and atmospheric variability

Four large production domains (Fig. 2) exist in the eastern North Pacific Ocean. These have been termed (i) the Coastal Downwelling Domain, (ii) the Transition Zone, (iii) the Coastal Upwelling Domain, and (iv) the Central Subarctic Domain (Ware and McFarlane 1989). Persistent surface currents in the northeast Pacific delineate the location of these domains. The Bering Sea can be considered a fifth domain, and is delineated by the Aleutian Islands and Alaskan Peninsula. All five domains are unique in terms of the dominant fish species and their response to regime shifts.

A zero in the wind stress curl near the Pacific coast of North America causes a bifurcation of the eastward flowing Subarctic Current, which creates the northward flowing Alaska Current and the southward flowing California Current (Thomson 1981). However, the location of the separation of the Subarctic Current is not well defined, and varies on a seasonal basis, because the location and intensity of the Aleutian Low and North Pacific high atmospheric pressure systems varies between summer and winter.

The dominant feature in the Central Subarctic Domain (Central Gulf of Alaska) is the Alaska Gyre, which rotates in a counter-clockwise (cyclonic) direction (Ware and McFarlane 1989). This circulation results in divergence (upwelling) in the core of the gyre, and may explain why this domain is relatively productive (Reid 1962). Intensification of the winds

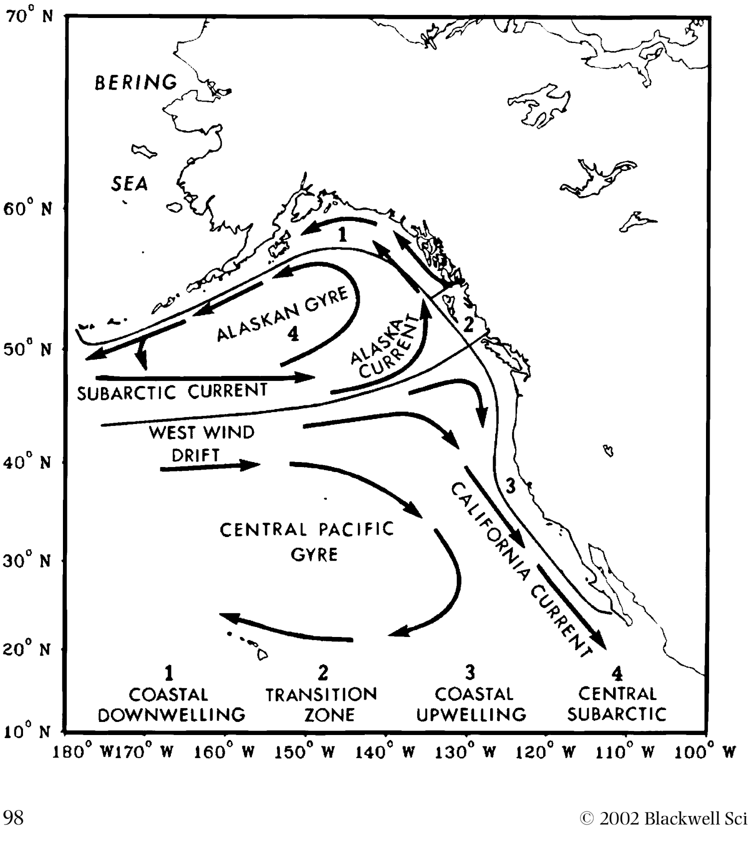

**Figure 2** Prevailing ocean currents and the four major domains defined by Ware and McFarlane (1989).

might improve productivity and result in increased divergence and upwelling of nutrient-rich water at the core of the gyre (Reid 1962; Brodeur and Ware 1992). Flow in the Alaska gyre was found to be stronger than usual after the 1977 regime shift, whereas no change was noted in the California Current (Coastal Upwelling Domain) (Miller 1996). This supports the hypothesis of Chelton and Davis (1982) that the Alaska and California Currents fluctuate out of phase.

The onset of the Aleutian Low results in increased precipitation in the Subarctic North Pacific. This input of freshwater has a strong, stabilizing effect on oceanographic conditions. As the Aleutian Low intensifies, wind patterns change further south along the coast of North America leading to decreased upwelling and increased water column stability. In the Gulf of Alaska, increased stability means that phytoplankton can be maintained in the euphotic zone for longer periods of time, which in turn increases the overall amount of primary production (Gargett 1997). However, off the coast of California, increased stability and less upwelling results in a decreased nutrient supply and a decline in primary production. Thus, a decline in phytoplankton in this area—related to limited nutrients and not light—leads by inference to a decline in secondary production.

The presence of winter sea-ice and a subsurface pool of cold (<2.0 °C) water in summer are significant characteristics of the Bering Sea (Wyllie-Echeverria and Wooster 1998). The extent of the sea-ice cover depends on the air temperature and the winter storm tracks that are generated by the Aleutian Low (Overland and Pease 1982). When the Aleutian Low is strong relative to the high-pressure systems that move in from the north, warm air is pumped northward and the sea-ice does not penetrate far south. During such warm years, the cold pool of water is not well developed (Wyllie-Echeverria and Wooster 1998). The cold pool of water is significant because of its size (in the order of hundreds of kilometre wide and up to 70 m thick) and because of its effects on temperature-sensitive species assemblages.

The timing of events in the Bering Sea are not necessarily synchronous with those further south (Wooster and Hollowed 1995). There are indications of a cool era in the Bering Sea from about 1965–1978, and of a warm period beginning in 1978 (Wooster and Hollowed 1995). Significant decreases in the winter ice cover were also reported after 1977 (Niebauer 1988). Variability in the climate–ocean conditions in the Bering Sea appears to be related to climate–ocean conditions further south, and the mechanism that connects the two may be the Aleutian Low.

## Ecological impacts of atmospheric variability

### Phytoplankton and zooplankton

The diversity and abundance of phytoplankton and zooplankton have been sporadically measured at various times and places in the North Pacific over the past century. However, as with most marine organisms, there are few if any assessments of abundance before the 1960s. In general, the available data suggest shifts in production that correspond to timing of regime shifts (Table 1).

*Central North Pacific*

Around the time of the 1977 regime shift, total chlorophyll *a* (a proxy for phytoplankton production) nearly doubled in the central North Pacific (just north of Hawaii) owing to a deepening of the mixed layer (Venrick *et al.* 1987; Venrick 1994). This deepening of the mixed layer resulted in increased phytoplankton production in deep water in the subtropical domain near the Hawaiian Islands and occurred with the intensification of the Aleutian Low and regime shift of 1977 (Polovina *et al.* 1995). At the same time as these changes were being reported, the mixed layer in the Gulf of Alaska was noted to be 20–30% shallower than normal (Polovina *et al.* 1995). Both deepening and shallowing of the mixed layers increased primary and secondary production in each of the respective regions. In the Gulf of Alaska, increased production was associated with increased exposure of phytoplankton to light, whereas in the subtropical North Pacific increased production was related to mixing deeper, nutrient-rich water into the euphotic zone (Polovina *et al.* 1995).

*California Current*

Biomass of zooplankton (measured as displacement volume) decreased by approximately 80% in the Coastal Upwelling Domain (California Current) between 1951 and 1993 (Roemmich and McGowan 1995). Roemmich and McGowan related this decline to coastal warming associated with the 1977 regime shift that increased stratification and reduced upwelling of nutrient-rich water in the California Current. They further noted that the stratification might

**Table 1** Changes in production indices of major species groups following the 1977 and 1989 regime shifts within the Bering Sea (BS), Gulf of Alaska (GOA) and California Current domains (British Columbia (BC) and areas off the west coast of North America (WCNAm.)).

| Production domain | Group | Region | Index | Species | 1977 | 1989 | Source |
|---|---|---|---|---|---|---|---|
| Bering Sea/ Alaska | Plankton | BS | Biomass | Jellyfish | ↑ | ↑ | Brodeur *et al.* (1999b) |
| | | GOA | Biomass | Zooplankton | ↑ | ↓ | Hare and Mantua (2000) |
| | | BS | Biomass | Zooplankton | ↓ | ↓ | Hare and Mantua (2000) |
| | Pelagic fish | W. Alaska | Catch | Coho salmon | ↑ | ↑ | Hare and Mantua (2000) |
| | | W. Alaska | Catch | Sockeye salmon | ↑ | ↑ | Hare and Mantua (2000) |
| | | C. Alaska | Catch | Chinook | ↑ | ↑ | Hare and Mantua (2000) |
| | | C. Alaska | Catch | Coho | ↑ | ↑ | Hare and Mantua (2000) |
| | | C. Alaska | Catch | Pink salmon | ↑ | ↑ | Hare and Mantua (2000) |
| | | C. Alaska | Catch | Sockeye | ↑ | ↑ | Hare and Mantua (2000) |
| | | SE Alaska | Catch | Chum | ↑ | ↑ | Hare and Mantua (2000) |
| | | SE Alaska | Catch | Coho | ↑ | ↑ | Hare and Mantua (2000) |
| | | SE Alaska | Catch | Pink salmon | ↑ | ↑ | Hare and Mantua (2000) |
| | | SE Alaska | Catch | Sockeye | ↑ | ↑ | Hare and Mantua (2000) |
| | | W. Alaska | Catch | Chinook salmon | ↑ | ↓ | Hare and Mantua (2000) |
| | | W. Alaska | Catch | Chum salmon | ↑ | ↓ | Hare and Mantua (2000) |
| | | W. Alaska | Catch | Pink salmon | ↑ | ↓ | Hare and Mantua (2000) |
| | | C. Alaska | Catch | Chum | ↑ | ↓ | Hare and Mantua (2000) |
| | | BS | Recruitment | Walleye pollock | ↑ | ↓ | Hare and Mantua (2000) |
| | | GOA | Recruitment | Walleye pollock | ↑ | ↓ | Hare and Mantua (2000) |
| | | BS | Recruitment | Herring | ↑ | – | Hare and Mantua (2000) |
| | | SE Alaska | Catch | Chinook | ↓ | ↓ | Hare and Mantua (2000) |
| | Demersal fish | GOA | Recruitment | Shortspine thornyhead | ↑ | ↓ | Hare and Mantua (2000) |
| | | GOA | Recruitment | Pacific Ocean Perch | ↑ | – | Hare and Mantua (2000) |
| | | BS | Recruitment | Pacific Ocean Perch | ↓ | ↑ | Hare and Mantua (2000) |
| | | BS | Recruitment | Pacific cod | – | ↓ | Hare and Mantua (2000) |
| | | GOA | Recruitment | Pacific cod | – | ↓ | Hare and Mantua (2000) |
| | | GOA | Recruitment | Sablefish | – | ↓ | Hare and Mantua (2000) |
| Bering Sea/ Alaska | Benthic fish | GOA | Recruitment | Arrowtooth flounder | ↑ | ↑ | Hare and Mantua (2000) |
| | | BS | Recruitment | Arrowtooth flounder | ↑ | ⇔ | Hare and Mantua (2000) |
| | | GOA | Recruitment | Halibut | ↑ | – | Hare and Mantua (2000) |
| | | BS | Recruitment | Yellowfin sole | ↓ | ↑ | Hare and Mantua (2000) |
| | | BS | Recruitment | Greenland turbot | ↓ | ↓ | Hare and Mantua (2000) |
| | | BS | Recruitment | Alaska plaice | ↓ | ↓ | Hare and Mantua (2000) |
| | | BS | Recruitment | Rock sole | – | ↓ | Hare and Mantua (2000) |
| | | BS | Recruitment | flathead sole | – | ↓ | Hare and Mantua (2000) |
| | Higher ORGS | GOA | Abundance | Marine birds | ↓ | – | Piatt and Anderson 1996) |
| | | GOA/BS | Abundance | Steller sea lion | ↓ | – | Trites and Larkin (1996) |
| | | GOA/BS | Abundance | Northern fur seal | ↓ | – | Trites (1992) |
| | | GOA/BS | Abundance | Harbour seal | ↓ | – | Pitcher (1990) |
| California Current | Plankton | BC | Biomass | Southerly copepods | – | ↑ | Mackas *et al.* (2001) |
| | | BC | Biomass | Euphausiids | – | ↑ | Mackas *et al.* (2001) |
| | | E. Pacific | Biomass | Zooplankton | – | ↓ | Hare and Mantua (2000) |
| | | BC | Biomass | Boreal copepods | – | ↓ | Mackas *et al.* (2001) |
| | | California | Biomass | Zooplankton | ↓ | ↓ | Hare and Mantua (2000) |
| | Pelagic fish | California | Abundance | Pacific sardine | ↑ | ↑ | Barnes *et al.* (1992) |
| | | WCNAm. | Recruitment | Mackerel | ↑ | ↓ | Hare and Mantua (2000) |
| | | WCNAm. | Recruitment | Pacific hake | ↑ | ↓ | Hare and Mantua (2000) |
| | | BC | Catch | Chum salmon | ↑ | ↓ | Beamish *et al.* (2000) |
| | | Wash. | Catch | Chum salmon | ↑ | ↓ | Hare and Mantua (2000) |
| | | BC | Catch | Pink salmon | ↑ | ↓ | Beamish *et al.* (2000) |
| | | BC | Catch | Sockeye salmon | ↑ | ↓ | Beamish *et al.* (2000) |
| | | BC | Recruitment | Pacific hake (SOG[1]) | ⇔ | ↑ | McFarlane *et al.* (2000) |
| | | BC | Catch | Pacific sardine | ⇔ | ↑ | McFarlane and Beamish (1999) |

**Table 1** continued.

| Production domain | Group | Region | Index | Species | 1977 | 1989 | Source |
|---|---|---|---|---|---|---|---|
| | | BC | Abundance | Pacific herring (SOG) | ↓ | ↑ | McFarlane *et al.* (2001) |
| | | BC | Abundance | Pacific herring (WCVI[2]) | ↓ | ↓ | McFarlane *et al.* (2001) |
| | | WCNAm. | Recruitment | Anchovy | ↓ | ↓ | Hare and Mantua (2000) |
| California Current | Pelagic fish | BC | Catch | Chinook salmon | ↓ | ↓ | Beamish *et al.* (2000) |
| | | BC | Catch | Coho salmon | ↓ | ↓ | Beamish *et al.* (2000) |
| | | Wash. | Catch | Chinook salmon | ↓ | ↓ | Hare and Mantua (2000) |
| | | Wash. | Catch | Coho salmon | ↓ | ↓ | Hare and Mantua (2000) |
| | | Wash. | Catch | Pink salmon | ↓ | ↓ | Hare and Mantua (2000) |
| | | Wash. | Catch | Sockeye salmon | ↓ | ↓ | Hare and Mantua (2000) |
| | | Oregon | Catch | Chinook salmon | ↓ | ↓ | Hare and Mantua (2000) |
| | | Oregon | Catch | Coho salmon | ↓ | ↓ | Hare and Mantua (2000) |
| | | California | Catch | Chinook salmon | ↓ | ↓ | Hare and Mantua (2000) |
| | | California | Catch | Coho salmon | ↓ | ↓ | Hare and Mantua (2000) |
| | Demersal Fish | WCNAm. | Recruitment | Pacific Ocean Perch | ↑ | ↑ | Hare and Mantua (2000) |
| | | BC | Recruitment | Sablefish | ↑ | ↓ | King *et al.* (2000) |
| | | WCNAm. | Recruitment | Widow rockfish | ↑ | ↓ | Hare and Mantua (2000) |
| | | WCNAm. | Recruitment | Sablefish | ⇔ | ↓ | Hare and Mantua (2000) |
| | | WCNAm. | Recruitment | Chilipepper | ↓ | ↓ | Hare and Mantua (2000) |
| | | WCNAm. | Recruitment | Bocaccio | ↓ | ↓ | Hare and Mantua (2000) |
| | | WCNAm. | Recruitment | Canary rockfish | ↓ | ↓ | Hare and Mantua (2000) |
| | | WCNAm. | Recruitment | Yellowtail rockfish | ↓ | ↓ | Hare and Mantua (2000) |
| | | BC | Recruitment | Pacific cod | ⇔ | ↓ | McFarlane *et al.* (2000) |
| | Benthic fish | BC | Recruitment | Dover sole | ↑ | ↓ | McFarlane *et al.* (2000) |
| | | BC | Recruitment | English sole | ↑ | ↓ | McFarlane *et al.* (2000) |
| | | BC | Recruitment | Rock sole | ↑ | ↓ | McFarlane *et al.* (2000) |
| | | WCNAm. | Recruitment | Dover sole | ↑ | – | Hare and Mantua (2000) |
| | Higher ORGS | SE AK | Abundance | Steller sea lion | ↑ | – | Calkins *et al.* (1999) |
| | | BC | Abundance | Steller sea lion | ↑ | – | Bigg (1988) |
| | | BC | Abundance | Harbour seal | ↑ | – | Olesiuk *et al.* (1990) |
| | | California | Abundance | California sea lion | ↑ | – | Stone *et al.* (1997) |
| | | California | Abundance | Northern elephant seal | ↑ | – | Stone *et al.* (1997) |

Arrows (↑ and ↓) indicate the direction of change in production from the previous regime; (⇔) indicates no change; and (–) indicates no data available). Data are attributed to the most recent publications containing either source data or updated time series. Further details about many of the listed species and additional sources of information are contained in the text.

[1] Strait of Georgia.

[2] West coast of Vancouver Island.

be the result of a climate-induced change in ocean circulation that brought warmer water into the area and limited the supply of nutrients and/or advected zooplankton away from the coast. Ongoing retrospective analyses (e.g. Rebstock 2001) of the California data suggest that much of the decline in biomass can be attributed to a decline in salps and doliolids, which are mainly composed of water and have relatively low 'meat' content (Rebstock 2001). It also appears that some taxa may have increased whereas others decreased in abundance (Rebstock 2001).

Zooplankton biomass and community structure anomalies were examined for a 15-year period (1985–1999) off southern Vancouver Island (at the northern tip of the California Current ecosystem) (Mackas *et al.* 2001). Species-specific anomalies (the 'type' of zooplankton present in a given year) were found to be much larger than the anomalies of the total annual biomass, meaning that there was more variability in the structure of the zooplankton community than in its total biomass. Species dominance shifted during 1990–1998 when 'boreal' zooplankton species (traditionally found from 40°N to the Bering Sea) declined by orders of magnitude, whereas southerly species of copepods and chaetognaths (more commonly found off California) exhibited order of magnitude increases. The shift occurred on a large spatial scale (>100 km), both on and seaward of the continental shelf, and reversed abruptly in 1999. Many of the zooplankton anomalies were found to correlate with both local (temperature, salinity, currents) and large scale (e.g. SOI, NOI, PDO) physical environmental indices (Mackas *et al.* 2001). Relative strength of the poleward versus equatorward longshore flow was believed to strongly affect the zooplankton community structure in this region.

There is a positive relationship between primary production and the strength of the northerly winds (upwelling favourable) in the Southern California Bight (Ware and Thomson 1991) – a result verified using the data from upwelling systems around the world that showed primary production is roughly proportional to upwelling (Ware 1992). Wind-induced upwelling relaxed in the Southern California Bight between 1916 and 1942, concurrent with a decline in primary production (Ware and Thomson 1991). Thus, it appears that a long-term cycle in wind-induced upwelling drives a similar long-period oscillation (in the order of 40 years) in primary and secondary production in southern California (Ware and Thomson 1991).

### *Alaska Gyre*

Biomass of copepods increased in the Alaska Gyre in 1976–1977, coincident with the cooling of the central North Pacific and intensification of the Aleutian Low (McFarlane and Beamish 1992). Large-scale sampling of oceanic areas in the North Pacific also found a significant increase in zooplankton biomass from 1956–1962 to 1980–1989 (Brodeur and Ware 1992; Brodeur *et al.* 1999a). Biomass continued to remain above the long-term mean after 1988, but varied from year to year.

From 1956 to 1962, high zooplankton biomass occurred in the central part of the Alaska Gyre, while in the 1980s the elevated biomass occurred in a steady band from the transition zone to the northern coast of Canada and Alaska (Brodeur *et al.* 1999a). Intensified wind mixing may have resulted in deeper mixed layer depths in the winter that retarded phytoplankton growth, and allowed grazers to more efficiently use the phytoplankton production (Brodeur and Ware 1992). Changes in mixed layer depths reported throughout the North Pacific likely affect the production and biomass of zooplankton (Polovina *et al.* 1995), and might explain the spatial differences in the peak zooplankton biomass between the 1960s and 1980s (Brodeur *et al.* 1999a).

### *Bering Sea*

Zooplankton biomass and chlorophyll concentration in the eastern Bering Sea and eastern Subarctic Pacific increased in the mid-1960s and remained high until the end of the 1980s (Sugimoto and Tadokoro 1997). Sugimoto and Tadokoro demonstrated a significant positive correlation between summer plankton biomass and winter wind speed in the eastern Bering Sea. They also found that the zooplankton biomass and chlorophyll concentration during the mid 1960s to early 1970s were higher than those in the preceding and following decades for the central and western Subarctic Pacific. The values declined in the late 1980s.

## Fish

### *Small pelagics*

Long-term variability has persisted in fish populations for centuries. Soutar and Isaacs (1974) analysed fish scale depositions (a proxy for fish abundance) in the anaerobic sediments of the Santa Barbara Basin and found evidence of large, natural, long-term fluctuations in the abundance of pelagic fishes, including Pacific sardine (*Sardinops sagax*, Clupeidae) and northern anchovy (*Engraulis mordax*, Engraulidae). Baumgartner *et al.* (1992) also examined these same scale depositions, but over a much longer time period, spanning over the last 1700 years. They found persistent variability in both sardine and anchovy deposition that showed peaks approximately every 60 years. Ware (1995) also identified a peak in the range of 50–75 years, while MacCall (1996) examined coastal pelagic fish abundance throughout the 1900s in the California Current ecosystem and found low frequency fluctuations in the dominant species that are cyclic and related to cold and warm periods that occur every 50–70 years. Interestingly, the cyclical sequence appears to alternate between planktivores (sardine and anchovy) and piscivores (Pacific bonito *Sarda chiliensis*, Scombridae, and Pacific mackerel *Scomber japonicus*, Scombridae).

Kawasaki (1991) examined catches from three sardine populations in the Pacific Ocean, and the European pilchard (*Sardina pilchardus*, Clupeidae) in the Atlantic Ocean from 1910 to the late 1980s, and found simultaneous changes in their abundance. In the same study, Kawasaki examined herring in the Atlantic and Pacific and showed that their abundance also fluctuated synchronously, although with a different phase than the sardines. Sardines were the focus of the largest fishery in British Columbia from the 1920s to the mid-1940s, after which they disappeared (McFarlane and Beamish 1999). This collapse occurred simultaneously off the coast of Canada and the US, and has traditionally been touted as a prime example of overfishing (e.g. Hilborn and Walters 1992).

The trends in abundance of sardine populations off Japan, California and Chile are synchronous—the collapse of the sardine stocks off the US and Canada was concurrent with the collapse of the Japanese stocks (Kawasaki and Omori 1988). This synchrony is strong evidence that the reason for the collapse had more to do with changes in ocean habitat than with fishing (McFarlane and Beamish 1999). In the early 1980s, the sardine population off the coast of California began to recover and has been steadily increasing (Barnes *et al.* 1992). A recovery in British Columbia began in 1992 when sardines were reported in catches of Pacific hake (*Merluccius productus*, Merluciidae) (McFarlane and Beamish 1999). The behaviour of sardines also changed at this time, as they shifted their distribution northward, moving into the Strait of Georgia and spawning off the west coast of Vancouver Island (McFarlane and Beamish 1999).

Data from the mid-1920s to 1999 suggest that sardines did not respond to every identified regime shift (McFarlane and Beamish 2001). However, the disappearance of sardines from British Columbia waters does correspond with the 1947 regime shift, and their reappearance corresponds with the (1989) regime shift. This suggests that the links between the sardine dynamics and climate are complex, and that variables such as temperature should be considered as proxies for ecosystem change, rather than as direct regulators of fish distribution and abundance. Favourable conditions for sardines are created by changes in the aggregate of factors that characterize the ecosystem, the specifics of which are unknown (McFarlane and Beamish 2001).

Zebdi and Collie (1995) examined variability in Pacific herring (*Clupea pallasi*, Clupeidae) recruitment in Sitka Sound from 1972 to 1990 and found a positive relationship with sea surface temperature. Based on the match–mismatch hypothesis (Cushing 1975), they concluded that warmer temperatures led to earlier spawning, which benefited herring survival because early hatched larvae could find conditions (plankton blooms) favourable to their survival. It is also possible that overall feeding conditions for larvae improved because of the increase that occurred in zooplankton biomass in the Gulf of Alaska (Brodeur and Ware 1992) during the same period. In the same study, Zebdi and Collie noted that herring recruitment was synchronous within, but not between production domains, and that the northern and southern stocks were out of phase by 1 year. In addition, the recruitment response to sea surface temperature differed between production domains. Sitka Sound herring responded positively to warmer temperatures whereas the southern stocks responded negatively to warmer temperatures.

### *Groundfish*

McFarlane *et al.* (2001) studied the effects on groundfish of the 1989 regime shift in the Strait of Georgia (SOG) and west coast of Vancouver Island (WCVI) ecosystems and found the two systems exhibited opposite responses to the change. Offshore, the distribution of Pacific hake shifted north (McFarlane and Beamish 1999), and resulted in a greater total abundance off the WCVI (McFarlane *et al.* 2000). Hake traditionally spawned offshore along the Californian coast. However, they have spawned off the WCVI since 1994 (McFarlane *et al.* 2000). The herring stocks off the WCVI declined throughout the 1990s, presumably owing to the increased predation pressure by migratory hake (McFarlane *et al.* 2001). Herring and the resident stock of hake in the SOG are now at high levels of abundance because of reduced predation on herring by hake, and a decline in mean body size of the SOG hake (McFarlane *et al.* 2001). Hake smaller than 40 cm feed primarily on euphausiids (Tanasichuk *et al.* 1991). McFarlane *et al.* (2001) suggest that herring had opposite responses in the two ecosystems owing to differing ecosystem organizations after the regime shift.

The study by McFarlane *et al.* (2001) was unusual in that it compared the response of two adjacent ecosystems within the same production domain. Much of the regime research has focused on comparing the response of stocks across production domains. For example, Hollowed and Wooster (1995) examined recruitment time series from 1950 to 1989 for six Pacific herring stocks, one northern anchovy stock and 16 groundfish stocks. They found parallel recruitment patterns in several groundfish species that were related to switching between two alternating (warm and cool) ocean states. They also found that strong year classes were infrequent in the northernmost regions (transitional and downwelling domains), whereas strong year classes were more common in the coastal upwelling domain. Most of the stocks that did exhibit strong year classes did so prior to 1977, but not after. Conversely, herring and widow rockfish in the Gulf of Alaska and off Prince Rupert had strong year classes only after 1977. This seems to indicate that there was a shift in production that differentially affected northern and southern stocks, although McFarlane *et al.* (2000) and Hare and Mantua (2000) suggest that, for the most part, the response of groundfish in the Gulf of Alaska was North Pacific-wide.

King *et al.* (2000) generated an index of year-class strength for sablefish (*Anoplopoma fimbria*, Anoplopomatidae) within British Columbia waters from 1960 through 1997. They found that year classes from 1960 to 1976 were weaker than average, and that the year classes were stronger than average from 1977 to 1989, with the 1977 year class being the largest on record. Sablefish year classes have been below average since 1990. The relative strength or weakness of the year class is related to climate–ocean conditions, as periods of above-average year-class strength were characterized by intense Aleutian Lows, more frequent south-westerly winds and warmer coastal sea surface temperatures off the west coast of Vancouver Island (King *et al.* 2000).

In a unique step towards incorporating regime shift effects in stock assessment, King *et al.* (2001) produced a 'report card' that grades the ecosystem of sablefish on decadal scales. The report card rates climate and ocean indices for the North Pacific, and regional biological and environmental indices, as good or bad depending on their effects on the critical life stage on the species of interest (in this case, the larval phase of sablefish). In agreement with the findings of King *et al.* (2000), the report card indicates that the conditions for sablefish year class were strong between 1977 and 1988. The climate–ocean conditions during this productive period were characterized by persistent, strong Aleutian Lows, more frequent south-westerly winds, warming along the coast, above-average abundance of Subarctic and boreal copepods, relatively weak winter downwelling and strong summer upwelling along the coast of British Columbia. The conditions did not persist into the 1990s (King *et al.* 2001). Armed with this report card, fisheries managers have more information on which to base their exploitation strategies. Because the year classes in the 1990s were below average and were produced in an unproductive regime, it is likely that recruitment to the fishery over the next few years will be low (King *et al.* 2001). Fishing plans for the near future can therefore be adapted to protect adult spawning biomass for more productive conditions in the future.

### *Pacific salmon*

Pacific salmon (*Oncorhynchus* spp., Salmonidae) inhabit or pass through at least two production domains in their lifecycle. For example, Alaska pink (*O. gorbuscha*) and sockeye (*O. nerka*) spend most of their life in the Central Subarctic Domain (Ware and McFarlane 1989), but pass through the Coastal Downwelling Domain on their seaward and return migrations (Fig. 6). Studies on the effects of climate on these species must therefore consider oceanographic conditions in both areas (Hare and Francis 1995). Fluctuations in Pacific salmon production trends, as they relate to large-scale climate variability, have been studied extensively (e.g. Beamish and Bouillon 1993; Francis and Hare 1994; Beamish and Bouillon 1995; Hare and Francis 1995; Mantua *et al.* 1997).

Evidence that large-scale salmon production is related to climate processes in the North Pacific comes from synchronous shifts in production among several species or stocks in response to a physical regime shift (Beamish and Bouillon 1995; Hare and Francis 1995; Hollowed and Wooster 1995). There are indications that salmon abundance has varied with climate for centuries (Beamish *et al.* 1999), and that large-scale climate impacts occur in the oceanic rather than the freshwater phase of the salmon lifecycle (at least for coho, *O. kisutch*) (Bradford 1999). It should be noted that production has generally been estimated by catches or by abundance of recruits because salmon exploitation rates are high and are therefore considered to track abundance well (Beamish *et al.* 1999). However, use of these simple indices of production have been criticized because these can be confounded by changes in spawner abundance (Peterman *et al.* 1998).

Salmon production trends in Alaska are generally the opposite of those in the northwest Pacific (Hare and Francis 1995) and correspond to the timing of regime shifts. Landings for the northern North Pacific and Alaskan salmon stocks were high in the 1930s and 1940s, low from the late 1940s through to the mid-1970s, and began to increase in the mid-1970s (Beamish and Bouillon 1993; Hare and Francis 1995). As the Alaskan landings increased in the 1970s, several North American west coast stocks, especially the Oregon coho salmon stock, began to decline (Pearcy 1992). The 1989 regime shift was associated with some of the lowest catches in the history of the Canadian fishery (particularly for the southern British Columbia stocks) (Beamish *et al.* 2000).

Two mechanisms have been proposed to explain the increased production in the northern salmon stocks in the late 1970s. The first involves improved feeding conditions owing to an increase in copepod production that was associated with the regime shift and the period of intense Aleutian Lows (McFarlane and Beamish 1992; Beamish and Bouillon 1993). The second proposed mechanism is that marine survival of migrating salmon improved in their last year at sea (Rogers 1984), and is based on the hypothesis that vulnerability to predation by marine mammals was reduced because warming of the surface waters in the Gulf of Alaska altered the timing and route of salmon migration following the 1977 regime shift (Hare and Francis 1995). Brodeur and Ware (1995) provide supporting evidence for both hypotheses.

### *Pollock and other northern species*

The Gulf of Alaska and the Bering Sea have both exhibited changes in their environment and biota in recent decades (Livingston *et al.* 1999; Trites *et al.* 1999). Brodeur *et al.* (1999b) surveyed catches of large medusae from the eastern Bering Sea from 1979 to 1997 and found a 10-fold increase in medusae biomass that began gradually from 1979 to 1989 and increased dramatically after 1990. It is unknown whether this increase was owing to human intervention or to environmental changes. However, the present authors point out that there were concomitant changes in atmospheric and oceanographic variables in 1990, and that these changes are strong indications of a regime shift. No negative effects on recruitment of any fish species were detected whereas the biomass of medusae increased. However, walleye pollock (*Theragra chalcogramma*, Gadidae) has only had one strong year class since 1989 and summer zooplankton biomass on the southeast Bering Sea shelf declined slightly in the 1990s (Brodeur *et al.* 1999b). Walleye pollock is still the single most abundant fish species in the eastern Bering Sea and is of great commercial importance (Wepestad *et al.* 2000). Owing to its large biomass, variations in the abundance of pollock are felt throughout the food web (Livingston 1991; Trites *et al.* 1999).

The distribution of Bering Sea fish is affected by variations in ice cover. As mentioned previously, the extent of ice cover in the Bering Sea was reduced beginning in 1976 (Niebauer 1988). Northward-blowing winds associated with intense Aleutian Lows pushed the ice northward and resulted in reduced ice cover in warm years (Wyllie-Echeverria 1995). Wyllie-Echeverria points out that pollock were not reported north of Bering Strait before 1976. Since then, pollock have been present north of the Strait in years of light ice cover. Additionally, larval pollock were found in the Chukchi Sea, north of Bering Strait in 1988, which suggests a change in the spawning distribution, at least for a portion of the population.

Wyllie-Echeverria and Wooster (1998) proposed that the distribution of fish stocks that are sensitive to temperatures around 2 °C should reflect ocean conditions. They found that Arctic cod (*Boreogadus saida*, Gadidae) are present only within the persistent winter pool of cold subsurface water (<2 °C), whereas the distribution of pollock, a Subarctic species, is more variable. Pollock were rarely found in the cold pool of water, but were more abundant on the outer continental shelf in cold years and dispersed across the entire shelf in warm years. Therefore, during the warmer regimes, the distribution of pollock appears to expand whereas the distribution of Arctic cod is compact.

Quinn and Niebauer (1995) found consistent relationships between pollock recruitment at age 2 and environmental variables on a 1-year lag, and suggested that age-2 pollock recruitment is related to the above-normal air and sea temperatures and reduced sea-ice extent 6–18 months earlier. They also found that environmental effects are ‘felt’ more strongly at the juvenile stage than at the larval or egg stage. Another factor that affects recruitment is density-dependent (biological) regulation (Livingston 1993).

The roles of environment and density dependence need not be considered separately. For example, Wepestad *et al.* (2000) proposed that water mass transport owing to wind forcing was the important regulating factor in pollock recruitment because transport is the mechanism that separates juvenile and adult pollock. They showed that strong year classes occur in warm years when juvenile pollock are transported inshore and away from the highly cannibalistic adults. In cold years, transport is reduced and the distributions of juvenile and adult pollock overlap, which can result in weak year classes as a result of adult on juvenile cannibalism.

The Gulf of Alaska nekton community structure changed after the 1977 regime shift from one that was dominated by forage species such as shrimps and capelin (*Mallotus villosus*, Osmeridae) to one dominated by piscivorous gadids and flatfish (Anderson *et al.* 1997; Anderson and Piatt 1999; Trites *et al.* 1999; Mueter and Norcross 2000). According to

Mueter and Norcross (2000), the observed decline in shrimp species can be attributed more to increased predation by the large piscivorous fish rather than to fishing, because the decline followed, rather than preceded, the increase in large piscivores. It is also possible that the shrimp populations were initially depressed by fishing and were therefore more vulnerable to predation by the increasing population of piscivores (Orensanz *et al.* 1998). Most of the declining species were pelagic, although the species on the rise tended to be benthic or demersal (cod and flatfish) (Anderson and Piatt 1999).

### Marine mammals and sea birds

Francis *et al.* (1998) acknowledged that the responses of apex predators to climate change are difficult to interpret owing to the confounding effects of natural responses and human influences (e.g. the 1989 Exxon Valdez oil spill, commercial pinniped harvests, etc.). In addition, the time scale on which birds and mammals respond to direct or indirect effects of climate change may be delayed or muted. For example, York (1995) correlated the survival rates of northern fur seals (*Callorhinus ursinus*, Otariidae) with environmental indices on time lags ranging from months to years before the birth of a cohort. Shorter time lags were used to relate direct effects of temperature on growth, although longer lags were used to account for possible changes in production that would affect the food supply of a growing cohort.

Piatt and Anderson (1996) found significant declines in the piscivorous marine bird population in the Gulf of Alaska between the 1970s and the 1990s concurrent with a shift in diet from one dominated by capelin, to one in which capelin was essentially absent. Changes in diets, along with reduced reproduction, were also noted in marine birds nesting on the Pribilof Islands beginning in 1978 (Decker *et al.* 1995).

Declines in the Bering Sea and Gulf of Alaska populations of Steller sea lions, fur and harbour seals (*Phoca vitulina*, Phocidae) have been observed since the mid-1970s (Pitcher 1990; Springer 1992; Trites 1992; Trites and Larkin 1996; Stone *et al.* 1997; Francis *et al.* 1998; Rosen and Trites 2000). The timing of the pinniped declines corresponds with the regime shift of 1977. Conversely, the portion of the Steller sea lion (*Eumetopias jubatus*, Otariidae) population breeding between southeast Alaska and Oregon has been increasing (Bigg 1988; Calkins *et al.* 1999).

Several hypotheses have been offered to explain the decline of the Steller sea lion in the northeast Pacific, such as a temporary population decline, delayed consequences of the pup harvest before 1972, short-term variability in environmental conditions, and deterministic changes in the environment (Pascual and Adkison 1994). The latter might result from either long-term global environmental changes or from human intervention. Testing the likelihood of each of these hypotheses suggests that either long-term change in the environment or a stochastic catastrophe is responsible for the sea lion decline (Pascual and Adkison 1994).

Merrick *et al.* (1997) found a significant correlation between diet diversity and sea lion population size in the Gulf of Alaska, and concluded that the population size declined in parallel with a decline in diet diversity. They also examined sea lion diets from six areas in the Aleutian Islands and the Gulf of Alaska between 1990 and 1993 and found that diet was dominated in every area by either walleye pollock or Atka mackerel (*Pleurogrammus monopterygius*, Hexagrammidae). Composition of the Steller sea lion diet differed prior to the population decline that began in the early 1970s in the eastern Aleutian Islands, and the early 1980s in the Gulf of Alaska (Merrick *et al.* 1987). Capelin were found in well over half the sea lion stomachs sampled near Kodiak Island in the Gulf of Alaska in the mid-1970s, but capelin have rarely been found since then (Merrick *et al.* 1997). In 1985–1986, researchers noted a high concentration of walleye pollock in the diet of sea lions in the Gulf of Alaska (Merrick and Calkins 1996), which became even more focused on pollock in 1990–1993 (Merrick *et al.* 1997). Merrick and Calkins (1996) also noted a decrease in the abundance of alternate prey (sandlance and capelin) that was concurrent with the decreasing diversity in the diet of sea lions.

According to Merrick *et al.* (1997), it is problematic that no sea lion population has shown an increasing trend when the diet consists mainly of walleye pollock or Atka mackerel. They suggest that a diverse diet is advantageous because of foraging efficiency, as diverse prey are easier to find, capture and handle. However, Rosen and Trites (2000) conclude that there are significant energetic deficiencies associated with consuming pollock and Atka mackerel. They found that captive Steller sea lions on a pollock-only diet showed metabolic depression and lost weight owing to the low caloric density of pollock. They further concluded that Steller sea lions would have to eat 35–80% more pollock than herring to maintain similar energy intakes. Thus, the low energy content of the prey available to Steller sea lions following the 1977 regime shift may have been inadequate to support large populations of Steller sea lions (Winship and Trites, unpublished data).

## Synthesis

Environmental variability occurs across many spatial and temporal scales (Francis *et al.* 1998). The research we reviewed focused on decadal or longer term variability in both physical and biological time series, although some (e.g. York 1995) concentrated on interannual variability. The intent of our review was to provide a synthesis of the current knowledge on the timing of the regime shifts that occurred in the 20th century, and to characterize the nature of the biological responses from primary producers through to the top predators in the food chain.

The regime shift literature provides evidence that large-scale changes in atmosphere–ocean conditions should not be considered as random variations. Instead, these should be thought of as long-term, stable conditions that can abruptly change state, such as occurred over the North Pacific in 1925, 1947, 1977, 1989, and possibly 1998 (Mantua *et al.* 1997; Minobe 1997; Beamish *et al.* 1999; Overland *et al.* 1999; McFarlane *et al.* 2000). Changes in atmosphere–ocean conditions appear to occur on a global scale as shown by the close correspondence observed in the trends in many of the climate–ocean indices for different parts of the world (Beamish *et al.* 1999). Changes in atmospheric pressure result in altered wind patterns that affect oceanic circulation and physical properties such as salinity and depth of the halo- and thermoclines. These in turn can affect phytoplankton productivity, the transport and survival of fish larvae, and ultimately, the survival of species that feed on lower trophic organisms.

Hare and Mantua (2000) note that there have been two interdecadal climatic oscillations operating at periods of 50–70 years (Minobe 1997) and 15–25 years. They found that the 1977 shift was evident in all biological and physical time series whereas the 1989 shift was most evident in the biological time series. As a result, they classified the 1977 shift as a major shift, and the 1989 shift as a minor shift. By way of explanation, Hare and Mantua (2000) proposed that the 1977 shift was stronger than 1989 because both the 50–70 year oscillation and the 15–25 year oscillation changed in 1977, while only the 15–25 year oscillation changed in 1989.

### 1977 and 1989 regime shifts

Changes in the dynamics of marine organisms following the 1977 and 1989 regime shifts in the Bering Sea/Gulf of Alaska and California Current regions are summarized in Table 1, and show that the (1989) regime shift was not a simple reversal of the 1977 regime shift (based on comparing the production indices of zooplankton, fish, and marine birds and mammals). The 1977 regime shift affected the biology of northern and southern areas of the North Pacific differently. After 1977, production of most zooplankton and fish increased in the Bering Sea and Gulf of Alaska. The increase in production is most evident for the pelagic fish species, and is less pronounced for demersal and benthic species. The higher organisms (birds and marine mammals) showed the opposite response. After 1977, the majority of pelagic, demersal, and benthic fish species in the California Current exhibited declines in production, whereas the productivity of pinnipeds (seals and sea lions) increased.

Harvesting probably confounds many of the data sets compiled in Table 1, and few data are available for species that were not commercially targeted. Despite such shortcomings, the available data reveal a number of interesting patterns when fish production is examined by regime. Based on the data compiled in Table 1, the 1977 regime shift was characterized as having a near balance in the number of stocks that increased and decreased, while the 1989 shift was characterized by widespread declines (cf. Hare and Mantua 2000). In the Bering Sea and northeast Pacific, 58% of assessed fish stocks increased after 1977, compared to only 36% after 1989 (Table 1). The nearly balanced response of fish production to the 1977 regime shift is also evident when the stocks are grouped and examined by habitat. After 1977, production increased for 60% of pelagic species and 55% of demersal and benthic species. However, after 1989, only 36% of the total pelagic species increased, while production increased in only 17% of the demersal and benthic species. The widespread decline in production after 1989 appears to be owing in large part to the decreases in the abundance of deep-water fishes.

Fish production not only appears to have responded differently to the 1977 and 1989 regime shifts, it also appears to have responded differently between the northern and southern ecosystems. Production increased after the 1977 shift for 69% of the assessed fish stocks in the Gulf of Alaska/Bering Sea and 45% of the California Current stocks. But after 1989, production increased in 40% of the Gulf of Alaska/Bering Sea stocks compared to 15% of the assessed California Current stocks.

For the most part, differences in the responses of the production domains can be attributed to the pelagic species. Production of essentially all (94%) assessed pelagic species in the Gulf of Alaska and Bering Sea increased after 1977, whereas increases in the California Current were observed for only 32% of the pelagic species. Responses of demersal and benthic species were similar across domains, where productivity improved by 56% in the Gulf of Alaska/Bering Sea and 54% in the California Current. In general, the response of pelagic species to the 1989 shift was positive in the northern area, although to a lesser extent than the previous shift (59%), and production improved for only 18% of pelagic species in the California Current. Although the latter proportion was small, the species involved (hake, herring, sardine) are the key species in this region.

Table 1 shows that regime shifts can have opposite effects on species living in different domains, or can affect different species living within a single domain in opposite ways. For example, the zooplankton biomass in the central North Pacific more than doubled between the 1950s and the 1980s (Brodeur and Ware 1992), whereas off the coast of California the biomass of zooplankton declined by more than 80% (Roemmich and McGowan 1995). Another example is the opposite direction of population trajectories of salmon populations in the California Current and Gulf of Alaska regions (Francis *et al.* 1998). Even within the same production domain, groups of species, such as hake and herring in the Strait of Georgia and off the west coast of Vancouver Island, can respond differently (McFarlane *et al.* 2001). Opposite responses of populations in different regions is also observed for the top predators in the system, such as for Steller sea lion and harbour seal populations that declined rapidly during the 1977 regime shift in the Bering Sea and Gulf of Alaska, whereas populations increased off southeastern Alaska, British Columbia and Oregon (Bigg 1988; Olesiuk *et al.* 1990; Pitcher 1990; Springer 1992; Trites and Larkin 1996; Stone *et al.* 1997; Francis *et al.* 1998; Calkins *et al.* 1999).

The effects of climatic forcing on fish are not necessarily predictable; nor does a shift necessarily mean that species abundance will necessarily revert back to those of a previous regime. Climate can indirectly affect fish populations through changes in predator distribution and abundance. Examples of indirect effects on fishes include the previously mentioned hake–herring interaction and the overlap of adult and juvenile walleye pollock distributions in the Bering Sea (Bailey 2000). Climate is also more likely to affect sea birds and mammals in the North Pacific and Bering Sea by affecting the quantity or quality of prey available to them (e.g. Rosen and Trites 2000).

The summary presented in Table 1 is useful, but masks the important changes in distribution and subsequent predator-prey interactions. For example, the distribution of certain key species in the California Current (hake, sardine) changed in response to the 1989 shift, and the change impacted commercially important herring stocks. This effect is lost when expressed in a simple tabular format. The large-scale response to climate change is important, but fisheries are not managed on a large scale. The localized responses are perhaps most important because these must be incorporated in stock assessment.

Fisheries stock assessment has traditionally focused on imposing controls and limits on the effects of fishing to maintain fish populations at fixed, viable levels. In addition, the yields from these populations are usually considered to be sustainable for an indefinite period of time. The key inputs required for traditional stock assessment models are the stock–recruitment relationship and the virgin unfished biomass, both of which are assumed to be constant. However, a growing body of scientific literature indicates that the productivity of fish stocks varies naturally in association with climate, and that the effects of fishing are superimposed on this natural regulation. A new approach that incorporates climatic as well as fishing effects is therefore required to manage the world's fisheries.

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