



Climate controls on marine ecosystems and fish populations

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ABSTRACT

This paper discusses large-scale climate variability for several marine ecosystems and suggests types of ecosystem responses to climate change. Our analysis of observations and model results for the Pacific and Atlantic Oceans concludes that most climate variability is accounted for by the combination of intermittent 1–2 year duration events, e.g. the cumulative effect of monthly weather anomalies or the more organized El Niño/La Niña, plus broad-band “red noise” intrinsic variability operating at decadal and longer timescales. While ocean processes such as heat storage and lags due to ocean circulation provide some multi-year memory to the climate system, basic understanding of the mechanisms resulting in observed large decadal variability is lacking and forces the adoption of a “stochastic or red noise” conceptual model of low frequency variability at the present time. Thus we conclude that decadal events with rapid shifts and major departures from climatic means will occur, but their timing cannot be forecast. The responses to climate by biological systems are diverse in character because intervening processes introduce a variety of amplifications, time lags, feedbacks, and non-linearities. Decadal ecosystem variability can involve a variety of climate to ecosystem transfer functions. These can be expected to convert red noise of the physical system to redder (lower frequency) noise of the biological response, but can also convert climatic red noise to more abrupt and discontinuous biological shifts, transient climatic disturbance to prolonged ecosystem recovery, and perhaps transient disturbance to sustained ecosystem regimes. All of these ecosystem response characteristics are likely to be active for at least some locations and time periods, leading to a mix of slow fluctuations, prolonged trends, and step-like changes in ecosystems and fish populations in response to climate change. Climate variables such as temperatures and winds can have strong teleconnections (large spatial covariability) within individual ocean basins, but between-basin teleconnections, and potential climate-driven biological synchrony over several decades, are usually much weaker and a highly intermittent function of the conditions prevailing at the time within the adjoining basins. As noted in the recent IPCC 4th Assessment Report, a warming trend of ocean surface layers and loss of regional sea ice is likely before 2030, due to addition of greenhouse gases. Combined with large continuing natural climate variability, this will stress ecosystems in ways that they have not encountered for at least 100s of years.

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1. Introduction

In September 2006 a Working Group composed of the authors met at a GLOBEC Workshop on Climate Variability and Marine Ecosystems to discuss and reach consensus on characterizing the spatial and temporal scales of the physical climate forcing of ocean ecosystems, the matching of physical to biological time scales, and where, when and how climate forcing might lead to synchrony of fisheries responses among widely-separated ocean regions. The Group included Pacific

and Atlantic climate scientists and those interested in lower trophic level and fisheries responses to climate.

Our paper is motivated by the concern of GLOBEC scientists and fisheries managers about the importance of detecting and interpreting apparent oscillations, low frequency red noise, and multiple-state “regime shifts” of climate in controlling the year-to-year and decade-to-decade evolution of regional ecosystems and fisheries. Our goal here is to develop a conceptual model of low frequency variability in the marine climate of the Atlantic and Pacific and relate these changes to responses in large biological populations and associated ecosystems. What follows represents a concept paper rather than a review paper.

The workshop was timely in that historical time series are available for a variety of indices describing ocean climate and for a variety of

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variables describing the composition and productivity of many regional ocean ecosystems. The Group was motivated by numerous fishery time series, some reaching hundreds of years including pre-industrial fisheries, which show large amplitude and sometimes abrupt changes in stock size and productivity at time scales ranging from years to multiple decades (Fig. 1). Local changes in catch and abundance of harvested species are often accompanied by changes in the atmosphere, and in physical oceanographic and lower trophic level biological variables. In many instances, region-to-region correlation and synchrony of low-frequency fluctuations and trends extend across large spatial scales. Conversely, between-variable associations that are strong in some regions and time intervals are often weaker or different at other times and places. The main difficulty with a direct time series analysis is that co-occurrence does not necessarily prove causality, and physical/biological correlations among temporally-autocorrelated and relatively short (multi-decadal) records are suspect, except for initial exploratory purposes. Humans like to look for, and often find, patterns and cycles in data, but environmental time series are in general too short or incomplete to conclude physical/biological relationships based on times series analyses alone (Overland et al., 2006). Despite these limitations, analyses should continue on the decadal relationship between climate and ecosystems based on a combination of process studies and data analysis; Beamish et al. (2004) go so far as to state that management practices that ignore the impacts of such climate variability on the abundance trends of commercially important species could lead to the collapse of major fisheries.

The need to anticipate upcoming hard times in the ocean environment is not unique to humans. Developmental, reproductive, and migratory strategies of many marine organisms show heavy evolutionary investment in prediction of and adaptation to periodic 'disturbances,' most notably, the annual seasonal cycle. In some cases, the adaptive responses are frequency and phase matched to a dominant environmental periodicity, while in other cases the organism relies on environmental 'leading indicators' such as changes in temperature or food availability. For marine organisms, a serious dilemma, and potential for large changes in growth and survival, occurs when a highly successful strategy for dealing with strong and predictable variability at one time scale (e.g. 'spring' reproduction) encounters and conflicts with unpredictable and spatially-extensive variability at a somewhat longer time scale such as a change in the timing of the spring transition to upwelling conditions (Mackas et al., 2007).

Because of its particular influence on recent scientific thinking, special attention was given to the 1970s to early 1980s period of rather

strong secular trends in several important climatic index time series that corresponded to a number of increases, as well as declines, in marine populations. Notable in these trends in climatic variables was a decadal-scale decline in the Southern Oscillation Index and decadal-scale increasing intensity of indices associated with the Aleutian Low and North Atlantic Oscillation. Over most of the Pacific, the trends appear to be initiated in the early 1970s or even in the late 1960s. In the Bering Sea and Gulf of Alaska regions, the strong teleconnection of the 1976 tropical El Niño to those regions, and the much weaker teleconnection of the 1972 El Niño, insert a step-like character centered on 1976 to the trends. Thus it appears that this apparent 1976 "regime shift," rather than being a consistent Pacific basin-wide feature, may be better characterized as a regional feature of the far Northeast Pacific. Physical changes in the North Atlantic in the late 1970s–1980s were intense and persistent enough to greatly impact species range and abundance of zooplankton, herring, and cod (Beaugrand, 2004; Heath and Lough, 2007); intrinsic climate fluctuations are confounded by warming trends from anthropogenic forcing from increases in greenhouse gases.

2. Climate variability

2.1. Atmospheric teleconnections

In the Northern Hemisphere (NH) during winter, there are clear and persistent climate patterns in the lower atmosphere with low-pressure over northeastern Canada and just east of Asia, and high-pressure just to the west of Europe and North America. These pressure differences reflect the so-called "stationary waves" in the atmosphere that are forced primarily by the continent–ocean heating contrasts and are spatially-locked to typical latitude and longitude ranges by the presence of the Rocky and Himalayan mountain ranges. Although these patterns are geographically anchored, they do change in time either because the details of heating over the ocean and land vary from year to year or because of internal, i.e. random or chaotic processes (Fig. 2).

A consequence of these pressure patterns is that differences in seasonal climate typically occur from year to year and decade to decade over large geographic regions. Some regions may be cooler or perhaps drier than average, while at the same time thousands of kilometers away, warmer and wetter conditions prevail. These simultaneous variations in climate, often of opposite sign, over distant parts of the globe are commonly referred to as teleconnections. Although their precise structure and shape vary to some extent from

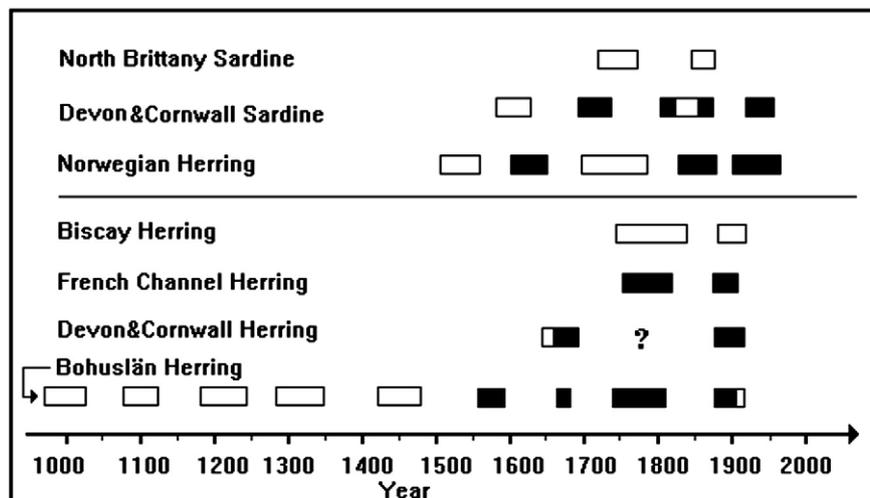


Fig. 1. Historical strength of northwestern European fish stocks. Shaded intervals represent periods of apparent high species abundance. Redrawn from Alheit and Hagen (1997).

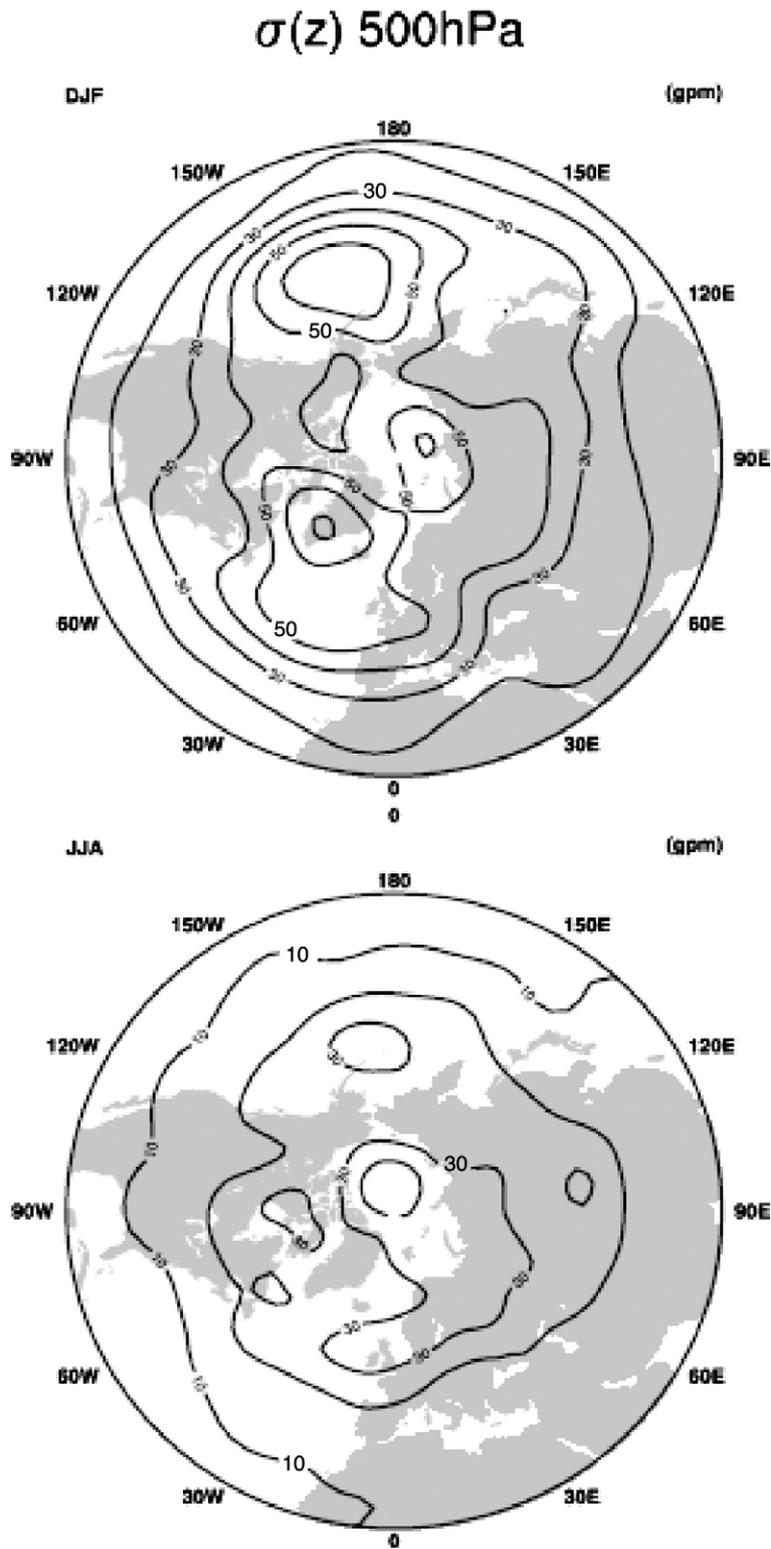


Fig. 2. Standard deviation of pressure (measured in geopotential meters) half way up in the atmosphere (500 hPa) for winter and summer. Regions of largest variability in winter are in economically important sub-Arctic Seas, the Icelandic region influencing the Labrador, Norwegian and Barents Seas and the Aleutian region influencing the Bering and Okhotsk Seas and Gulf of Alaska. Summer has less variability than winter but all sub-Arctic Seas show continued variability.

episode to episode, consistent regional characteristics that identify conspicuous patterns emerge.

Arguably the most prominent teleconnections over the NH are the North Atlantic Oscillation (NAO) and the Pacific–North American (PNA) patterns (Barnston and Livezey, 1987). Both patterns are of largest amplitude during the winter months. The NAO is primarily

characterized by north–south differences in pressure between temperate and high latitudes over the Atlantic sector (Hurrell and Deser, 2010-this issue). Thus, swings in the NAO index from one sign to another correspond to large changes in the mean wind speed and direction over the Atlantic, the heat and moisture transport between the Atlantic and the neighboring continents, and the intensity and

number of Atlantic storms, their paths, and their weather. It appears that the NAO does not owe its existence primarily to coupled ocean–atmosphere–land interactions: it arises from processes internal to the atmosphere, in which various scales of motion interact with one another to produce random and thus largely unpredictable variations with a fundamental time scale of 10 days and longer.

The PNA teleconnection pattern has a connection of four centers of high and low pressures in a roughly great circle route from the central Pacific, through the Gulf of Alaska and western Canada to the southeastern United States. Over the North Pacific Ocean pressures near the Aleutian Islands vary out-of-phase with those to the south, forming a seesaw pivoted along the mean position of the Pacific subtropical jet stream, the center of the main westerly (coming from the west) winds in the atmosphere. Over North America, variations over western Canada and the northwestern U.S. are negatively correlated with those over the southeastern U.S., but are positively correlated with the subtropical Pacific center. At the surface, the signature of the PNA is mostly confined to the Pacific. Like the NAO, the PNA is an internal mode of atmospheric variability.

The NAO and PNA also have several related names based on different definitions. The NAO is closely identified with a somewhat larger scale definition referred to as the Arctic Oscillation (AO) or Northern Annular Mode (NAM). The PNA is closely related to an index consisting of just the sea level pressure in a region near the Aleutian Islands, the North Pacific (NP) Index and a pattern of variability in North Pacific sea surface temperatures (SST), the Pacific Decadal Oscillation (PDO). Secondary SST and pressure patterns can also be found, like the Atlantic Tripole SST pattern (Peng et al., 2006), the Victoria pattern (Bond et al., 2003), or the Northern Oscillation Index (Schwing et al., 2002).

While over the years scientists have suggested a large number of additional climate patterns, analysis of NH-wide pressures show that the NAO and PNA and their aliases provide a robust characterization of the primary climate variability during the 20th Century, representing about 35% of the monthly variability in sea level pressure (Quadrelli and Wallace, 2004). “Third” patterns, computed either from objective (EOF) or heuristic analyses, are not consistent when analyses are compared between different periods within the 20th Century (Overland and Wang, 2005). Thus climatologists are basically limited to a conceptual model with the NAO, PNA, and “other” large scale climate patterns representing about half the signal of NH climate variability. The remainder is “climate noise.” In seasons where the NAO and/or the PNA are weak the observed climate pattern may be more local in character or there may be considerable month-to-month variation in the sign of the principal patterns. Even if a single climate index is

strong, the details of its spatial pattern may vary somewhat, giving different conditions on local scales. For example local weather can differ in the western North Atlantic for different episodes of a negative NAO.

Fig. 3 shows a convenient method to characterize the state of the NH climate in any given year by plotting the NAO on the abscissa and the Pacific NP index on the ordinate. Data for the first half of the 20th century are shown on the left and for the second half on the right. During the early 1990s the NAO was strong and positive and it was negative in the 1960s. The NP was negative (indicating low pressure and strong Aleutian low storm systems) in the 1980s with weak Aleutian lows in the 1950s. Since strong NAO-plus and NP-minus patterns provide enhanced warming over Eurasia and North America, the trends in the NAO and NP indices contribute to the observed overall NH warming trend in the last 50 years (Hurrell, 1996). In years when the values of both the NAO and NP are near the origin, such as the 1930s and 2000s, less organized climate patterns are present. There are also times when the NAO and PNA are both strong; considerable interest has been directed to teleconnections between ocean basins for these periods (Honda et al., 2005). However, by inspection of the data in the four quadrants of each panel in Fig. 3, it is clear that there is no consistent covariability between ocean basins when the entire 20th century is considered.

2.2. Decadal and longer-term variability

Considerable decade to decade variability is found in climate indices and various ecosystem/fisheries time series, for example the PDO for 1901–2006 (Fig. 4). There is much debate about whether such physical changes as those near the mid-1940s and 1970s in the PDO constitute a *regime shift* (Mantua et al., 1997; Steele, 2004). The question is in part semantical, but also important, as such climate changes are associated with synchronous shifts in ecosystems over the ocean basins (Overland et al., in press). A strict definition of regime implies the existence of *multiple stable states*. If we look at short pieces of a record (several decades), however, we can also have a *displacement* definition of regime shift where a change in mean state is statistically significant relative to the variance of the signal on each side of the shift. The straight lines in Fig. 4 illustrate a method of applying the displacement definition to find such shifts in the PDO for the mid 1940s and 1970s (Rodionov, 2004). One can have large local displacement regime shifts even if the time series of the underlying physical process on hundreds of years were from a Gaussian statistical distribution (i.e. without multiple equilibria) but with a large variance. What is somewhat troubling, however, is if we relax the

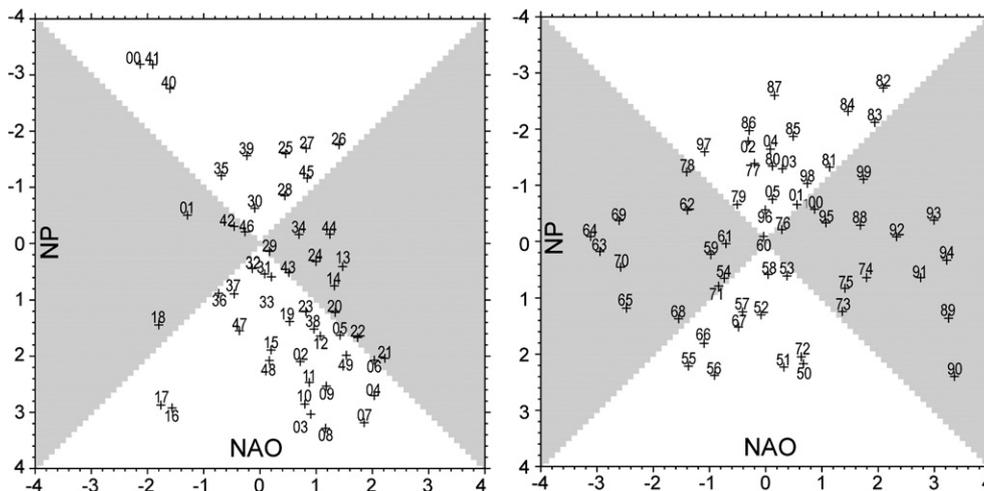


Fig. 3. Phase space diagrams that plot the state of winter climate for any given year in the 20th century in terms of the North Atlantic Oscillation (NAO) and North Pacific (NP) climate indices. Numbers are the year in the 20th century, with the first half of the century plotted on the left.

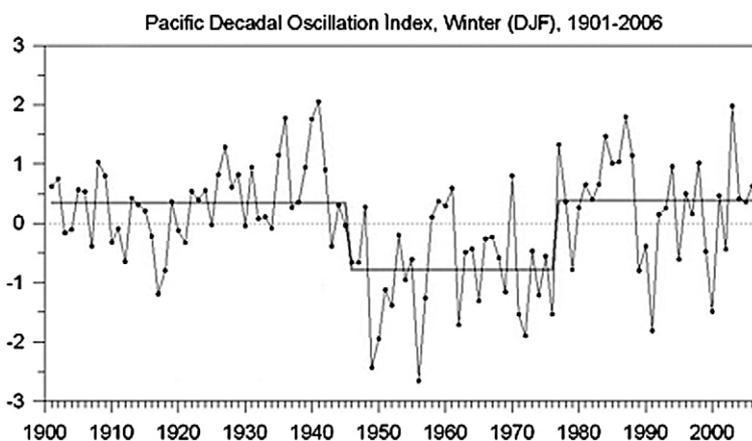


Fig. 4. Plot of the time series of the winter Pacific Decadal Oscillation for 1901–2006. The net displacements or “regime shifts” in the series near 1945 and 1976 (straight lines) are computed by the method of Rodionov (2004).

selectivity parameter in Rodionov’s method for selecting shifts, we can pick up additional potential changes (1934 and 1999), i.e. the analysis is sensitive to changes in analysis parameters (Overland et al., *in press*).

One can use statistical models to test the ability of the multiple stable state hypothesis versus red noise hypotheses to explain or at least represent the underlying physical processes contributing to time series such as the PDO. Red noise considers that the signal has contributions from many frequencies and that considerable contributions come from low frequencies (here decadal to multi-decadal). Positive extreme values or rapid shifts would occur at random when the contributions from each frequency are combined with fortuitous random phasing. Conversely, if the underlying process were more cyclic and deterministic, then there would be more possibility to say when a future shift might occur. But with red noise, the large shifts occur when the different contributions add together in a random manner, with little potential predictability. Thus if the true underlying climate process was close to red noise, predictions from extrapolation by curve fitting of 20th century data would be a misleading and dangerous exercise. We have fit a statistical model of multiple stable states, as well as long memory and first order autoregressive red noise models to the 100 year PDO record (Overland et al., 2006). Unfortunately, all models statistically fit the data rather well and it would take an observed time series of several hundred years to distinguish which is the “best” model for representing the underlying process of the PDO. Thus the PDO time series is “too short” to clearly determine the underlying climate process for the North Pacific from time series analysis alone.

Due to this relative “shortness” of available physical time series the best we are able to do is to recommend a conceptual model for climate on monthly and longer time scales as a red noise process, but with some multi-year memory, internal feedbacks and non-linearities. The climate systems for both the Pacific and Atlantic are characterized by large decadal variability but unknown timing. A weakly non-linear system implies that there may be some physical processes that help reinforce variability on decadal time scales. Some of these potential processes are discussed in the next section.

2.3. The role of ocean forcing on climate variability

Since both the NAO and the PNA arise from the intrinsic and nonlinear dynamics of the atmosphere, observed interannual and longer time scale fluctuations of these teleconnection patterns are mostly a remnant of the energetic weekly atmospheric variability, i.e. climate noise. However, feedback by the ocean has likely reddened the spectra of atmospheric events (Barsugli and Battisti, 1998).

The argument for an oceanic influence goes as follows: while intrinsic atmospheric variability exhibits temporal incoherence, the

ocean tends to respond to it with marked persistence or even oscillatory behavior. The time scales imposed by the heat capacity of the upper ocean, for example, lead to low frequency variability of both SST and lower tropospheric air temperature. The key question, then, is the sensitivity of the middle latitude atmosphere, away from the surface, to slower changes in SST and other surface boundary conditions including sea-ice and land surface snow cover. Most evidence is that the SST feedback, for instance, on the atmosphere is quite small compared to internal atmospheric variability (e.g., Lau, 1997; Peng et al., 1997). Nevertheless, the interaction between the ocean and atmosphere is likely important for understanding the details of the observed amplitude and persistence of NH teleconnection patterns and their longer-term temporal evolution, as well as the prospects for predictability.

Adding to the complexity of ocean–atmosphere interaction is the role of remote forcing from the tropical oceans. Several recent studies, for instance, have concluded that NAO variability is closely tied to SST variations over the tropical oceans (Liu and Alexander, 2007). The importance of tropical versus extratropical ocean–atmosphere interaction for the NAO, however, has not yet been fully determined.

In contrast, fluctuations in the PNA can be linked to changes in tropical Pacific SSTs, which are related to the occurrence of El Niño (EN) (Horel and Wallace, 1981; Lau, 1997). During EN, the equatorial surface waters warm considerably from the International Date Line to the west coast of South America. The atmospheric phenomenon tied to El Niño is termed the Southern Oscillation (SO), which is a global-scale east–west see-saw in atmospheric mass involving exchanges of air between eastern and western hemispheres centered in tropical and subtropical latitudes. During an EN event, the sea level atmospheric pressure tends to be higher than usual over the western tropical Pacific and lower than usual over the eastern Pacific, and warmer-than-average SSTs cover the near equatorial Pacific. While changes in equatorial Pacific SSTs can occur without a swing in the SO, EN and the SO are linked so closely that the term ENSO is used to describe the atmosphere–ocean interactions over the tropical Pacific. Warm ENSO events, therefore, are those in which both a negative SO extreme and an EN occur together. The interval between ENSO events is typically 2–7 years.

During the warm phase of ENSO, the warming of the waters in the central and eastern tropical Pacific shifts the location of the heaviest tropical rainfall eastward from its climatological position centered over Indonesia and the far western Pacific. This shift in rainfall and the associated latent heat release alters the heating patterns that force large-scale waves in the atmosphere, producing an amplification of the PNA (Hoerling et al., 1997). The PDO has been described as either a long-lived El Niño-like pattern of Indo-Pacific climate variability or a low frequency residual of ENSO variability on multi-decadal time

scales (Newman et al., 2003). It has also become clear that tropical Indo-Pacific SSTs vary on the same time scale as is evident in the PDO index, and this coupled with symmetrical SST signatures in the Southern Hemisphere point toward a common tropical forcing (e.g., Deser et al., 2004). The interdecadal timescale of tropical Indo-Pacific SST variability is likely due to oceanic processes.

Extratropical ocean influences play a role in the evolution of the PDO as changes in the ocean gyre evolve (Latif and Barnett, 1994) and heat anomalies are subducted and re-emerge (Alexander et al., 1999). There is also the possibility that there is no well-defined coupled ocean–atmosphere “mode” of variability in the Pacific on decadal-to-interdecadal time scales, since instrumental records are too short to provide a robust assessment and paleoclimate records conflict regarding time scales (section 2.2). It is possible, for instance, that the PDO is not itself a mode of variability but is a reflection of combined forcing by variability of the Aleutian low, ENSO, and oceanic zonal advection in the Kuroshio–Oyashio Extension (Schneider and Cornuelle, 2005). The latter results from oceanic Rossby waves that are forced by North Pacific Ekman pumping (Schneider and Miller, 2001). The SST response patterns to these processes are not completely independent, but they determine the spatial characteristics of the PDO.

3. Ecosystem responses

In contrast to climate forcing, there are numerous examples of apparent step-like or multiple-stable-state behaviors in fisheries and biological oceanography (Beamish et al., 2004; Beaugrand, 2004; Mackas et al., 2007). Bakun (2004) uses *climatic regime shifts* to signify apparent transitions between differing average climatic characteristics and *ecosystem regime shifts* to signify drastic large time- and space-scale shifts in abundances of major components of marine biological communities. For yellow fin sole (*Limanda aspera*) in the Bering Sea (Fig. 5) there appear to be separate relevant stock/recruit curves for different decadal-mean wind conditions (Wild-

erbuer et al., 2002). Thus while the winds represent a red noise process for forcing the ocean, the biological response seems to be bimodal. For Georges Bank haddock (*Melanogrammus aeglefinus*) there was not a return to high yields as fishing mortality was reduced after 1971, suggesting a hysteresis in the biological response to climate forcing and fishing pressure (Collie et al., 2004). Other examples are as dispersed as the North and Baltic Seas, Korean waters, and north of Hawaii (Rebstock and Kang, 2003; Alheit et al., 2005; Polovina, 2005). Such considerations are not new; Steele and Henderson (1984) showed that a simple population model exhibited multiple equilibrium states when driven by stochastic (red noise) environmental fluctuations. Thus we can anticipate that fisheries impacts from climate variability will be diverse and complicated, based on local ecosystem structure (Drinkwater et al., 2010–this volume). When a climatic variation occurs, potential marine ecosystem responses include the following (Bakun, 2004; Collie et al., 2004):

- *Directly-driven responses.* Some biological responses may have periods and phases that are directly coupled to those of the forcing process. For example, a period of poor reproductive success at the high-latitude (cooler) end of the range of a species may rather precisely coincide with a period of anomalously cold temperatures.
- *Transient responses.* A climatic “impulse” may set in motion a sequence of transient responses in predator–prey interactions, etc., that may persist after the initiating impulse has been terminated.
- *Nonlinear feedback responses.* A climatic impulse may excite self-enhancing (i.e., self-sustaining) nonlinear feedback loops within the ecosystem that may be reflected as durable shifts in ecosystem structure and trophic flows (Bakun, 2010–this issue).

Generally, more than one of these classes and often all of them may be operating in a given region and time period. While beyond the scope of this article, several authors discuss possible fisheries management responses to such climate variability (MacCall, 2002; Miller and Munro, 2004; Freon et al., 2005; King and McFarlane, 2006; Perry et al., 2010–this issue). For purposes of illustration of direct climate effects, we offer three regional examples.

3.1. El Niño and Peru

El Niño episodes typically last about a year and feature a radical deepening of the ocean thermocline and the associated nutricline along the Peruvian coast. As a result, the coastal upwelling that normally cools and enriches the local marine ecosystem no longer transports nutrient-rich thermocline waters to the near-surface zone.

The *directly-driven* ecosystem responses, occurring within the El Niño episode itself, are among the most dramatic effects of short-period climatic variability that occur anywhere in the world's oceans. These include collapse of local primary production and resulting population collapses of a variety of small planktonic herbivores and low-trophic level carnivores. The normally-dominant Peruvian anchoveta population that has, in its high biomass phase, supported the largest fishery that has ever existed on earth (Paulik, 1971) likewise experiences drastic declines in population size and may collapse completely, partly through reduced food supply, and partly through enhanced vulnerability to fishing pressure caused by aggregation of the fish in the remaining foraging areas. Sardines on the other hand often enjoy strong, sometimes spectacular, reproductive success (as described by Agostini et al. (2007) for sardines in the California Current System). Associated warming of the local habitat tends to displace resident fishes toward more southerly latitudes. Substantial advective influx and recruitment of warmer-water organisms from the tropics, notably shrimps and scallops, may occur (Arntz et al., 1988).

The effects of the episode do not terminate at the end of the El Niño. When an El Niño episode has subsided, the subsurface density structure rebounds upward, returning cool nutrient-rich subsurface

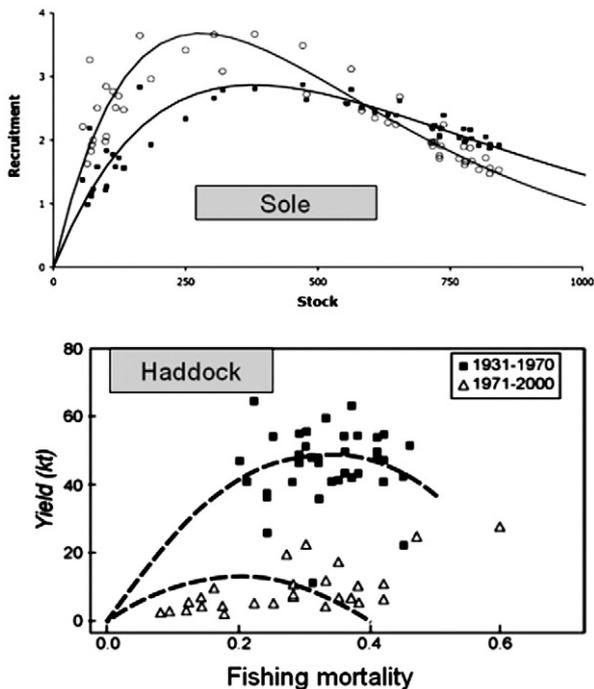


Fig. 5. Examples of potential multiple stable states for fisheries: Bering Sea yellow fin sole (*Limanda aspera*) and Georges Bank haddock (*Melanogrammus aeglefinus*). Plots are revisions from Wilderbuer et al. (2002) and Collie et al. (2004). The open and closed symbols represent data from different years, implying that the fish populations can have two distinct states based on the functional relationships of system variables.

waters to a shallow enough level to allow them to be effectively entrained in the upwelling process. The warm, nutrient-depleted near-surface waters are replaced by cool, nutrient-rich conditions. Primary production proceeds with renewed vigor and the normal planktonic community becomes reestablished. Displaced fish populations find their way back to the local ecosystem. Sequences of *transient responses* of varying duration carry effects forward into ensuing years. For example, the anchoveta begins vigorously rebuilding its population. This is a several-year process, and so in the year following the El Niño, anchoveta may still be in relatively low abundance. This offers a window for an exceptional recruitment of the invertebrates that had become established. In subsequent years as the habitat fills up with filter-feeding anchoveta, the water column becomes a poor place for shrimp and scallop larvae to survive, and so the invertebrate population outburst tends to be only a short-lived transient. Other transients may occur as segments of displaced fish populations, which may attempt to maintain themselves in locations to which they had been displaced during the El Niño, may briefly “hang on” but gradually fade away over the following several years, particularly when fishing is involved. The good sardine recruitment during the El Niño episode leads to increasing sardine population biomass as individuals of that particular cohort grow in age and size.

These vigorously productive transient responses within the renewed, re-enriched Peruvian ecosystem may continue until the next El Niño episode truncates the sequences of transient responses to the previous episode and begins the process anew. This continuous “resetting” of the Peru system by recurring El Niño episodes before internal *nonlinear feedback responses* can arise and impose potentially adverse “malignant”-type controls (Bakun and Weeks, 2006), may be one of the keys to the unique capacity of the Peruvian marine ecosystem to continue to provide remarkable quantities of fish.

There are evidently feedback processes that produce interdecadal-scale “regime”-like features in the Peruvian ecosystem. For example, there appear to be so-called “sardine periods” and “anchovy periods” (Alheit and Niquen, 2004) where one or the other of the two small pelagic clupeoid species may tend to dominate the “small nektonic planktivore” position in the ecosystem. Climate events are involved (e.g., Alheit and Bakun, 2010–this issue). There also may be an element where adverse interspecies *feedback* interactions such as the “school trap” may allow one or the other species to temporarily maintain a position of dominance despite declining competitive fitness (Bakun and Cury, 1999).

In summation, these various processes, as well as other similar ones not elaborated here, act to spread the effects of annual El Niño episodes to multi-annual time scales and even to multi-decadal time scales covering a series of individual El Niño episodes in a way that may appear to resemble a simple mixture of autoregressive and moving-average type processes acting on various time-scales. The continual resetting of the system by the recurrent El Niño may in fact be what has maintained that appearance and hypothetically prevented the type of abrupt adverse “phase shift” to a durably-altered less-desirable state such as has apparently afflicted the northern Benguela Current System, the Peru Current System’s Atlantic counterpart (Bakun and Weeks, 2008).

3.2. Southeastern Bering Sea

The ecosystem of the Bering Sea went through a structural shift after 1976 in response to a change in the PNA/NP/PDO toward lower atmospheric pressures in the Aleutian Low region, and after 2000 in response to warmer temperatures associated with weaker northerly winds which were not related to these major indices. While it is uncertain what the food web/species abundances were before the 1976 shift, after the shift walleye pollock (*Theragra chalcogramma*) had a major increase in abundance, which has been generally maintained near 10 million metric tons (Fig. 6). The physical climate changed in

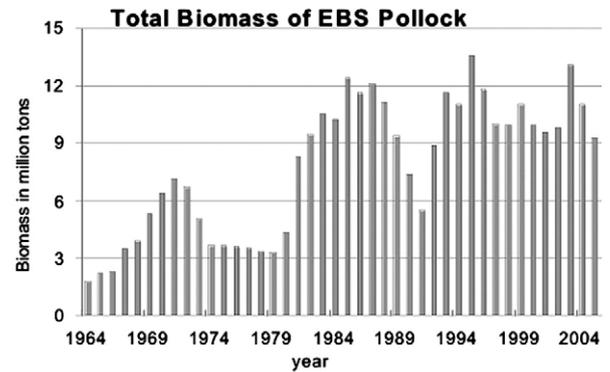


Fig. 6. Pollock (*Theragra chalcogramma*) biomass for the eastern Bering Sea.

1976, but the first strong pollock year class was 1978; it seems that the explosive increase depended both on warmer winter sea temperatures associated with the PDO and increased wind mixing in early summer, and thus enhanced lower trophic level productivity (Bond and Overland, 2005). Thus the PDO climate shift may have been a necessary but not sufficient condition for the ecosystem shift. One interpretation for the continued high pollock abundance is that their range on the Bering Sea shelf has increased due to loss of sea ice and warmer temperatures. After the ten-year almost exponential increase, pollock populations appear stable in the 1990s based on top down control through cannibalism. This shift was summarized as the “Oscillating Control Hypothesis” of Hunt et al. (2002). The second period of even warmer temperatures with an additional increase of 2 °C for 2000–2005 contributed to the continued expansion in habitat (Stabeno et al., 2006).

Of particular interest for the Bering Sea is that there was not just a latitudinal shift in species range but also a fundamental reorganization from an Arctic-type benthic ecosystem to a pelagic sub-Arctic structure attributable to the loss of sea ice (Fig. 7) and to associated altered seasonal match between algal production, zooplankton grazing, and growth and development of juvenile pollock (Hunt and Stabeno, 2002). Pollock were not the only species affected. Greenland Turbot, a cold-water species has decreased to 17% of its early 1970s values. Snow crab, a benthic species, have declined 60% from its earlier highs. Walrus have lost both their ice habitat and benthic food supply.

The recent six-year warm period with extensive ice retreat came to an end in 2006 and 2007. We can anticipate that different species will recover at different time intervals, depending on their ability to ride out this next cold period before the return to warmer conditions. Pollock show a recent decrease in abundance. But low recruitment started before 2006, in part due to a reduction in zooplankton and an increase in predators.

The species in the Bering Sea exhibit all three responses to climate variability. Northward relocations of bottom species are connected to warmer temperatures, a *directly driven* response. Fur seals have been in major decline since the 1970s; the mechanism is uncertain, but the coincidence with the NP index is striking. Pollock recruitment took advantage of warmer conditions after 1976, but by the mid 1980s top down control reduced the direct impact of climate, i.e. a *transient* response followed by an ecosystem restructuring. The recent reductions in pollock may have started as an ecosystem reorganization after a sustained warm period, i.e. a *non-linear effect*. This change combined with the recent shift to colder conditions suggests major uncertainty for the near future state of the Bering Sea ecosystem.

3.3. North Atlantic cod, *Calanus finmarchicus*, and the NAO

In the North Sea there is a negative correlation between cod (*Gadus morhua*) recruitment and the NAO (Fig. 8). The 1960s was a period of a

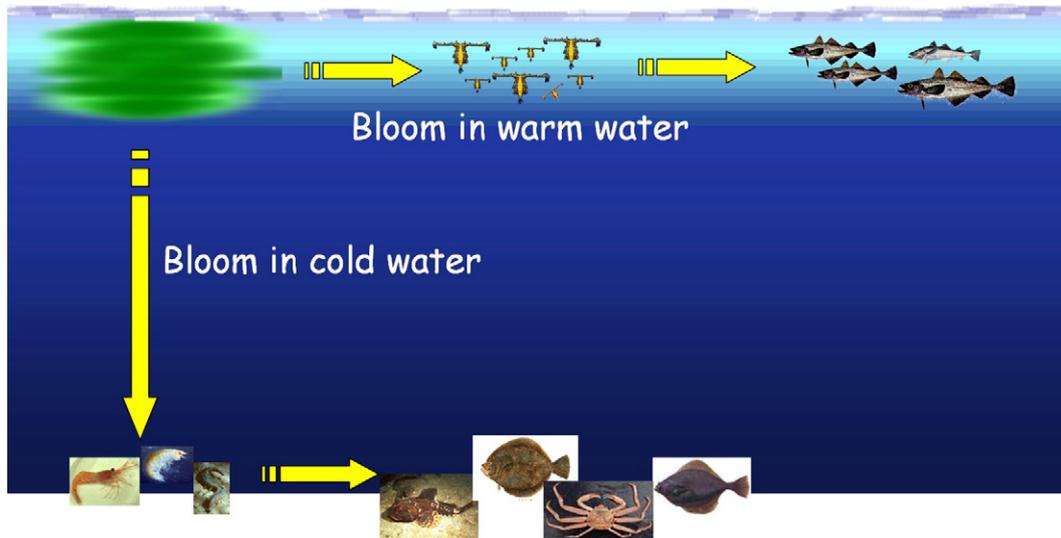


Fig. 7. Conceptual diagram for the ecosystem reorganization for the Bering Sea, with ice cover (benthic energy route) and without ice cover (pelagic energy route). Courtesy F. Mueter (University of Alaska Fairbanks, Fairbanks, Alaska; pers. comm.).

gadoid outbreak in the North Sea during a persistent negative phase of the NAO. Increasing sea temperature associated with positive NAO has a double negative impact on larval cod survival (Lehodey et al., 2006). Warmer temperatures increase metabolic rates and therefore increase their energy demand, while simultaneously decreasing the quality and quantity of their available prey. Beaugrand et al. (2003), Beaugrand (2004), and Heath and Lough (2007) show that the large decadal fluctuations in cod recruitment were accompanied, and probably caused, by synchronous changes in the zooplankton eaten by larval and juvenile cod. There are multiple components of the zooplankton changes, including poleward shifts in species distribution; changing life history timing; and changing size composition (Mackas and Beaugrand, 2010-this issue).

Further north in the Barents Sea, favorable cod recruitment is considered to be associated with warmer sea temperature and the positive NAO. It is hypothesized that this is due to higher primary production in larger ice free areas, a larger influx of zooplankton carried by increased current inflow from the southwest associated with positive NAO, and higher general biological activity with warmer temperatures. Intra-ecosystem shifts may be complex. Increases in cod have led to episodes of high predation and the collapse of the

capelin stock, with subsequent impacts on the Barents Sea community assemblage and food web structures (Ciannelli et al., 2005).

Historically, a positive NAO with strong north winds and colder temperatures is considered to be unfavorable for the Labrador-Newfoundland cod stock. The coupling between stocks and the NAO off of eastern Canada is in fact strongest at the northern and southern extremes of the species range (Fig. 8). Zooplankton biomass time series again show parallel spatial and temporal responses to NAO variability (Piontkovski et al., 2006; Mackas and Beaugrand, 2010-this issue). Stige et al. (2006) and Frank (Fisheries and Oceans Canada, Dartmouth, NS, personal communication) note *non-stationary relationships* between cod recruitment and the NAO, suggesting that effects such as age structure or species diversity dampen the climate-cod relationships.

The positive NAO is an increase in the strength (lower atmospheric pressure) of the Icelandic low which tends to organize the large scale wind fields over the entire North Atlantic. Wind pattern anomalies are not particularly symmetrical for the negative NAO state, where the seasonal average strength of the Icelandic low is reduced. This weaker Icelandic low can be considered to be made up of weaker and more variable storm systems with more variable tracts. Some of the cod/NAO uncertainty may be due to this asymmetry.

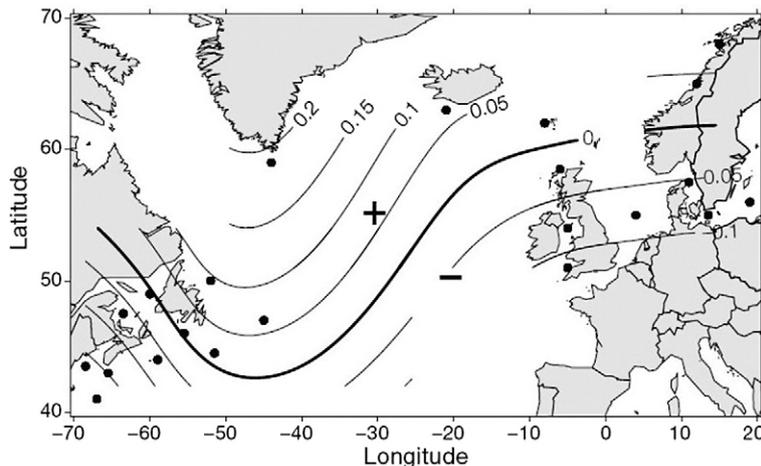


Fig. 8. The effect of the NAO on the spatial pattern of cod recruitment (after Stige, et al., 2006). The figure implies that when the NAO is positive, conditions are favorable for cod stocks northward from Newfoundland to Iceland and northern Norway, and are unfavorable near the North Sea and in southern Maritime Canada and the eastern United States. Opposite conditions would hold for negative NAO values.

4. Future climate change: forced (greenhouse gases) and intrinsic variability

4.1. Warming patterns

The Intergovernmental Panel on Climate Change Fourth Assessment Report (IPCC, 2007) concludes that present climate change *most likely* has an anthropogenic component due to increases in greenhouse gases, principally CO₂ and methane. A first look at 21st century climate for major ecosystem regions are discussed in an accompanying article (Wang et al., 2010–this issue). Here we present a summary of several marine ecosystem related issues.

One hypothesis of the nature of global warming is that changes might occur in the frequency distribution of the principal climate patterns, for example the positive phase of the NAO would occur more often (Palmer, 1999). While there is minor evidence that this may happen (IPCC, 2007), a primary response in the IPCC climate models is a rather spatially uniform warming trend throughout the ocean basins combined with the continued presence of decadal variability similar to that of the 20th century, NAO, PDO, etc. (Overland and Wang, 2007).

Fig. 9 shows the projected 21st century increases in SST for the winter southeastern Bering Sea; graphs are similar for the remainder of the North Pacific and North Atlantic. The IPCC models are each run several times from nearly the same starting conditions. Because the climate is chaotic in the models as in the real atmosphere, the range of variability in future SST projections will be similar for these individual runs, but the timing of events will differ among both the different IPCC models and runs of the same model. Therefore the thin lines in Fig. 9 representing single model runs are examples of possible futures events. If one averages over all the possible futures, one gets the thick line, which represents the trend from the anthropogenic contribution to future climate. A key result is that species will not just react to a global warming trend, but to the combination of the trend plus the continuing large, unpredictable interannual and decadal variability. By 2030 the influence of the trend will be as large as the decadal variability; coldest years in the future will be no colder than previous average temperatures and new positive extremes will be reached.

We anticipate several potential ecological impacts. The most obvious physical changes will be related to warming of the upper ocean, which will likely increase stratification. This will generally inhibit the mixing of nutrients from the deep ocean to the photic zone, probably reducing overall productivity on a global scale (Pierce,

2004). Since the warming trends appear more uniform than the climate patterns, species will encounter more spatially uniform patterns of change compared to the historical NAO or PNA influences. Species will still be impacted by the combined effect of life history and decadal climate variability, but new extreme states are much more possible as the first half of the 21st century unfolds. Plankton, fish, and benthic invertebrate species are all likely to shift their distributions poleward, although probably at different rates and over different distances, expanding less-productive tropical and subtropical ecosystems, and decreasing the highly productive subarctic and arctic ecosystems. Differential poleward–equatorward movement has in the recent past caused major disruptions of local ecosystems and fisheries (McFarlane and Beamish, 2002; Peterson and Schwing, 2003; Mackas and Beaugrand, 2010–this issue).

4.2. Effect of natural patterns of variability

Although the somewhat modest but rather uniform warming over the ocean basins (~1.5 °C increase by 2050), due to the atmospheric long wave radiation physics of an increasing greenhouse “blanket,” is a robust result of the IPCC climate models, the models are less reliable in resolving changes in the physics of climate patterns such as ENSO and the NAO, as well as in simulating changes in regional physics such as coastal upwelling. Thus one might encounter unexpected regional interactions and feedbacks. Recent research has emphasized exactly this point, under the term “Abrupt Climate Change” or “Black Swans” (Taleb, 2007).

Paleoclimate records, archaeological evidence, and instrumental data all indicate variations in the ENSO behavior of past centuries. Much of this variability appears to be internal to the Earth's climate system. But there is also evidence that changes in exogenous forcing affect ENSO, implying that small changes in forcings are able to cause large alterations in the behavior of this nonlinear system. Statistical analyses of the instrumental ENSO record have been used to assess the likelihood that its behavior since the mid-1970s is part of a natural decadal time scale variation. The recent trend for more warm ENSO events since 1976 and the prolonged warm conditions of the early 1990s is inconsistent with natural variability as measured before 1970. Yet, attribution remains uncertain. Many global climate models, for instance, project changes in the statistics of ENSO variability with global warming, some indicating greater ENSO activity marked by larger interannual variations relative to the warmer mean state. Yet,

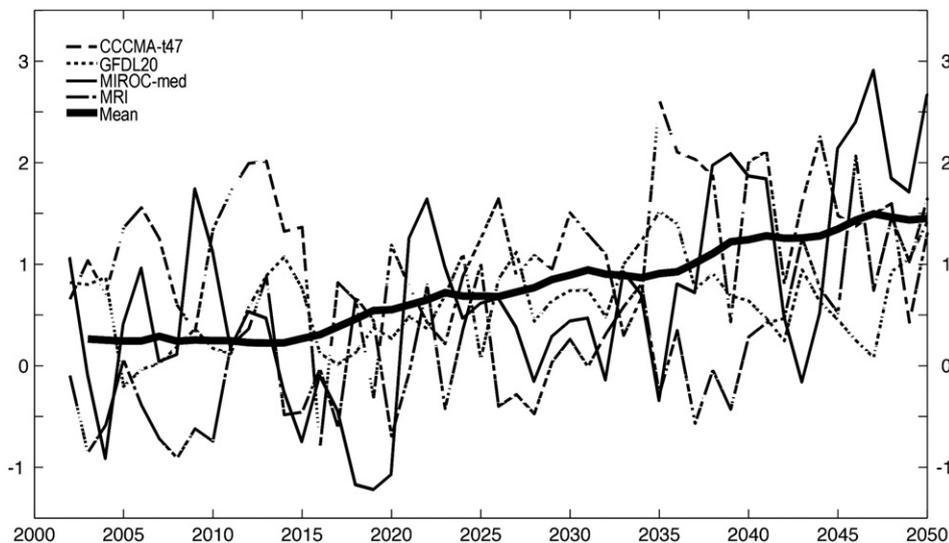


Fig. 9. Projected 21st century sea surface temperatures (°C) for the winter southeastern Bering Sea. The thin lines are possible future scenarios from different individual projections from different IPCC climate models. The thick line is the average of all the possible projections and represents the trend from the anthropogenic (greenhouse gases) contribution to change.

ENSO is not well enough simulated in climate models to have full confidence in these projected changes, in part because the positive atmosphere–ocean feedbacks involved with ENSO mean that small errors in simulating the relevant processes can be amplified. Thus, while it is likely that changes in ENSO and hurricanes will occur as a result of anthropogenic climate change, their nature, how large and rapid they will be, and their implications for regional climate change around the world are quite uncertain.

Of relevance is that several recent studies have shown that some of the upward trend in the NAO index over the last half of the 20th Century arose from tropical SST forcing. Averaged over the tropics, SSTs have warmed nearly 0.25 °C since 1950, with parts of the equatorial Indian and Pacific Oceans warming about 1 °C. While the possibility cannot be dismissed that the oceanic behavior is due purely to intrinsic coupled ocean–atmosphere interactions, it is not unreasonable to claim that part of the North Atlantic climate change, forced by the imposed slow warming of tropical SSTs, constitutes an anthropogenic signal that has just begun to emerge during the last half century. Moreover, as both ENSO and the NAO are key determinants of regional climate, our ability to detect and distinguish between natural and anthropogenic regional climate change is limited.

4.3. Other effects

As greenhouse gases continue to increase in the atmosphere, they will affect oceanic ecosystems in a variety of ways. Warming will also severely reduce sea ice extents, which control nutrient fluxes in subarctic and arctic regions, and the seasonality of lower trophic level production in fundamental ways that are still poorly understood. Loss of sea ice will impact local fish populations and sea-ice dependent communities. Many coastal regions will be affected by changes in the magnitude and seasonal timing of runoff and streamflow, which are vital for maintaining oceanic ecosystem productivity because they transport limiting nutrients such as iron to the open ocean, affect coastal mixing processes, and influence salmon spawning conditions. Coastal upwelling in eastern boundary currents could increase due to enhanced upwelling favorable winds driven by changes in the cross-shore atmospheric temperature and pressure gradients. This may result in the increased nutrient supply within these highly productive regions. The acidification of the ocean by increasing CO₂ will reduce the ability of carbonate shell producing organisms, such as corals and foraminifera, to successfully produce skeletons, thus potentially crippling ecosystems that rely on their health, particularly in the northern North Pacific. These and other possible impacts on future marine populations must be studied and monitored to prepare for their effects on exploited marine fisheries.

5. Conclusions

In looking back over our overview, one might be disappointed in the ability to forecast ecosystem changes. Organized NH climate is limited primarily to two climate patterns, the NAO and PNA, which account for less than 50% of the monthly variance. Further, we propose a primarily long memory red noise model for the temporal variability of atmosphere/ocean climate, which emphasizes the presence of large swings or shifts on decadal scales but rejects the ability to predict the timing of these events. While there are hypothesized ocean/atmospheric processes which bring some memory, feedback, and non-linearity to the coupled ocean/atmosphere system, we see no strong evidence for large discrete multiple stable states in the climate system, at least on annual to multi-decadal time scales. Ecosystems, however, respond in a variety of ways with multi-year restructuring being but one possible result to a short-lived transient climate event.

Although the temporal variability in atmospheric climate is noisy, the spatial patterns of the PNA and NAO impose preferred spatial forcing patterns on the ocean. The oceanic response patterns, which

depend on the local oceanic response to surface heating, wind stress and freshwater flux, can also have large spatial organization resulting from such features as the NAO, PDO, Victoria pattern and the Atlantic Tripole SST. Oceanic ecosystems can therefore respond synchronously in space to these large-scale oceanic patterns, adapting to not only changes in SST, but also to changes in upwelling, advective transport by mean currents, mesoscale eddy variance, thermocline structure, and mixed-layer depth. Some of these oceanic changes occur with lags induced by oceanic processes, such as Rossby waves, Kelvin waves or advection by mean flows. These lags can inject a component of predictability into the oceanic system that may be exploitable in anticipating ecosystem changes over periods of months or even years. Thus, noisy atmospheric behavior can still generate useful information on basin-scale and interbasin oceanic ecosystem synchronies if ocean dynamics and thermodynamics were more thoroughly understood and monitored.

We chose to see the cup half full and take note of the advancement in understanding over the previous 5 years. That the climate system is primarily red noise, but has large amplitude decadal events, provides understanding about the episodic temporal nature of climate forcing of ecosystems, and the difficulty of explicit, as opposed to statistical, forecasts. As suggested by Fig. 9, in the future there will be large decadal climate events but their timing is uncertain. Due to global warming, we expect new record maximums in ocean temperatures with ocean basin scale extents. The matching of climate and species with the potential for ecosystem reorganization after such a transient climate event will be of particular importance, with a range of potential responses.

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