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REVIEW

Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific

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ABSTRACT

A major reorganization of the North-east Pacific biota transpired following a climatic ‘regime shift’ in the mid 1970s. In this paper, we characterize the effects of interdecadal climate forcing on the oceanic ecosystems of the NE Pacific Ocean. We consider the concept of scale in terms of both time and space within the North Pacific ecosystem and develop a conceptual model to illustrate how climate variability is linked to ecosystem change. Next we describe a number of recent studies relating climate to marine ecosystem dynamics in the NE Pacific Ocean. These studies have focused on most major components of marine ecosystems – primary and secondary producers, forage species, and several levels of predators. They have been undertaken at different time and space scales. However, taken together, they reveal a more coherent picture of how decadal-scale climate forcing may affect the large oceanic ecosystems of the NE Pacific. Finally, we synthesize the insight gained from interpreting these studies. Several general conclusions can be drawn.

1 There are large-scale, low-frequency, and sometimes very rapid changes in the distribution of atmospheric pressure over the North Pacific which are, in turn, reflected in ocean properties and circulation.

2 Oceanic ecosystems respond on similar time and space scales to variations in physical conditions.

3 Linkages between the atmosphere/ocean physics and biological responses are often different across time and space scales.

4 While the cases presented here demonstrate oceanic ecosystem response to climate forcing, they provide only hints of the mechanisms of interaction.

5 A model whereby ecosystem response to specified climate variation can be successfully predicted will be difficult to achieve because of scale mismatches and nonlinearities in the atmosphere–ocean–biosphere system.

INTRODUCTION

In this paper, we characterize the effects of interdecadal climate forcing on the oceanic ecosystems of the NE Pacific Ocean. Our approach is first to reflect on a number of recent studies relating climate to marine ecosystem dynamics. These studies have focused on most major components of marine ecosystems – primary and secondary producers; primary, secondary and top-level predators. They have been undertaken at different time and space scales. However, taken together they begin to reveal a more coherent picture of how decadal-scale climate forcing may affect the large oceanic ecosystems of the NE Pacific. We then synthesize the insight gained from these studies with what we know about atmospheric and oceanic physics and how they affect these marine ecosystems.

Of particular importance to this paper is the concept of scale. Ricklefs (1990) defines scale as the characteristic distance or time associated with variation in natural systems. He goes on to make three important points about why the concept of scale is so important to developing an understanding of ecosystem structure and dynamics.

- Every process and pattern has a temporal and spatial extent.

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- Patterns and processes that occur on different scales of time and space are linked and rules governing these relationships may help to define ecosystem boundaries.
- Scales change as signals propagate through ecosystems, particularly as they move from physical to biological components of the ecosystem.

To characterize the scales upon which the studies we report were undertaken, we define their temporal and spatial extents as well as the oceanic ecosystems in which the studies were made.

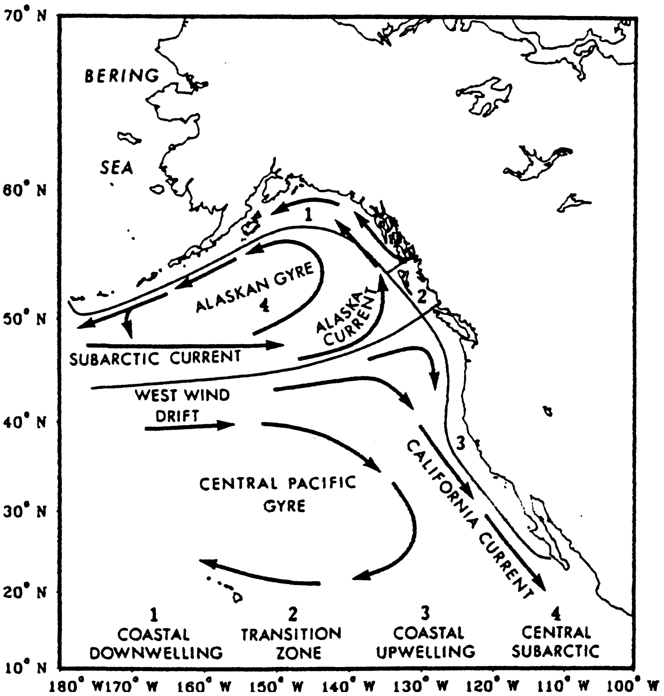
Time

All of the studies we report on focus on some aspect of variation at the decadal time scale. Some focus solely at that scale. Others attempt to characterize and compare the nature of variability at multiple time scales, either longer (centennial) or shorter (annual). Some collapse observations over spans of time, whereas others maintain the original time resolution of the data and attempt to characterize the nature of variability and connections at different time scales. One thing that becomes particularly apparent upon review of a number of these studies is that the nature of the relationships between atmosphere/ocean physics and ecosystem biological processes can be very different at different time scales.

Space

We characterize biological response in space at the level of the oceanic and fishery production domains of the NE Pacific described by Ware and McFarlane (1989). The southern region of the subarctic North Pacific is defined by a narrow zonal transPacific transitional domain between the Alaskan and Central Pacific gyres (Ward, 1993). This transitional domain lies just north of the Subarctic Boundary (Fig. 1). The eastward zonal flow in this region is referred to as the Subarctic Current. In the western Pacific, this region is defined by the confluence of the Oyashio and Kuroshio Currents. In the NE Pacific, the eastward-flowing Subarctic Current separates into two streams ≈800 kilometres offshore. One branch (Alaska Current) veers northward and flows into the Gulf of Alaska, forming the cyclonic Alaska Gyre, while the other branch flows southward to form the California Current. This frontal structure, strong eastward zonal flow, and bifurcation at the North American coast are the major physical features that define a number of oceanic domains critical to NE Pacific fisheries production (Central Subarctic, Transitional, Coastal Upwelling, Coastal Downwelling) as described by Ware and McFarlane (1989) (Fig. 1). These oceanic domains define three fish-production regions: the coastal upwelling region

Figure 1. Prevailing ocean currents and four major oceanic domains as defined by Ware and McFarlane (1989).



off the coast of Vancouver Island, Washington, Oregon and California, which is dominated by a unique assemblage of pelagic species (Pacific hake, *Merluccius productus*; Pacific sardine, *Sardinops caerulea*; northern anchovy, *Engraulis mordax*; and Pacific mackerel, *Scomber japonicus*); the coastal downwelling region of the Gulf of Alaska, which supports large domestic groundfish (walleye pollock, *Theragra chalcogramma*, Pacific cod, *Gadus macrocephalus*, Pacific halibut, *Hippoglossus stenolepis*, and sablefish, *Anoplopoma fimbria*) and herring fisheries; and the central subarctic region, which serves as an oceanic pasture for many of the Pacific salmon stocks harvested along the North-east Pacific coast from Alaska to California.

While different studies refer to ecosystem processes in various subsets of these domains, for the most part one can extrapolate findings to the oceanic domain scale. In addition, while a particular biological response can generally be limited to the domain scale, physical forcing often occurs on a much larger spatial scale.

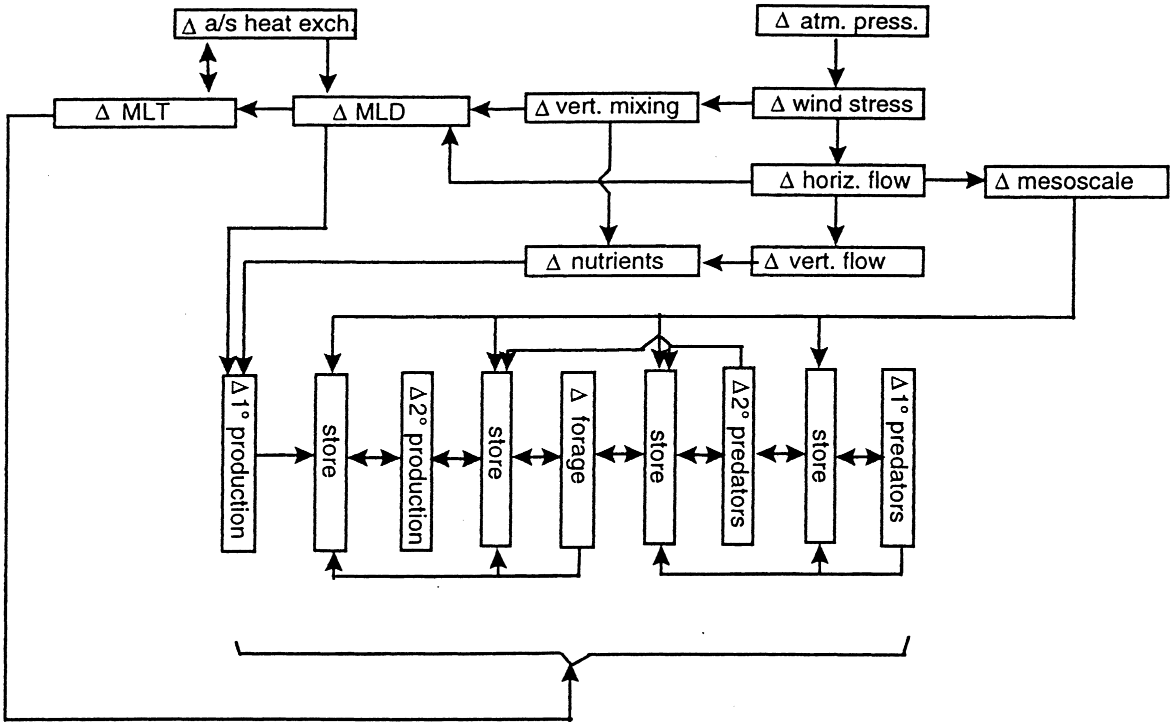
Oceanic ecosystems

The crucial questions in these studies are to identify mechanisms whereby climate variability (the physical forcing) is linked to ecosystem change (the biological response). We have developed a conceptual model (Fig. 2) to illustrate how these physical–biological linkages may manifest themselves, and it is elaborated upon in the following scenario.

1 *The primary forcing function resulting from climate change (ΔC) is a change in surface wind stress which affects horizontal and vertical flow and mixing in the surface layer of the ocean, and the depth of the surface layer. Air–sea heat exchange will also be altered, as will the location and character of oceanic fronts and other mesoscale features.*

A major characteristic of ΔC is the redistribution of atmospheric pressure (Δ*atm. p.)* leading to changes in surface wind stress (Δ*wind stress*) and hence in the wind-driven surface circulation (Δ*horiz. flow*). Surface horizontal currents can change in location and intensity (and sometimes in direction). For example, the frequency of mesoscale physical processes that concentrate or disperse organisms may increase or decrease; these processes include eddies, localized

Figure 2. A model illustrating potential pathways by which effects of climate can be mechanistically transmitted to marine biota. See text for definitions of abbreviations.



upwelling jets, and storm events. Altered location and intensity of surface divergences, convergences, and oceanic fronts respond to altered horizontal and vertical circulation and affect vertical circulation (upwelling). Intensity of surface winds and stability of the surface layer determine vertical mixing and, with changes in air–sea heat exchange (Δ*a/s heat exch.*), the depth of the surface layer. Note that changes in air–sea heat exchange affect both mixed-layer temperature (Δ*MLT*) and depth of the mixed layer (Δ*MLD*), while changes in atmospheric pressure are expressed through their effects on wind stress, which in turn influences ocean circulation and mixing. Within the coastal margins of oceanic ecosystems, precipitation, run-off, and tides also affect vertical mixing.

2 ΔC *leads to changes in primary production, the timing of blooms, mixture of phytoplankton species, and their concentration and larger-scale distributions.*

Primary production is controlled by the supply of nutrients, usually provided from below the surface by upwelling, convective overturn, or vertical mixing. With an adequate supply of nutrients, plankton blooms depend on adequate incoming radiation and a shallow, stable surface layer. The timing and intensity of these processes can be altered by ΔC. The relative abundance of phytoplankton species (e.g. diatoms vs. flagellates) is also affected. The concentration of phytoplankton cells is affected by convergences and the intensity of vertical mixing, and circulation determines the larger-scale distribution. In the trophic ladder component of the model, 'store' boxes have been inserted between levels, because the effects of climate variation may be felt differently by the actual production process and by storage and dispersal of accumulated biomass (by analogy, the difference between the factory and the retail outlet).

3 *These changes are reflected in the secondary production (zooplankton) level and in transfer efficiencies between levels.*

Secondary production is dependent upon primary production, and changes at the primary level will lead to different abundances and distributions of the zooplankton species present. Climatic conditions may favour some types of zooplankton or individual species over others.

4 *Thus before and after a major shift in climate, the upper trophic levels are likely to be supported by substrates that differ in abundance, concentration, and location of key zooplankton and the associated small nektonic species.*

Not only forage species but also larvae and, in some cases, adults of higher levels feed on zooplankton, with several species of copepods and euphausiids being the principal prey. The availability of preferred food will determine the growth and reproduction of species depending on it.

5 *Upper-trophic-level species will be selectively favoured by changed conditions before and after a climate regime shift, so one might expect different total production and species mixture in the two states. In the case of sustained large changes in abundance of certain key species, there should be changes, possibly compensatory, in other components.*

To the extent that the production of a given upper-trophic-level species depends on the availability of desired food in adequate concentrations, different species will be favoured by changes in habitat and feeding conditions before and after a regime shift. Unless there is a major change in underlying productivity, a major increase in one population should be accompanied by decreases in other components of that or neighbouring trophic levels.

6 *Growth and survival of upper trophic levels are affected by* ΔC *primarily through direct effects on the metabolic requirements of larvae and juveniles, the availability of adequate food to satisfy those needs, the local distribution and abundance of predators and competitors, and the availability of suitable habitat for protection from predators.*

Environmental effects on recruitment may work primarily through the availability (in terms both of quantity and of appropriate spatial distribution) of suitable food to larvae and juveniles. Environmental effects may also influence local abundance of predators and competitors of larvae. Changes in the zooplankton base resulting from ΔC should play a major role in determining year-class strength and growth of upper-trophic-level species with some being favoured, others disfavoured by the changed conditions. These differences will subsequently be reflected in the biomass of the adult populations.

7 *In the absence of lags and nonlinearities, the system would be expected to track* ΔC*, especially at the lower trophic levels where replacement time is short. At higher trophic levels, replacement times are longer and differ by species. Thus change at higher trophic levels can be out of phase with that at lower levels, leading eventually to changes in species mixture and dominance and to the possibility of ecosystem regime shifts and of changes in carrying capacity.*

Systems must differ in the extent to which such regime shifts are evident. Whereas clupeoids in coastal ecosystems clearly exhibit regime shifts, the evidence is less clear with groundfish in subarctic oceanic systems. Certainly, populations of upper-trophic-level species vary significantly, and mechanisms must exist for control of their magnitude. The carrying capacity of ecosystems for these species must vary with the supply of appropriate food and with the local abundance of predators and competitors, and all of these interacting components of the ecosystem respond to the bottom-up consequences of ΔC, as described above.

8 *With different mixes of key upper-trophic-level species before and after a regime shift, top-down effects occur, with different pressures on stocks of forage of those predators and their competitors. Such intermediate-level stocks are subject to both top-down and bottom-up effects.*

The changing abundance of upper-trophic-level populations, because of recruitment differences as well as fishing removals, must be felt among populations of their predators, prey, and competitors. Because of specific differences in response to ΔC, as well as the lags and nonlinearities mentioned above, these effects could occur even with no changes in underlying primary and secondary production, and should lead to changes in species mixture in the affected lower trophic levels.

In summary, as illustrated in our model (Fig. 2), the primary effect of physical forcing is on lower trophic levels working its way up through the trophic ladder. In addition, changes in mixed-layer temperature affect rates of processes at all trophic levels, and changes in mesoscale circulation features affect the distribution and availability of prey at all levels. There are also top-down effects, as changes in distribution and abundance of higher levels affect predators, competitors, and prey at other levels. Changes in abundance at higher trophic levels may result from fishing as well as from climatic variation, the latter acting particularly through its impact on recruitment success.

Nothing in the discussion thus far is specific to one or another time scale. However, we will provide evidence that ecosystems in the North-east Pacific respond to decadal and longer time scales of physical forcing. One might expect the bottom-up response to follow the forcing, especially at lower trophic levels. Top-down response, on the other hand, can get out of phase with the forcing because of different rates of response from species to species.

SOME OBSERVATIONS ON THE NE PACIFIC

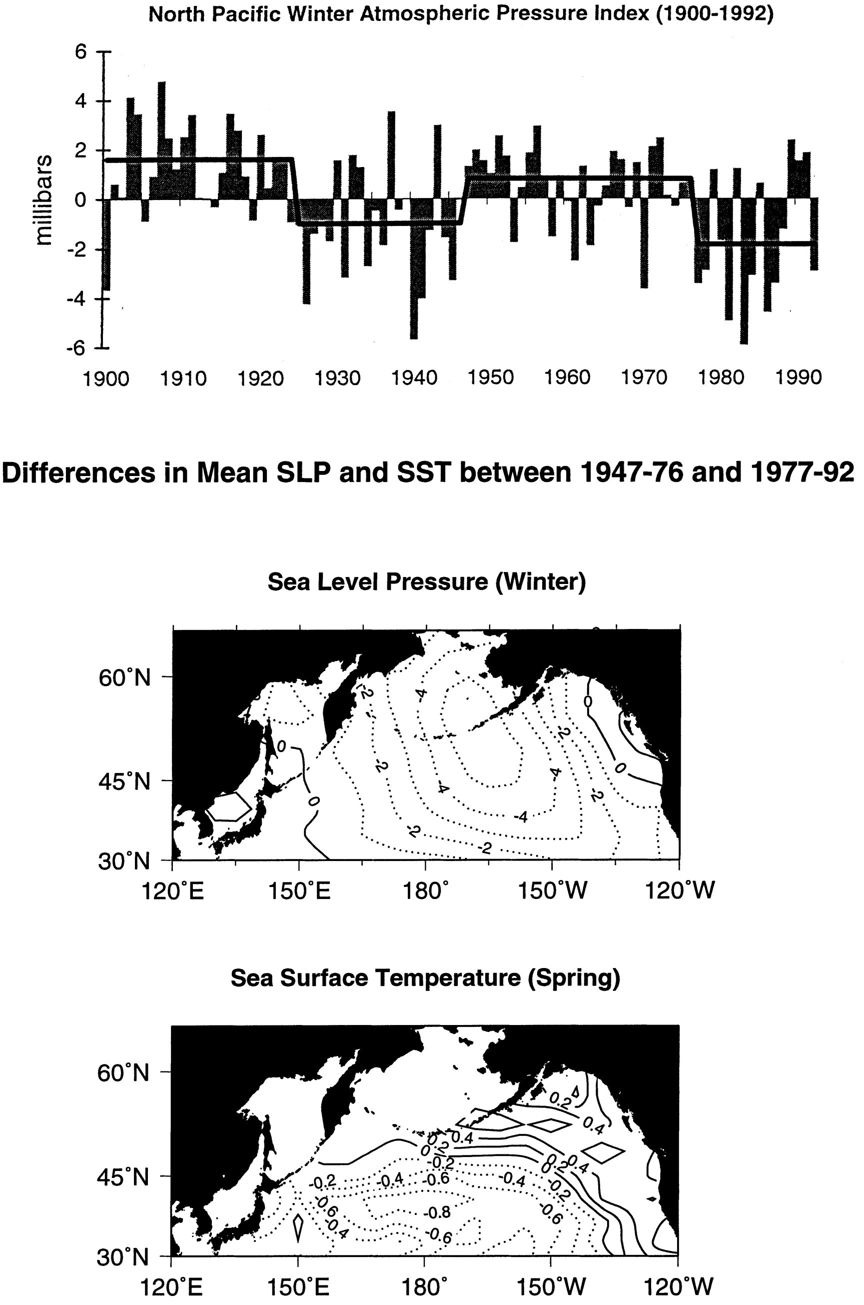
There are many natural frequencies of variability in the NE Pacific and Bering Sea. Those that are most intensively studied by fishery oceanographers occur at the annual and decadal scales, with a focus on biological components of oceanic ecosystems which supply commercial fisheries. Obviously, quantifying seasonal- and annual-scale variability is critical for providing stock assessments to annual fishery management cycles. Studies of seasonal responses of fish populations are critical for examining fine-scale match/mismatch hypotheses concerning larval and juvenile fish and their potential food supplies. However, it is the decadal- (and longer) scale variability that seems to provide more insight into ecosystem processes, and is rapidly becoming the focus of fishery oceanographers in both the North Pacific and North Atlantic. The fundamental question being asked is: does climate effect rather rapid shifts in the organization of marine ecosystems and, if so, on what time and space scales can these effects be measured?

In this section, we report on a number of recent (and a few not-so-recent) studies which, when taken together, begin to give a more coherent view of ecosystem response to decadal-scale climate forcing. Many of these studies focus on oceanic ecosystem responses to the apparent climate regime shift of 1976/77 (Beamish, 1993; Francis and Hare, 1994; Graham, 1994; Miller *et al.*, 1994; Trenberth and Hurrell, 1994), the physics of which are reported in more detail elsewhere. Briefly, during the 1976/77 winter season, the atmosphere–ocean climate system over the North Pacific was observed to shift its basic state abruptly. The Aleutian Low deepened and its centre moved eastward, causing storm tracks to shift southward and increase in intensity. In addition, a fundamental change occurred in the sea surface temperature (SST) pattern in the NE Pacific. Prior to the regime shift, SSTs were anomalously cold along the North American coast and anomalously warm in the central North Pacific. This pattern was reversed after the shift, and appears to have persisted to the present. Figure 3 documents both the atmospheric (SLP, sea level pressure) and oceanic (SST) responses.

Plankton

Recent studies on both phytoplankton and zooplankton dynamics provide much of the evidence for the strong linkage between decadal-scale climate change and the production of fish populations in the large oceanic ecosystems of the NE Pacific. The three major studies reported in this section (Brodeur and Ware, 1992; Polovina *et al.*, 1995; Roemmich and McGowan, 1995) focus on changes in plankton production which occurred in response to the NE Pacific climatic regime shift of 1976/77.

Figure 3. Three indicators of large-scale, long-term climate variability over the North Pacific Ocean in the 20th century. The top panel shows Trenberth and Hurrell's (1994) North Pacific Index and a time series of intervention model fits similar to Francis and Hare (1994). The two bottom panels illustrate atmospheric (mb) and oceanic (°C) effects of the 1976/77 climate regime shift.


North Pacific Winter Atmospheric Pressure Index (1900-1992)

Differences in Mean SLP and SST between 1947-76 and 1977-92

Sea Level Pressure (Winter)

Sea Surface Temperature (Spring)

Venrick *et al.* (1987) show significant shifts in phytoplankton production (integrated chlorophyll *a*) just north of Hawaii at about the time of the 1976/77 regime shift (Fig. 4). Subsequent analysis (Venrick, 1994) reveals that this response was due to increased phytoplankton production in deep (75–200 m) water in response to a shift in ocean mixing and a deepening of the mixed layer. Polovina *et al.* (1995) further support this and report that, associated with the 1976/77 regime shift and intensification of the Aleutian Low Pressure System, was a 30–80% deepening of the winter and spring mixed layer in the Subtropical Do-

Figure 4. Observations of integrated chlorophyll *a* in the central North Pacific. Bars represent 95% confidence intervals based on number of observations (shown above bars). From Venrick *et al.* (1987).

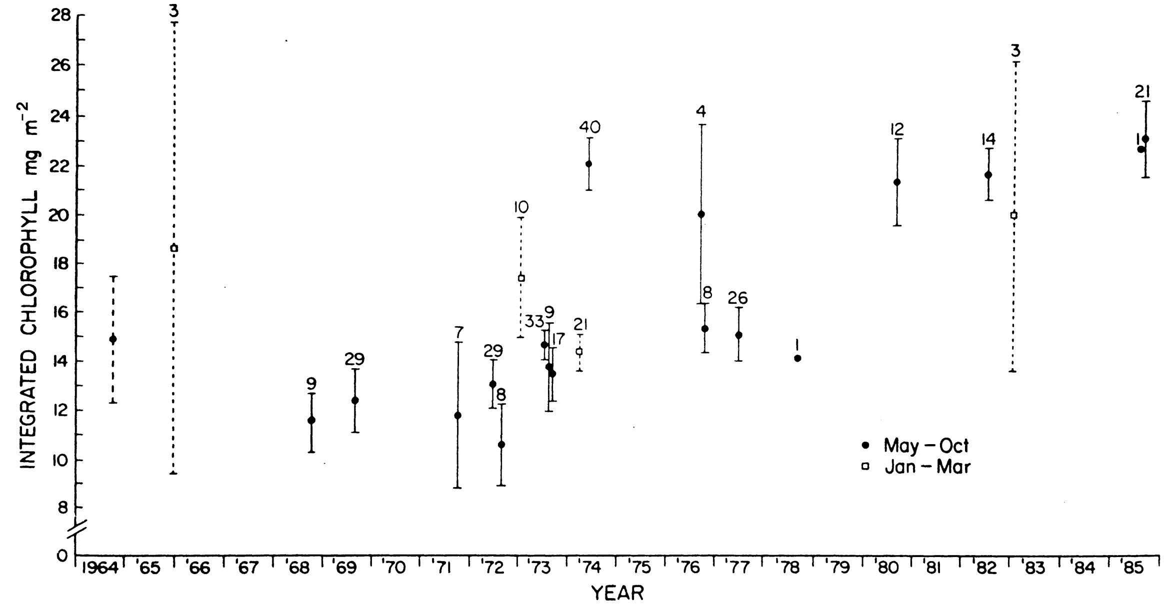
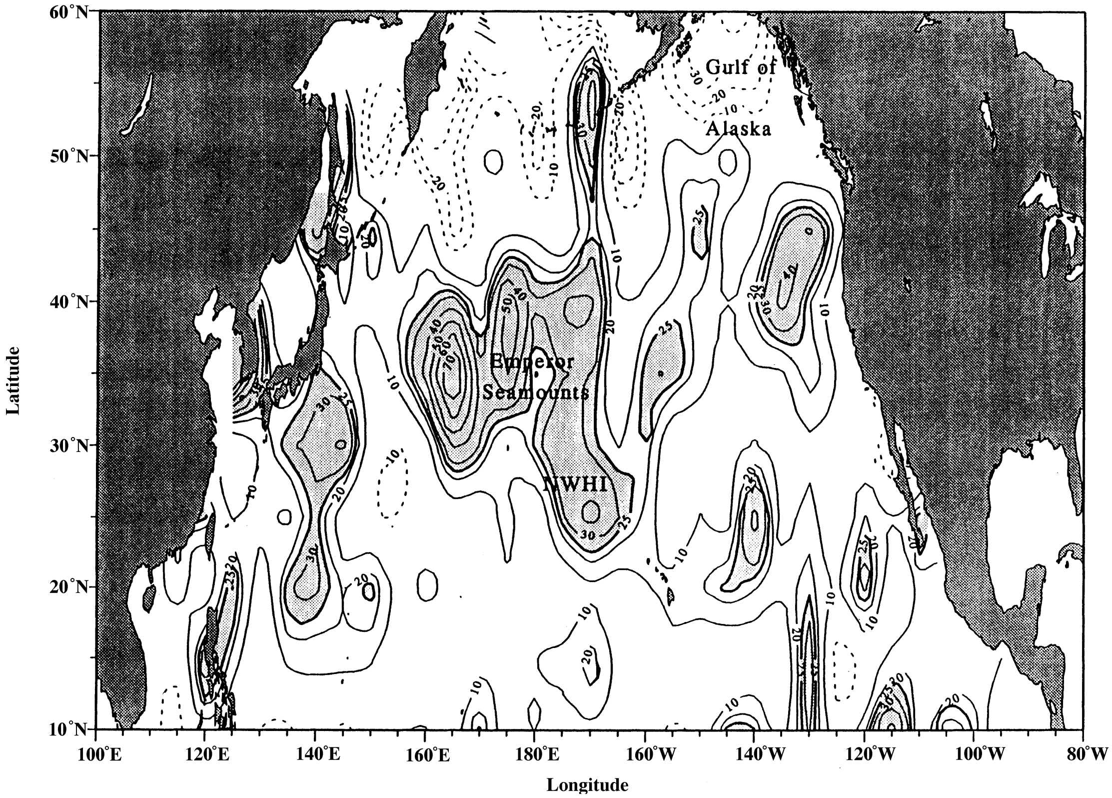


Figure 5. Per cent change in mean winter and spring mixed-layer depth (MLD) between 1977–1988 and 1960–1976, relative to 1960–1976 levels. Shading for 1977–1988 MLD that are more than 25% deeper than 1960–1976 MLD. Dashed contours are negative. From Polovina *et al.* (1995).



main (North-western Hawaiian Islands) and central Transition Zone (Emperor Seamounts) and a 20–30% shoaling of the mixed layer in the northern Subarctic Domain (Gulf of Alaska) (Fig. 5). Based on modelling of phytoplankton response to these changes, they speculate that these physical conditions would increase primary and secondary production in the northern Subtropical and northern (central) Subarctic Domains and decrease them in the Transition Zone. This is primarily due to the fact that at higher latitudes, light tends to be limiting to primary production, whereas at lower latitudes nutrients tend to be limiting.

Brodeur and Ware (1992), Roemmich and McGowan (1995) and Brodeur *et al.* (1996) have been able to show that zooplankton biomasses in the Central Subarctic Domain (central Gulf of Alaska) and Coastal Upwelling Domain (California Current) seem to have responded in opposite directions to the 1976/77 regime shift. In the Central Subarctic Domain, summer zooplankton biomass more than doubled between the late 1950s and the 1980s (Brodeur *et al.*, 1996, Fig. 6). The mechanism proposed to underlie the interpretation of these phenomena involves variation in the circulation of the subarctic gyre in the NE Pacific – a speeding up and slowing down of the Subarctic and Alaska Currents. This would affect both Ekman pumping at the centre of the gyre, leading to increased upwelling and divergence in the centre, and advection (transport of nutrients, phytoplankton, zooplankton) around the circumference of the gyre. Associated with this would be a shoaling of the euphotic zone (MLD) and a resultant increase in the exposure of phytoplankton cells to light.

On the other hand, in the southern Coastal Upwelling Domain the biomass of macrozooplankton has decreased by as much as 70% between the early 1950s and the early 1990s (Roemmich and McGowan, 1995, Fig. 7). The authors provide several mechanistic hypotheses for their observations. First, they suggest that the coastal warming associated with the 1976/77 regime shift may have caused increased stratification in the California Current, a sharper thermocline with less vertical displacement of nutrient-rich waters due to wind stress (coastal upwelling), and a resultant decrease in the fraction of the year when wind stress is strong enough to lift nutrient-bearing waters to the sea surface near the coast. Second, they speculate that a climate-induced shift in ocean circulation, such as the bifurcation of the West Wind Drift (Subarctic Current), might import warmer water into the California Current, thus decreasing the supply of either nutrients and/or the volume of zooplankton carried by the California Current.

Both of these findings are consistent with the earlier results of Wickett (1967), who studied the interannual variation in zooplankton volumes off California, in the western Bering Sea, and at Ocean Station P (50°N, 145°W) in the central Gulf of Alaska during the 1950s and early 1960s. By studying the relative abundances of zooplankton in these regions and relating them to zonal and meridional components of surface winds in a region upstream of the bifurcation of the Subarctic Current, he found that a major cause of zooplankton variation downstream of the division point (bifurcation of the Subarctic Current into the California and Alaska Currents) is the change in the proportion of surface-layer, wind-driven water (Ekman transport) that is swept southward (escaping) out of the subarctic circulation. The implication is that zooplankton and nutrients are carried with the surface waters and that forcing conditions (surface winds) which favour a high 'escapement' of subarctic water into the California Current will increase zooplankton production in that region and decrease it in the region of the Alaska Current.

Finally, McFarlane and Beamish (1992) identify a significant relationship between larval marine fish survival (sablefish off the British Columbia coast), zooplankton (copepod) abundance, and climate conditions (Aleutian Low intensity) for the years 1965–80. In particular, they suggest that larval sablefish survival improves when there is an abundant supply of copepod eggs and nauplii which are associated with a combination of strong winter Aleutian lows and warm sea surface temperatures in coastal waters. These effects seem to be particularly pronounced at the time of an abrupt change from cold to warm coastal ocean surface temperatures such as occurred in the 1976/77 regime shift.

In summary, three things are quite clear from these studies.

1 Both phytoplankton and zooplankton changed in response to a fundamental reorganization of the upper ocean of the NE Pacific in response to the 1976/77 climate regime shift.

2 The nature of the response was not the same in different production domains of the NE Pacific. In particular, zooplankton biomass in the coastal upwelling domain (California Current) and central subarctic domain (offshore Gulf of Alaska) appeared to respond in opposite directions to the abrupt changes in climatic forcing.

3 The role of changes in horizontal transport and its effects on primary and secondary production is very difficult to assess. The relative importance of horizontal advection and vertical transport (Ekman pum-

Figure 6. Large-scale distribution of zooplankton biomass from sampling during the six-week period beginning 1 June for the period 1956–1962 (top) and 1980–1989 (bottom) (Brodeur *et al.*, 1996).

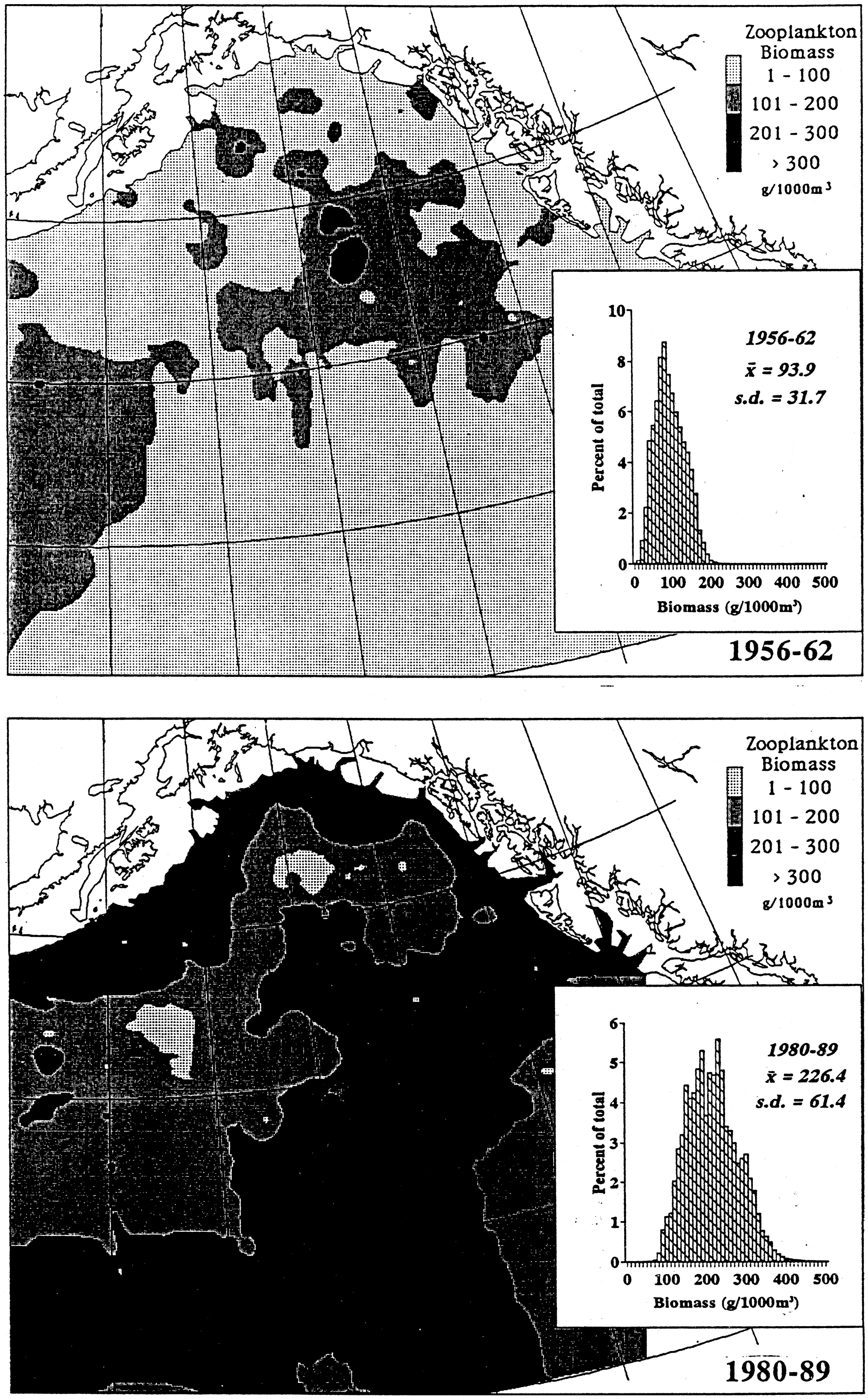
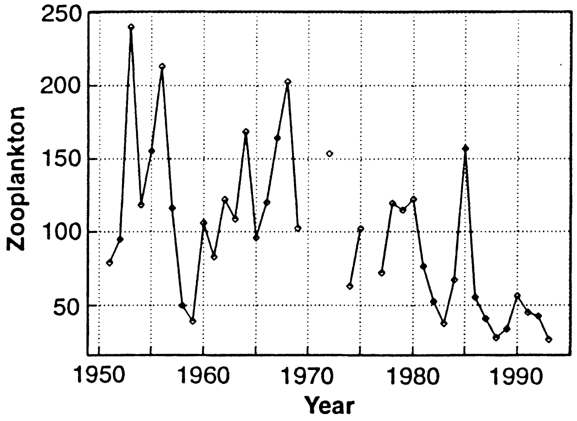


Figure 7. Time series of average annual zooplankton volume (cm^3 per 1000 m^3) along CalCOFI line 90 (located off Southern California). From Roemmich and McGowan (1995).



ping, coastal upwelling) perhaps relates to the relative importance of the production and storage (delivery) boxes for each trophic level as well as the Δ mesoscale box in the diagram at the bottom of Fig. 2.

Fish

Hollowed and Wooster (1992) studied the relationships between winter atmosphere/ocean conditions and strong year classes of NE Pacific groundfish. To do so, they first postulated two mean states of winter atmospheric circulation in the North Pacific – termed Type A and Type B (Fig. 8 – top panels)[1]. These states are identified by the frequency of intense winter 'Aleutian Low Pressure' events and their resultant surface ocean temperature and wind field responses (Type B warm eras are characterized by more intense winter Aleutian lows, warmer than average coastal SSTs, enhanced south-westerly winter winds in the NE Pacific with increased advection into the Alaska Current). They then characterized the period between 1932 and 1988 into an alternating sequence of cool and warm eras, each era ranging in length between 6 and 12 years. They have since extended this series back to the turn of the century (Fig. 8 – bottom panel). They point out that the three most recent warm eras appear to have been initiated by specific El Niño events, suggesting that the timing of the observed decadal pattern of variation in the North-east Pacific might be governed by teleconnections with the Southern Oscillation (Wooster and Hollowed, 1995). Then, between 1950 and 1984, Hollowed and Wooster (1992, 1995) were able to show a linkage between the timing of cool and warm eras and years of simultaneous strong year classes in 15 groundfish stocks ranging from California to the Bering Sea (1961, 1970, 1977 and 1984) (Fig. 9). Interestingly, each of these years occurred during a warm era when Type B circulation prevailed and three of the four years were associated with El Niño events. Hollowed and Wooster (1995) make the point that the relationships between climate forcing and marine biological response at higher trophic levels are not as clear as those at lower trophic levels. They speculate that ocean conditions associated with warm temperature may be a necessary but not sufficient condition for strong year classes in NE Pacific marine fishes. And in that strong year classes tend to occur infrequently, their findings suggest that in iteroparous species with moderate life spans, changes in stock abundance associated with decadal-scale climate variability may be associated with the 'storage effect' of a few exceptionally strong year classes (Chesson, 1984).

Beamish and Bouillon (1993) demonstrate that smoothed trends in North Pacific salmon production from 1925 to 1989 were not primarily anthropogenic in basis but, rather, were strongly linked to the marine environment, and in particular to similarly smoothed trends in the winter Aleutian Low. Hare and Francis (1995) and Francis and Hare (1994) have used the methods of time series analysis to attempt to understand the spatial and temporal dimensions of the relationship between NE Pacific salmon production and atmosphere/ocean physics. They have been able to show that there are very significant and coherent linkages between relatively sudden interdecadal shifts in the North Pacific atmosphere (Fig. 3) and ocean physics and marine biological responses as evidenced by indices of Alaska salmon production (Fig. 10). Three points which stand out from these analyses are:

- Coherence between physical and biological variables appears to predominate at the decadal (regime) scale and not the annual scale.
- Salmon appear to be affected by climate early in their marine life history.
- During the 20th century, there appear to have been four interdecadal regimes (Fig. 3 – top) in the North Pacific coupled atmosphere/ocean system:

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[1] The observation of Roemmich and McGowan (1995) that there was no change in net transport off southern California between the eras of 1951-57 and 1987-93 appears to contradict this conceptual model: the explanation, which requires further investigation, may lie in the different scales involved.

Figure 8. Two alternating patterns of atmospheric circulation postulated by Hollowed and Wooster (1992). An example winter sea-level pressure pattern is illustrated for each circulation type (reproduced from Emery and Hamilton, 1985). The bottom time series is Hollowed and Wooster's classification of cool (Type A) and warm (Type B) eras superimposed on Trenberth and Hurrell's (1994) North Pacific Index. See also footnote 1.

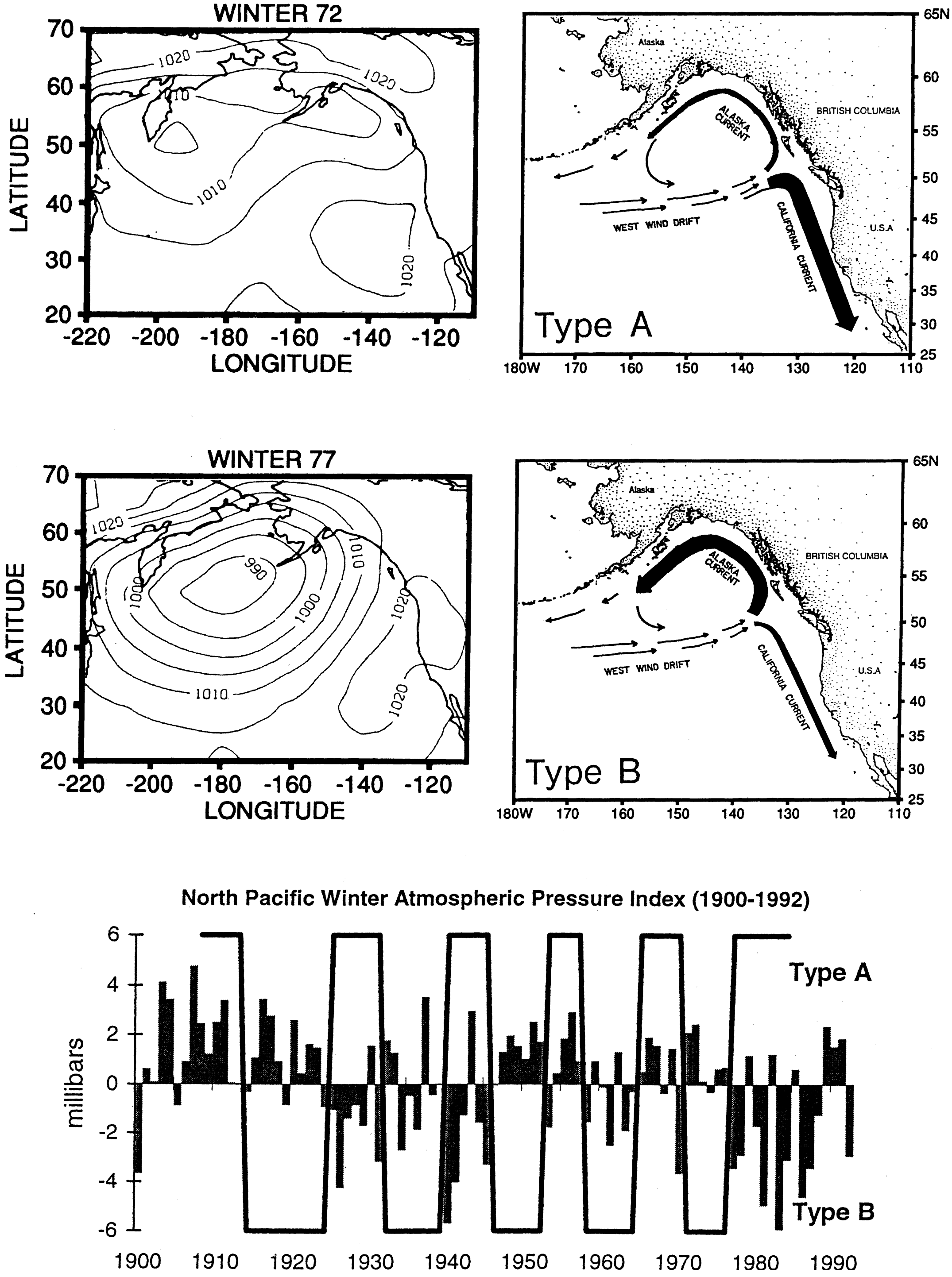
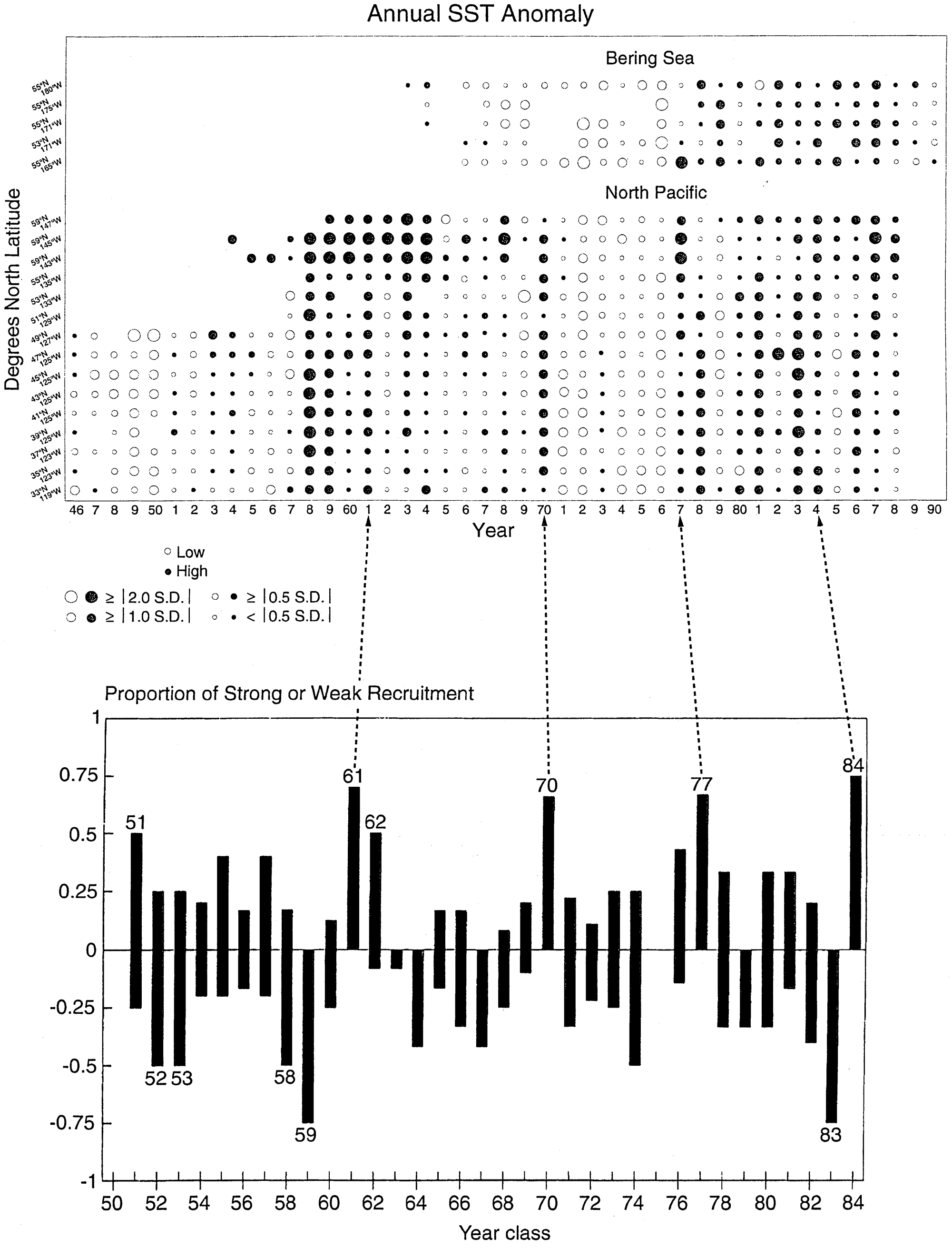


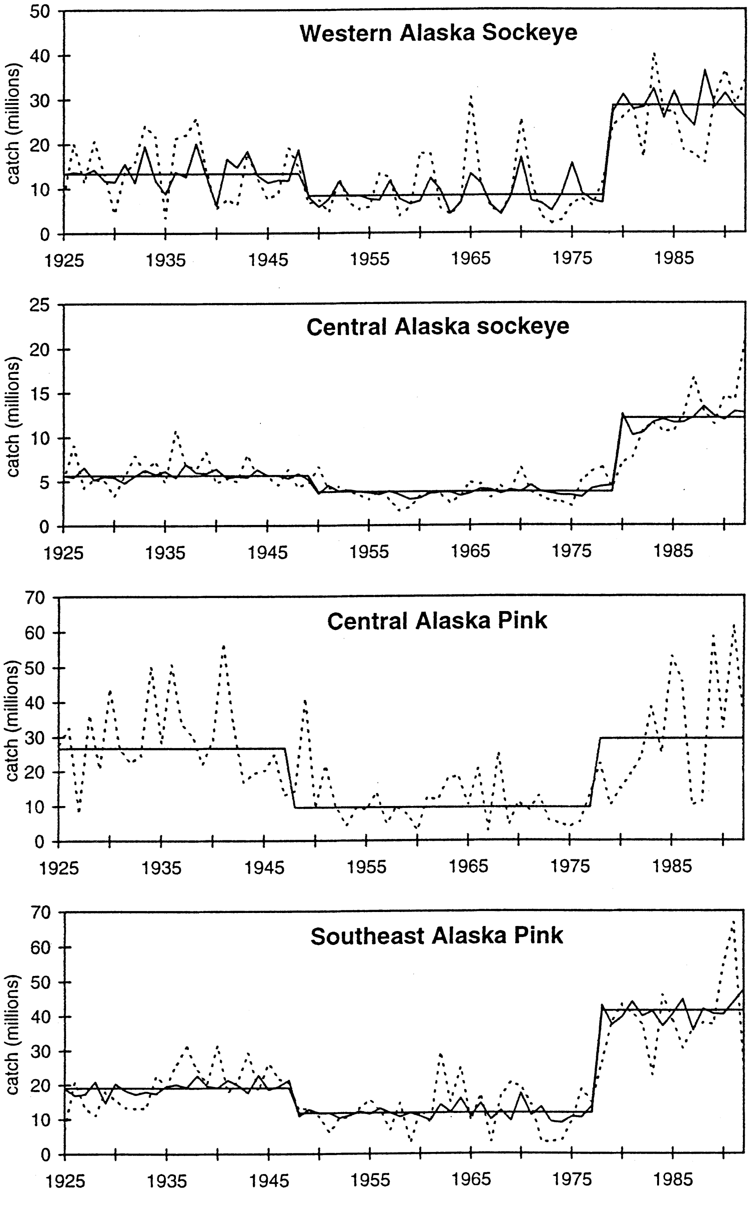
Figure 9. Pattern of sea surface temperature anomalies along the west coast of North America (upper panel) and subsequent year-class strength of North-east Pacific groundfish stocks (lower panel). From Hollowed and Wooster (1992).



1900–1924, 1925–1946, 1947–1976, 1977–present. The lower two panels of Fig. 3 show differences in mean winter sea level pressure and spring sea surface temperature between the two most recent regimes.

In several recent studies (Hare, 1996; Zhang, 1996; Mantua *et al.*, 1997), the climatic variability described above was named the Pacific Decadal Oscillation (PDO) and was shown to affect sea surface and land temperatures, sea level pressure and streamflow from Alaska to California. Further, the PDO was shown to be essentially independent of the ENSO (El Niño–Southern Oscillation) phenomenon. It is of considerable interest that NE Pacific groundfish populations appear to follow the Hollowed and Wooster (1992)

Figure 10. Time history of catches (dashed lines), intervention model fits (thin solid lines), and estimated interventions (thick solid lines) for the four major Alaska regional salmon stocks. From Hare and Francis (1995).



cold/warm era scale of variability while NE Pacific salmon population fluctuations mimic the PDO regime-scale variability.

Finally, in an earlier paper, Francis and Sibley (1991) noted an apparent opposite decadal-scale response in salmon production between the California and Alaska Current domains. This corresponds to similar spatial responses in ocean physics (Chelton and Davis, 1982) and zooplankton production reported above. Hare *et al.* (unpublished data) have recently advanced this model for salmon, showing that over the historical instrumental record, the prevailing coastal ocean conditions in Alaska and along the Pacific North-west coast are inversely favourable to salmon production. For the past 20 years, conditions have been favourable for Alaskan salmon and unfavourable for Pacific North-west salmon. They point out that a significant shift in zooplankton biomass as well as its distribution around the Subarctic Gyre has provided favourable feeding conditions for migrant salmon smolts during a highly critical stage in their life history. Conversely, the dramatic decrease in zooplankton biomass off the Pacific North-west coast due to stratification of California Current waters and loss of advective products from the West Wind Drift presents a relatively barren oceanic environment for Pacific North-west smolts. A conceptual extension to this model has recently been advanced by Gargett (1997). The key notion is the possible existence of an 'optimum window' for coastal water column stability, driven by large-scale fluctuations in Pacific basin climate, which affect both light levels and nutrient supply for phytoplankton growth. Assuming that the physical stability of the entire coastal NE Pacific varies 'in phase' in response to decadal-scale variation in the Aleutian Low/PDO process, she hypothesizes that northern (Gulf of Alaska/Bering Sea) and southern (California Current) phytoplankton populations occupy opposite ends of this 'window'. Because those in the Gulf of Alaska are light limited whereas those in the California Current are nutrient limited, this produces variations in primary (and secondary) production in the two regions which are out of phase.

Beamish (1993) focused on the 1976/77 regime shift and its effects on marine fish (both salmonid and nonsalmonid species) production in the NE Pacific and Eastern Bering Sea. He documents that the period 1976–78 was a time of exceptional productivity for fishes found off the Pacific coast of Canada and the US, ranging from the Bering Sea to the coast of California. He relates this marine biological response to changes in primary and secondary production in response to climate-induced changes in upper ocean heat storage and resultant changes in the depth of the euphotic zone over vast regions of the NE Pacific. Along the same lines, Bakkala (1993), NPFMC (1993) and Alton *et al.* (1988) provide tantalizing indications that the flatfish complex of the E. Bering Sea may have significantly changed in both its composition and its spatial distribution at the time of the 1976/77 regime shift. In essence, they report that the biomasses of five of the six major flatfish species of the region increased significantly in the late 1970s and early 1980s. The only species that did not increase was Greenland turbot, *Reinhardtius hippoglossoides*, the one species that seems to prefer colder ocean regimes (an amphiboreal species – Alton *et al.*, 1988). The top panel of Fig. 11 shows recruitment estimates for Greenland turbot from 1970 to 1993 (NPFMC, 1993). Recruitment decreased significantly at the time of the climate regime shift in the late 1970s. What is perhaps more interesting is how the distribution of (primarily) juvenile Greenland turbot seems to have been pushed to the north-west along the outer Bering Sea shelf as the ocean climate warmed in the late 1970s and early 1980s (Fig. 11 – bottom panel).

Baumgartner *et al.* (1992) have analysed natural frequencies in climate-driven fish populations of the NE Pacific over a much longer time frame. Through the analysis of fish scale deposition rates in anaerobic sediments in the Santa Barbara Basin off southern California, they have been able to develop a 1750-year time series proxy of pelagic fish abundance in the California Current (Fig. 12 – top panel for Pacific sardine and northern anchovy). They have partitioned this variability into low frequency (>150 years) and high frequency (<150 years). The low-frequency variability reflects the centenary-scale climate epochs of the last 2000 years (e.g. Medieval Warm Period, Little Ice Age) and relates very closely to bristlecone pine tree ring widths, which reflect prevailing atmospheric temperature regimes (Fig. 12 – bottom right panel). The high-frequency power spectra for both sardine and anchovies show peaks at around 60 and 75 years (Fig. 12 – lower left panel). During the 20th century, the pelagic fish populations of the California Current have tended to vary in response to atmospheric forcing regimes similar to Alaskan salmon populations (Ware and Thomson, 1991). This being the case, one might speculate that the kind of decadal-scale atmospheric forcing in the North Pacific that we have seen during the 20th century has probably persisted for centuries.

In summary, perhaps the most important point to be revealed by these studies which focus on climate and marine fish is that there clearly is a hierarchy of natural frequencies in the coupled atmosphere/ocean to which fish populations and oceanic ecosystems are responding (Ware, 1995). Hollowed and Wooster's (1992) warm–cool eras (approx 20-year period) are similar to Royer's (1993) low-frequency ocean temperature signal (related to the 18.6 year nodal tidal cycle) as well as Latif and Barnett's (1994) 20 year (approx.) oscillation in the SST of the North Pacific forced by extra-tropical ocean–atmosphere interactions. Interestingly, Ware (1995) points out that the onset and duration of these warm and cool periods along the west coast of North America may vary with latitude (shorter to the south). Likewise, the Francis and Hare (1994) and Mantua *et al.* (1997) interdecadal climate regimes appear to be similar to Baumgartner *et al.*'s (1992) strong 60 year peak in the power spectrum of the 1750-year anchovy and sardine abundance time series from the California Current. The tantalizing similarities are not definitive, but are difficult to ignore.

Figure 11. Two indices of E. Bering Sea Greenland turbot, *Reinhardtius hippoglossoides*, production. The upper panel shows annual estimates of recruitment under three different population dynamics models (reproduced from NPFMC, 1993). The lower panel shows the estimated density distribution of Greenland turbot during National Marine Fisheries Service summer bottom trawl surveys in 1979, 1982, 1985 and 1986. From Alton *et al.* (1988).

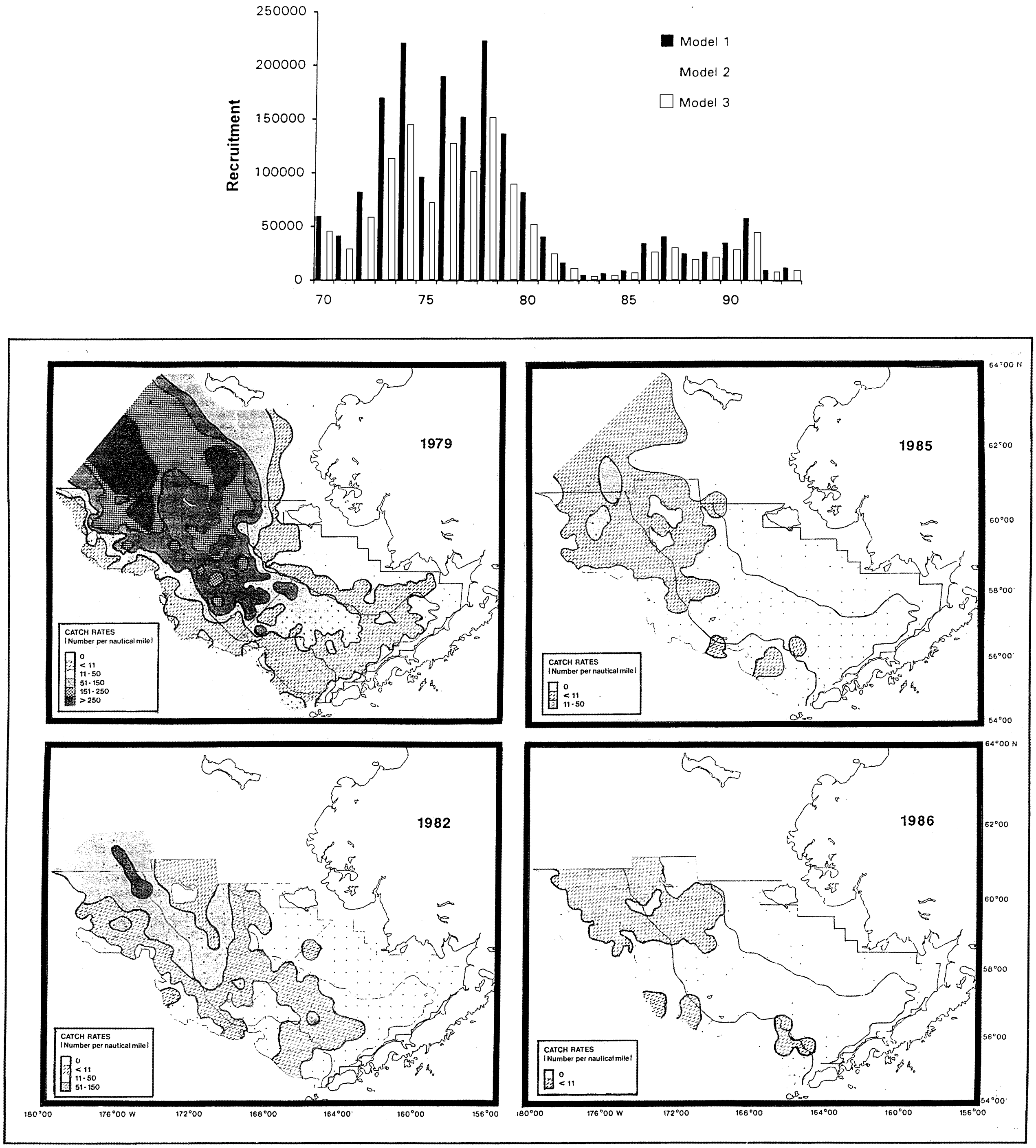
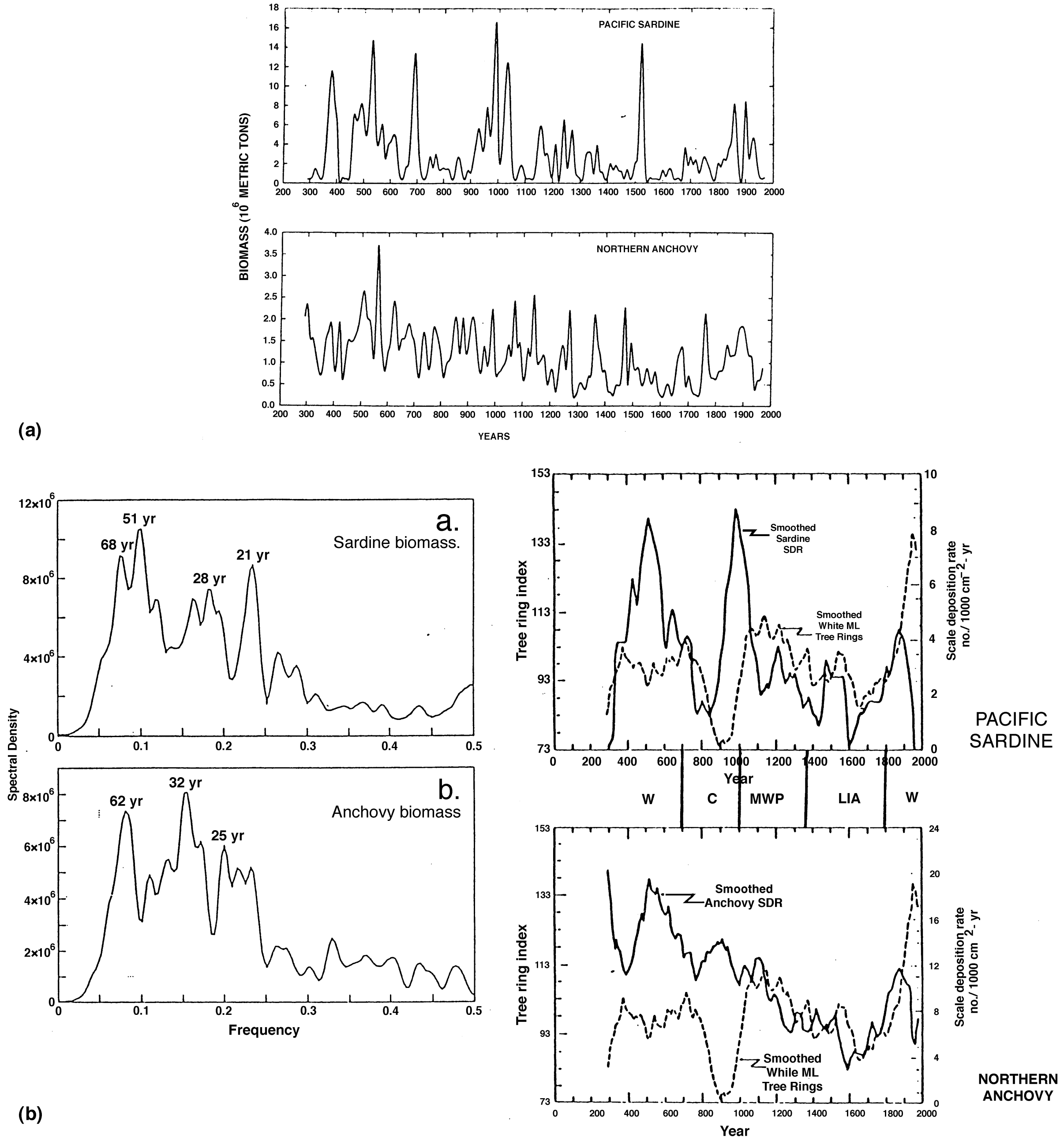


Figure 12. Proxy time series of pelagic fish abundance in the California Current (top), power spectra for high-frequency (< 150 year) variability (lower left), and low-frequency (> 150 year) variability compared with White Mountain (California) bristlecone pine tree ring widths (lower right). From Baumgartner *et al.* (1992) and T. Baumgartner (personal commun.). Warm = W, C, cold; MWP, Medieval warm period; LIA, Little ice age.



Marine birds and mammals

Declines in the populations of some pinnipeds (Steller sea lions, fur and harbour seals) and sea birds have been observed during the last few decades in the Bering Sea and Gulf of Alaska, with numbers of Steller sea lions so depressed that the species was listed as threatened under the Endangered Species Act in spring 1990. Excellent reviews of the nature of these declines are given by Springer (1992) and Alaska Sea Grant (1993).

Studies of top trophic level responses to climate change are often difficult to interpret because natural responses could be masked by anthropogenic influences on marine populations. For example, the commercial harvest of subadult male northern fur seals (*Callorhinus ursinus*) in the Pribilof Islands (Bering Sea) clearly altered natural trends in population dynamics over time. Since the cessation of harvest in 1984, the population of male fur seals increased rapidly and did not stabilize until about 1993. In addition, commercial harvest of potential fur seal prey such as walleye pollock affect both prey distribution and abundance.

Direct and indirect impacts of climate on the survival of marine birds and mammals are expected but difficult to discern. Changes in mixed-layer temperature could directly influence metabolic rates of marine mammals (York, 1995). However, it is the indirect responses of top-trophic-level species to climate-driven changes at lower trophic levels that are the most likely significant impacts of decadal-scale climate variability. These indirect effects could result from at least one of three principal processes: changes in prey availability, changes in prey abundance and changes in the mix of available prey. Examples of these three indirect processes are found in studies of seabird and marine mammal populations before and after the regime shift of 1976/77.

1 *Prey availability*

The abundance and/or distribution of prey affected by the 1976/77 regime shift appears to have influenced seabird populations off the coast of central California. Dr David Ainley (H.T. Harvey and Associates, Alviso, CA, personal commun.) connected top-level predator population dynamics to climatic effects on California Current (Farallone Islands) zooplankton reported earlier (Roemmich and McGowan, 1995). He reports that since the late 1970s, the proportion of the coastal euphausiid, *Thysanoessa spinifera* (a key species in the coastal food web whose production is related to the intensity of coastal upwelling), in the diet of Cassin's auklet (*Ptychoramphus aleuticus*) at the Farallones has declined and the proportion of the oceanic euphausiid, *T. pacifica*, has increased. At the same time, the auklet population has decreased by as much as 50%. Variation in the availability of *T. spinifera* is likely linked to the timing of the spring transition and onset of coastal upwelling and, in turn, the auklet's reproductive phenology (Ainley and Boekelheide, 1990). Ainley (personal commun.) concludes that

> … the auklet breeds successfully in years when *T. spinifera* is available in great quantity near to the surface, and poorly or not at all when the euphausiid is not available, as during ENSO and warming events forced by anomalies in the Aleutian Low Pressure system.

2 *Prey abundance*

Hunt *et al.* (1996) examined the hypothesis that changes in the diets of four species of sea birds in the vicinity of the Pribilof Islands (black-legged kittiwakes, red-legged kittiwakes, common murres and thick-billed murres) between the 1970s and 1980s were linked to changes in the distribution of age-1 walleye pollock. They observed that the proportion of age-1 pollock in seabird diets decreased over this time period and that, during the same period, the proportion of age-1 pollock in the National Marine Fisheries Service summer bottom trawl survey decreased as well in the vicinity of the Pribilofs. Because this decrease in juvenile pollock was observed in the diets of both surface-feeding and subsurface-feeding sea birds, they concluded that the change resulted from a change in the horizontal distribution of juvenile pollock in the vicinity of the Pribilofs.

3 *Species mixture of available prey*

A recent paper by Piatt and Anderson (1995) examines possible relationships between significant declines in top predators (marine birds and mammals) in the northern Gulf of Alaska during the past 20 years and a climate-induced shift in the structure of forage components of the oceanic ecosystem upon which these species depend. The initial intent of Piatt and Anderson's research was to determine the effect of the 1989 *Exxon Valdez* oil spill on population dynamics of seabird populations in the Gulf of Alaska. The estimated changes in population size of common murre colonies in the Gulf of Alaska before and after the *Exxon Valdez* oil spill are illustrated in

Figure 13. Per cent change in common murre populations before and after *Exxon Valdez* oil spill. From Piatt and Anderson (1995).

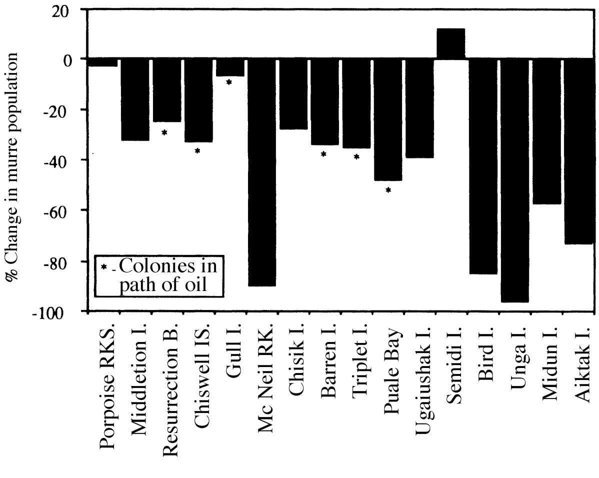


Figure 14. Trends in numbers of piscivorous birds and marine mammals in the Bering Sea and Gulf of Alaska. From data summarized by Springer (1992).

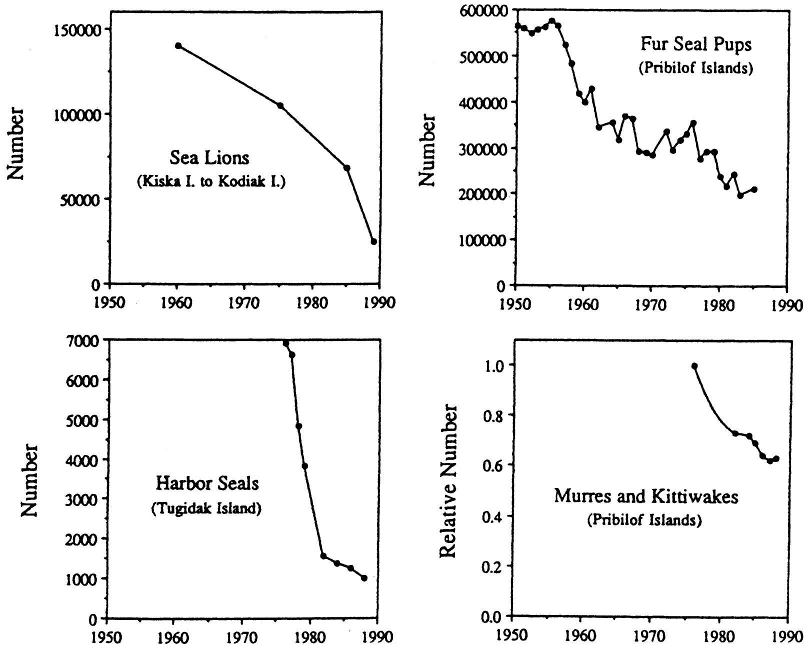
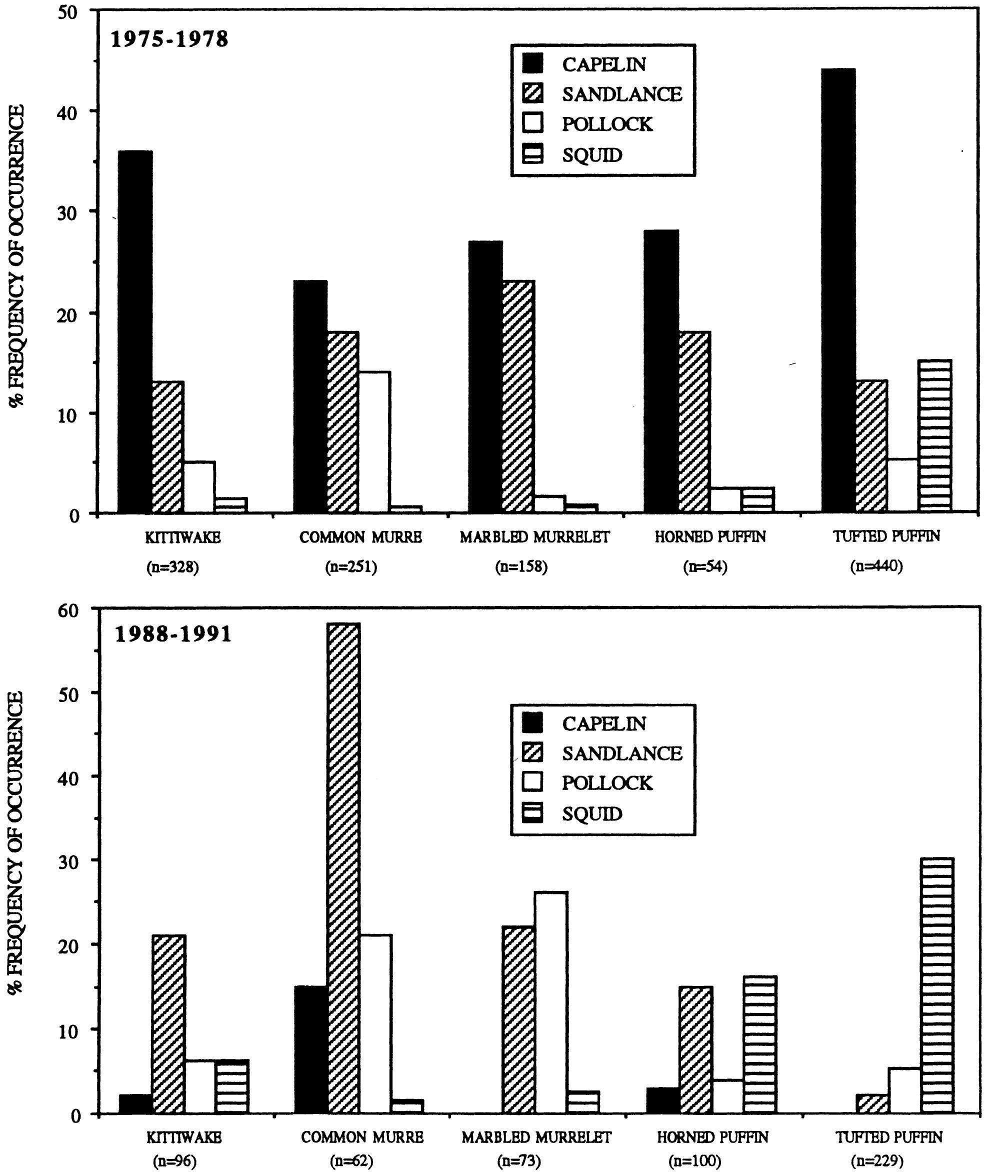


Fig. 13. The starred values are those colonies that would have been in the path of the spill. It is clear that the most significant declines occurred in colonies not in the path of the spill. In addition, most of the prespill censuses were taken as part of the US Department of Interior Outer Continental Shelf Environmental Assessment Program (OCSEAP) of the mid and late 1970s. And so what is apparent here is that significant declines in common murre populations occurred between the mid-to-late 1970s and the early 1990s. Combining this with recent declines in numbers of piscivorous marine birds of the Bering Sea (Pribilof Islands) and marine mammals of the Bering Sea and Gulf of Alaska (Springer, 1992; Fig. 14), it is clear that these could be related to fundamental reorganizations of these large oceanic ecosystems in response to the climate regime shift of the late 1970s. Piatt and Anderson (1995) give a clue as to how this might have occurred. They demonstrated that a significant change occurred in the diet composition of five seabird species collected in the Gulf of Alaska between 1975–1978 and 1988–1991 (Fig. 15). Clearly there was a fundamental shift in diet, from one dominated by capelin in the late 1970s to one where capelin was virtually absent in the late 1980s. Catch-per-unit-effort of capelin in midwater shrimp trawls along the Alaska Peninsula (Gulf of Alaska) between 1972 and 1992 is illustrated in Fig. 16. Clearly, capelin virtually disappeared from these surveys in the late 1970s, similar to the findings of Hunt *et al.* (1996) for the Eastern Bering Sea.

In a similar study, Merrick and Calkins (1994) examined the prey of Steller sea lions during 1975–78 and 1985–86. They showed that walleye pollock were the most common prey in sea lion diets in virtually all seasons and areas of the Gulf of Alaska before and after the 1976/77 regime shift. In addition, there was an increase from the 1970s to the 1980s in the proportion of animals sampled that consumed pollock, despite a decrease in the abundance of juvenile pollock. Most interesting was their observation of a simultaneous decline in the abundance of alternative prey (forage species such as capelin and sand lance), suggesting that the change in the mixture and diversity of available prey species may have been a significant contributor to the overall decline in sea lion populations.

These papers provide evidence that the climate regime shift of the late 1970s could have brought about a restructuring of the oceanic ecosystems of the Gulf of Alaska and E. Bering Sea such that either the abundance or availability of forage fish declined to the point where juvenile sea birds and marine mammals were significantly affected. These (and other) observations have led Dr Scott Hatch (National Biological Service, Anchorage, AK, personal commun.) to put

Figure 15. Change in diet composition of five Gulf of Alaska seabird populations. From Piatt and Anderson (1995).



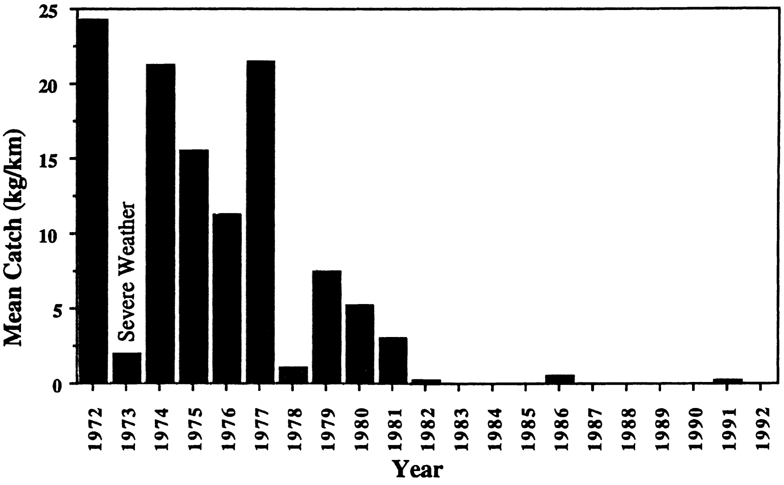
forward the following ecosystem-level hypothesis to explain recent trends in Alaska region marine birds and mammals:

> The principal factor responsible for unfavourable trends in marine birds and pinnipeds in the Gulf of Alaska is availability of suitable food resources. Food limitation, in turn, may be caused by recent climatically driven ecosystem shifts favouring increased production of pelagic and demersal predatory fish (e.g. adult pollock, cod, salmon, and various flatfishes, especially arrowtooth flounder and halibut) at the expense of forage species (capelin, sand lance, juvenile pollock, herring, and myctophids) on which marine bird and mammal species depend.

CONCLUSIONS

It has been argued that understanding biological patterns and how they change across measurement scales is the fundamental conceptual problem in ecology (Levin, 1992). This generalization surely holds true for climatic variability and its analysis as well. It is axiomatic that climate variability occurs across all temporal and spatial scales. This is not to say, however, that all scales are equally interesting or important.

Figure 16. Trends in catch-per-unit-effort of capelin in midwater shrimp trawls in Pavlof Bay, Alaska Peninsula, from 1972 to 1992. From Piatt and Anderson (1995).



Temporally, there has been a growing recognition of the special importance in climatic variability of the scale of decades to centuries (Stockton, 1990). This perceived importance reflects both effects for mankind and the accumulation of observations on decadal-long trends. Our intent in this review was to demonstrate the importance of decadal-scale climatic variability on biological production along the entire food chain, i.e. its effects on ecosystems. From this review, several general conclusions can be drawn.

1 There are large-scale, low-frequency, and sometimes very rapid changes in the distribution of atmospheric pressure over the North Pacific Ocean which are, in turn, reflected in ocean properties (e.g. MLT and MLD) and circulation. Of particular importance are changes on decadal and longer time scales.

2 Oceanic ecosystems respond on similar time and space scales to variations in physical conditions. The limited evidence available for the NE Pacific suggests that responses occur at all trophic levels and are most rapid at lower trophic levels.

3 Linkages between the atmosphere/ocean physics and biological responses are often different at different time and space scales. Even at the decadal scale, it is becoming clear that there may be more than one important natural climate frequency in the NE Pacific by which the large oceanic ecosystems are driven. In addition, there are indications that a number of these biological responses are different in different regions of the NE Pacific (e.g. opposite responses of both zooplankton and salmon production to climate forcing in the California and Alaska Current regions).

4 Although the principal effect of climatic variation appears to be at lower trophic levels (bottom-up effect), there is ample reason to believe that significant top-down effects also occur. The hypothesized relation in the Gulf of Alaska, referred to in the previous section, linking climate to increases in predatory fishes, subsequent decreases in forage fishes and resultant declines in top-level bird and mammal populations, is a case in point.

5 While the cases presented here demonstrate oceanic ecosystem response to climatic forcing, they provide only hints of the mechanisms of interaction. Elaboration of those mechanisms should be the target of research.

6 A model whereby ecosystem response to specified climate variation can be successfully predicted will be difficult to achieve because of scale mismatches and nonlinearities in the atmosphere–ocean–biosphere system. In fact, these systems may be inherently unpredictable in a strict sense. Even with an appropriate model, greatly enhanced monitoring of physical forcing and ecosystem response will be required to provide the data necessary for useful operational predictions.

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