



# Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea

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## Abstract

This paper provides a retrospective analysis of the relationship of physical oceanography and biology and recruitment of three Eastern Bering Sea flatfish stocks: flathead sole (*Hippoglossoides elassodon*), northern rock sole (*Lepidopsetta polyxystra*), and arrowtooth flounder (*Atheresthes stomias*) for the period 1978–1996. Temporal trends in flatfish production in the Eastern Bering Sea are consistent with the hypothesis that decadal scale climate variability influences marine survival during the early life history period. Density-dependence (spawning stock size) is statistically significant in a Ricker model of flatfish recruitment, which includes environmental terms. Wind-driven advection of flatfish larvae to favorable nursery grounds was also found to coincide with years of above-average recruitment through the use of an ocean surface current simulation model (OSCURS). Ocean forcing of Bristol Bay surface waters during springtime was mostly shoreward (eastward) during the 1980s and seaward (westerly) during the 1990s, corresponding with periods of good and poor recruitment. Distance from shore and water depth at the endpoint of 90-day drift periods (estimated time of settlement) were also found to correspond with flatfish productivity. © 2002 Elsevier Science Ltd. All rights reserved.

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## Contents

1. Introduction . . . . .	236
2. Rationale for analysis . . . . .	237
3. Methods . . . . .	237
4. Results . . . . .	239

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## 1. Introduction

Reasonably accurate methods for simulating annual production of commercially exploited marine fishes are needed not only to protect the reproductive potential of the stock from overfishing, but also to develop realistic models of the impact of commercial fishing on marine ecosystems. Stock assessment analysts commonly use two types of simulation methods. In the first approach, projections are based on random draws from a distribution with statistical properties that match historical observations of year-class strength. This approach can be extended to address decadal scale variability in ocean conditions by partitioning the time series into periods of climatic conditions that are favorable or unfavorable to survival. Partitioning the time series in this manner assumes that over the range of expected spawning biomass levels, the influence of climate on oceanographic conditions and the carrying capacity is the overriding factor influencing fish production. The second approach assumes a relationship between some measure of reproductive potential (typically spawning biomass) and recruitment. Neither of these approaches is fully representative of the combined role of physical and biological regulation of fish production. There is growing recognition of the need for stock projection models that address the role of reproductive potential and oceanography on year-class strength (Iles & Beverton, 1998).

This study provides a comprehensive retrospective analysis of the relationship of physics and biology and recruitment of three flatfish stocks: flathead sole (*Hippoglossoides elassodon*), northern rocksole (*Lepidopsetta polyxystra*), and arrowtooth flounder (*Atheresthes stomias*). These three species comprise an important segment of the Bering Sea ecosystem. Rock sole consume benthic infauna (primarily polychaetes and other marine worms), whereas flathead sole and arrowtooth flounder consume pelagic prey (Lang, Livingston, & Miller, 1995). Arrowtooth flounder, in particular, is a large piscivorous species capable of consuming large numbers of juvenile fish annually (Yang & Livingston, 1986). Also these species are the target of a high value commercial fishery. Bering Sea flatfish have been lightly exploited because of by-catch restrictions that limit the annual amount of Pacific halibut that can be taken in groundfish fisheries. In the last decade, the combined annual catch of these three species has averaged over 80,000 ton.

The variability of the Bering Sea climate during spring is just beginning to receive significant attention (Bond & Adams, in press). Both the air–sea processes that dominate the climate forcing, and the modes that characterize the climate variability, vary with season (Overland, Bond and Adams, in press). Retrospective studies have revealed that these three periods of different forcing patterns may be linked to key oceanographic features of the region including: (a) the timing of the spring bloom (Stabeno, Bond, Kachel, Salo, & Schumacher, 2001); (b) sea surface temperature anomalies; (c) the extent of sea ice (Stabeno et al., 2001); and (d) patterns of cross-shelf advection (Rozenkranz, Tyler, & Kruse, 2001; Wespestad, Fritz, Ingraham, & Megrey, 2000).

Retrospective analysis of the influence of climate forcing on marine fish recruitment has revealed that year-class success (measured by recruitment) of flathead sole, rock sole, and arrowtooth flounder follows a pattern that is consistent with shifts in atmospheric forcing in the region (Hare & Mantua, 2000; Hollowed, Hare & Wooster, 2001). These findings illustrate the need for focused retrospective analyses to reveal potential mechanisms underlying the apparent association between recruitment patterns of winter—spawning flatfish and climate variability. The dominant modes of climate forcing in the southeastern Bering Sea during the winter are the Arctic Oscillation (AO) and the Pacific Decadal Oscillation (PDO) (Overland, Adams, & Bond, 1999). These modes influence the distribution and intensity of winter storms represented by the position and intensity of the Aleutian Low (AL). Overland et al. (1999) identified three periods of different patterns of winter climate forcing during the last 30 years: 1967–1976 (negative PDO, mixed AO,

and positive AL), 1977–1988 (positive PDO, negative AO, and negative AL), and 1989–1998 (mixed PDO, positive AO, and mixed AL).

This analysis represents the first phase of what we hope will lead to detailed process studies targeting flatfish recruitment processes. We recognize that retrospective analyses of this sort have mixed success (Drinkwater & Myers, 1987; Myers, 1991). However, some of the failures of retrospective models may be attributable to climate scale variability that had not been recognized at the time these studies were carried out. The role of climate variability will be formally considered in our analysis. Further, recent studies have shown that the likelihood of spurious correlation occurring can be reduced by limiting the analysis to factors that are likely to influence survival during the early life history phase (e.g. Megrey, Hollowed, Hare, Macklin, & Stabeno, 1996; Rozenkranz et al., 2001; Tyler, 1992).

## 2. Rationale for analysis

To explore the potential mechanisms underlying the apparent associations between the recruitment patterns of winter and spring/summer spawning flatfish and climate variability, we formulated the following hypotheses:

1. Wind-driven advection of larvae during spring to favorable near-shore settlement habitat is an important requirement for good survival.
2. The availability of food (zooplankton) for larvae is important for good survival.
3. Sea surface temperature has been identified as a major determinate of year-class production for rock sole (Fargo & McKinnell, 1989), because it influences both metabolic and growth rates.
4. The location and intensity of the Aleutian low pressure center are primary indicators of the winter climate system in the Bering Sea (Overland et al., 1999). The AO index has been linked to the variability in the Aleutian low pressure center and has exhibited changes over decadal time periods that appear to be in-phase with periods of favorable recruitment of winter spawning flatfish. Thus the AO index was examined as a variable for possible correspondence with recruitment productivity.

## 3. Methods

Estimates of Bering Sea flatfish recruitment are available from age-structured statistical models used in the annual stock assessments of the Bering Sea/Aleutian Islands flatfish resources (NPFMC, 2000). These assessments utilize fishery and NMFS trawl survey age composition data as well as biomass estimates based on trawl surveys and fishery catch information to produce numerical estimates of age-specific abundance from 1970–2001 (shown relative to the strongest year class for each species in Fig. 1). These flatfish species are not captured by the survey trawls until ages four or five, so recruitment information for this study are included up to 1996.

It is well known that shallow sea areas, such as estuaries and bays, are important nursery habitats for the early life-history stages of flatfish species worldwide (Norcross, Holladay, Dressel, & Frandsen, 1996; several papers in NJSR, Vol. 27, 1991). To analyze the potential advection of flatfish larvae from spawning areas to nursery grounds in a given year, the ocean surface current simulation (OSCURS) model was employed in conjunction with known temporal and spatial information on flatfish spawning. The OSCURS model calculates 24 h water movement in the North Pacific Ocean and Bering Sea by converting the daily sea level pressure grid to east–west wind and surface mixed layer current velocity and then adding the long-term mean geostrophic currents (Ingraham & Miyahara, 1988).

The estimated center of spawning concentrations and known larval duration of winter spawning flatfish

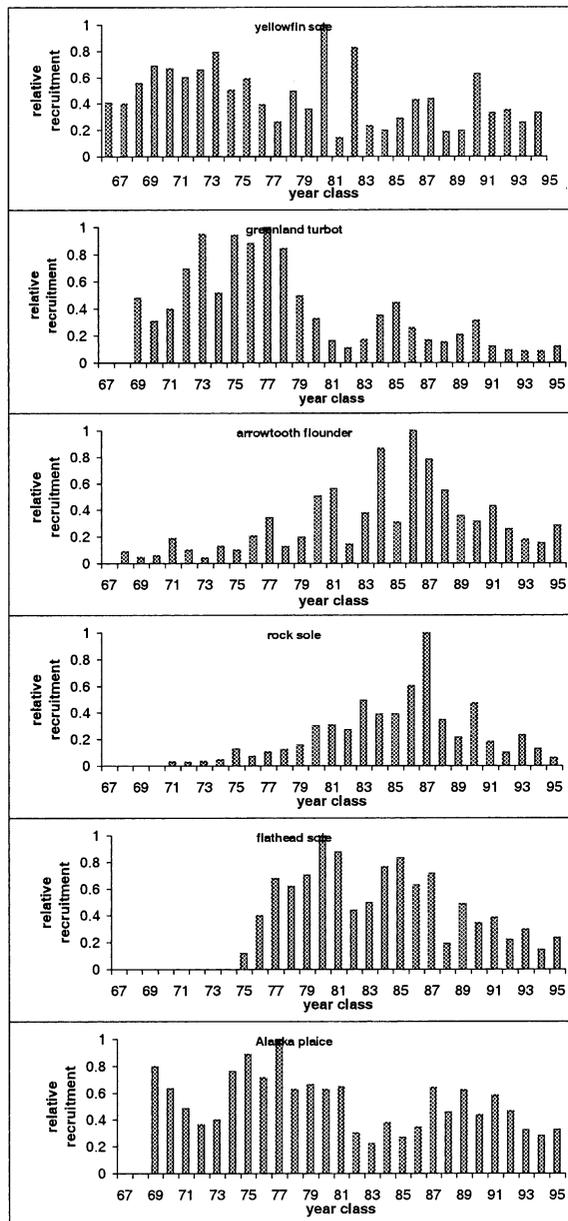


Fig. 1. Estimated relative recruitment of Eastern Bering Sea flatfish species from stock assessment models of population abundance.

were used to determine the starting point and duration for the wind-drift surface current simulations. Simulations were started at 56°N, 164°W for a 90-day period from April 1 to June 30. End points of the simulated drift were used as an estimator for location of settlement after 90 days by calculating depth, distance from land and compass direction from start point to end point.

A time series of sea ice retreat was used to index prey availability. This index is based on the assumption that zooplankton production is proportional to primary production. At high latitudes characteristic of the Bering Sea, primary productivity in the spring is determined by a combination of the date of the ice retreat

and the end of strong storm activity, which prevents stabilization of the water column. Hunt et al. (in press) determined that the timing of the spring phytoplankton bloom, characterized as either early or late, can be estimated by the date of ice retreat at a oceanographic station located at 56.88°N and 164.03°W. Ice retreat after 27 March corresponds to an early plankton bloom, whereas if it occurs prior to this date the bloom tends to be delayed until the water column becomes thermally stratified. We extended their work from weekly ice coverage data to include years from 1982–1994 to discern if the early or late spring phytoplankton blooms corresponded to years of enhanced or depressed flatfish productivity. Observations of sea surface temperature taken at the Pribilof Islands were averaged for each year from 1972–1996 for inclusion in the analysis, as were data for the AO Index.

We applied a rank-based nonparametric procedure to look for change points in each environmental and recruitment time series (Lanzante, 1996). This procedure assumes a step-change in the median of the time series; it uses a statistic based on the sum of the ranks before and after each time step to determine the point of greatest change and test the significance of the change.

To evaluate the effects of the environmental variables on estimated recruitment, a nonlinear statistical model was employed. A Ricker stock recruitment curve with environmental factors was fitted for stocks of each of the three species—the arrowtooth flounder, flathead sole, and rock sole:

$$R = \alpha S e^{(-\beta S + e_1 V_1 + e_2 V_2 + \dots + e_9 V_9)}$$

where  $R$  and  $S$  are recruitment and stock in millions of fish and kilotons of female spawning biomass, respectively,  $\alpha$  is a density-independent parameter,  $\beta$  is a density-dependent parameter, and  $V_1$ – $V_9$  are the following environmental variables:  $V_1$ , compass direction of larval endpoint;  $V_2$ , ending larval drift depth (m);  $V_3$ , ending larval drift distance in nautical miles from land (nmi = 1.83km);  $V_4$ , AO;  $V_5$ , Pribilof Islands Sea Surface temperature (°C);  $V_6$ , Early spring bloom (1=early spring bloom, 0 otherwise);  $V_7$ , May spring bloom (1=May spring bloom, 0 otherwise);  $V_8$ , Late spring bloom (1=late spring bloom, 0 otherwise); and  $V_9 = V_2^* V_3$ .

The probability of a particular model being correct given the recruitment data, assuming the models considered have equal prior probability, was estimated with the standard Bayesian formula:

$$\Pr(\text{Model}_i | \text{data}) = \frac{L(\text{data} | \text{Model}_i)}{\sum_i L(\text{data} | \text{Model}_i)}$$

where  $L(\text{data} | \text{Model}_i)$  is the maximum likelihood of the data given Model  $i$ ; the prior probabilities cancel because of the assumption of equal probability (Hilborn & Mangel, 1997). First, a series of models that include  $\alpha$  and either  $\beta$  or one of the environmental variables was considered for each species to determine which model had the highest probability (>90%) of being correct for each species. Second, a series of models that included the highest probability coefficients from the first analysis and one of the environmental variables was considered.

After an initial examination of the temporal and spatial trends in spawning and larval stages and consideration of the mechanisms hypothesized for flatfish recruitment, we have restricted our analysis to the winter spawning flatfish (rock sole, flathead sole and arrowtooth flounder). Yellowfin sole have not been included because they spawn in the nursery area and their larvae are mostly unaffected by the advective properties of the Bering Sea oceanography and climate. Alaska plaice species were also not included, but this was because of our lack of knowledge of their early life histories.

#### 4. Results

The rank based nonparametric change point analysis gave results consistent with most published environmental indices, which indicate that a climatic shift occurred in the oceanography of the Bering Sea in the

late 1980s. Significant changes were also found for the AO in 1988, the Pribilof Island sea surface temperature in 1987, the ending larval drift depth in 1989 and the interaction of ending larval drift depth and distance in 1988 ( $\alpha = 0.05$ ). A significant change point was identified for flathead sole in 1987 from the recruitment time series. These results are broadly consistent with those of Hare and Mantua (2000).

Spawner-recruit modeling results indicate that the density-dependent  $\beta$  term provide a better fit than any particular environmental variable; the probability was >90% that the standard Ricker model (with  $\alpha$  and  $\beta$  only) was the correct model when compared to models that estimated  $\alpha$  and a single environmental parameter (Table 1). This is because of the low to moderate levels of spawning biomass when recruitment was high during the 1980s and the high levels of spawning biomass in the 1990s when recruitment was at lower levels.

This finding is symptomatic of most highly autocorrelated time series of recruits. Recent efforts have focused on distinguishing temporal shifts resulting from changes in oceanographic forcing to shifts caused by fluctuations linked to variations in spawning biomass (Bakun, 1996; Clark, Hare, Parma, Sullivan, & Trumble, 1999). Decadal scale changes in springtime climate may establish these patterns in flatfish production. Simulations of ocean surface current trajectories indicate decadal differences in springtime drift patterns over the Bering Sea shelf that may determine flatfish larvae advection to favorable nursery areas. From 1980 to 1989 the springtime surface current flow pattern over the Bering Sea shelf was generally on-shelf (except for 1984), whereas for the years 1990–1997 it was off-shelf (except for 1994, Fig. 2). Average estimated recruitment for each of the winter spawning flatfish species were higher during the years of on-shelf flow; being double for rock sole, 35% higher for arrowtooth flounder, and 8% higher for flathead sole.

Further examination of the relationship between the endpoints of larval drift and recruitment success, where the endpoint of larval drift is measured as the interaction between the distance from shore at the end of the drift trajectory and depth, indicates that strong year-classes did not result from those years when larval settlement occurred distant from nursery areas (Fig. 3). Although strong and weak recruitment may result from near-shore settlement, advection to nursery areas appears to be a likely candidate as a mechanism governing winter-spawning flatfish production over the time period examined.

Table 1  
Results of the Ricker spawner recruit model fit to the data

Model parameters	Arrowtooth flounder probability	Rock sole probability	Flathead sole probability
$\alpha$ and compass direction of drift	0.0000464	0.0000005	0.0000000
$\alpha$ and ending drift depth	0.0012249	0.0000129	0.0000000
$\alpha$ and ending drift distance from land	0.0003199	0.0000007	0.0000000
$\alpha$ and arctic oscillation	0.0025921	0.0000013	0.0000000
$\alpha$ and sea surface temperature	0.0096058	0.0000252	0.0000000
$\alpha$ and spring bloom	0.0002010	0.0000028	0.0000000
$\alpha$ and drift*distance interaction	0.0060895	0.0000314	0.0000000
$\alpha + \beta$ (density dependence)	0.9799203	0.9999250	1.0000000
$\alpha + \beta$ and compass direction of drift	0.1443127	0.0438241	0.0454624
$\alpha + \beta$ and ending drift depth	0.0478778	0.0646543	0.0675984
$\alpha + \beta$ and ending drift distance from land	0.0473398	0.0481376	0.0726813
$\alpha + \beta$ and AO	0.4313135	0.0439540	0.0257384
$\alpha + \beta$ and sea surface temperature	0.1112469	0.0482731	0.0257358
$\alpha + \beta$ and spring bloom	0.1162825	0.0787300	0.2363195
$\alpha + \beta$ and drift*distance interaction	0.0505550	0.4390198	0.0795420
$\alpha + \beta$ and spring bloom* $\beta$ interaction	0.0510718	0.0487344	0.4469222

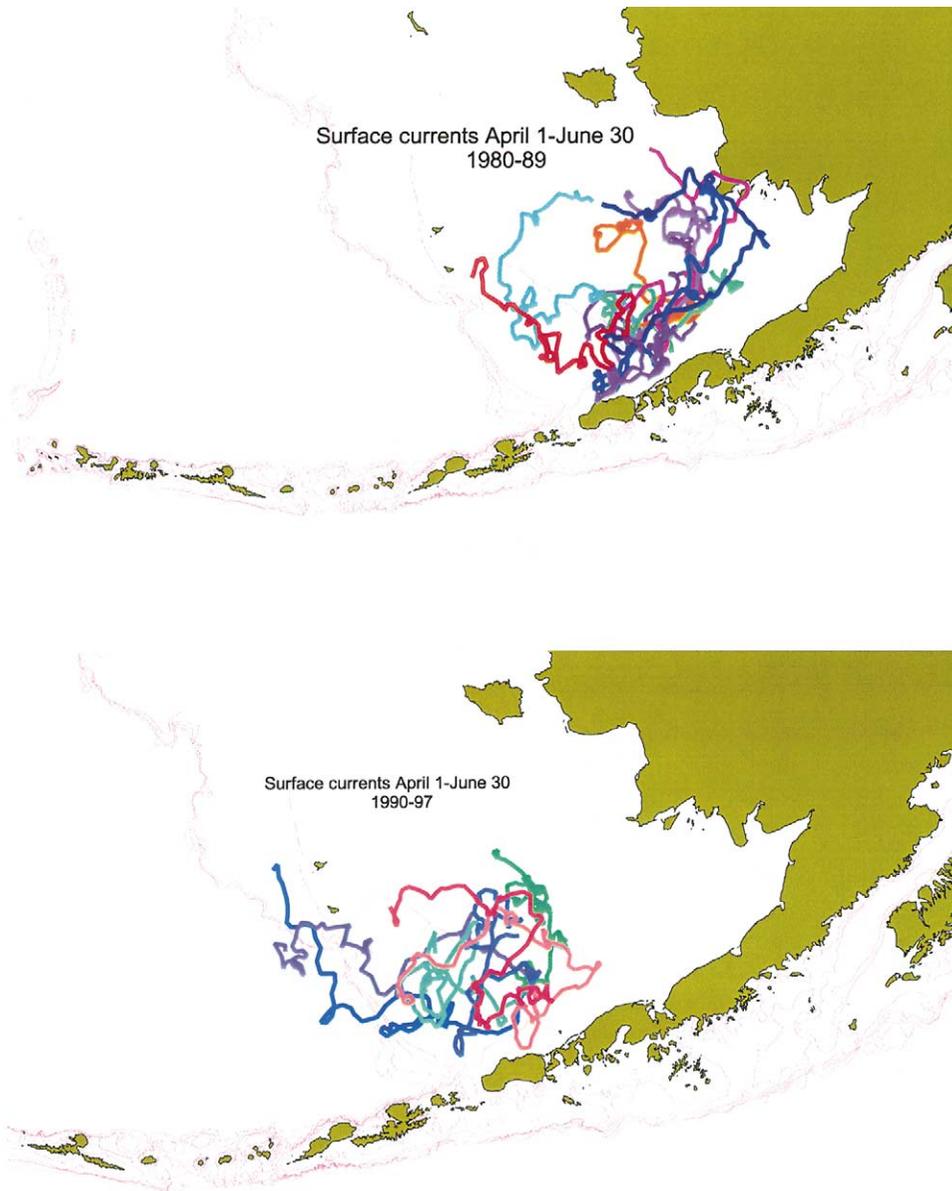


Fig. 2. Results of the OSCURS drift trajectories for April 1–June 30 1980–1989 (top panel) and April 1–June 30 1990–1997 (bottom panel).

There is an indication that the environment has played a major role in the reproductive success of the winter-spawning flatfish over a decadal scale. This leads to consideration of fitting spawner–recruit relationships for years consistent with each oceanic regime. Standard Ricker curves were fitted to data for both 1978–1988 and 1989–1996 for arrowtooth flounder and rock sole, but only for 1978–1988 for flathead sole (Fig. 4). The higher recruitment levels estimated for both rock sole and arrowtooth flounder in the earlier period suggest a more productive stock using these data.

Modeling results further indicated that adding the environmental data to the standard Ricker model (using

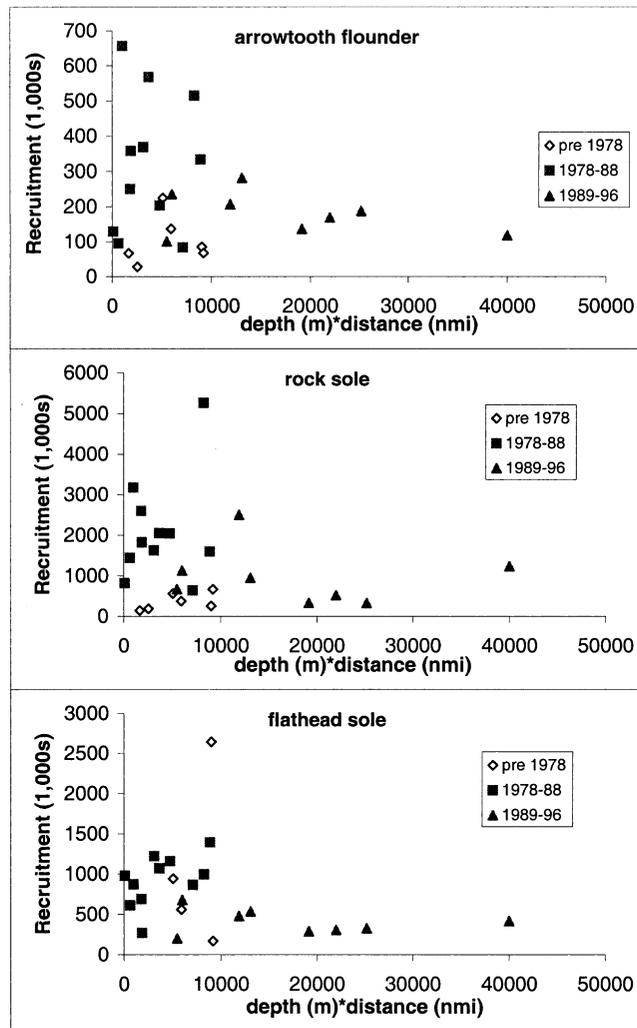


Fig. 3. Relationship between estimated recruitment and the location of the ending larval drift position in terms of the interaction between distance from land (nautical miles) and depth (m) for arrowtooth flounder, rock sole and flathead sole.

data from all years) after the inclusion of the density-dependent  $\alpha$  term identified the AO as an important explanatory variable for arrowtooth flounder. Likewise, the ending depth multiplied by distance from land interaction was an important factor for rock sole, and the timing of the spring plankton bloom was important for flathead sole.

To further examine how patterns of local climate have affected cross-shelf advection, we contrasted the location of the springtime signature of the Aleutian low-pressure field from composites of sea level pressure anomalies for April–June 1977–1988 and 1989–1996 (Fig. 5). Anomalous sea level pressure implies that westerly to south-westerly surface winds (on-shelf) predominated during 1977–1988, whereas during 1989–1996 easterly (off-shelf) winds were predominant. This obvious change in the sea level pressure regime appears to be related to changes in the direction of the larval transport mechanism.

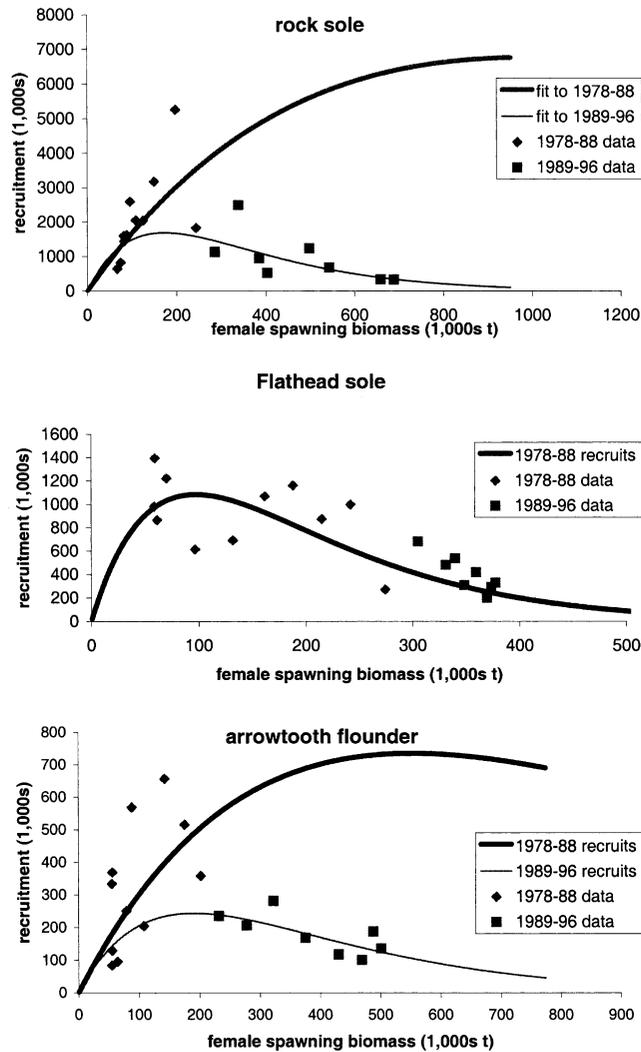


Fig. 4. Ricker model fit to the spawner-recruit data points for the years 1978–1988 for rock sole, arrowtooth flounder and flathead sole and 1989–1996 for rock sole and arrowtooth flounder.

## 5. Discussion

Synchronous strong year-classes have been identified for many marine fish stocks and have been related to oceanic conditions (Hollowed & Wooster, 1992). Four hypotheses have been presented here to better understand the mechanisms at work when alternating cycles of consecutive, strong and weak year-classes have occurred in Bering Sea shelf flatfish stocks, which have coincided with known changes in the dominant modes of forcing in the Southeastern Bering Sea ocean environment.

Strong year-classes have been found to correspond with years 1978–1989, when the springtime cross-shelf advection was predominately to the east or northeast, i.e. towards the extensive nursery areas surrounding Bristol Bay. When springtime cross-shelf wind patterns changed to the west that is the off-shelf direction (1989–1996) recruitment declined. Other Bering Sea fish and invertebrate stocks have also exhibited per-

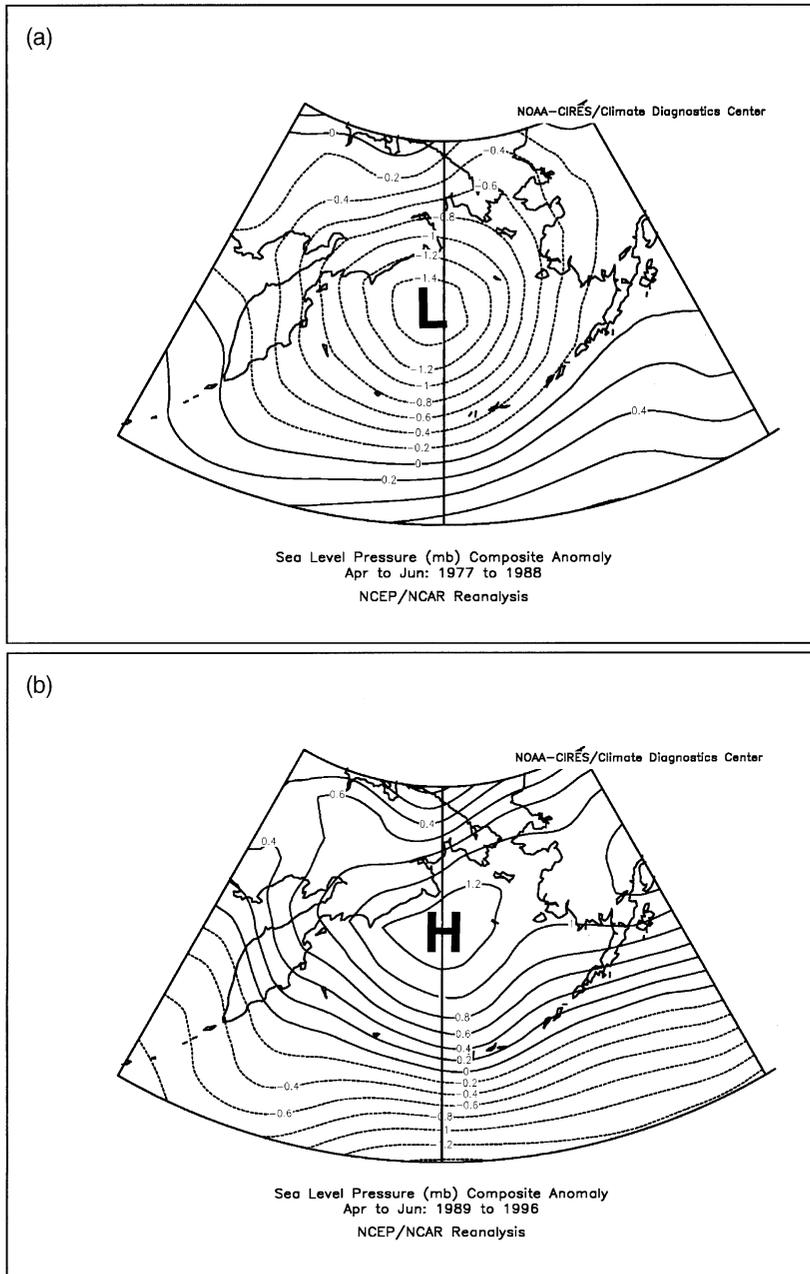


Fig. 5. Sea level pressure (mb) composite anomalies for the Bering Sea for April–June 1977–1988 (top panel) and April–June 1989–1996 (bottom panel).

iodic and autocorrelated trends in productivity that have been linked to the environment. Zheng and Kruse (2000) reported that decadal scale climate shifts played a major role in recruitment trends in seven of the 15 crab stocks they studied. Rosenkranz, Tyler, Kruse, and Niebauer (1998) found that northeast wind direction and water temperature explained 50% of the variability in the year-class strength of the Tanner

crab index. Northeast winds were considered favorable for advection of crab larvae to regions of fine sediments.

The spring ice retreat, thought to be associated with the spring bloom and increased food availability, was only found to be an important factor for flathead sole in our stock-recruitment model with environmental variables. The availability of suitable prey at the time of first feeding has been shown by Lasker (1975) to be essential for larval survival. Our attempt to characterize the match–mismatch hypothesis of Cushing (1975) where ecological conditions (spring bloom) match the timing of larval emergence may not have been captured by our ice-edge analysis. The spawning period of North Pacific flatfish is usually protracted over several months. This may produce a persistent cohort of larvae that may be less sensitive to the timing of the initial spring bloom, but is better able to take advantage of the blooms that results from the onset of thermal stratification, which occur later in the spring. Our knowledge of the phytoplankton bloom dynamics over the inner and middle fronts of the eastern Bering Sea shelf must be improved if we are better to characterize the timing of larval emergence as it relates to future year-class strength.

Decadal length periods of intense Aleutian low pressure have been associated with years of synchronous strong year-classes for many fish stocks (Hollowed & Wooster, 1995). Evidence of decadal shifts in the abundance of fish and invertebrate species of the eastern Bering Sea shelf during the last positive phase of the Aleutian low pressure Index (1977–1989) is provided by Conners, Hollowed, and Brown (2002). In the case of winter-spawning shelf flatfish species, the primary mechanism may be the on-shelf advection associated with the position and intensity of the springtime signature of the AL. The change in the wind and drift pattern since 1989 can be attributed to the general location of the AL, which has, on the average, shifted to the west and south relative to the previous regime. It should be noted that the actual location of the center of the AL between April 1 and June 30 in any year may not have been in the average locations shown in Fig. 5.

The fits to the spawner-recruit data in Fig. 4 suggest that variability in productivity may be linked to the decadal patterns in the ocean environment. There was a good fit between higher productivity and the better rock sole and arrowtooth flounder recruitment during the 1978–1988 decadal period compared to the 1989–1996 period. In contrast, possible links between the productivity differences between the two periods and flathead sole are difficult to discern because of large confidence bounds on the spawner-recruit curve for the 1989–1996 period. Unfortunately, information acquired from processes operating on a decadal scale allows only limited data from which to discern such relationships. This problem becomes even more tenuous for North Pacific flatfish species because their slow growth and late maturation may reduce the range of responses in the spawning stock dynamics over the decadal scale. However, it has been shown in longer time series that marine fish populations obtain different productivity states through changes in the environment or intense harvest. Pacific halibut have been found to have recruitment productivity related to climate regimes in the North Pacific Ocean that is independent of stock size (Clark et al., 1999). Georges Bank haddock were displaced from a long-term (>30 year) production equilibrium by large catches in the mid 1960s, from which the stock has not fully recovered (Fogarty, Rosenberg, & Sissenwine, 1992; Spencer & Collie, 1997).

These temporal shifts in the reproductive potential of fish stocks are crucial to fishery managers who use average recruitment over specified time periods to calculate target levels of spawning biomass, which can be sustained at various harvest levels. The level of spawning biomass, which can be sustained under a productive climatic regime at a given harvest level, is of course, much greater than under a less productive regime. Monitoring the relationship between ocean environment and stock productivity can help reduce the risk of overfishing. This has become particularly evident in cases such as Georges Bank haddock in which the stock has already been perturbed into a less productive state by intensive harvesting in the past, and could be pushed into an even less productive state by environmental shifts (Fogarty et al., 1992).

For Bering Sea rock sole, flathead sole and arrowtooth flounder, there is a strong underlying association of density dependence between effective spawning stock size and subsequent recruitment. The consecutive

years of strong recruitment during the 1980s resulted in the build-up of large spawning stock sizes in the 1990s, such that the condition of the spawning stock in any given year became clearly autocorrelated with the previous years. Through not accounting for this autocorrelation in the spawning stock in our spawner-recruit model we may have overestimated the density-dependence in this relationship and masked the ability to detect the role of oceanography on reproductive success.

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