Environmentally induced recruitment variation in petrale sole, *Eopsetta jordani*

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Abstract.—Potential effects of parental stock size and environmental factors on year-class strength (YCS) of petrale sole, *Eopsetta jordani*, were investigated in two areas off Oregon and Washington (Pacific States Marine Fisheries Commission areas 2B: 42°50'N–44°18'N, and 3A: 45°46'N–47°20'N). Parental egg production indices and YCS were not consistently correlated over the period 1970 to 1977. Variation in YCS between 1958 and 1977 was associated with oceanographic conditions from winter to early spring, the period in which pelagic larval stages are most abundant. A regression model based on indices of offshore Ekman transport from January to March and alongshore transport from December to February accounted for nearly 55% of the YCS variation in Area 2B. In Area 3A, the previous two indices plus sea surface temperature from December to February explained about 65% of the YCS variation. Inshore advection of eggs and larvae could favor settlement of juveniles into nearshore areas and increase the subsequent recruitment strength of petrale sole.

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Recruitment fluctuations in fish populations are ascribed to many physicochemical factors and biological processes, including parental stock size and fishing (Ricker, 1975; Shepherd et al., 1984). However, the importance of various factors to the recruitment of most species of fish is virtually unknown. Although year-class strength (YCS) of many fishes is thought to be determined at the egg and larval stages (Sharp[1]; Rothschild and Rooth, 1982), it may also be significantly affected during the postlarval stages (Smith, 1981; Sissenwine, 1984).

Increasing evidence suggests that oceanographic conditions affect the recruitment of many fishes in the Northeast Pacific Ocean (e.g. Parrish et al., 1981; Bailey and Incze, 1985; Hollowed et al., 1987; Botsford et al., 1989). A recent hypothesis suggests that recruitment of groundfish off the west coast of the United States is related to the timing of the spring transition, a period of major changes in oceanographic conditions.[2] On the Oregon–Washington shelf oceanographic conditions exhibit strong seasonal patterns (e.g. Huyer et al., 1975; Halpern, 1976; Huyer, 1977; Landry et al., 1989). In winter, alongshore currents are northward at all depths, and cross-shore surface currents flow inshore resulting in downwelling. In spring, flow is southward at all depths but stronger near the surface. The spring transition usually occurs within a one week period during March or April (Strub et al., 1987; Strub and James, 1988). In summer, a surface coastal current flows southwestward and the attendant offshore transport causes upwelling; however, deep flow is northward. In fall, alongshore currents are northward at all depths.

Petrale sole, *Eopsetta jordani*, Pleuronectidae, is a commercially important flatfish of the northeast Pacific Ocean (Ketchen and Forrester, 1966). It is continuously distributed from the Bering Sea (58°N–152°W) to Baja California (32°26'N–117°16'W) (Roedel, 1953; Hitz and

[1] Sharp, G. D. 1980. Report of the workshop on effects of environmental variation on survival of larval pelagic fishes. *In* Sharp, G. D. (rapporteur), Report and supporting documentation of the workshop on the effects of environmental variation on the survival of larval pelagic fishes, p. 15–59. Int. Ocean. Comm. Workshop Rep. 28.

[2] Lynn, R. J. Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038. Personal commun., 1991.

Rathjen, 1965). Recruitment fluctuations of petrale sole appear to be strongly related to environmental factors (Ketchen and Forrester, 1966). Ketchen (1956) demonstrated a positive correlation between winter sea surface temperature and recruitment of petrale sole off British Columbia from the middle 1940's to the middle 1950's. In the same area, Ketchen and Forrester (1966) postulated that warmer sea surface temperatures and onshore transport of pelagic early life stages could favor recruitment of this species.

Two central spawning areas of petrale sole, Heceta Bank and Willapa Deep, are located off Oregon and Washington (Fig. 1). Petrale sole spawn from late fall to early spring at depths of about 300–450 m (Cleaver, 1949; Harry, 1959; DiDonato and Pasquale, 1970; Pedersen, 1975). The incubation period of newly fertilized eggs ranges from about 6 to 13 days (Alderdice and Forrester, 1971). The eggs and yolk-sac larvae are stenohaline and stenothermal (Alderdice and Forrester, 1971). Development of pelagic eggs and larvae occurs mainly from winter to spring, followed by the presettlement and postsettlement juvenile stages from summer to fall respectively (Fig. 2). Although petrale sole larvae have been found from 2 to 120 km offshore, Pearcy et al. (1977) collected nearly 50% of them 83–120 km offshore. However, postsettlement juveniles have only been found at 18–90 m depth in the inner continental shelf (Ketchen and Forrester, 1966; Gregory and Jow, 1976; Pearcy et al., 1977).

The recruitment patterns of petrale sole off Oregon and Washington demonstrated consecutive series of cohorts alternating between below average (weak) YCS and above average (strong) YCS over the base period 1958–77 (Castillo, 1992). Possible causes for such recruitment variations have not yet been studied. Our objectives were to determine 1) if spawning biomass of petrale sole is correlated with YCS, 2) if YCS fluctuations are associated with selected environmental factors, and 3) the percentage of YCS variation explained by environmental factors.

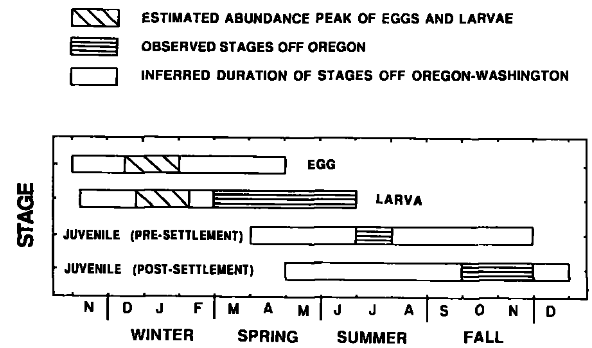

Figure 2

Estimated duration of life stages of petrale sole, *Eopsetta jordani*, off Oregon and Washington from the beginning of the spawning period to the time in which most age-0 juveniles are found settled in the inner continental shelf. The inferred temporal occurrence of life stages was based on the reported duration of spawning, incubation period and presence of presettlement and postsettlement juveniles in the Northeast Pacific Ocean (based on Cleaver, 1949; Harry, 1959; Best, 1963; Porter, 1964; Ketchen and Forrester, 1966; Alderdice and Forrester, 1971; Gregory and Jow, 1976; and Pearcy et al., 1977).

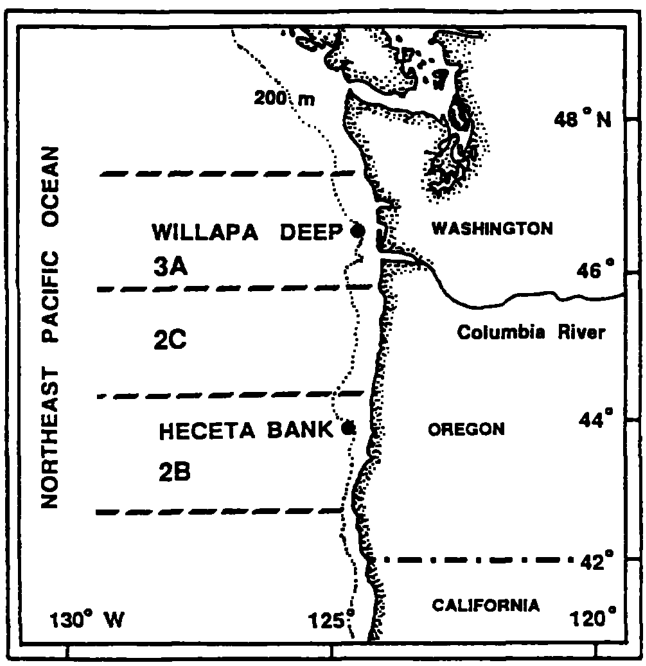

Figure 1

Location of Willapa Deep and Heceta Bank spawning grounds of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 3A and 2B. Spawning areas are located nearly 50 km offshore (modified from Pedersen, 1975).

Data and methods

We selected two locations off Oregon and Washington to investigate the effect of environmental factors on YCS of petrale sole: Pacific States Marine Fisheries Commission[3] areas 2B (42° 50'N–44°18'N) and 3A (45°46'N–47°20'N) (Fig. 1). Indi-

[3] Named Pacific Marine Fisheries Commission (PMFC) areas until 1990.

ces of YCS for petrale sole were obtained from cohort analyses of numbers of females recruited to six years of age in areas 2B and 3A (Table 1). These YCS indices represent the recruitment strength of year classes hatched from 1958 to 1977. Males were excluded from these YCS indices because of problems of increasing age underestimation in fish over 8 years.[4] However, because recruitment variation was similar in males and females of younger age groups, the YCS indices should be representative of both sexes.

Potential egg production was used as a proxy for spawning biomass (e.g. Hayman and Tyler, 1980). Egg production was estimated from fecundity and maturity information (Porter, 1964) and from cohort analyses of the parental stock for years 1970 to 1977 (Castillo, 1992). Annual potential egg production was estimated as the sum of the age-specific products of the numbers of females, their fecundity, and their percent maturity. The number of females was estimated from the observed annual sex ratio in the commercial landings. Females composed on average 58% of petrale sole landed. Egg production was averaged for fish over age 13 years because of the scarcity of older females.

Eight environmental indices available within, or near, areas 2B and 3A were used to investigate possible correlations with petrale sole YCS (Table 2). Ocean transport calculations provided by The Pacific Fisheries Environmental Group (PFEG) were based on Bakun (1973; after Fofonoff[5]). Sverdrup transport was calculated by PFEG by using a finite difference form of equation six in Nelson (1977)[6]. A proxy for salinity was based on observations of water density at constant temperature available at the Columbia River estuary (Table 2, Fig. 1). The timing of the spring transition was obtained from Strub and James

[4] Recent use of the break-and-burn technique for aging otoliths showed that males grow more slowly and lay down less yearmarks (annuli) on the surface of the otolith than females (William H. Barss, Oregon Department of Fish and Wildlife, Newport, OR 97365, unpubl. data).

[5] Fofonoff, N. P. 1960. Transport computations for the North Pacific Ocean—1958. Fish. Res. Board Can. Manuscr. Rep. Oceanogr. and Limnol. No. 80.

[6] $M_y = \vec{k}(\nabla \times \vec{\tau})/\beta$ where: M_y is the meridional component of the vertically integrated mass transport, $\vec{k}(\nabla \times \vec{\tau})$ is the vertical component of the wind stress curl, and β is the meridional derivative of the Coriolis parameter.

Table 1

Cohort analyses of numbers of female petrale sole, *Eopsetta jordani,* reaching 6 years of age in Pacific States Marine Fisheries Commission areas 2B and 3A (Castillo, 1992; after Jones, 1981). Both year-class strength indices were significantly correlated with Summed-CPUE indices ($P \leq 0.05$, Castillo, 1992; after Hayman et al., 1980).

Cohort (year)	Year-class strength (thousands of fish) Area 2B	Area 3A
1958	208	543
1959	278	544
1960	309	624
1961	385	692
1962	231	333
1963	296	421
1964	240	365
1965	280	547
1966	487	954
1967	352	703
1968	419	737
1969	349	558
1970	426	651
1971	421	570
1972	373	463
1973	356	415
1974	259	326
1975	193	332
1976	157	286
1977	223	424

Table 2

Environmental indices used in correlations with year-class strength of petrale sole, *Eopsetta jordani.* Recruitment areas include Pacific States Marine Fisheries Commission areas 2B and 3A. (Source of data is indicated for each environmental factor.)

Environmental index	Recruitment area
Sea surface atmospheric pressure[1, 3]	2B, 3A
Alongshore coastal transport indices	
Mean sea level[2]	
Neah Bay (48°22'N–124°38' W)	3A
Crescent City (41°45'N–124°12' W)	2B
Northward Ekman transport[1, 3]	2B, 3A
Northward Sverdrup transport[1, 3]	2B, 3A
Offshore Ekman transport[1, 3]	2B, 3A
Cube of wind speed[1, 3]	2B, 3A
Water properties	
Sea surface temperature[3]	
(43°N–44.9°N), (124°W–124.9°W)	2B
(46°N–47.9°N), (124°W–124.9°W)	3A
Salinity index Columbia River[2]	
Estuary (46°13'N–123°45'W)	2B 3A

[1] Computed at 45° N–125° W.
[2] Tidal Datum Quality Assurance Section, NOAA, Rockville, MD 20852.
[3] Pacific Fisheries Environmental Group, P.O. Box 831, Monterey, CA 93942.

(1988). However, for years not available from Strub and James, it was estimated from weekly upwelling indices (at 45°N 125°W, Bakun, 1975; Mason and Bakun, 1986). In the latter case the time of spring transition was assigned to the first week of the year in which the weekly upwelling index became positive and remained positive for at least another week. The spring transition dates reported by Strub and James (1988) were highly correlated with our estimates (r=0.80; P<0.01). Because March is usually a month of predominant onshore Ekman transport prior to the spring transition (i.e. negative offshore Ekman transport), we determined whether YCS variation was correlated with mean onshore Ekman transport during March.

Analytical methods

Spearman's correlation analyses (Tate and Clelland, 1957) were used to account for linear and nonlinear monotonic associations between YCS and independent variables (i.e. potential egg production, environmental factors, and timing of the spring transition). Independent variables were lagged to the first year of life of each cohort to determine potential influences on YCS at the time year classes were born. Exploratory Spearman's correlation analyses were used for each season of the year because of the seasonality of different early life stages and environmental factors (Fig. 2, Appendix A).

Because many environmental-YCS relationships showed anomalous correlations during the 1958 El Niño, one of the largest El Niño events in the twentieth century (Cannon et al., 1985), this year was not included in Spearman's correlation analyses. However, after the most consistent Spearman's correlations for 1959–77 were established, all years from 1958 to 1977 were considered in regression analyses. Such regressions consisted of estimated YCS on environmental anomalies. These anomalies were computed as the actual seasonal value of a given factor minus its long-term mean for 1958–77. The use of anomalies as independent variables was justified to reduce multicollinearity effects in polynomial regressions (Neter et al., 1989).

The Bonferroni correction and the P-value plot of Schweder and Spjotvoll (1982) required individual P-values ≈0.001 for an overall P-value = 0.05 in multiple comparisons between YCS and environmental factors. Since such P-values would have made it difficult to detect meaningful ecological relationships, significance of correlations was based on individual P-values ≤0.05. Although statistical significance in our study was based on nonfiltered data (here after referred to as original series), unrelated trends in original series often cause spurious correlations and conceal the extent of year-to-year associations (Dickey et al., 1986; Norton[7]; Cohen et al., 1991). Therefore, first-order differencing was used to evaluate the reliability of correlations based on the original series (Chatfield, 1989; here after referred to as filtered series). By this criterion, a significant correlation for original series was deemed reliable only if the attendant correlation for the filtered series had the same correlation sign and a minimum absolute value ($|r|$ > 0.10). Although this procedure does not account for P-values of filtered series, it provides a more consistent selection of factors potentially associated with recruitment variation.

Results

Potential spawning biomass

The effect of spawning biomass on subsequent recruitment strength was minimal as indicated by similar variations from 1970 to 1977 in YCS per parental egg and the YCS index (Fig. 3). The initial decline in YCS in the 1970's was not linked to a de-

[7] Norton, J. 1990. Relationship between California Current temperatures and intensity of the Aleutian Low. Southwest Fisheries Science Center. Report of activities. March–April 1990. La Jolla, CA, p. 16–18.

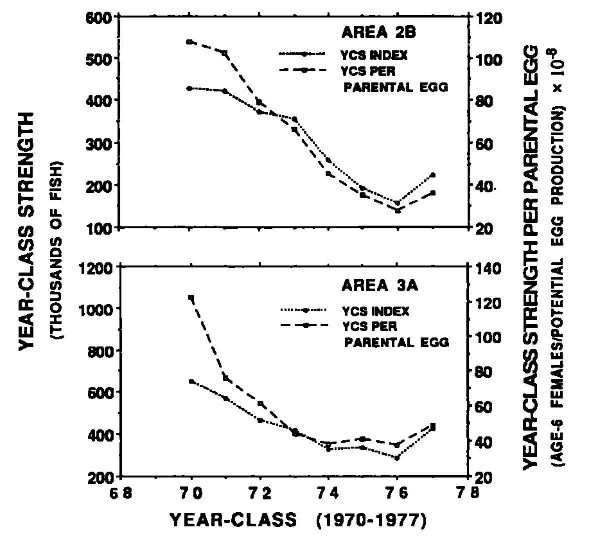

Figure 3

Comparison between year-class strength indices of petrale sole, *Eopsetta jordani*, with the attendant number of fish reaching age 6 per parental egg in Pacific States Marine Fisheries Commission areas 2B and 3A. (Cohorts considered in year-class strength indices were hatched between 1970 and 1977.)

crease in parental-stock size, as negative trends between YCS and potential egg production were observed for year classes from 1970 to 1977 (Area 2B: r=–0.81, P<0.05; Area 3A: r=–0.57, P<0.20; Fig. 4A). Examination of the attendant filtered series did not support a density-dependent relationship when the size of the parental stock was large (e.g. Ricker, 1954; Area 2B: r=0.21, Area 3A: r=0.07; Fig. 4B).

Environmental-YCS fluctuations (1959–1977)

Alongshore transport indices

1 Mean sea level height The strongest northward and southward coastal flow generally coincide with the highest and lowest mean sea levels off Oregon (Huyer et al., 1975). Long-term seasonal sea levels indicated that stronger northward and southward flows from 1959 to 1977 occurred in winter and summer, respectively (Appendix A). Correlations between YCS and mean sea level were highest in winter for both study areas (Fig. 5A). The attendant filtered series showed lower but consistent correlations for winter (Fig. 6A). Thus, recruitment strength of petrale sole seems to be associated with interannual variation in nearshore northward transport during winter.

2 Northward Ekman transport This index indicates the alongshore flow of surface mixed layers driven by wind stress. Unlike sea level height, there was no correlation between northward Ekman transport and YCS (Figs. 5B and 6B). The four long-term seasonal means of this index indicated predominantly negative northward transport (i.e. southward transport) of surface waters at offshore areas (45°N–125°W, Appendix A).

3 Northward Sverdrup transport This index measures alongshore transport over the entire water column by adding geostrophic flow to Ekman transport. For nonwinter seasons, the long-term seasonal means of this index showed southward transport of offshore waters (45°N–125°W, Appendix A). Northward Sverdrup transport and YCS were not consistently correlated (Figs. 5C and 6C).

Offshore Ekman transport The long-term seasonal means of this index indicated average offshore transport of surface waters and upwelling from spring to summer followed by onshore transport and downwelling from fall to winter (Appendix A). Winter offshore Ekman transport and YCS showed clear and consistent negative correlations in both study areas (Figs. 5D and 6D).

Cube of wind speed This index reflects the turbulence transferred to the sea surface by the wind (Niiler and Kraus, 1977). Although cube of wind speed was correlated with YCS for winter and spring (Figs. 5E and 6E), these correlations were largely explained by onshore Ekman transport during this period. Moreover, correlations for spring vanished in both areas when March was excluded from the analyses. Thus, cube of wind speed seems to be spuriously correlated with YCS.

Sea surface temperature Long-term seasonal means of sea surface temperature increased from winter through summer and decreased from fall through winter (Appendix A). Correlations between YCS and sea surface temperatures for winter and spring showed high positive

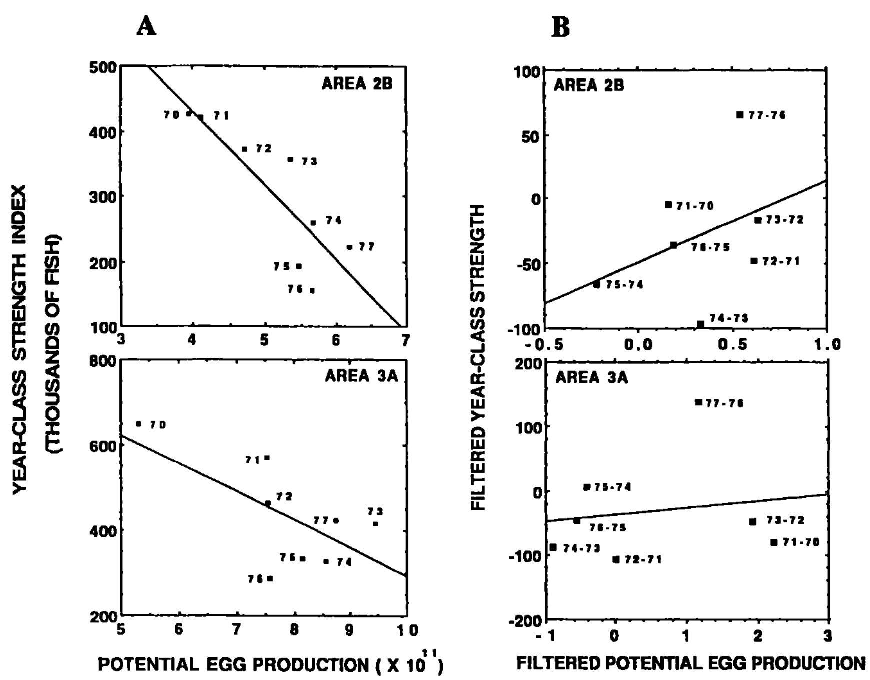

Figure 4

Variation of year-class strength of petrale sole, *Eopsetta jordani*, in relation to potential parental egg production in Pacific States Marine Fisheries Commission areas 2B and 3A. Comparison is shown for (**A**) original and (**B**) filtered series. Cohorts hatched between 1970 and 1977 (years are identified by the last two digits).

values only in Area 3A, particularly during winter (Figs. 5F and 6F). Therefore, warmer temperatures may result in increased survival of eggs and/or larvae of petrale sole in Area 3A.

Nearshore salinity index This index reflects nearshore salinity variations caused by the Columbia River plume. Although high correlations between filtered YCS and the salinity index were detected for winter and summer, no significant correlations were observed for original series (Figs. 5G and 6G).

Sea surface atmospheric pressure Nearshore transport and water properties such as temperature, salinity and density are greatly influenced by the North

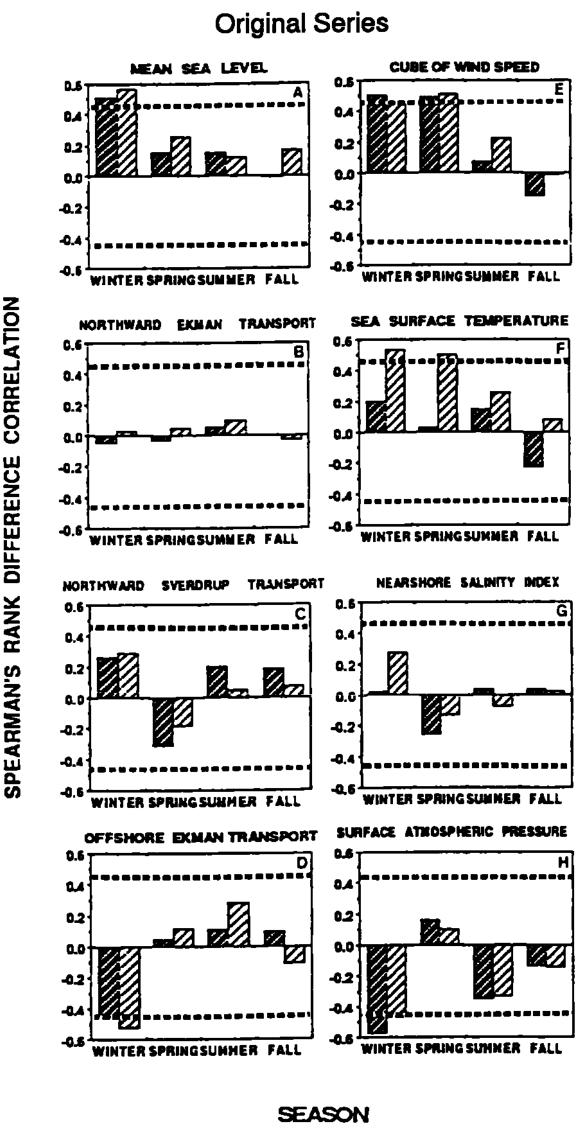

Figure 5

Spearman's correlations between year-class strength indices of petrale sole, *Eopsetta jordani*, and seasonal averages of environmental factors lagged to the first year of life (Table 2). Correlation for cohorts 1959 to 1977 are compared for Pacific States Marine Fisheries Commission areas 2B (dark bar) and 3A (light bar). Dashed lines correspond to $P = 0.05$ for individual correlations.

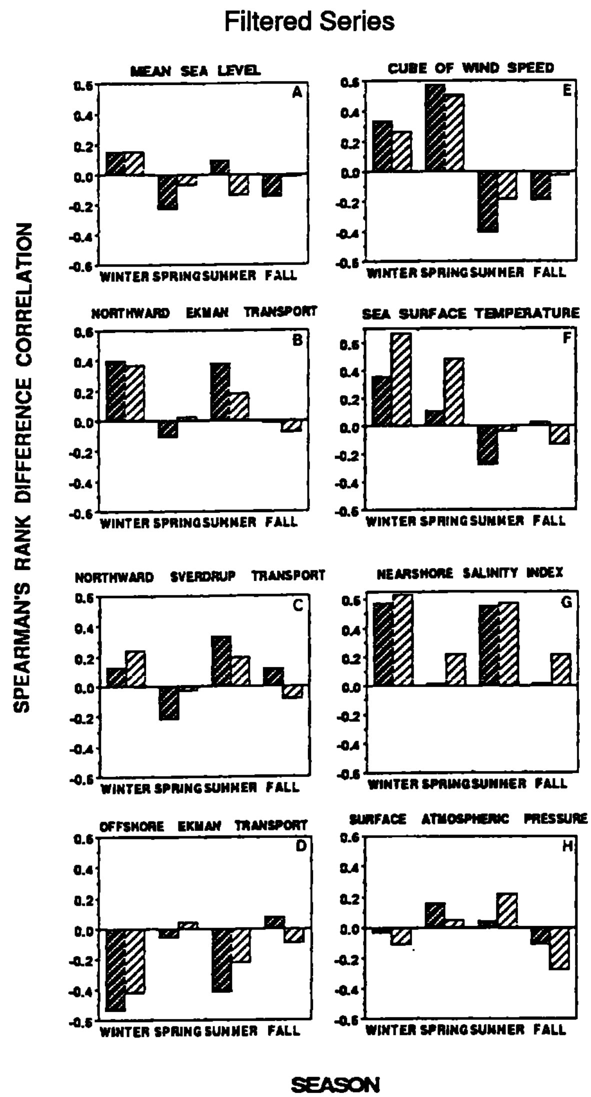

Figure 6

Spearman's correlations between filtered year-class strength indices of petrale sole, *Eopsetta jordani*, and filtered seasonal averages of environmental factors lagged to the first year of life for cohorts from 1959 to 1977 (Table 2). Areas compared are Pacific States Marine Fisheries Commission 2B (dark bar) and 3A (light bar). Significance of correlations was based on original series (see analytical methods).

Pacific high and Aleutian low pressure systems (Huyer, 1983). Large negative correlations between YCS and winter sea surface atmospheric pressure were evident in both areas (Fig. 5H). However, filtered series suggested that this index was spuriously correlated with recruitment strength (Fig. 6H).

Effects of the spring transition on YCS Correlations between YCS and the week of the spring transition from 1967 to 1977 were not significant (Area 2B: r=0.27, Area 3A: r=0.22; P>0.20; Fig. 7A). Moreover, correlations for attendant filtered series were negative (Area 2B: r=–0.18, Area 3A: r=–0.32; Fig. 7B). However, onshore transport during early spring can affect YCS as recruitment strength was correlated with mean onshore Ekman transport during March in both study areas (Area 2B: r=0.55, Area 3A: r=0.50; P<0.05). Such correlations were also supported by the attendant filtered series (Area 2B: r=0.58, Area 3B: r=0.42).

Environmental-YCS series Based on exploratory correlation analyses for original and filtered series, winter offshore Ekman transport seemed to be the main factor affecting YCS of petrale sole in areas 2B and 3A. In subsequent analyses, the period January–March was chosen for describing the association between YCS and offshore/onshore Ekman transport. This period was selected because of the importance of onshore transport on YCS during March. Moreover, correlations between offshore Ekman transport and YCS tended to be higher during January–March (original and filtered series respectively: Area 2B, r=–0.48 and –0.67; Area 3A: r=–0.52 and –0.65; P<0.05) than December–February (original and filtered series respectively: Area 2B, r=–0.46 and –0.53; Area 3A: r=–0.52 and –0.42; P≤0.05).

Comparing onshore Ekman transport with YCS, we found that two periods of reduced onshore Ekman transport (1962–65 and 1974–77) coincided with weak year classes of petrale sole (Fig. 8). The years 1958, 1961, and 1968 showed the largest positive anomalies in onshore Ekman transport from 1958 to 1977. However, unlike 1961 and 1968, the 1958 El Niño produced weak YCS in Area 2B and near-average YCS in Area 3A. Other anomalies for indices such as winter and spring sea surface temperature and winter sea level height showed some correspondence with YCS anomalies in Area 3A. In Area 2B, only onshore Ekman transport and sea level height suggested some association with YCS (Figs. 8 and 9).

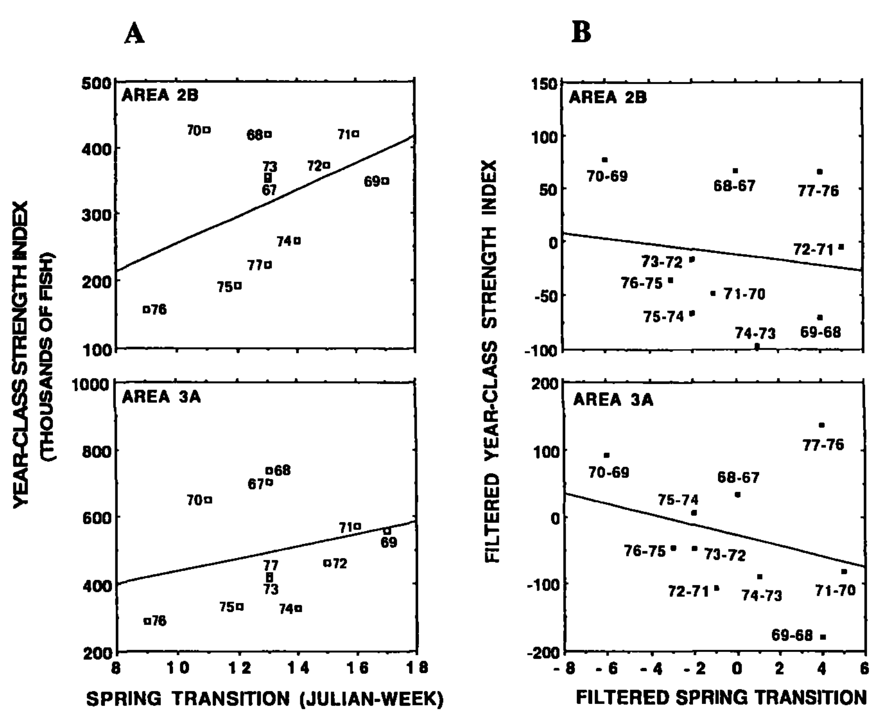

Figure 7

Variation of year-class strength for petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A in relation to the week of the year in which the spring transition occurred. Comparison is shown for (**A**) original and (**B**) filtered series. Year classes are considered hatched between 1967 and 1977 and are identified by the last two digits.

Percentage of YCS variation explained by environmental factors The relationship between YCS and January–March offshore Ekman transport anomalies was best described by second-order polynomial regressions (Fig. 10, Table 3). Associations between YCS and winter sea level height anomalies in areas 2B and 3A, were also described by second-order polynomials (Fig. 11, Table 3). Although the association between YCS and winter sea surface temperature in Area 3A was better described by a second-order polynomial than by a linear regression, only the latter was significant (Fig. 12, Table 3). Except for the year 1958, and for the years with large anomalies in offshore Ekman transport

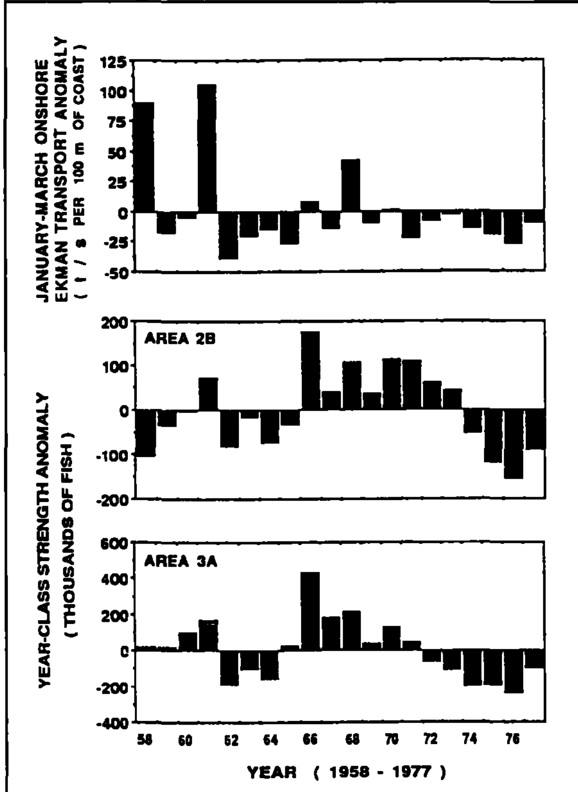

Figure 8

Anomalies for mean onshore Ekman transport off Oregon (January to March), and for year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A. (Values computed from the long-term mean 1958–77.)

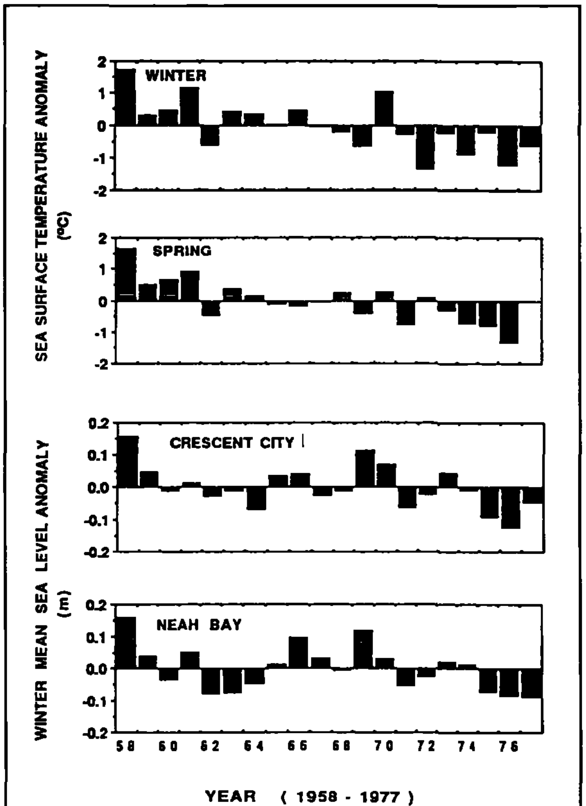

Figure 9

Anomalies of sea level height (Crescent City and Neah Bay), and winter and spring sea surface temperature off Oregon-Washington (considered for Area 3A). Values based on the long-term mean 1958–77. (Locations for environmental indices are shown in Table 2.)

(i.e. 1961, 1968; Fig. 10) and sea level height (i.e. 1969; Fig. 11), a common feature in these regressions is the nearly linear association for most of the studied period.

Regressions for individual environmental factors explained less than 40% of the YCS variation in each area from 1958 to 1977 (Table 3). However, a regression model including offshore Ekman transport and sea level height accounted for nearly 55% of the YCS in Area 2B (Fig. 13). Over the same period in Area 3A, these two environmental factors plus sea surface temperature explained about 65% of the variation in YCS.

Discussion

Recruitment variation of petrale sole in areas 2B and 3A was correlated with oceanographic conditions from winter to early spring, the period in which egg and larval stages of this species are most abundant. Since postsettlement, age-0 petrale sole have only been found within the inner continental shelf (Ketchen and Forrester, 1966; Gregory and Jow, 1976; Pearcy et al., 1977), and YCS and offshore Ekman transport were consistently and negatively correlated, it is possible that inshore advection of eggs and larvae toward nearshore settlement areas may be the major factor determining YCS in this species.

A critical assumption for establishing spawner-recruit relationships is that density-independent survival variation at early life stages is negligible when compared with variation in spawning biomass. This assumption is not consistent with the results obtained in our study, with the lack of spawner-recruit relationships for petrale sole in other areas (Ketchen and Forrester, 1966), and with the results of most flatfish studies (Cushing, 1971; Roff, 1981).

Our findings support the hypothesis that recruitment of petrale sole is dependent on northeastward

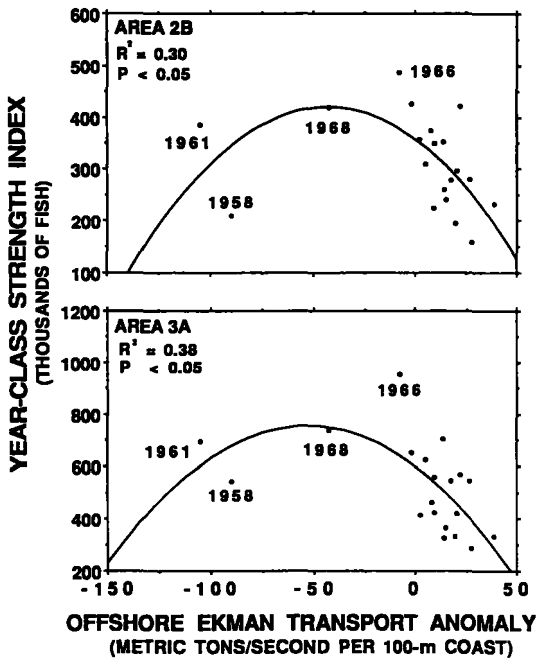

Figure 10

Relations between year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A and mean offshore Ekman transport anomaly off Oregon from January to March. (Regression parameters are shown in Table 3.)

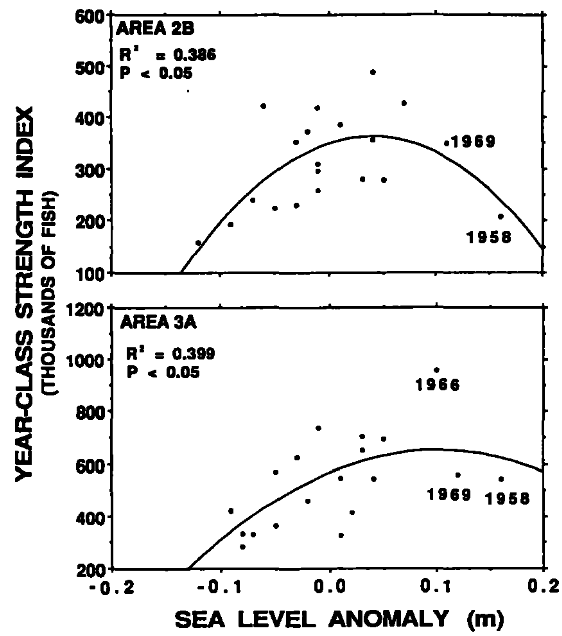

Figure 11

Relations between year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A and winter mean sea level height anomalies. (Regression parameters are shown in Table 3.)

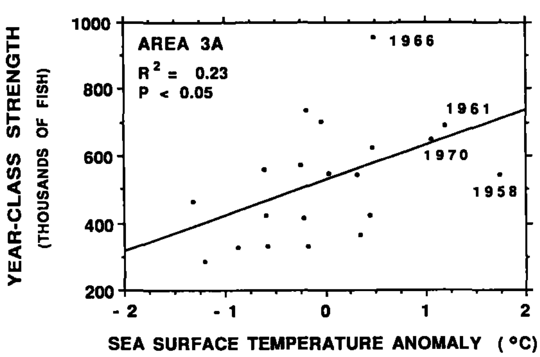

Figure 12

Relation between year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission Area 3A and mean winter sea surface temperature anomaly off Oregon-Washington (December-February). (Regression parameters are shown in Table 3.)

transport during winter (Ketchen and Forrester, 1966). The analyses in Area 3A are also consistent with an association between temperature and survival of early life stages of petrale sole (Ketchen and Forrester, 1966; Alderdice and Forrester, 1971). Considering the discharge of the Columbia River into Area 3A and the stenohaline condition of eggs and larvae in this species, possible salinity-YCS associations may be overridden by cross-shore and alongshore advection and sea temperature.

Recruitment strength of petrale sole was correlated between areas 2B and 3A (r=0.82, P<0.01). However, the highest determination coefficient for regression models of YCS on environmental factors was obtained in Area 3A. Although the proportion of variation in YCS explained by second-order polynomial regressions was significant for both offshore Ekman transport and sea level height, filtered series suggest that year-to-year variation in YCS were better explained by the former. Unlike Area 3A and off British Columbia (Ketchen and Forrester, 1966), no regression models of YCS on sea surface temperature were significant or marginally significant in Area 2B. The higher positive temperature-YCS association for Area 3A compared with Area 2B is consistent with temperature differences between areas (Appendix A). These observations suggest a latitudinal effect of temperature on the recruitment of petrale sole, that is, higher recruitment toward the poleward range of the

Table 3

Regressions of year-class strength (YCS) for petrale sole, *Eopsetta jordani* (thousands of females attaining age 6), on environmental anomalies in Pacific States Marine Fisheries Commission areas 2B and 3A from 1958 to 1977. Environmental anomalies are based on the long-term mean 1958–77. SST = sea surface temperature anomaly (Dec.–Feb.), SL = mean sea level height anomaly (Dec.–Feb.), Me = offshore Ekman transport anomaly (Jan.–Mar.). $P \le 0.05$ for significant correlations (n = 20 years). In the last regression model, $R^2 = 0.667$ between predicted YCS ($e^{\ln(YCS)}$) and YCS index ($P<0.05$).

Area	Regression model	R^2	P
	YCS on SST		
3A	YCS = 524.5048 + 104.8226 SST	0.231	<0.05
	YCS on SST and SST²		
3A	YCS = 550.4459 + 116.8338 SST – 44.9699 SST²	0.270	0.06*
	YCS on Me and Me²		
2B	YCS = 357.0224 – 2.9121 Me – 0.0340 Me²	0.302	<0.05
3A	YCS = 576.0152 – 4.3035 Me – 0.0391 Me²	0.381	<0.05
	YCS on SL and SL²		
2B	YCS = 347.0157 + 625.3314 SL – 8103.1487 SL²	0.386	<0.05
3A	YCS = 565.1595 + 1686.4019 SL – 8512.4524 SL²	0.399	<0.05
	YCS on Me, Me², SL and SL²		
2B	YCS = 377.9325 – 2.3712 Me – 0.0255 Me² + 346.4281 SL –7477.8599 SL²	0.549	<0.05
3A	YCS = 608.3490 – 3.8546 Me – 0.0378 Me² + 1104.2691 SL –7115.5843 SL²	0.508	<0.05
	Ln (YCS) on Me, Me², SL, SL², SST and SST²		
3A	Ln (YCS) = 6.4115 – 0.0068 Me – 6x10–5 Me² + 1.9585 SL –9.0066 SL² + 0.1069 SST – 0.1321 SST²	0.648	<0.05

* Nonsignificant.

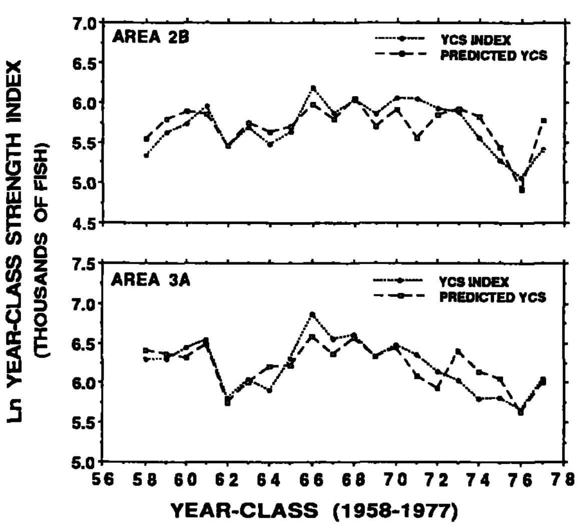

Figure 13

Log-transformed estimated and predicted year-class strength for petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A. Area 2B: prediction is based on anomalies of offshore Ekman transport and sea level height and their attendant squared values. Area 3A: predicted values are based on anomalies of offshore Ekman transport, sea level height, sea surface temperature, and their attendant squared values. (Regression parameters are shown in Table 3.)

species' distribution in warmer years (Cushing, 1982; Bailey and Incze, 1985; Frank, 1991).

The interrelation among oceanographic factors (e.g. Huyer, 1977; Kruse and Huyer, 1983) makes it difficult to determine the importance of any single environmental factor to YCS variation. Hence, the more consistent negative correlation between YCS and offshore Ekman transport in Area 3A than in Area 2B could be due in part to a higher correlation between YCS and sea surface temperature in Area 3A.

Primary production and usable solar radiation seem to be positively correlated during winter and spring off Oregon (Small et al., 1972). However, no associations between YCS of petrale sole and mean usable radiation were observed from solar radiation estimates for winter or spring near areas 2B[8] and 3A[9] (Castillo, unpubl. data). On the other hand, although a nearly tenfold increase in zooplankton production from winter to summer may be stimulated by coastal upwelling off Oregon (Peterson and Miller, 1977), correlations between YCS of petrale sole and spring or summer upwelling indices did not suggest that recruitment strength is primarily controlled by

[8] U.S. Weather Bureau. 1961–1964. Local climatological data, Medford, Municipal Airport, Oregon, U.S. Dep. Commerce. USCOMM-WB-Asheville.

[9] U.S. Weather Bureau. 1958–1964. Local climatological data, Clatsop County Airport, Astoria, Oregon, U.S. Dep. Commerce. USCOMM-WB-Asheville.

zooplankton production. Such inference is consistent with observations for two other species of flatfish in Area 3A (Hayman and Tyler, 1980).

Years of strong cohorts of petrale sole and other flatfishes tended to co-occur off Oregon during the 1960's (e.g. 1961, 1966, and 1968).[10] Year class 1961 was strong for nearly 85% of 13 groundfish species from the Northeast Pacific (Hollowed et al., 1987). The high onshore Ekman transport in winter 1961 (Fig. 10) suggests that major factors controlling YCS in petrale sole are the same for other groundfish species.

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Appendix A

Long-term seasonal means (1959–77) of environmental indices used in exploratory correlation analyses. Except for mean sea level height and sea surface temperature, only one index per environmental factor was considered for Pacific States Marine Fisheries Commission areas 2B and 3A. (Geographical locations and sources for environmental indices are shown in Table 2.)

	Environmental indices									
	Mean sea level height[1]						Sea surface temperature[6]			
Season	Area 2B	Area 3A	Northward Ekman tran.[2]	Northward Sverdrup tran.[3]	Offshore Ekman tran.[4]	Cube of wind speed[5]	Area 2B	Area 3A	Nearshore salinity index[7]	Sea surface atmos. pressure[8]
Winter	2.09	2.33	– 26.09	18.43	– 72.31	155.16	10.40	9.38	9984.63	1017.60
Spring	1.93	2.19	– 20.02	– 117.43	9.97	46.17	10.73	10.16	9990.12	1018.65
Summer	1.88	2.25	– 14.24	– 200.35	61.28	104.99	13.67	13.85	10102.03	1018.58
Fall	1.98	2.29	– 10.69	– 15.63	– 19.71	53.31	13.22	12.87	9999.48	1017.17

[1] Meters.
[2] Value × 10 = metric tons per second per kilometer.
[3] Value × 100 = metric tons per second per kilometer.
[4] Metric tons per second per 100 meter of coast width.
[5] $(\text{meters/second})^3$.
[6] Value = Celsius degrees.
[7] Value/10,000=water density (grams/cm^3) at 15°C.
[8] Millibars.