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Pacific Basin climate variability and patterns of Northeast Pacific marine fish production

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Abstract

A review of oceanographic and climate data from the North Pacific and Bering Sea has revealed climate events that occur on two principal time scales: a) 2–7 years (i.e. El Niño Southern Oscillation, ENSO), and b) inter-decadal (i.e. Pacific Decadal Oscillation, PDO). The timing of ENSO events and of related oceanic changes at higher latitudes were examined. The frequency of ENSO was high in the 1980s. Evidence of ENSO forcing on ocean conditions in the North Pacific (Niño North conditions) showed ENSO events were more frequently observed along the West Coast than in the western Gulf of Alaska (GOA) and Eastern Bering Sea (EBS). Time series of catches for 30 region/species groups of salmon, and recruitment data for 29 groundfish and 5 non-salmonid pelagic species, were examined for evidence of a statistical relationship with any of the time scales associated with Niño North conditions or the PDO. Some flatfish stocks exhibited high autocorrelation in recruitment coupled with a significant step in recruitment in 1977 suggesting a relationship between PDO forcing and recruitment success. Five of the dominant gadid stocks (EBS and GOA Pacific cod, Pacific hake and EBS and GOA walleye pollock) exhibited low autocorrelation in recruitment. Of these, Pacific hake, GOA walleye pollock and GOA Pacific cod exhibited significantly higher incidence of strong year classes in years associated with Niño North conditions. These findings suggest that the PDO and ENSO may play an important role in governing year-class strength of several Northeast Pacific marine fish stocks. © 2001 Published by Elsevier Science Ltd.

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1. Introduction

Marine organisms show a broad range of responses to spatial and temporal changes in the environment. The nature and intensity of each response stems from the specific life history of the organism and how directly coupled its life history process is to the forcing (Steele & Henderson, 1984; Francis & Hare, 1994; Francis, Hare, Hollowed, & Wooster, 1998). For example, several studies have demonstrated a coupling between atmospherically-driven changes in ocean conditions and changes in lower trophic level abundance and distribution (Brodeur & Ware, 1992; Sugimoto & Tadokoro, 1997). In contrast, higher trophic level species show more varied responses to atmospheric forcing (Hollowed & Wooster, 1995). Differences in the sensitivity of species to spatial and temporal forcing may explain the complex patterns of recruitment (Caddy & Gulland, 1983) and biomass variations (Spencer & Collie, 1997) observed in marine fish.

The ecological literature provides a framework for categorizing the types of responses of higher trophic level species to ocean forcing (for review see Rice, 2001). Chesson (1982) identified three modes of variability: spatial, temporal and population. Chesson (1991) extended this concept further by defining five sources of variability in populations: within individuals, between individuals, within patches, between patches, and pure temporal variation. Higher trophic level organisms may be influenced by each of the sources of variation to a lesser or greater extent. Chesson noted that for large populations, within individual variability does not lead to significant fluctuations on the population scale, whereas, environmental variation on large spatial scales can lead to population fluctuations that are independent of population size. He called this type of environmental variation Pure Temporal Variation (PTV). PTV occurs over time and spatial scales sufficiently

large to contain essentially closed communities. PTV is the variation that remains once all effects of space have been accounted for. The purpose of this paper is to examine the reproductive history of the major Northeast Pacific marine fish stocks in an attempt to identify those stocks that show strong influence from PTV.

Evidence that marine populations have evolved in an environment where PTV plays an important role in marine production is found in the observed synchrony of anomalous recruitment events (Hollowed, Bailey, & Wooster, 1987; Koslow, 1987; Hollowed & Wooster, 1992; Beamish, 1994) and synchronous temporal shifts in fish production (Kawasaki, 1991; Hare & Francis, 1995; Bakun, 1996; Steele, 1998). The apparent shift in marine ecosystems in response to short-term events and decadal scale atmospheric variations suggests that large-scale climate/ocean events may be the principal sources of PTV. In this paper two sources of PTV are identified and we examine how the dominant fish species of the north Pacific respond to these sources of variability.

The two major large-scale climate phenomena influencing the North Pacific are the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) (Mantua, Hare, Zhang, Wallace, & Francis, 1997). The SO is an oscillation of atmospheric pressure between the central and western tropical Pacific while El Niño refers to an associated warming of the waters of the equatorial Pacific from the dateline to the coast of Peru. ENSO events tend to occur every 2–7 years though their frequency has apparently increased since the mid-1970s (Trenberth & Hare, 1996). In contrast to ENSO, the PDO is a decadal-scale oscillation in the North Pacific SST with alternating positive and negative phases that have lasted 20–30 years during the 20th Century. The physical signature of the PDO generally resembles ENSO's signature with two differences. Firstly the PDO signal is strongest in the North Pacific and decreases in magnitude towards the equator in contrast to the ENSO signal. Secondly the PDO has little physical impact outside of the Pacific basin whereas ENSO has well known global impacts. The positive phase of the PDO is associated with a deepening of the Aleutian Low pressure cell, and warming along the shelf and slope regions of the U.S. west coast and Gulf of Alaska. Polovina, Mitchum, and Evans (1995) noted that this phase also corresponds to a shoaling of the mixed layer in the Gulf of Alaska.

Fish populations may respond differently to PTV forcing linked to either the PDO or ENSO. In some stocks it is possible the PTV has little significance relative to the remaining sources of variability (e.g. within individual variations or between individual variations). In this study we examine the hypothesis that North Pacific marine fish stocks are influenced by PTV. We predict that those marine fish populations that are found to be influenced by PTV, will exhibit recruitment fluctuations on a temporal scale consistent with the principal atmospheric and oceanic processes influencing the system.

2. Methods

We initiated our study by reviewing ENSO variations and those in sea surface temperature and sea level pressure data from the North Pacific and Bering Sea. We examine these data to identify shifts in large scale physical forcing. Next, we examine time series of commercial fishery data (catch, recruitment and biomass) for evidence of coherence with one or more of the time scales noted in oceanographic and climate data.

2.1. ENSO

In a recent paper, Trenberth (1997) provided a definition of El Niño, and listed the events since 1950. He defined an El Niño event as the occurrence of a period when the running mean of SST anomalies exceeded 0.4°C in the Niño 3.4 region (5°N – 5°S , 120°W – 170°W) for at least five consecutive months. The timing and duration of the conditions are important in characterizing their potential influence on extra-tropical latitudes. We compare Trenberth's classification with one that we have derived from another data source, the Japanese Meteorological Agency's (JMA) monthly database for a similar region, region B (4°N – 4°S , 150°W – 90°W) in an attempt to arrive at agreed values (Table 1).

Using the JMA data, we have identified El Niño (La Niña) events by a 0.5°C sea surface temperature (SST) anomaly persisting in region B for five months or longer. Since the SST data used both analyses were basically the same, it is not surprising that in most cases, the results are similar. We also assigned a measure of intensity, computed as the average of the highest anomaly during three consecutive months.

2.2. Niño North

To test the view that unusually warm or cool conditions on the eastern side of the North Pacific, which we shall call Niño North and Niña North respectively, are commonly generated by tropical events, we have examined monthly sea surface temperature (SST) anomalies in coastal locations north of the tropics. The SST data were obtained from two recently completed re-analyses of the Comprehensive Ocean Atmosphere Data Set (COADS, Woodruff, Slutz, Jenne, & Steurer, 1987).

Table 1

Timing, duration, and intensity of El Niño events in equatorial regions of the Pacific. The year and month when warming was identified using the format MM/YY, the duration of the event in months is in parentheses

Year	Trenberth (months)	JMA (months)	Intensity ($^{\circ}\text{C}$)
1951–52	8/51–2/52 (7)	6/51–2/52 (9)	1.2
1953	3–11/53 (9)	4–9/53 (6)	0.8
1957–58	4/57–6/58 (15)	4/57–4/58 (13)	1.3
1963–64	6/63–2/64 (9)	6/63–1/64 (8)	0.9
1965–66	5/65–6/66 (14)	4/65–2/66 (11)	1.4
1968–70	9/68–3/70 (19)	11/68–1/70 (15)	1.0
1972–73	4/72–3/73 (12)	4/72–2/73 (11)	2.2
1976–77	8/76–3/77 (8)	6/76–3/77 (10)	1.0
1977–78	7/77–1/78 (7)	Not evident	NA
1979–80	10/79–4/80 (7)	Not evident	NA
1982–83	4/82–7/83 (16)	5/82–9/83 (17)	3.0
1986–88	8/86–2/88 (19)	9/86–1/88 (17)	1.5
1991–92	3/91–7/92 (17)	5/91–6/92 (14)	1.4
1993	2–9/93 (8)	3–7/93 (5)	1.1
1994–95	6/94–3/95 (10)	10/94–2/95 (5)	1.0
1997–		5/97–	3.4

For the period 1950–1981, we have used the Reconstructed SST (RSST) data of Smith, Reynolds, Livezey, and Stokes (1996), and for 1982–1999 we have used the Optimum Interpolation SST (OISST) of Reynolds and Smith (1994). The RSST data have the same temporal and spatial dimensions as COADS data, i.e., monthly averages on a worldwide $2^\circ \times 2^\circ$ grid. The OISST data are computed on a $1^\circ \times 1^\circ$ grid. We averaged the OISST onto the COADS grid so that we could combine the RSST and OISST datasets. For our analysis, we computed SST anomalies at selected coastal locations between 26°N and 54°N (Fig. 1). SST anomalies were computed as monthly deviations from the 1950–1997 averages, which included 27 years prior to the 1976/77 regime shift and 21 years after it.

Three regions were selected for analysis of the timing and presence of Niño North:

1. The west coast (WC) region, which included the COADS squares centered at 27°N , 117°W ; 33°N , 121°W ; 39°N , 127°W and 45°N , 127°W .
2. The Eastern Gulf of Alaska (EGOA) region, which included squares referenced at 51°N , 131°W ; 57°N , 139°W and 59°N , 147°W .
3. The Western Gulf of Alaska and Eastern Bering Sea (WGOA/EBS) region, which included squares referenced at 55°N , 163°W ; 55°N , 167°W and 59°N , 171°W .

Niño North conditions were identified by when anomalies >0.5 EC persisted for at least two months at two adjacent extra-tropical rectangles.

Fig. 1. Location of squares used to summarize sea surface temperature anomalies from the Comprehensive Ocean Atmosphere Data Set.

2.3. *Pacific Decadal Oscillation*

Time series of the PDO were calculated from parallel EOF analyses of the monthly SST and SLP anomaly fields based on the temporal covariance matrix from the 1900–1997 period of record as described by Mantua et al. (1997) and Zhang, Wallace, and Battisti (1997). They note that reversals in the polarity of the PDO occurred in 1925, 1947 and 1977, the most recent shift being from a negative to a positive phase. The 1977 shift was most relevant to this analysis because the time series of marine fish data seldom extend back to 1947.

Recent studies have provided evidence of another regime shift in the North Pacific ecosystem in 1989 (Overland, Adams, & Bond, 1999; Minobe, 1999; Hare & Mantua, 2000; McFarlane, King, & Beamish, 2000). Overland et al. (1999) observed that the signature of this most recent shift in climate forcing was most persistent in the Arctic Oscillation and was short-lived in the Pacific North American index. Hare and Mantua (2000) showed that this shift was most evident in stocks from the western GOA and Bering Sea.

2.4. *Recruitment time series*

Indicators of population trends for Pacific salmon, groundfish, and pelagic species were used in this analysis. Time series of catch (salmon) and recruitment (pelagic and groundfish stocks) are subject to a variety of sources of error (see Hare, Mantua, & Francis, 1999, for salmon and assessment documents referenced in Table 2 for groundfish stocks). For our purposes, the absolute value of recruitment or catch is less important than their temporal patterns. We assume that the time series presented here are reasonable approximations to the real temporal patterns of recruitment or catch.

Salmon trends previously described in Hare et al. (1999) have been included here to provide a comprehensive examination of PTV in a variety of marine fish species. Briefly, Hare et al. (1999) analyzed time series of salmon catch for 5 species from 7 geographic regions. They examined a total of 30 region/species groups (5 of the species/region combinations had no historical record of catches). In all cases, the catch time series was lagged to the year of ocean entry. Recruitment time series for 29 groundfish species and five non-salmonid pelagic species from the WC, GOA and EBS were assembled for this analysis. The groundfish and pelagic species recruitment time series were based on length-based or age-based statistical stock assessment models (Table 2).

Evidence of a response at the population level to forcing at the decadal scale was measured using a variety of techniques. Time series of recruitment and stock biomass were visually compared for trends over a latitudinal gradient. Salmon catch and groundfish recruitment data were analyzed statistically by computing, a) the lag-1 autocorrelation coefficient, and b) the coefficient of variation, and by conducting an intervention analysis.

2.4.1. *Relation of recruitment to PDO*

The lag-1 autocorrelation coefficient measures the degree of correlation between adjacent year classes. Strong autocorrelation in catch and/or recruitment time series would be expected if a stock is responding to a low frequency climate signal such as the PDO. However, high levels of lag 1 autocorrelation can be generated by a variety of other processes unrelated to atmospheric forcing such as fishing mortality and strong density dependence. For example, when a stock

Table 2
Summary of sources of groundfish and pelagic fish recruitment data

Stock	Time period	Source
AI Atka mackerel	1977–94	Lowe & Fritz, 1998
AI POP	1957–93	Ito & Ianelli, 1998
EBS Alaska plaice	1969–96	Wilderbuer & Walters, 1998
EBS arrowtooth flounder	1968–95	Wilderbuer & Sample, 1998
EBS flathead sole	1975–97	Walters & Wilderbuer, 1998
EBS Greenland turbot	1969–95	Ianelli, Wilderbuer, & Sample, 1998
EBS Pacific cod	1975–95	Thompson & Dorn, 1998
EBS Pacific herring	1956–91	Zheng, 1996; Wespestad, 1991
EBS pollock	1963–96	Ianelli, Fritz, Honkalehto, Williamson, & Walters, 1998
EBS POP	1959–90	Ito & Ianelli, 1998
EBS rock sole	1973–96	Wilderbuer & Walters, 1997
EBS yellowfin sole	1953–94	Wilderbuer & Nichol, 1998
GOA arrowtooth flounder	1970–93	Turnock, Wilderbuer, & Brown, 1998
GOA halibut	1966–89	S. Hare, International Pacific Halibut Comm., Seattle, WA, Pers. Comm., 1998
GOA Pacific cod	1975–95	Thompson, Zenger, & Dorn, 1997
GOA pollock	1962–96	Hollowed, Brown, Ianelli, Megrey, & Wilson, 1998
GOA POP	1960–92	Heifetz, Ianelli, & Clausen, 1997
GOA PWS Pacific herring	1969–92	F. Funk. Pers. Comm., Alaska Department of Fish and Game, Juneau, AK 1998
GOA sablefish	1977–96	Sigler, Fujioka, & Lowe, 1998
GOA Sitka Pacific herring	1969–92	F. Funk. Pers. Comm., Alaska Department of Fish and Game, Juneau, AK 1998
GOA thornyhead	1962–93	Ianelli & Ito, 1998
WC chillipepper rockfish	1969–97	Ralston, Pearson, & Reynolds, 1998
WC northern anchovy	1963–94	Jacobson, Lo, Herrick, & Bishop, 1995
WC Dover sole	1962–91	Brodziak, Jacobson, Lauth, & Wilkins, 1997
WC Pacific hake	1981–93	Dorn & Saunders, 1997
WC sablefish	1970–96	Crone et al., 1997
WC sardine	1970–94	Deriso, Barnes, Jacobson, & Arenas, 1996
WC widow rockfish	1969–96	Ralston & Pearson, 1997
WC yellowtail rockfish	1963–93	Tagart, Ianelli, Hoffman, & Wallace, 1997

collapses, the recruitment time series may have consistently low values until the stock rebuilds. Thus, strong autocorrelation is considered to be a necessary, but an insufficient, criterion for the identification of those stocks that are being influenced by decadal scale shifts in atmospheric forcing.

Time series that exhibited strong autocorrelation (≥ 0.4) were further analyzed using intervention analysis. Intervention analysis is an extension of autoregressive integrated moving average time-series models (ARIMA) (Box & Tiao, 1975), and Hare and Francis (1995) have documented the history of its application in fisheries science. Intervention analysis was used to determine if

changes in production of North Pacific marine fish stocks were coincident with the change in the phase in the PDO in 1977. Specifically we test whether step interventions have resulted in shifts in the mean level of production of these fish stocks. The test is analogous to a two-sample *t* test applied to autocorrelated data (Mantua et al., 1997).

Hollowed and Wooster (1995) reasoned that if recruitment success is dependent on a sequence of events, then a prolonged semi-permanent shift in ocean conditions will influence only one of several conditions necessary for successful recruitment. Stocks that exhibit this type of recruitment response would show change either in the probability of a strong year class, or in the amplitude of strong year classes when they do occur (expressed as a change in the mean level of recruitment). The statistical signature of this type of recruitment response would be a measurable change in the coefficient of variation in the recruitment time series. To test for this type of response, we calculated the coefficient of variation for three time periods: 1965–1976, 1977–1988 and 1989 to present. These periods coincide with different phases in North Pacific ecosystem forcing. A shift in either the amplitude of strong year classes or the frequency of strong year classes would influence the coefficient of variation.

2.4.2. Relation of recruitment to Niño North

Evidence of a relationship between Niño North and marine fish production necessitated a comparison of the frequency of strong year classes during Niño North conditions with the frequency of strong year classes in other years. Years of possible forcing related to Niño North were identified using the monthly SST anomalies derived from coastal COADS data. Recruitment time series were compared with SST data from the region closest to the spawning location of the fish stock or, in the case of salmon, the location of their entry into the open ocean. Following Hollowed and Wooster (1995), the recruitment time series were log-transformed and standard deviates were estimated for each year using the mean and standard deviation for the period 1970–1983. This time period was selected because it includes seven years both before and after the 1976/77 shift. Strong year classes were defined as years when the standard deviates were ≥ 0.5 (i.e. at or above the median of the time series before transformation). Statistical comparisons of the probability of strong year classes when Niño North conditions were present to the probability in other years were performed, using a test of differences between proportions and the Fisher Exact test (Zar, 1984).

3. Results

3.1. El Niño

Analysis of the duration and timing of El Niño events in the tropics based on the JMA data, revealed several notable features (Table 1). The duration of El Niño events ranged from 5 to 17 months, with an average duration of 11 months. Of the fourteen events identified, four lasted less than 9 months, and five lasted for 13 months or longer. Most of the events started in spring or early summer; ten starting between March and June. The 1993 event started early, in March, whereas three events (1968–70, 1986–88, and 1994–95) started late (September and November). Most events ended early in the year, with nine ending in January–April. Three ended in July–September (1953, 1982–93, and 1993).

Estimates of the frequency and intensity of El Niño events in the tropics also revealed some notable common characteristics. The average intensity (temperature anomaly) of El Niño events was 1.5°C, and ranged from 0.8° to 3.4°C. Intense events were in 1972–73, 1982–83 and 1997–98, whereas the 1953 and 1963–64 events were relatively weak. The duration of tropical El Niño events, measured in the number of Niño months in five-year periods from 1950, ranged from 8 to 24, with an average of 16 months. The numbers of Niño months were low during 1960–64 (8 months) and 1970–79 (12 months) but high during 1965–69 and from 1980 onwards (18–24 per five years).

3.2. *La Niña*

Analysis of the duration and timing of La Niña conditions in the tropics revealed eleven events occurred between June 1949 and February 1996 (Table 3). The average duration of La Niña conditions was 11.7 months, ranging from 6 to 23 months. Two events were particularly long, 1954–56 (23 months) and 1970–72 (21 months). The average intensity was 1.3°C, with a range 0.6° to 1.9°C. Particularly intense La Niña events occurred in 1954–56 (1.9°C) and 1973–74 (1.7°C). The average number of La Niña months per five years was 14.7 with a range of none (1990–94) to 33 (1970–74).

3.3. *Niño North*

During the period 1950–1998, the El Niño events associated with maximum warming at higher latitudes, a condition we call Niño North, were those of 1957–58, 1963, 1982–83, 1993, and 1997 (Fig. 2). The intense tropical El Niño event of 1972–3 had little influence north of 32°N. On the other hand, there were periods of extensive warming at higher latitudes, as in 1959 and 1981, that appeared to be unrelated to El Niño events (Fig. 2), but in several examples (e.g. 1954, 1967, 1981, and 1994) the warming appeared to originate in the north and spread southward (Fig. 2).

The average duration of Niño North conditions varied between region; being eight months in

Table 3
Timing, duration and intensity of La Niña events in equatorial regions of the Pacific

Year	JMA (months)	Intensity (°C)
1949–50	6/49–6/50 (13)	1.5
1954–56	4/54–1/56 (23)	1.9
1956–57	7/56–1/57 (7)	0.8
1964–65	4/64–1/65 (10)	1.1
1967–68	8/67–3/68 (8)	1.1
1970–72	5/70–1/72 (21)	1.5
1973–74	4/73–3/74 (12)	1.7
1975–76	5/75–3/76 (11)	1.6
1978	4/78–9/78 (6)	0.6
1988–89	5/88–4/89 (12)	1.6
1995–96	9/95–2/96 (6)	0.7

Fig. 2. Monthly sea surface temperature anomalies in 0.5°C increments for the years 1950–1999 for COADS regions 1–10 (locations shown in Fig. 1).

the WC region, ten months in the EGOA region, and five months in the WGOA/EBS region (Table 4). In the WC region Niño North conditions were observed after all but three of the tropical events (1951–52, 1953–54 and 1986–88) (Table 4). Whereas in the EGOA region, Niño North conditions were observed after only six out of the sixteen tropical events, and after nine of the sixteen in the WGOA/EBS region. It is interesting to note that the strong 1972–73 El Niño event had little impact on either the EGOA or the WGOA/EBS regions.

The lag time between tropical El Niño events and Niño conditions in the North ranged from 0 to 14 months (Table 4), and in most years the ocean warming was detected in the WC region before the EGOA or WGOA/EBS regions. In 1963, ocean warming was detected in the EGOA and the WGOA/EBS regions eight months in advance of the tropical event (Table 4). But in 1993, ocean warming was detected in WC only one month before the tropical event (Table 4).

3.4. Decadal variability

Winter SST (January–March) temperature anomalies have a low frequency variability (Figs. 3a–c). Below average temperatures were observed in 1950–1956, in 1969–1976 (except in 1970) and in 1989–1991. Warm temperature anomalies were observed in several regions in 1957–1964, in 1977–1984. Trends in variability are consistent along the coast. It is interesting to note that after 1988, cool temperatures prevailed until 1998 in the two highest latitude locations (the Bering Sea and Prince William Sound) (Figs. 3b and c).

3.5. Autocorrelation analysis

The amount of autocorrelation between the catch and recruitment time series ranged from 0.9 (Central Alaskan pink) to -0.24 (WC sablefish) (Fig. 4). Salmon, flatfish and Gulf of Alaska

Table 4

Timing and duration of anomalous warm conditions related to tropical El Niño events. Tropical events are identified in the first column. The year and month when warming was identified for each region using the format MM/YY, the duration of the event in months is in parentheses

Equatorial Region B	West coast	Eastern GOA	Western GOA and EBS	Lag WC	Lag GOA	Lag EBS
6/51–2/52 (9)		9/51–12/51 (4)			3	
4–9/53 (6)			7/53–9/53 (3)			3
4/57–4/58 (13)	6/57–9/59 (28)	5/57–8/58 (16)	6/57–6/58 (13) ^b	2	1	2
6/63–1/64 (8)	9/63–1/64 (5)	10/62–2/64 (17)		3	–8	
4/65–2/66 (11)	11/65–12/65 (2) ^a			7		
11/68–1/70 (15)	12/69–3/70 (4)		1/70–4/70 (4)	13		14
4/72–2/73 (11)	10/72–1/73 (4)			6		
6/76–3/77 (10)	11/76–2/77 (4)		6/77–10/77 (5)	5		12
7/77–1/78 (7) ^c	12/77–6/78 (6)		2/78–5/78 ^b	5		7
			12/78–9/79 (10)			
10/79–4/80 (7) ^c	1/80–3/80 (3)			3		
5/82–9/83 (17)	1/83–3/84 (15)	3/83–8/83 (6)	5/83–8/83 (4)	8	10	12
			12/83–1/84 (2) ^a			
9/86–1/88 (17)			10/86–12/86 (3)			1; 6
			3/87–5/87 (3)			
5/91–6/92 (14)	2/92–11/92 (10)			9		
3–7/93 (5)	2/93–7/93 (6)	5/93–8/93 (4)	11/93–12/93 (2) ^a	–1	2	8
10/94–2/95 (5)	2/95–4/95 (3)			4		
	7/95–9/95 (3)					
	12/95–9/96 (10)					
[5/97–]	5/97–8/98 (16)	6/97–4/98 (11)	6/97–8/97 (3)	0	1	1

^a Only 2 month duration.

^b Includes a 2 month gap.

^c Evident in Trenberth's analysis only.

rockfish stocks tended to have high autocorrelation coefficients (≥ 0.4) (Table 5). Gadid stocks, west coast sablefish, Atka mackerel, Pacific herring, west coast flatfish and west coast rockfish stocks all tended to have low autocorrelation coefficients (< 0.4) (Table 6). Washington sockeye, eastern Bering Sea cod, and some west coast rockfish stocks exhibited negative autocorrelation. Three of the five British Columbian salmon stocks had autocorrelation coefficients of < 0.4 . Three of the four chum stocks had low autocorrelation coefficients. In all, 23 of the 29 salmon time series had lag-1 autocorrelation coefficients greater than the cutoff value of 0.4. Of the five eastern Bering Sea flatfish stocks; three showed high autocorrelation, and two had low autocorrelation.

3.6. Coefficient of variation

Hare et al. (1999) estimated coefficients of variation for 28 salmon stocks. Three exhibited a coefficient of variation for the 1977–1988 period that was $> 50\%$ of the pre-1977 level (Table 7). The stocks that showed the most notable increases in variation were the Oregon and California chinook stocks (133% and 171% respectively). Three stocks exhibited a 50% or more decline in

(a)

Temperature Anomalies (Jan - Mar)

Fig. 3. a. Comparison of winter temperature anomalies 1950–1999 for four coastal locations along the U.S. west coast. b. Comparison of winter temperature anomalies 1950–1999 for three coastal locations in the Eastern Gulf of Alaska. c. Comparison of winter temperature anomalies 1950–1999 for three coastal locations in the Western Gulf of Alaska and Bering Sea.

variation during the 1977–1988 period relative to the pre-1977 period (Table 7)—two were from Alaska and one from Washington.

Comparisons of run size variability in 1989–1998 relative to 1977–1988 showed most stocks exhibited greater variability in their run sizes in the 1989–1998 period. Eleven stocks exhibited a coefficient of variation for the 1989–1998 period that was >50% of the 1977–1988 level (Table 7). Three stocks, all from Alaska, showed a 50% decrease in variation for the latter period compared to 1977–1988 (Table 7).

Of the thirty-two time series of recruitment for stocks of pelagic fish and groundfish, only

(b)

Fig. 3 (continued)

twenty-six included seven or more records from before and after 1977. Six of the groundfish stocks showed a coefficient of variation for the 1977–1988 period that exceeded that of the pre-1977 period by $>50\%$ (Table 8), whereas only two stocks showed coefficient of variation that declined from the pre-1977 level by $>50\%$ (Table 6). In 1989–1998, nine groundfish and pelagic stocks exhibited a greater than 50% drop in variability relative to the previous time period. Only three stocks exhibited a $>50\%$ increase in recruitment variability.

3.7. Intervention analysis

We have fitted the salmon catch data using an intervention model that incorporated a 1977 step. Sixteen of the twenty-one salmon stocks analyzed exhibited a significant step change in 1977 ($p < 0.1$) (Table 9). Significant positive steps occurred in eleven of the thirteen Alaskan salmon stocks, whereas a significant negative step occurred in coho stocks in California, Oregon and Washington, and chinook stocks in Oregon and Washington (Table 9).

Intervention analyses were performed on eight groundfish stocks for which there were at least eight data points from prior to 1977. Of these, four stocks showed a significantly positive step in 1977 ($p < 0.05$) (Table 10). It was interesting to note that heavily fished stocks (Pacific ocean perch and thornyhead) showed high autocorrelation but an insignificant step in 1977 (Table 10).

(c)

Fig. 3 (continued)

3.8. Short-term recruitment events

All five of the dominant gadid stocks (EBS and GOA Pacific cod, Pacific hake and EBS and GOA walleye pollock) exhibited low autocorrelation in recruitment. The proportion of strong year classes was higher in years associated with Niño North conditions. Statistical analysis supports the hypothesis that the proportion of strong year classes is statistically higher during years of Niño North conditions for GOA pollock ($p \leq 0.1$), GOA Pacific cod ($p \leq 0.1$) and WC Pacific hake ($p \leq 0.05$) (Table 11). The data for Bering Sea gadid populations do not support the hypothesis that the proportion of strong year classes in years of Niño North conditions is significantly higher than the proportion of strong year classes in other years.

4. Discussion

In this paper we have examined trends in time series of recruitment and stock biomasses for evidence of that climatic shifts induce responses in production of commercial marine fishes. We have found several indications that North Pacific fish stocks have responded to PTV stemming from El Niño and PDO forcing. The apparent relationship between extra-tropical forcing and

Fig. 4. Lag-1 autocorrelation for Northeast Pacific and Bering Sea fish stocks. Time series of catch data were used in the analysis of salmon stocks whereas time series of recruitment were used in the analysis of groundfish and pelagic fish.

recruitment success requires more study to confirm these relationships. This analysis provides a basis for an initial conceptual model that may explain the coherent recruitment patterns observed in marine fish stocks between widely separated distant regions of the North Pacific.

In a recent study McGowan, Cayan, and Dorman (1998) compared SST anomalies from coastal stations along the West Coast to ENSO events. Our study has extended this analysis to include the Gulf of Alaska and Bering Sea regions. We have found a pattern of ocean warming based on COADS data that is similar to that observed at coastal stations, and evidence of ENSO forcing at high latitudes in both in the Gulf of Alaska and in the Bering Sea.

Wallace (1985) presented evidence that El Niño forcing can be transmitted to higher latitudes through: a) the propagation of coastally trapped Kelvin waves, or b) through local forcing of coastal phenomena by anomalous surface winds associated with planetary-scale teleconnection patterns in the atmosphere. Evidence for both these two sources of distant ocean forcing was observed in our study. Niño North conditions were most prevalent in the WC region, followed by the WGOA/EBS region. We interpret this finding as follows. Since Niño North conditions can result from both coastally trapped waves and shifts in atmospheric forcing in the WC region, it

Table 5

Results of autocorrelation analysis. Rho is the lag-1 autocorrelation coefficient. CV is the coefficient of variation. Regional abbreviations same as Table 7

Stock	Pts.	Rho	CV
W. AK chinook	47	0.71	0.37
W. AK chum	47	0.81	0.66
W. AK coho	49	0.69	1.00
W. AK pink	49	0.59	1.45
W. AK sockeye	48	0.75	0.78
C. AK chinook	47	0.74	0.67
C. AK chum	47	0.44	0.41
C. AK coho	49	0.76	0.68
C. AK pink	49	0.91	0.73
C. AK sockeye	48	0.67	0.72
S. AK chinook	47	0.47	0.20
S. AK chum	47	0.77	1.04
S. AK coho	49	0.67	0.60
S. AK pink	49	0.66	0.83
S. AK sockeye	48	0.82	0.51
BC chinook	47	0.89	0.37
BC chum	47	0.17	0.58
BC coho	48	0.48	0.28
BC pink	49	0.42	0.53
BC sockeye	48	0.36	0.56
WA chinook	47	0.87	0.36
WA chum	47	0.55	0.63
WA coho	49	0.72	0.42
WA pink	49	0.59	1.26
WA sockeye	48	0.04	0.59
OR chinook	47	0.60	0.39
OR coho	49	0.60	0.74
CA chinook	47	0.34	0.36
CA coho	46	0.49	1.06

is here that there is the highest probability of observing such conditions. In the northern regions, Niño North conditions depend on the influence of atmospheric forcing on the position and intensity of the Aleutian low.

Surface flow trajectories simulated using the Ocean Surface CUREnt Simulations (OSCURS) model reveal that Niño North conditions coincide with years of strong northward advection directed into the head of the Gulf of Alaska (Ingraham, Ebbesmeyer, & Hinrichsen, 1998). These simulations are consistent with Strub's review (pers.com.) in which he found that the signal of ENSO is transmitted along the boundaries of the NE Pacific by a mix of poleward transport and anomalous poleward winds. OSCURS model simulations indicate that shifts in wind forcing will accelerate coastal currents in the WGOA region more intensely than in the EGOA. This may explain why Niño North conditions were more prevalent in the WGOA/EBS region (Table 4).

The frequency of El Niño events may influence the interpretation of decadal ocean temperature

Table 6

Results of autocorrelation analysis on Northeast Pacific groundfish and small pelagic species. Definitions same as Table 7

Stock	pts	Rho	CV
AI Atka mackerel	21	−0.10	0.77
AI POP	32	0.01	1.05
EBS Alaska plaice	26	0.68	0.63
EBS arrowtooth flounder	28	0.40	0.75
EBS flathead sole	21	0.50	0.48
EBS Greenland turbot	27	0.75	0.79
EBS Pacific cod	21	−0.07	0.64
EBS Pacific herring	36	0.42	0.91
EBS POP	39	0.53	0.75
EBS rock sole	23	0.48	0.67
EBS walleye pollock	34	0.06	0.69
EBS yellowfin sole	42	0.19	0.57
GOA arrowtooth flounder	24	0.73	0.39
GOA Pacific cod	21	−0.10	0.38
GOA Pacific halibut	42	0.81	0.44
GOA PWS herring	24	−0.17	1.39
GOA Sitka herring	28	−0.07	1.44
GOA POP	33	0.34	1.14
GOA sablefish	20	0.74	0.72
GOA thornyhead	32	0.48	0.34
GOA walleye pollock	35	0.40	1.01
WC bocaccio	28	−0.09	1.62
WC canary rockfish	31	0.18	0.62
WC Dover sole	30	0.13	0.44
WC northern anchovy	32	0.16	1.05
WC Pacific hake	27	−0.21	1.59
WC Pacific mackerel	48	0.37	1.94
WC widow rockfish	28	0.45	0.67
WC yellowtail rockfish	31	0.31	0.34
WC sablefish	27	−0.24	0.84

data. Wooster and Hollowed (1995) hypothesized that eras of warm ocean conditions have been initiated by ENSO events. The data presented here suggest that prolonged periods of warm coastal conditions at northern latitudes have been associated with periods of highly frequent El Niño events (e.g., 1965–1969 and 1980–1999). This suggests that low frequency trends in extra-tropical ocean temperature in the North Pacific may be partially explained by the frequency of El Niño events as manifested in Niño North conditions.

Several authors have noted decadal scale shifts in the abundance of marine fish populations (Hare et al., 1999; Francis, Hare, Hollowed, & Wooster, 1998; Andersen & Piatt, 1999; Beamish et al., 1999; Bakun, 1996). Numerous hypotheses have been proposed to explain the apparent relationship between decadal scale shifts in ocean conditions and marine fish production (for overviews see Hayward, 1997; Francis et al., 1998; McGowan et al., 1998). Our study suggests that, the underlying cause of changes in fish biomass can not always be attributed to a persistent

Table 7

Summary of total data points and total coefficient of variation (CV) for Pacific salmon stocks based on all data and three time periods: 1965–1976, 1977–1988, 1989–1998 for Pacific salmon stocks. Values in parentheses represent the proportional change from the previous period. Regional abbreviations are as follows: W. AK=western Alaska, C. AK=central Alaska, S. AK=southeast Alaska, BC=British Columbia, WA=Washington, OR=Oregon, CA=California

Stock	Pts. 65–98	CV 65–98	Pts. 65–76	CV 65–76	Pts. 77–88	CV 77–88	Pts. 89–98	CV 89–98
W. AK Chinook	47	0.37	12	0.27	12	0.20 (–0.26)	7	0.35 (0.75)
W. AK Chum	47	0.66	12	0.41	12	0.22 (–0.46)	7	0.57 (1.62)
W. AK coho	49	1.00	12	0.56	12	0.41 (–0.27)	9	0.37 (–0.10)
W. AK pink	49	1.45	12	1.25	12	1.23 (–0.02)	9	0.62 (–0.50)
W. AK sockeye	48	0.78	12	0.82	12	0.30 (–0.63)	8	0.41 (0.37)
C. AK chinook	47	0.67	12	0.35	12	0.29 (0.17)	7	0.13 (–0.55)
C. AK chum	47	0.41	12	0.39	12	0.32 (–0.18)	7	0.22 (–0.31)
C. AK coho	49	0.68	12	0.38	12	0.34 (–0.11)	9	0.35 (0.03)
C. AK pink	49	0.73	12	0.58	12	0.18 (–0.69)	9	0.33 (0.83)
C. AK sockeye	48	0.72	12	0.38	12	0.31 (–0.18)	8	0.21 (0.32)
S. AK chinook	47	0.20	12	0.13	12	0.14 (0.08)	7	0.15 (0.07)
S. AK chum	47	1.04	12	0.55	12	0.43 (–0.22)	7	0.32 (–0.26)
S. AK coho	49	0.60	12	0.35	12	0.36 (0.03)	9	0.33 (–0.08)
S. AK pink	49	0.83	12	0.69	12	0.62 (–0.10)	9	0.27 (–0.57)
S. AK sockeye	48	0.51	12	0.29	12	0.25 (–0.14)	8	0.24 (–0.04)
BC chinook	47	0.38	12	0.17	12	0.22 (0.28)	7	0.73 (2.32)
BC chum	47	0.58	12	0.69	12	0.56 (–0.19)	7	0.43 (–0.23)
BC coho	48	0.28	12	0.24	12	0.14 (–0.42)	8	0.56 (3.00)
BC pink	49	0.53	12	0.48	12	0.45 (–0.06)	9	0.78 (0.73)
BC sockeye	48	0.56	12	0.29	12	0.45 (0.55)	8	0.56 (0.24)
WA chinook	47	0.36	12	0.22	12	0.17 (–0.23)	7	0.27 (0.59)
WA chum	47	0.63	12	0.70	12	0.34 (–0.51)	7	0.37 (0.09)
WA coho	49	0.42	12	0.24	12	0.20 (–0.17)	9	0.88 (3.40)
WA pink	49	1.26	12	1.21	12	1.14 (–0.06)	9	1.08 (–0.05)
WA sockeye	48	0.59	12	0.36	12	0.47 (0.31)	8	0.78 (0.65)
OR chinook	47	0.39	12	0.24	12	0.56 (1.33)	7	0.38 (–0.32)
OR coho	49	0.74	12	0.34	12	0.39 (0.15)	9	1.51 (2.87)
CA chinook	47	0.36	12	0.17	12	0.46 (1.71)	7	0.53 (0.16)
CA coho	46	1.06	12	0.54	12	0.65 (0.20)	6	1.68 (1.59)

shift in year-class strength. For example, strong autocorrelation in recruitment coupled with a significant intervention in 1977 was only observed in salmonids and some flatfish. The dominant gadid species in the WC and GOA regions exhibited an intermittent recruitment pattern punctuated by strong year classes that may be associated with Niño North conditions.

Our results suggest that the increase in gadid stock biomass is a consequence of the storage of biomass in the population resulting from these fishes' moderate longevities (maximum age ca. 20 years). Strong year classes may play an important role in ensuring that iteroparous species survive periods of unfavorable environmental conditions (Leaman & Beamish, 1984; Fogarty, 1993). Chesson (1983) termed this phenomenon the 'Storage Effect'. He noted that co-existence

Table 8

Summary of total data points, and coefficient of variation (CV) for groundfish and pelagic stocks based on all data and three time periods: 1965–1976, 1977–1988 and 1989–1998. Values in parentheses represent the proportional change from the previous period. Regional abbreviations are as follows: AI=Aleutian Islands, EBS=Eastern Bering Sea, GOA=Gulf of Alaska, WC=west coast

Stock ^a	Pts.	CV 65– 98	Pts. 65– 76	CV 65– 76	Pts. 77– 88	CV	Pts.	CV 89–98
AI Atka mackerel	21	0.77	2		12	0.75	7	0.56 (–0.25)
AI POP	32	1.05	12	0.58	12	0.60 (0.03)	2	
EBS Alaska plaice	26	0.63	8	0.33	12	0.47 (0.42)	6	5.01 (9.66)
EBS A. flounder	28	0.75	9	0.48	12	0.60 (0.25)	7	0.54 (–0.10)
EBS flathead sole	21	0.48	2		12	0.32	7	0.36 (0.13)
EBS Greenland turbot	27	0.79	8	0.41	12	0.84 (1.05)	7	0.72 (–0.14)
EBS Pacific cod	21	0.64	2		12	0.66	7	0.45 (–0.32)
EBS Pacific herring	36	0.91	12	0.79	12	0.77 (–0.03)	3	
EBS POP	39	0.75	12	0.81	12	1.11 (0.31)	7	0.05 (–0.96)
EBS rock sole	23	0.67	4		12	0.53	7	0.49 (–0.08)
EBS walleye pollock	35	0.69	12	0.44	12	0.78 (0.77)	9	0.89 (0.14)
EBS yellowfin sole	42	0.57	12	0.27	12	0.63 (1.33)	6	0.52 (–0.18)
GOA A. flounder	24	0.39	7	0.48	12	0.31 (–0.35)	5	0.12 (–0.61)
GOA Pacific cod	21	0.38	2		12	0.35	7	0.42 (0.20)
GOA Pacific halibut	42	0.44	12	0.30	12	0.16 (–0.47)	2	
GOA PWS herring	24	1.39	8	1.16	12	1.33 (0.15)	4	0.74 (–0.44)
GOA Sitka herring	28	1.44	9	1.90	12	1.33 (–0.30)	7	0.67 (–0.50)
GOA POP	33	1.14	12	1.07	12	0.76 (–0.29)	4	0.32 (–0.58)
GOA sable fish	20	0.72	0		12	0.60	8	0.46 (–0.23)
GOA thornyhead	32	0.34	12	0.35	12	0.37 (0.06)	5	0.13 (–0.65)
GOA walleye pollock	35	1.01	12	0.88	12	0.86 (–0.02)	8	1.27 (0.48)
WC bocaccio rockfish	28	1.62	9	0.87	12	1.80 (0.52)	7	1.10 (–0.39)
WC canary rockfish	32	0.61	11	0.44	12	0.55 (0.25)	9	0.51 (–0.07)
WC chilipepper	29	0.84	8	0.56	12	1.12 (1.00)	9	0.56 (–0.50)
WC Dover sole	30	0.44	12	0.22	12	0.13 (–0.41)	3	0.34 (1.62)
WC Pacific hake	27	1.59	7	1.29	12	1.57 (0.22)	8	0.62 (–0.61)
WC Pacific mackerel	49	1.92	12	2.79	12	1.04 (–0.63)	9	0.26 (–0.75)
WC POP	40	1.01	12	0.49	12	0.32 (–0.35)	7	0.17 (–0.47)

(continued on next page)

between competing species could be enhanced if extreme year classes of competing species were favored by opposing forcing factors. Recent harvest strategies for gadids in the North Pacific and Bering Sea are allowing a high percentage of survival of adults thus maintaining the contributions of strong year classes to future generations. Fogarty (1993) suggested that strong year classes may occur when a species' abundance is sufficient to overwhelm their competitors or predators. This process may be particularly important for gadid populations that experience intense juvenile

Table 8 (continued)

Stock ^a	Pts.	CV 65–98	Pts. 65–76	CV 65–76	Pts. 77–88	CV	Pts.	CV 89–98
WC northern anchovy	32	1.05	12	1.08	12	0.73 (–0.32)	6	0.71 (–0.47)
WC sablefish	27	0.84	7	0.47	12	0.80 (0.70)	8	1.70 (1.13)
WC widow rockfish	28	0.67	8	0.93	12	0.47 (–0.50)	8	0.22 (–0.53)
WC yellowtail rockfish	31	0.34	12	0.39	12	0.31 (–0.21)	5	0.34 (0.10)

^a A. flounder=arrowtooth flounder; POP=Pacific ocean perch; PWS=Prince William Sound.

Table 9

Results of intervention analysis on Northeast Pacific salmon. ARMA is the type of Autoregressive Moving Average model fit to the time series. $p(\text{Step77})$ is the significance of a 1977 step intervention. Direction is the change in catch level if a 1977 intervention was statistically significant at a 0.10 level or greater. Regional abbreviations same as Table 5

Stock	Pts.	ARMA	$p(\text{Step77})$	Direction
W. AK chinook	45	(1,0)	0.070	+
W. AK chum	45	(1,0)	0.041	+
W. AK coho	45	(1,0)	0.001	+
W. AK sockeye	45	(5,0)	0.001	+
C. AK chinook	45	(0,1)	0.058	+
C. AK coho	45	(1,0)	0.001	+
C. AK sockeye	45	(0,1)	0.001	+
C. AK Pink	45	(0,2)	0.001	+
S. AK chinook	45	(0,1)	0.198	
S. AK chum	45	(1,0)	0.487	
S. AK coho	45	(1,0)	0.001	+
S. AK sockeye	45	(1,0)	0.001	+
S. AK pink	45	(0,0)	0.001	+
BC chinook	45	(1,0)	0.356	
BC coho	45	(1,0)	0.347	
WA chinook	45	(0,0)	0.001	–
WA coho	45	(0,1)	0.072	–
OR chinook	45	(0,1)	0.017	–
OR coho	45	(1,0)	0.018	–
CA chinook	45	(0,1)	0.163	
CA coho	45	(1,0)	0.028	–

predation, as is the case for Bering Sea pollock where cannibalism prevails (Livingston, Ward, Lang, & Yang, 1993).

Evidence of a higher probability of strong year classes of major gadid species during Niño North conditions is consistent with previous studies of WC and GOA gadids. Bailey (1981) found that strong year classes of Pacific hake were associated with winters of warm ocean conditions. He hypothesized that the strong recruitment resulted from a reduction in offshore advection. Horne

Table 10

Results of intervention analysis on Northeast Pacific groundfish and small pelagic species. Definitions same as Table 7

Stock	Pts.	ARMA	$p(\text{Step77})$	Direction
EBS Alaska plaice	28	(1,0)	0.799	
EBS arrowtooth flounder	28	(0,0)	0.002	+
EBS Greenland turbot	26	(0,1)	0.016	–
EBS POP	38	(1,0)	0.836	
GOA arrowtooth flounder	30	(0,0)	0.001	+
GOA halibut	24	(1,0)	0.049	+
GOA POP	33	(1,0)	0.487	
GOA thornyhead	31	(1,0)	0.912	

Table 11

Results of Fisher exact tests of the following hypothesis. Ho: The proportion of strong year-classes in years of Niño North conditions is not greater than the proportion of strong year-classes in other years. Ha: The proportion of strong year-classes in years of Niño North conditions is greater than the proportion of strong year-classes in other years

Period	Species	P value
All Years	WC Pacific hake	0.02
All Years	GOA Pacific cod	0.05
All Years	GOA walleye pollock	0.09
All Years	EBS Pacific cod	0.10
All Years	EBS walleye pollock	0.45
Post 76	GOA Pacific cod	0.07
Post 76	GOA walleye pollock	0.06
Post 76	EBS Pacific cod	0.12
Post 76	EBS walleye pollock	0.41

and Smith (1997) observed that the locations of spawning populations of Pacific hake shifted polewards during warm years. However they also noted that warm-water years do not guarantee that recruitment is higher than usual. Megrey, Hollowed, Hare, Macklin, and Stabeno (1996) proposed that strong year classes of GOA pollock are associated with years when periods of vigorous Gulf circulation, which replenishes nutrients in shelf waters, are followed by periods of relaxed circulation in the spring. As noted earlier, several of the years associated with Niño North conditions were also years when circulation in the Gulf of Alaska gyre was directed to the head of the Gulf and surface flow was accelerated.

5. Conceptual model

Based on the findings of our study, we offer a conceptual model to explain patterns of marine fish production in different regions of the North Pacific. Under conservative exploitation strategies, recruitment of marine fish in the Northeast Pacific is influenced by two sources of large scale

atmospheric forcing: the PDO and ENSO. These forcing factors can be considered sources of PTV. The influence of PTV caused by atmospheric phenomena is retained in iteroparous stocks through the storage effect. The frequency of ENSO events increased coincidentally with a major shift to the positive phase of the PDO in the late 1970s.

The coupling of forcing events resulted in a dramatic shift in the abundance trends of marine fish stocks in the North Pacific. Pacific salmon and selected flatfish stocks show production patterns that are consistent with the oscillations of the PDO. When ocean conditions are favorable for survival in the Gulf of Alaska and Bering Sea, they are less favorable along the U.S. West Coast. This phase mismatch may be attributed to differential responses by zooplankton to the oceanic conditions associated with the positive phase of the PDO (Brodeur, Frost, Hare, Francis, & Ingraham, 1996). Some gadid populations appear to respond to large-scale forcing at the temporal scale of ENSO forcing. When ENSO forcing induces Niño North conditions in the North Pacific, ocean conditions favor recruitment of gadid populations in the WC and GOA regions. This process may explain the synchronisation observed in the occurrence of extreme year classes of Pacific hake, GOA Pacific cod and GOA pollock stocks. Biomass trajectories of major gadid populations within the region have increased in recent decades, because of a higher frequency of ENSO events. Verification of this model through mechanistic research is a necessary next step. Differentiating between shifts in production caused by annual events and those caused by long-term changes in marine production is critical for designing and implementing successful process oriented research on the effects of climate.

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