

AN ABSTRACT OF THE THESIS OF

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Title: Fluctuations of Year-Class Strength in Petrale Sole
(*Eopsetta jordani*) and Their Relation to Environmental Factors

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The effects of potential parental egg production 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). Indices of YCS based on Summed-CPUE (summed catch rates of females for ages 6 + 7) and cohort analysis (numbers of females attaining age-6) tended to be significantly correlated within and between areas 2B and 3A ($r \geq 0.45$, $P \leq 0.06$). Since cohort analyses were deemed more reliable YCS indices than Summed-CPUE indices, only cohort analyses were used to determine the role of potential parental egg production and environmental factors on YCS variations. Large YCS fluctuations were evident from 1958 to 1977. Year-classes born from 1962 to 1965 and from 1973 to 1977 were intermediate to weak cohorts in areas 2B and 3A. In both areas, estimates of commercial catch rates suggested a substantial decline of abundance from the middle 1970's to the middle 1980's. The fact that the large decrease of YCS for cohorts born from 1973 to 1977 was not preceded by a decline in commercial catch rates, and that spawner-recruit relations were not detected, suggested that density-independent factors were more important than parental-stock size during the initial decrease of YCS in the 1970's and the subsequent decline of catch rates

in the late 1970's. For cohorts born from 1958 to 1977, 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 variations in area 2B. For area 3A, sea surface temperature from December to February along with the previous environmental factors explained about 65 % of the YCS variation. In a lower extent, winter salinity variations due to the Columbia River also appeared to be related to recruitment strength in area 3A. These findings suggested that YCS fluctuations of petrale sole from 1958 to 1977 may have been primarily forced by winter and early spring oceanographic conditions affecting distribution and/or survival of eggs and early larval stages.

Fluctuations of Year-Class Strength in Petrale Sole (Eopsetta jordani)
and Their Relation to Environmental Factors

by

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Fluctuations of Year-Class Strength in Petrale Sole (*Eopsetta jordani*)
and their Relation to Environmental Factors

GENERAL INTRODUCTION

Basis for Recruitment Variation in Fishes

An outstanding, yet little understood problem in fisheries science and ecology is the recruitment process by which new individuals or recruits are added to the older portion of the population through successful reproduction and immigration. Although in fisheries literature recruitment is often referred to as the addition of new individuals to the vulnerable population (e.g., Ricker 1975), the recruitment level is commonly referred in fisheries science and ecology as to year-class strength (e.g., Ketchen and Forrester 1966) or brood strength. (e.g., Carruthers et al. 1951).

Despite the fact that many studies on year-class strength (YCS) variations in fishes tend to support Hjort's (1914) belief that year-class fluctuations among cohorts can be traced back to early life stages (e.g., Bannister et al. 1974, Lasker 1981), the complexity of the recruitment process in fishes has prevented a definite answer as to whether Hjort's (1914) "critical period" concept has general validity. Briefly, this concept states that the early life stages of fishes are subject to high mortality. Hjort (1914) hypothesized that this high mortality could be due both to lack of food after hatching, or to drift of larvae and young fry away from areas favorable for further growth.

Several studies suggest that individual species characteristics and environmental factors could affect the validity of Hjort's critical-period concept (Sette 1943, May 1974). However, the idea that drift of larvae may affect subsequent recruitment has been supported by many studies (e.g., Parrish et al. 1981, Bailey 1981, Parrish et al. 1983). Moreover, several interrelated processes could also affect early survival of fish and recruitment strength. Some of these

processes could include spawning biomass (Ricker 1954, Cushing 1971), predation of early fish stages (e.g., Hunter 1981, Bailey and Houde 1989), diseases (Lindquist 1978) and many other environmental conditions (e.g., Shepherd et al. 1984, Bakun 1985).

The difficulty in determining the relative importance of density-independent and density-dependent factors on fish recruitment could be due to the different importance of these processes among species (Cushing 1971, Cushing 1973), temporal changes between density-dependent and density-independent processes in a single species (e.g., Gulland 1982, Rothschild et al. 1989), or to different importance of these processes in each life stage of cohort (e.g., Sissenwine 1984, Houde 1987). Besides, Wooster and Bailey (1989) have pointed out that a meaningful integration of density-dependent and density-independent processes in recruitment studies has been limited by reduced multi-disciplinary research.

Although human-induced climatic change could have potentially dramatic consequences on marine ecosystems and fisheries (e.g., McGlade 1990, Bakun 1990, Gucinski et al. 1990), long-term historical records of fisheries (Cushing 1982) and evidence from fish scales found in anoxic sediment (Soutar and Issacs 1974) strongly suggest that several commercially important fishes have experienced remarkable abundance changes in past centuries, which presumably were largely unrelated from human activities.

Despite the recent development of Northeast Pacific fisheries, evidence of climatic and oceanographic influences on the abundance and/or recruitment of many fishes has become increasingly apparent (e.g., Ketchen 1956, Bailey and Incze 1985, Hollowed et al. 1987, Botsford et al. 1989). In the case of flatfishes from the Northeast Pacific and other oceans, it has been generally reported that recruitment may have been more influenced by environmental factors than by parent stock size (e.g., Johansen 1927, Sissenwine 1974, Ketchen and Forrester 1966, Hayman and Tyler 1980). This apparent lack of spawner-recruit relation is further supported by the non-correlated variability between YCS and reproductive life span of pleuronectids (Roff 1981).

Introduction and Objectives

The present study deals with the recruitment process and abundance fluctuations of petrale sole (*Eopsetta jordani*), as well as with the identification of factors related to recruitment variations in this species. Petrale sole is a relatively large flatfish from the Northeast Pacific. It is reported from Coronado Island (32°N, 26'N - 117°, 16'W) off Baja California to Kodiak Island (58°N - 152°W) off Alaska (Roedel 1953, Hitz and Rathjen 1965). However, it is commercially fished only from Santa Barbara, California, to Hecete Strait, British Columbia (Pedersen 1975-a). After Pacific halibut (*Hippoglossus stenolepis*), petrale sole has consistently obtained the highest per unit value of any groundfish in the Northeast Pacific coast (Demory 1984). Six offshore spawning locations for this species have been reported along the Pacific coast of the United States and Canada (Pedersen 1975-b). The present work will focus on the two central spawning grounds reported by Pedersen (1975-b); (Figure I.1).

The general objectives of the present research are: i) to determine YCS and relative abundance variations of petrale sole off Oregon and Washington, ii) to synthesize available information relevant to the recruitment process of this species iii) to ascertain the extent to which potential egg production and environmental factors could have influenced YCS from the late 1950's to the late 1970's, and to ascertain whether recruitment variation could have been reflected in commercial catch rates in this species.

Organization of Thesis

This research is based on interpretation of information from the fishery, research surveys from larval to adult stages, and from available knowledge on petrale sole. Section I considers estimates of YCS indices and annual catch rates from the fishery and relative YCS indices from surveys. Section II deals with the effects of potential egg production and environmental factors on recruitment strength.

Section III summarizes the findings of this thesis. Sections IV and V contain respectively the references and the appendices of Sections II and III.

I. COMPARISON OF YEAR-CLASS STRENGTH AND CATCH RATES FOR PETRALE SOLE (Eopsetta jordani) IN TWO AREAS OFF OREGON AND WASHINGTON

Abstract

Year-class strength for petrale sole (Eopsetta jordani) off Oregon and Washington (Pacific States Marine Fisheries Commission area 2B: 42°50'N - 44°18'N, and area 3A: 45°46'N - 47°20'N) showed large interannual fluctuations from cohorts born during 1958 to 1982. Summed-CPUE indices (summed catch rates for ages 6 + 7) and cohort analysis indices (age-6) tended to be significantly correlated within and between areas 2B and 3A ($r \geq 0.45$, $P \leq 0.06$). Comparisons with survey data indicated that cohort analysis provided more reliable year-class strength estimates than Summed-CPUE indices. Cohort analysis calculations from year-class 1958 to 1977 showed that cohorts born during 1962 to 1965 and 1973 to 1977 were intermediate to weak in areas 2B and 3A. However, the decrease of year-class strength for these cohorts was not consistent with trends of commercial catch-per-effort in both areas, which suggested that fishery independent factors may have been more important for the initial decrease of year-class strength and catch rates than parental stock size.

Introduction

The study of year-class strength (YCS) is central for understanding the role of recruitment on population fluctuation and for the long-term management of fisheries. Petrale sole (Eopsetta jordani) is commercially caught from the multispecies groundfish fishery off the Northeast Pacific coast. The effect of fishing upon the abundance and YCS of this species is unclear. For petrale sole off British Columbia and Washington, Cleaver (1949) suggested that decreased yields may have been caused mainly by fishing, but Barraclough (1954) ascribed the decline in availability both to heavy exploitation and long-term recruitment failure. Ketchen and Forrester (1966) questioned the role of the fishery because of the large variations of YCS seen in stocks with different exploitation history. Pedersen (1975-a) indicated that variations in yield were a result of recruitment variations during the 1950's and 1960's. He further suggested that variable recruitment to

the stocks may have been more important on production trends than the spawning ground fishery. For petrale sole off Oregon, Demory et al. (1976) reported that year-classes born in 1961, 1966, 1968 and 1970 appeared to be stronger than adjacent cohorts, and Lenarz (1978) indicated important YCS variations. Demory (1984) also suggested variable recruitment, but no trends from year-class 1960 to 1975 off Oregon-Washington (Columbia area 43° 00'N - 47° 30'N). Yet, he indicated a general decrease in relative abundance of petrale sole since the late 1970's.

YCS indices based on catch tend to be overestimated during upwards trends in effort on a stock, and YCS indices based on catch-per-effort can be affected by opposite bias (Pedersen 1975-a). On the other hand, estimates of YCS derived from virtual population analysis (e.g., Pope 1972) have been considered more reliable than catch-per-effort indices (Hayman et al. 1980) and have often been utilized in fish recruitment studies (e.g., Koslow 1984, Hollowed et al. 1987). In spite of this, only catch rates (Ketchen and Forrester 1966) and landings of partially recruited ages (Demory 1984) have been used as quantitative indices to estimate YCS in petrale sole. Although over 98 % of the catches for petrale sole have come from otter trawling (Pedersen 1975-a), the orientation of fishing effort to different species has changed through time, making it difficult to obtain a consistent measure of relative abundance. In addition, landing statistics have not accounted for all groundfish catches taken by offshore foreign fleets. Besides, both fishing depth ranges and fishing power of domestic vessels have increased since the late 1970's. Therefore, new analyses of the role of fishing and natural factors on the decrease of abundance of petrale sole require the use of alternative YCS estimates to those derived from catch and catch-per-effort.

The objectives of this study were to determine and compare the magnitude of YCS variations for petrale sole in Pacific States Marine Fisheries Commission (PSMFC) areas 2B and 3A (formerly called PMFC areas). A complementary goal was to estimate general changes in

relative abundance using two different estimates based on catch rates. PSMFC areas 2B and 3A have supported the highest landings of petrale sole off Oregon and southern Washington. Moreover, each one of these areas surrounds a winter spawning ground (Figure I.1). Long-term tagging studies in spawning sites within PSMFC area 2B (Oregon Fish Commission 1970) and PSMFC area 3A (DiDonato and Pasquale 1970) have shown that most migrations of petrale sole are restricted within each of these two areas.

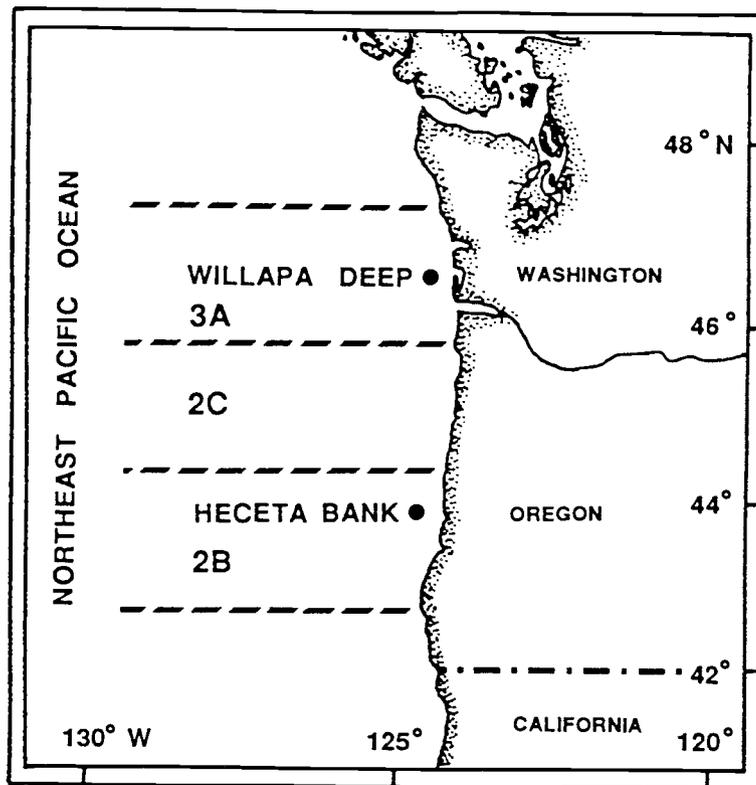


Figure I.1. Location of Willapa Deep and Heceta Bank spawning grounds of petrale sole in Pacific States Marine Fisheries Commission (PSMFC) areas 3A and 2B. (Modified from Pedersen 1975-a).

Methods

Indices of YCS derived from fishery data were based on summed-CPUE (Hayman et al. 1980) and on the cohort analysis version II of Jones (1981, after Pope 1972). Data from groundfish surveys conducted by the Oregon Department of fish and Wildlife, ODFW, (Demory et al. 1976) were used to compute YCS from year to year. Survey data collected by ODFW were also used to evaluate YCS indices based on relative abundance and to calibrate cohort analysis indices for year-classes born from 1960 to 1971. YCS indices based on Summed-CPUE and cohort analyses were estimated separately from fishery data for PSMFC areas 3A ($45^{\circ} 46'N - 47^{\circ}20'N$) and 2B ($42^{\circ} 50'N - 44^{\circ}18'N$). Herein after referred to as areas 2B and 3A.

Age estimations of petrale sole used in this study were based on the surface aging method of otoliths (blind side sagitta). However, the break and burn technique showed that surface aging of otoliths is only reliable for females, at least up to 18 years old, and for males under 9 years of age. (William H. Barss, ODFW, unpublished data). Therefore, YCS indices from surveys and fishery data were based on the age composition of females. Variation of YCS in females should be reflected in males since male and female numbers were significantly correlated in landings. This conclusion was also supported by age frequencies of males and females up to age-8 obtained from surveys. These showed that strong year classes in females were seen also in males.

The age composition from commercial bottom trawl landings was provided by ODFW from 1966 to 1981, and for 1987 and part of 1986. However, the age composition for 1976 in area 3A was obtained from sampling conducted by the Washington Department of Fisheries (WDF). The remaining age composition from 1982 to 1989 was estimated as a part of this study using available otolith samples provided by ODFW (Appendices I.1 and I.2).

Although petrale sole start recruiting to the trawl fishery at age-3, full recruitment is not completed until ages 6 or 7. However,

due to the discard of small fish at sea by fishermen, the recruitment appears to be completed at age 8 in landings. Estimation of the numbers of younger fish caught were based on available discard rate estimates for the studied period. No YCS estimates were computed for age groups under age-6 due to potentially higher discard rates for stronger cohorts. The estimated percentage of weight discarded for the whole catch of petrale sole in 1982 (Barss and Demory 1985) was similar to those reported in 1960-61 (Herrmann and Harry 1963). This suggested that total discard rates may have changed little from 1966 to 1982. Thus, discard rates at-age (TenEyck and Demory 1975) were used to account for the original catches from 1966 to 1981. These latter authors reported that the discarded proportion for females at ages 6, 7 and 8 were 22 %, 10 % and 3% respectively, which were very similar to those of males. The discard rates estimates of TenEyck and Demory (1975), along with those available for 1987 (Robert L. Demory, ODFW, unpublished data) were used to estimate changes in discards of small fish after 1981. A discard of about 6 % was calculated for age-6 in 1987, and no evidence of older age-groups being discarded was detected in that year. Therefore, the decrease in discards for the period 1982-87 was estimated by linear interpolation of discard estimates between 1981 and 1987. The same discard rate at age-6 for 1987 was assumed for 1988-89 because it was deemed more conservative than projecting the previous linear interpolation.

The annual contribution in weight and numbers of females and males in the landings is required to compute the Summed-CPUE and cohort analysis indices. The weight contribution of females in landings was calculated as weight proportion (WP):

$$WP_f = (N_f \times W_f) / (N_f \times W_f + N_m \times W_m) \quad (1)$$

where N_f and N_m are the respective numbers of females and males in samples from commercial landings, and W_f and W_m are the corresponding mean observed (or estimated) total fish weights. The sex ratios used to calculate the weight contribution of female petrale sole in landings

were based on the original proportions of fish in samples. However, in some annual samples unusually large departures from the average sex ratio were adjusted using the mean numbers of females and males sampled in the six adjacent years (Appendices I.3 and I.4).

The total weight of female petrale sole landed per age group in a given year and area was computed as the total weight of females landed times the fraction of female weight per age group obtained from samples of females. The total number of females at a given age was computed as the total weight of all females at the same age divided by the mean weight of females for the attendant age group (Appendices I.5 and I.6).

ODFW survey data were available within areas 3A and 2C in 1971 and 1973, and within area 2B in 1972 and 1974. Since annual age frequencies from surveys were not affected by discard rates and were computed from a larger number of samples than those from the fishery, survey data were deemed more reliable indicators of year to year differences in YCS than landing data. General differences in YCS were estimated from surveys by comparing and following individual brood years through the years (Demory et al. 1976). However, unlike the latter work, only female age composition was utilized to compute relative YCS indices because of the unreliable aging of male fish mentioned previously. As age frequencies in areas 2B, 2C and 3A showed common strong year-classes in succeeding years, the age frequencies for areas 3A and 2C were combined to increase the representation for years 1971 and 1973.

Landing data from 1966 to 1981 were obtained from PMFC (1964-84). Total landing estimates from 1982 to 1989 were obtained from reports and unpublished data furnished by ODFW and WDF. Changes in relative abundance were estimated using non-standardized and standardized catch rates. Non standardized catch rates were computed dividing the total annual landing of petrale sole in areas 2B and 3A by the attendant total annual bottom trawl fishing effort. Since the range of fishing depths increased through the studied years, standardized catch rates consider a constant depth range of fishing per area, and only include the fishing effort in which petrale sole catches were reported. The

latter was done to reduce the effect of changes in orientation of total fishing effort to other species. As the landings of petrale sole in areas 2B and 3A during the middle 1960's occurred at depths shallower than 420 m, this depth was selected as a limit to standardize catch and fishing effort information through time. For each PSMFC area, the standardized annual fishing effort (Oregon-Washington fleets) directed toward petrale sole (f) was computed as fishing days (24 hr/day) by the relation:

$$f = (f_o \times C) / C_o \quad (2)$$

where f_o is the annual Oregon groundfish fishing effort in which attendant Oregon landings of petrale sole (C_o) were reported in logbooks at depths of up to 420 m, and C is the estimated total landing of petrale sole per area (2B or 3A) up to 420 m of depth, C was calculated as the total annual landing of petrale sole at all depths multiplied by the annual proportion of Oregon landings up to 420 m of depth (computed from Oregon fishing log-books). Since both f_o and C_o were based on partial annual sampling of Oregon logbooks, they do not reflect interannual changes in total fishing effort and landings in equation 2, but changes in their annual ratio (f_o / C_o). This procedure allowed to estimate both standardized annual catch rates (C / f); (appendices I.3 and I.4), and summed-CPUE indices for cohort born in year i . The latter was computed as:

$$\text{Summed-CPUE}_i = \sum_j^{j+1} (N_j / f_{i+j}) \quad (3)$$

where N_j is the number of females at age j and f_{i+j} is the corresponding standardized fishing effort for year $i+j$. Summed-CPUE indices were computed for ages (6 + 7) and for ages (8 + 9).

Cohort analysis requires estimates of instantaneous rates of natural mortality (M), fishing mortality at a terminal age (F_t) and the numbers of fish caught at different ages for a given year-class. The number of females was back-calculated by cohort analysis from age 12 to age 6 for cohorts born from 1960 to 1977, and from age 12 until ages 7

and 8 for cohorts born in 1959 and 1958 respectively. The previous difference in back-calculations is due to lack of age composition prior to 1966. The estimate of natural mortality was based on Pauly (1980). Preliminary estimation of M by plotting total annual instantaneous mortality (Z) against fishing effort (Gulland, 1983), and Z estimates based on the early age structure in the fishery (Demory and Bailey 1967) produced unreliable values for age groups entirely recruited to the fishery.

As indicated by Jones (1981) and evidenced in the present study, potential errors in the estimated catch at older ages in some cohorts may prevent the use of a standard method for computing F_t for all cohorts. In the case of most cohorts, terminal fishing mortality was computed as $F_t = Z - M$, where Z was calculated as the slope of the regression: $\ln [N_j / f_{i+j}]$ on age j , and where j ranges from age 8 to 12, and f_{i+j} is as described in equation 3. The first reason for not using the previous method in estimating F_t for the remaining cohorts was the disagreement between the resultant YCS and the relative YCS determined from surveys. The second reason was the improbably low (or high) catch estimate at older ages which could produce large bias in the back-calculated number of fish at smaller ages.

In the case of cohorts with available survey information, the selection of F_t was based on values producing a similar difference in YCS for adjacent cohorts than those observed from relative YCS age frequencies for the attendant cohorts. By this procedure, age frequencies from age groups 3 to 11 obtained from surveys were computed from year-classes born between 1960 to 1971. Then, the ratios of age frequencies for adjacent cohorts at the same age were calculated to estimate relative YCS ratios. Since these YCS ratios are relative indices, the attendant differences in YCS were only used to compare adjacent cohorts (Table I.1). Selection of F_t estimates by this procedure were based on values producing cohort analyses back-calculations consistent with the difference in YCS for adjacent cohorts observed from relative YCS indices.

For cohorts showing unlikely catch at older ages, but for which no survey information was available, estimates of F_t were based on values reflecting increase (or decrease) in summed commercial catches between adjacent cohorts. As catches for younger age-groups were not available for all cohorts, only ages 8 to 12 were included in the previous summed-catches.

The agreement between YCS indices within and between areas was compared by Spearman-rank difference correlations (Tate and Clelland 1957).

Results

Age-Weight Relations

On average, females accounted for 58 % of the numbers and 65 % of the weight landed of petrale sole in each area. When comparing the numbers of males and females for all years, significant differences from the proportion 1 : 1 were detected in both areas (G-test; $P < 0.05$; Sokal and Rohlf 1981). Estimates of YCS indices required annual data on mean weight of females at-age from total annual landings. As this information was not available for all years, it was also necessary to estimate age-weight relations of females, and length-weight relations for both sexes. In the case of years with weight information, the best age-weight fitting to estimate weight at-age was obtained by linear regressions of fish weight on age ($r > 0.65$, $P < 0.01$). In years without weight information, mean fish weight was estimated by common length-weight regressions using data for available years. The regression of fish weight on fish length used is $W = aL^b$, where W is the total fish weight in grams and L is the total (center) fish length in millimeters. The parameters a and b were computed from log-transformed weight and length data as: $\ln [W] = \ln a + b \ln [L]$, ($r > 0.90$ $P < 0.01$). There were significant differences between the slope parameters for each area and sex ($P < 0.05$). The transformed regression parameters by area and sex were:

	Females:	Males:
Area 2B:	$W = 2.6773 \times 10^{-6} L^{3.248384}$	$W = 6.8999 \times 10^{-6} L^{3.082794}$
Area 3A:	$W = 1.4963 \times 10^{-6} L^{3.348022}$	$W = 9.7836 \times 10^{-6} L^{3.027382}$

Catch Rate Estimates

Non-standardized annual catch rates of petrale sole were similar to standardized annual catch rates for areas 2B and 3A. However, interannual variation was greater in area 3A than in area 2B (Figure I.2). Although relative abundance could have been increasingly underestimated by non-standardized catch rates from the late 1970's due

Table I.1. Ratios of percentage of age frequencies between adjacent cohorts, and for a same age group of female petrale sole. Only cohorts with age groups ranging from age-3 (1971 and 1970) to age-11 (1961 and 1960) were compared. (Based on survey data in PSMFC areas 3A+2C and 2B provided by Robert L. Demory, ODFW, Newport, OR 97365).

Cohorts compared	Survey Comparison			Median	Mean
	1971-72	1972-73	1973-74		
1971 / 1970	-	-	1.06	1.06	1.06
1970 / 1969	-	3.18	1.63	2.40	2.40
1969 / 1968	0.33	0.58	0.43	0.43	0.44
1968 / 1967	1.34	1.19	0.65	1.19	1.06
1967 / 1966	0.44	0.77	0.60	0.60	0.60
1966 / 1965	1.74	1.28	1.84	1.74	1.62
1965 / 1964	1.78	2.51	1.24	1.78	1.84
1964 / 1963	0.66	0.63	2.61	0.66	1.30
1963 / 1962	2.80	0.67	2.61	2.61	2.03
1962 / 1961	0.69	0.33	-	0.51	0.51
1961 / 1960	2.68	-	-	2.68	2.68

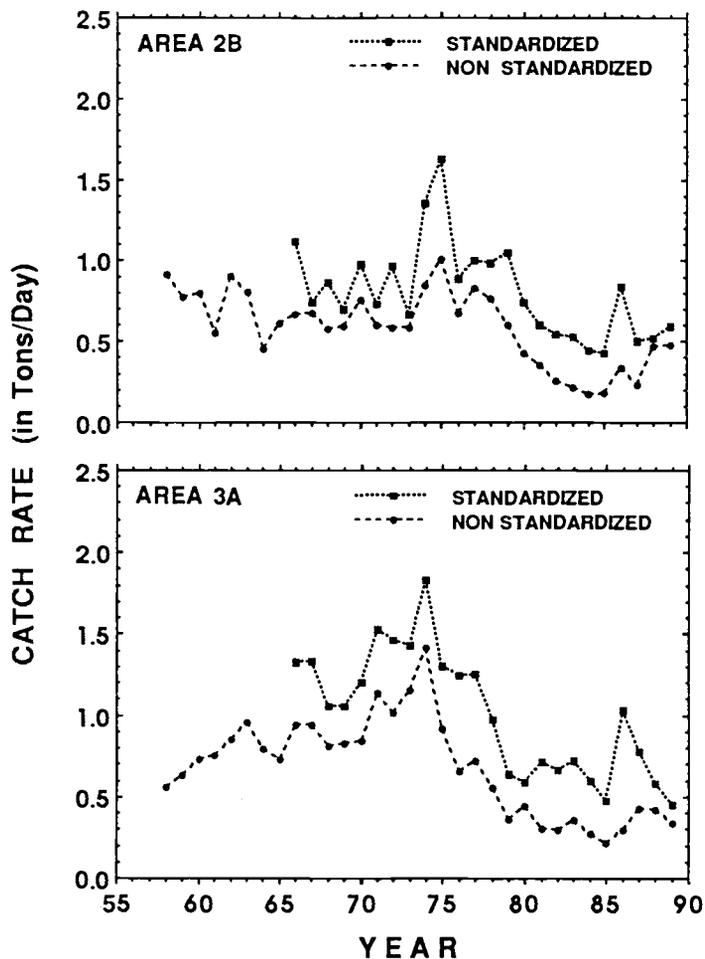


Figure I.2. Catch rates of petrale sole in PSMFC areas 2B and 3A. Standardized values consider all fishing effort in which petrale sole was present up to a depth of 420 m. Non standardized values consider all groundfish effort and fishing depths per area (including fishing trips that did not capture any petrale sole).

to the greater number of species landed, or due to the attendant increase in fishing effort, standardized catch rates also supported a substantial decrease in catch rates since the late 1970's in areas 2B and 3A. After 1985 a slight increase in catch rates was observed in both areas, but it persisted until 1989 only in area 2B.

Relative YCS from Surveys

This index was used to compare YCS between adjacent cohorts from year-classes born from 1960 to 1971. Large differences in relative YCS were shown from these age frequencies, cohorts born in 1961, 1966, 1968, 1970 and 1971 appeared to be consistently strong (Figure I.3). These YCS patterns were also supported by ratios of age-frequency percentages between adjacent cohorts (Table I.1). Due to the potentially high bias of mean ratios of age-frequency percentages, the attendant median values were selected as relative YCS indices for adjusting cohort analyses estimates.

YCS Indices Based on Summed-CPUE

Both the indices for ages (6 + 7) and ages (8 + 9) showed a decreasing trend in YCS from cohorts born in the middle 1960's to the middle 1970's. From this last period until 1982, these two indices suggested a small recruitment increase in area 2B (Figure I.4). The correlation between Summed-CPUE indices for year-classes born from 1960 to 1980 was higher for area 3A ($r = 0.83$, $P < 0.01$) than for area 2B ($r = 0.38$, $P < 0.09$). The lower consistency between indices for area 2B suggested that these could be less reliable than those for area 3A. Despite the differences in each area, older age groups are more susceptible to differences in fishing mortality among cohorts, thus, the index for ages (6 + 7) was considered more reliable than the index for ages (8 + 9). It must be pointed out that relative differences in YCS from year to year seen from survey data were generally not reflected in Summed-CPUE indices, particularly in area 2B, which further supports the lower reliability of summed-CPUE indices for this latter area.

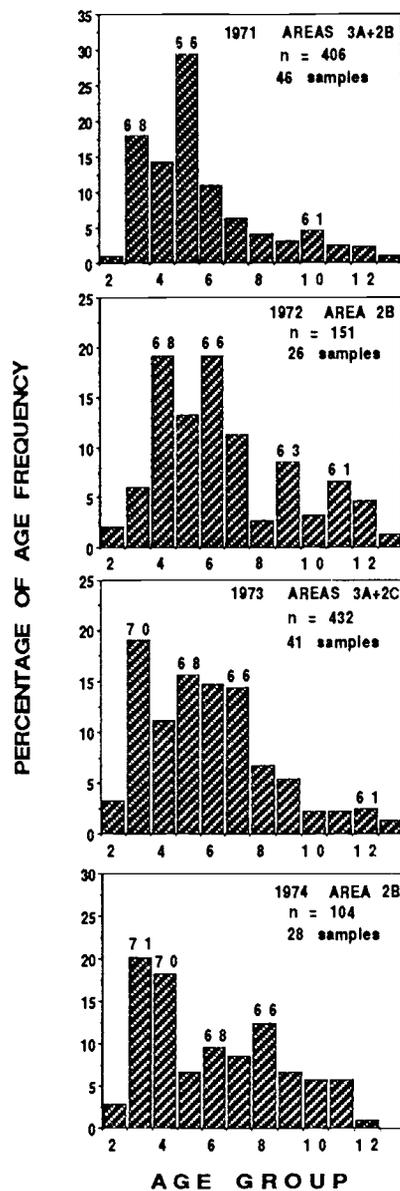


Figure I.3. Percentage of age frequency of female petrale sole obtained from surveys in PSMFC areas 2B, 2C and 3A. (Computed from data furnished by R. L. Demory, ODFW, Newport, OR).

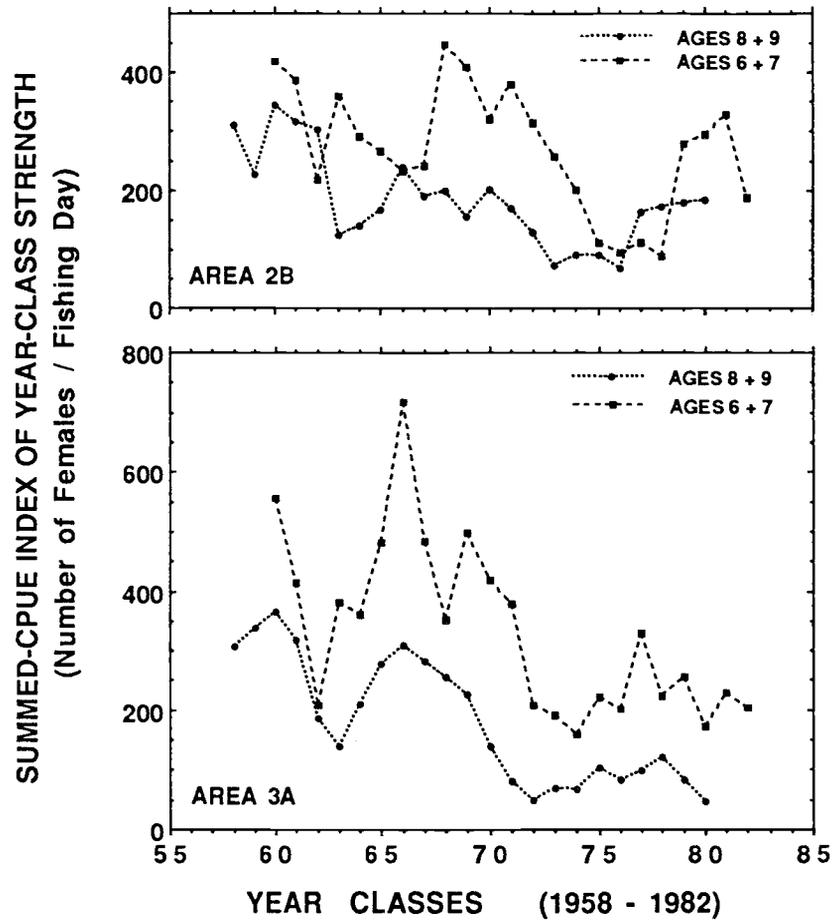


Figure I.4. YCS of petrale sole based on Summed-CPUE indices for females of ages (6 + 7) and (8 + 9). The indices are shown for PSMFC areas 2B and 3A.

YCS Indices Based on Cohort Analysis

Estimates of instantaneous natural mortality rate by the method of Pauly (1980) require values of the von Bertalanffy growth parameters k (metabolic coefficient) and L_{∞} (asymptotic length) and mean annual water temperature ($^{\circ}\text{C}$) from the location where fish are caught. To account for discard of small fish from landings, k and L_{∞} estimates were obtained by combining age-length data from surveys up to age-8, and age-length data from ages 9 to 13 obtained from landings (Appendix I.7).

Based on data given in Huyer (1977), the approximate mean annual temperature at depths where petrale sole is caught is nearly 8°C . The estimate of annual instantaneous natural mortality (M) of female petrale sole in area 3A and 2B was 0.16. This value is also the mean estimate obtained when using the present estimates for parameters k and L_{∞} and other values reported in the literature (Table I.2).

For most cohorts in which adjusted terminal fishing mortalities were used to correct YCS indices, the adjusted fishing mortalities greatly differed from those of other cohorts (Tables I.3. and I.4). However, since estimated values of annual instantaneous fishing mortality derived from cohort analyses tend to converge toward smaller age groups (Pope 1972), temporal comparisons among fishing mortalities should be more reliable for the smaller age group considered. Predictably, annual instantaneous fishing mortalities for age-6 were similar between estimates based on non-adjusted fishing mortalities and adjusted fishing mortalities. The mean estimate of annual instantaneous fishing mortality for age-6 for year classes 1960 to 1977 was smaller and less variable for area 2B ($\bar{x} = 0.16$, s.d. = 0.07) than for area 3A ($\bar{x} = 0.24$, s.d. = 0.12). Temporal variations in fishing mortality further suggested that year-classes born in the 1970's had higher fishing mortalities than cohorts born in the 1960's.

YCS indices between age-6 and age-8 were significantly correlated in area 3A ($r = 0.93$, $P < 0.001$) and area 2B ($r = 0.94$, $P < 0.001$). Since the back-calculation until age-6 also depends on age-8, these

Table I.2. Estimates of annual instantaneous natural mortality rate (M) for female petrale sole based on Pauly (1980). Von Bertalanffy coefficients L_{∞} and k are also shown. The mean environmental temperature used was 8°C.

Area	L_{∞} (cm)	k	M	Reference for L_{∞} and k
PSMFC Area 3A	72.8	0.079	0.16	1
PSMFC Area 2B	69.1	0.083	0.16	1
PSMFC Area 3C inshore	58.6	0.167	0.26	2
Cape Flattery inshore	70.7	0.092	0.16	3
Cape Flattery Spit Deep	83.2	0.047	0.10	3
Esteban Deep	79.5	0.048	0.10	3
Esteban inshore	65.3	0.117	0.20	3

1: Present study, 2: Ketchen and Forrester (1966), 3: Pedersen (1975-a).

Table I.3. Estimated annual instantaneous fishing mortality for female petrale sole in PSMFC area 2B derived from cohort analyses. Values of terminal fishing mortality with suprascript (a) were adjusted by relative YCS indices.

Cohort	Age Group						
	6	7	8	9	10	11	12
Annual Instantaneous Fishing Mortality							
1958	-	-	0.36	0.15	0.20	0.34	0.38
1959	-	0.22	0.13	0.16	0.25	0.21	0.33
1960	0.08	0.12	0.18	0.21	0.60	0.22	0.38
1961	0.05	0.12	0.14	0.29	0.30	0.11	0.28
1962	0.06	0.14	0.60	0.39	0.49	0.67	1.20 ^a
1963	0.08	0.32	0.14	0.20	0.17	0.59	0.25 ^a
1964	0.23	0.23	0.29	0.21	0.30	0.32	0.45
1965	0.15	0.23	0.17	0.26	0.32	0.17	0.08 ^a
1966	0.22	0.23	0.25	0.49	0.63	1.16	0.72 ^a
1967	0.06	0.15	0.21	0.17	0.09	0.14	0.19 ^a
1968	0.11	0.26	0.26	0.18	0.30	0.20	0.25
1969	0.24	0.29	0.18	0.30	0.44	0.57	1.20 ^a
1970	0.18	0.15	0.26	0.24	0.23	0.28	0.32
1971	0.15	0.24	0.28	0.17	0.23	0.15	0.32
1972	0.17	0.32	0.22	0.21	0.19	0.32	0.22
1973	0.19	0.19	0.17	0.12	0.23	0.22	0.23
1974	0.22	0.23	0.25	0.49	0.63	1.16	0.72
1975	0.24	0.21	0.38	0.45	0.66	0.54	0.38
1976	0.29	0.23	0.25	0.33	0.55	0.16	1.19
1977	0.15	0.17	0.26	0.52	0.25	0.75	0.38

Table I.4. Estimated instantaneous fishing mortality for female petrale sole in PSMFC 3A derived from cohort analyses. Values of terminal fishing mortality with suprascript were adjusted by relative YCS indices (a), or by summed catch from age 8 to 12 (b).

Cohort	Age Group						
	6	7	8	9	10	11	12
Annual Instantaneous Fishing Mortality							
1958	-	-	0.30	0.50	0.41	0.47	0.48 ^b
1959	-	0.31	0.46	0.46	0.54	1.44	0.55
1960	0.15	0.38	0.42	0.49	0.97	0.45	0.55
1961	0.15	0.16	0.26	0.22	0.24	0.21	0.23
1962	0.12	0.22	0.25	0.35	0.33	0.40	1.20 ^a
1963	0.22	0.29	0.15	0.23	0.48	0.75	0.36
1964	0.24	0.29	0.33	0.47	1.61	2.35	0.97
1965	0.24	0.21	0.31	0.39	0.19	0.20	0.02 ^a
1966	0.18	0.18	0.20	0.19	0.06	0.05	0.11 ^a
1967	0.17	0.22	0.27	0.23	0.08	0.32	0.36
1968	0.09	0.19	0.21	0.12	0.21	0.19	0.36
1969	0.21	0.35	0.30	0.58	0.60	0.60	1.20 ^a
1970	0.10	0.26	0.24	0.25	0.19	0.13	0.24
1971	0.24	0.20	0.30	0.14	0.10	0.34	0.21
1972	0.19	0.42	0.27	0.10	0.09	0.16	0.20
1973	0.52	0.27	0.21	0.35	0.59	0.88	0.33
1974	0.39	0.35	0.32	0.39	0.27	0.37	0.26
1975	0.28	0.51	0.75	0.70	0.57	2.17	0.92
1976	0.37	0.58	0.90	0.76	1.46	0.62	0.97
1977	0.41	0.64	0.38	0.29	0.04	0.30	0.03 ^b

high correlations are not unexpected. For reasons similar to those applied to the Summed-CPUE indices, numbers of fish attaining age-6 estimated from cohort analysis were considered more reliable indices of YCS than older ages. Yet, due to the high correlation between indices for ages 6 and 8, the numbers of fish at ages 6 and 7 for cohorts 1958 and 1959 were estimated by simple linear regressions of ages 6 and 7 on age 8 ($r > 0.93$, $P < 0.001$, Tables I.5 and I.6).

Due to the back-calculation from age 12 to age 6, no YCS estimates were computed by this method after the year-class born in 1977. Cohorts born from 1962 to 1965 and from 1973 to 1977 were intermediate to weak year-classes in areas 2B and 3A (Figure I.5). The declining trend of YCS in the latter cohorts was reflected in lower catch rates since the late 1970's (Figure I.2). Thus, despite the relatively large number of age groups of petrale sole in the Oregon-Washington fishery, the cooccurrence of weak cohorts may have substantial effects on commercial catch rates.

Comparison of YCS Indices Between Areas

Variations in YCS were common in areas 2B and 3A (Figures I.4 and I.5). Area 3A consistently showed larger Summed-CPUE indices and number of fish reaching age-6 than area 2B (Tables I.5 and I.6). With the exception of a marginally significant correlation between the Summed-CPUE indices of area 3A and the cohort analysis index for area 2B ($P = 0.06$) all other YCS indices were significantly correlated (Table I.7). The exception is apparently due to the relatively lower decrease in YCS in area 2B than in area 3A for cohorts born since the early 1970's. The large YCS decline beginning from this latter period appears to have occurred first in area 3A and next in area 2B and it is supported both by Summed-CPUE and cohort analysis indices.

Table I.5. Numbers of female petrale sole (thousands) reaching ages 6 to 12 in PSMFC area 2B. Values were based on cohort analyses. (Ages 6 and 7 of cohort 1958 and age-7 of cohort 1959 are regression estimates based on age-8).

Cohort	Age Group						
	6	7	8	9	10	11	12
Thousands of Fish							
1958	208	142	90	53	39	27	16
1959	278	199	137	103	75	50	34
1960	309	243	184	130	90	42	29
1961	385	312	236	175	112	70	53
1962	231	185	137	64	37	19	8
1963	296	233	144	106	74	53	25
1964	240	162	110	71	49	31	19
1965	280	206	139	101	66	41	30
1966	487	379	300	230	171	132	107
1967	352	284	207	144	103	80	60
1968	419	321	211	139	99	63	44
1969	349	234	149	106	67	37	18
1970	426	303	222	146	98	67	43
1971	421	307	205	132	95	64	47
1972	373	269	166	113	79	55	34
1973	356	251	177	127	95	65	44
1974	259	178	120	80	41	19	5
1975	193	129	90	52	28	12	6
1976	157	101	68	45	28	13	10
1977	223	165	118	78	40	26	11

Table I.6. Numbers of female petrale sole (thousands) reaching ages 6 to 12 in PSMFC area 3A. Estimated were based on cohort analyses. (Ages 6 and 7 of cohort 1958 and age-7 of cohort 1959 are regression estimates based on age-8).

Cohort	Age Group						
	6	7	8	9	10	11	12
Thousands of Fish							
1958	543	379	247	155	80	45	2
1959	544	394	248	134	72	36	7
1960	624	459	268	150	79	25	14
1961	692	508	370	243	166	111	76
1962	333	251	172	114	69	42	24
1963	421	288	183	134	91	48	19
1964	365	245	156	95	51	9	1
1965	547	365	253	158	92	65	45
1966	954	678	482	336	238	191	155
1967	703	508	348	227	154	121	75
1968	737	573	404	280	211	145	103
1969	558	386	231	146	70	32	15
1970	651	503	329	221	147	103	77
1971	570	382	267	168	124	95	58
1972	463	327	183	119	92	71	52
1973	415	209	136	94	57	27	10
1974	326	188	113	70	40	26	16
1975	332	213	109	44	18	9	1
1976	286	168	81	28	11	2	1
1977	424	241	108	63	41	33	21

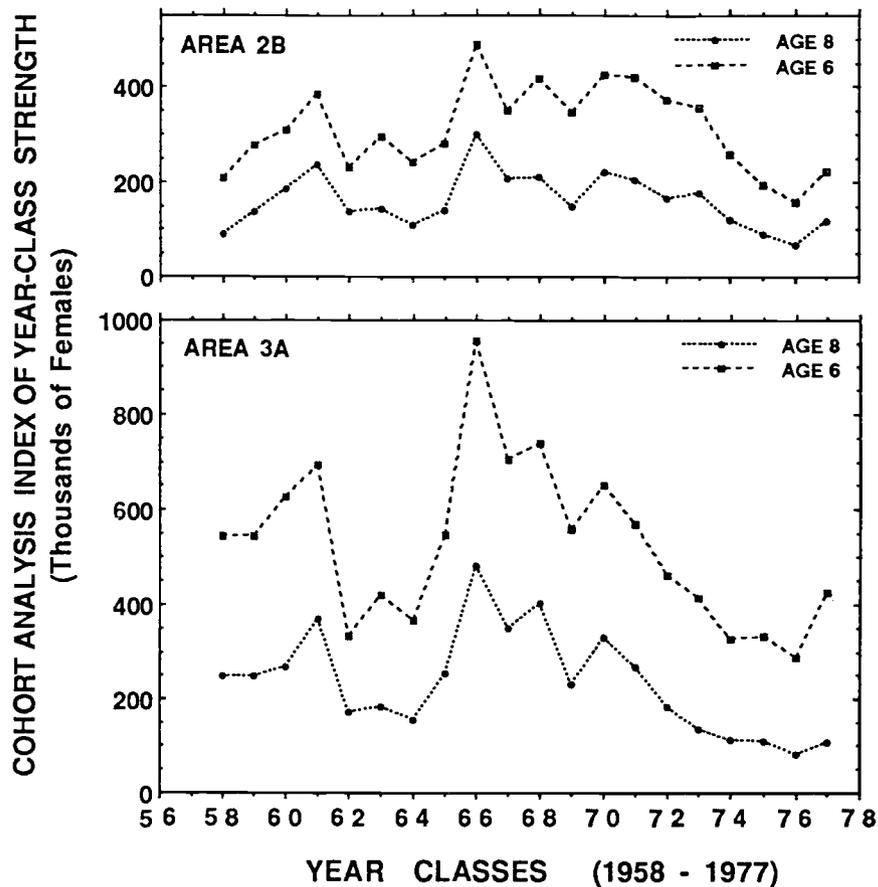


Figure I.5. YCS indices of petrale sole based on cohort analyses estimates of the numbers of females reaching ages 6 and 8. The estimates are shown for PSMFC areas 2B and 3A.

Table I.7. Spearman's correlations among YCS indices of petrale sole in PSMFC areas 2B and 3A. Indices used are the summed-CPUE index for ages 6 + 7 (Summed-CPUE) and cohort analysis estimates for age group 6 (N-6). Cohorts included in the correlations were born from 1960 to 1977. (n = 18, P-values are shown in parenthesis).

YCS Indices	YCS Indices		
	Summed-CPUE Area 3A	N-6 Area 2B	N-6 Area 3A
Summed-CPUE Area 2B	0.49 (0.04)	0.61 (0.01)	0.61 (0.01)
Summed-CPUE Area 3A	-	0.45 (0.06)	0.76 (<0.01)
N-6 Area 2B	-	-	0.82 (<0.01)

Discussion

Cohort analysis estimates at age-6 appeared to be the most reliable YCS indices of petrale sole in this study. This index considers differences in fishing mortality among cohorts, as well as differences in YCS based on surveys and summed catches between adjacent cohorts. Thus, it is unlikely that errors in YCS estimates at age-6 could be large enough to confuse weak and strong year-classes. The similarity between the relative YCS indices of Demory et al. (1976), based on both sexes, and the present relative YCS estimates, based on females, is ascribed to the small contribution of older males in survey samples.

The recruitment index of Demory (1984) based on summed-catch of females from ages 5 to 7 in the Columbia area was correlated both with the present calibrated cohort analysis indices from 1960 to 1971 (area 2B: $r = 0.82$, $P < 0.01$; and area 3A: $r = 0.65$, $P = 0.03$). Yet, for most cohorts born in the 1970's, YCS estimates using the summed-catch index could be overestimated due to a substantial increase in fishing effort and landings (Appendices I.3 and I.4). Conversely, YCS estimates based on the present Summed-CPUE indices could be underestimated for cohorts born in the 1970's and 1980's. Yet, the decline in YCS shown by Summed-CPUE indices during the 1970's was consistent with cohort analyses indices, and with higher fishing mortalities for these cohorts.

Rivard (1989) indicated that calibration of cohort analysis may be required for recent abundance estimates in fishes. Although no survey data were available to evaluate cohort analyses indices of year-classes born after 1972, Summed-CPUE also supported the decline of YCS detected from cohort analysis in areas 2B and 3A during the 1970's. Similarly, the decrease in YCS shown by cohort analysis for year-classes born since the early 1970's was reflected in the decline of standardized and non-standardized commercial catch rates since the late 1970's, which supports a general decrease in abundance of petrale sole (Figure I.2).

Comparisons of YCS among year-classes by the Summed-CPUE indices are more likely to be biased due to temporal differences in mortality rates among cohorts (presumably mainly fishing mortality) and changes in catchability through time, both of which further assume no trends for the comparisons to be reliable. Thus, the present Summed-CPUE indices must be considered general measures of YCS. The fact that similar conclusion was reported in area 3A by Hayman et al. (1980) for Dover sole (Microstomus pacificus), but not for English sole (Parophrys vetulus), supports their idea that species distribution may affect the reliability of Summed-CPUE indices. Like Dover sole, petrale sole has wider bathymetric distribution than English sole (Alverson 1960).

Nearly 57 % of the recoveries of petrale sole tagged in area 2B during its spawning period in Heceta Bank were obtained in this same area over a nine-year period (Oregon Fish Commission 1970). For area 3A, the attendant recovery over a period of eight years following a tagging in Willapa Deep was nearly 69 % (DiDonato and Pasquale 1970). In both tagging studies, most of the remaining percentage of fish showed a northward migration pattern from areas 2B (34 %) and 3A (29 %). The fact that only 2 % of the recoveries tagged in area 3A showed southward migration, and that only 13.6 % of the recoveries tagged in area 2B were captured farther north than area 2C (Figure I.1) suggests that similar YCS variations of petrale sole between areas 2B and 3A are largely due to common recruitment patterns, rather than to fish migration between areas. On the other hand, Best (1963) reported that most northward post-spawning migrations from the nearest southern spawning ground are restricted to areas south of Cape Blanco (i.e., south from area 2B). Thus, although the previous tagging studies showed incomplete isolation between spawning groups of petrale sole, the use of separate YCS indices for areas 2B and 3A is a better approach than a combined YCS index between areas.

Although area 2B could have been grouped with area 2C to compute a more representative YCS index for the spawning group of Heceta Bank, insufficient age structure from commercial catches for area 2C did not allow the inclusion of this latter area. It must be pointed out that

despite the greater catches and relative abundance of petrale sole in area 3A than in area 2B, the latter area appear to have experienced less drastic changes in recruitment and abundance. Yet, similar fishing effort and catch rate trends in these two areas from 1966 to 1989 (Appendices I.3 and I.4) makes it difficult to infer from such comparison the extent to which YCS patterns have been affected by natural and fishing mortality. However, the declining trend in catch rates in both areas did not occur until the late 1970's. This suggests that the decrease in YCS detected for cohorts born since the early 1970's may have been initially more related to natural factors than to potential recruitment overfishing (as defined by Cooke 1984).

For intermediate to weak year-classes born from 1962 to 1965, no associated decline in catch rates was evident when these year-classes entered the fishery. A reason for this may be the rapid recovery in YCS for cohorts born from 1966 to 1971. On the other hand, inverse trends in catch rates prior to 1966 in areas 2B and 3A (Figure I.2) disagree with a simultaneous decline of YCS from 1962 to 1965. This fact is consistent with the suggestion that the recruitment in petrale sole appears to be independent of the exploitation history (Ketchen and Forrester 1966, Pedersen 1975-a).

The present findings support the belief that the observed range of parent-stock sizes in flatfishes generally does not determine the number of recruits that survive to reproduce (Cushing 1973, Roff 1981). Evidence of spawner-recruit relations have neither been found for petrale sole off British Columbia (Ketchen and Forrester 1966), nor for petrale sole off Oregon-Washington (Section II of thesis). Yet, the two latter studies have strongly suggested the existence of environmental-recruitment relations for this species.

II. ENVIRONMENTALLY INDUCED RECRUITMENT VARIATIONS IN PETRALE SOLE (Eopsetta jordani)

Abstract

Potential effects of parental stock size and environmental factors on recruitment strength of petrale sole (Eopsetta jordani) were investigated in two areas off the Pacific Coast of the United States (Pacific States Marine Fisheries Commission areas 2B: 42° 50'N - 44° 18'N, and 3A: 45° 46'N - 47° 20'N). Although spawner-recruit relations were not evident, a regression model based on indices of offshore transport from January to March, and alongshore transport from December to February, accounted for nearly 55 % of the variation of year-class strength in area 2B from 1958 to 1977. For Area 3A, the previous indices plus sea surface temperature from December to February explained about 65 % of the variation in year-class strength. Nearshore salinity variations caused by the Columbia River from December to February also appeared to be related to the recruitment in area 3A. This study suggested that the recruitment of petrale sole is primarily controlled by oceanographic factors from winter to early spring, period in which the egg and early larval stages of petrale sole appear to be most abundant in surface mixed layers. Autocorrelation in environmental and YCS series emphasized the need for long-term recruitment-environmental studies.

Introduction

Recruitment fluctuations in fish populations is ascribed to many physico-chemical factors and biological processes (Shepherd et al. 1984), as well as to parental stock size and fishing (Ricker 1975). Yet, the relative importance of these factors and processes on the recruitment strength of most species is virtually unknown. Although survival at the egg and larval stages may be critical for subsequent year-class strength (YCS) in fishes (e.g., Sharp 1980, Rothschild and Rooth 1982), post-larval survival in some species could disrupt recruitment estimates based on earlier life stages (Smith 1981, Sissenwine 1984).

Petrale sole (Eopsetta jordani, Pleuronectidae) is a commercially important flatfish from the Northeast Pacific. Spawning occurs during

winter months in deep waters (300-450 m). Two central spawning areas, from a total of six reported for this species (Pedersen 1975-b), are located off Oregon and Washington (Figure I.1). Only environmental factors have appeared to be related to recruitment fluctuations in petrale sole. Ketchen (1956) suggested a positive correlation between winter sea surface temperature and recruitment off British Columbia from the middle 1940's to the middle 1950's. In the same area, Ketchen and Forrester (1966) postulated that sea surface temperature and onshore transport of pelagic early life stages could favor YCS. Subsequently, Alderdice and Forrester (1971) determined that eggs and yolk-sack larvae of petrale sole are stenohaline and stenothermal. These findings are consistent with the belief that oceanographic conditions may influence the recruitment of many Northeast Pacific fishes (e.g., Parrish et al. 1981, Bailey and Incze 1985, Hollowed et al. 1987, Botsford et al. 1989). A recent hypothesis suggests that recruitment in groundfishes off the West Coast of the United States could be related to the timing of the spring transition, as well as to attendant interannual variations in advection of early life stages of fishes (Ronald J. Lynn, Southwest Fisheries Science Center, La Jolla, CA, pers. Comm. 1991).

Although large YCS fluctuations have been reported for petrale sole off Washington and Oregon (Pedersen 1975-a, Section I of this thesis), no studies have examined possible causes for such variations. The main interest of the present study is to ascertain whether YCS variations of petrale sole off Oregon and Washington tend to be associated with parental spawning biomass, and with environmental conditions present at early life stages. Specific objectives of this study are: 1) Synthesize information relevant to the recruitment process. 2) Determine if petrale sole exhibit a spawner-recruit relation. 3) Evaluate if YCS fluctuations are related with potentially important environmental factors, and with the timing of the spring transition.

Methods

The two studied locations are Pacific States Marine Fisheries Commission (PSMFC) areas 2B ($42^{\circ} 50'N - 44^{\circ} 18'N$) and 3A ($45^{\circ} 46'N - 47^{\circ} 20'N$), herein after referred to as areas 2B and 3A (Figure I.1). For each of these areas, YCS indices of petrale sole were obtained from cohort analyses estimates of numbers of females attaining 6 years of age (Section I). These two YCS indices represent the recruitment strength of year-classes born from 1958 through 1977. The exclusion of males from the previous YCS indices was justified due to increasing age underestimation in fish over eight years old (William. H. Barss, Oregon Department of Fish and Wildlife, Newport, OR, unpubl. data). However, age-frequencies for younger age-groups indicated that the present YCS indices should be representative for both sexes.

Potential egg production was used as proxy for spawning biomass. Egg production was estimated from fecundity and maturity data (Porter 1964) and from cohort analyses calculations for the parental stock (Section I). Annual potential egg production was estimated as the sum of the age-specific product of the numbers of females, their fecundity, and their maturity proportion. Egg production was averaged for fish over age 13 due to the scarcity of older females.

Information on distribution and length composition of petrale sole larvae off Oregon was furnished by William G. Pearcy and Douglas F. Markle (School of Oceanography, and Department of Fisheries & Wildlife, respectively, Oregon State University). Eight oceanographical and meteorological indices available within or near areas 2B and 3A (Table II.1), were used to determine potential environmental-YCS relations for petrale sole. The timing of the spring-transition was estimated from weekly upwelling indices computed at $45^{\circ} N 125^{\circ} W$ from 1967 to 1977 (Bakun 1975, Mason and Bakun 1986). The spring transition was assigned to a given week based on the high temporal coincidence between weekly changes in upwelling indices, and available dates for the spring transition (Strub and James 1988).

Table II.1. Environmental indices used in correlations with YCS of petrale sole. Recruitment area refers to PSMFC areas 2B and 3A.

Environmental Index	Recruitment Area
Sea surface atmospheric pressure ^{a,c}	2B, 3A
Alongshore Coastal Transport Indices:	
1- Mean sea level ^b	
Neah Bay (48° 22'N - 124° 38'W)	3A
Crescent City (41° 45'N - 124° 12'W)	2B
2- Northward Ekman transport ^{a,c}	2B, 3A
3- Northward Sverdrup transport ^{a,c}	2B, 3A
Offshore Ekman transport ^{a,c}	2B, 3A
Cube of wind speed ^{a,c}	2B, 3A
Water Properties:	
1- Sea surface temperature ^c	
(43° N - 44.9° N), (124° W - 124.9° W)	2B
(46° N - 47.9° N), (124° W - 124.9° W)	3A
2- Salinity index Columbia River ^b	
Estuary (46° 13'N - 123° 45'W)	2B 3A

^a Computed at 45° N - 125° W.

^b Tidal Datum Quality Assurance Section. NOAA, Rockville, MD 20852.

^c Pacific Fisheries Environmental Group. P.O. Box 831. Monterey, CA 93942.

Spearman's correlation analyses (Tate and Clelland 1957) were utilized to account both for linear and non-linear monotonic associations between YCS and independent variables lagged to the first year of life for each cohort (i.e., potential egg production, environmental factors and the timing of the spring transition). Since many of the environmental-YCS plots in this study showed extreme values during 1958, that year was not included in the previous correlations analyses. However, after the most consistent Spearman's correlations for the period 1959 to 1977 were established, all years from 1958 to 1977 were considered in polynomial regression analyses. Such regressions consisted of estimated YCS on environmental anomalies. Environmental anomalies were computed as the actual seasonal value of a given factor minus its long-term mean 1958-1977. The use of anomalies as independent variables was justified to reduce multicollinearity effects in polynomial regressions (Neter et al. 1989). Adjusted P-values for the correlation coefficients of such regressions were based on the estimated number of independent observations (n^* , formula 14 in Bayley and Hammersley 1946). Since the error in the autocorrelation coefficient can increase as more lags are added, calculations of n^* considered up to lag $(n / 10)$ suggested by Blackman and Tukey (1958) and Sutcliffe et al. (1976). Where n is the total number of observations. The estimate of n^* for each regression model was obtained from the dependent or independent variable with the largest autocorrelation coefficient. Lag 2 was deemed to produce conservative estimates of n^* , as equal values were obtained up to lag 4 for the most autocorrelated variables.

Since the spawning period of petrale sole is not restricted to a particular month, it was deemed adequate to utilize seasonal averages of environmental factors in exploratory Spearman's correlation analyses (i.e.; winter: December to February, and so on). In spite of the use of seasonal averages in these correlation analyses, an overall P-value equal to 0.05 for multiple comparisons of YCS with eight environmental factors and four seasons required very small individual P-values (c.a.

0.001 based on the Bonferroni correction or the P-value plot method of Schweder and Spjøtvoll, 1982). Moreover, as estimates of n^* in exploratory correlations would have compounded the difficulty for detecting biologically meaningful relations, the attendant uncorrected P-values of the present exploratory correlations are not indicative of strict statistical relations. However, in addition of exploratory correlation analyses based on original data, a second kind of Spearman's correlations was based on first-order differencing (Chatfield 1989, herein after referred to as correlation for filtered series). Correlations for filtered series reflect the degree of high-frequency associations (i.e., from year to year), as potential trends which may cause spurious correlations in the original data have been removed (Dickey et al. 1986, Cohen et al. 1991). Thus, a same sign in Spearman's correlations for original and filtered series should further support a relation between YCS and independent variables.

Results

Recruitment Process off Oregon-Washington

Information on early life history and spawning of petrale sole allowed to infer the approximate duration of the egg, larval and juvenile stages during the first year of life (Figure II.1, Appendix II.1). Most petrale sole larvae were concentrated in the upper 50 m of the sea surface (Table II.2). Thus, larval stages in this species appear to be predominantly pelagic at least from spring to early summer months.

Winter transport and cross-shelf water density gradients off Oregon (Huyer et al. 1975, Huyer 1977) are similar to those reported off British Columbia (Alderdice and Forrester 1971). Thus pelagic eggs and larvae off Oregon and Washington also experience northward and onshore advection during winter. After the spring transition, which occurs within approximately one week period (Strub et al. 1987), eggs and larvae are subject to predominant offshore and southward transport.

The size of petrale sole larvae collected off Oregon tended to be consistent both with inshore advection from winter to early spring, and with offshore advection from middle spring to summer. In general, all years combined (1961-1976), showed that individuals found both in nearshore areas (< 50 km offshore), and offshore areas (> 100 km offshore), were in average larger, and tended to be collected after than those caught at intermediate locations, closer to spawning grounds (Table II.3). The fact that two of the largest individuals (25-28 mm total length) were caught at 47 km offshore in March and at 306 km offshore in June, suggests large differences in spatial and temporal distribution of larvae and pre-settlement juveniles. Cross-shore distribution of petrale sole larvae showed that most of them occurred in offshore areas in relation to either spawning areas or juvenile settlement areas (Figure II.2A). Moreover, ichthyoplankton surveys off Oregon did not suggest a demersal distribution of larvae in nearshore areas (Figure II.2B). Thus, instead of a potential sinking of eggs and small larvae on the continental shelf, as speculated by Alderdice and

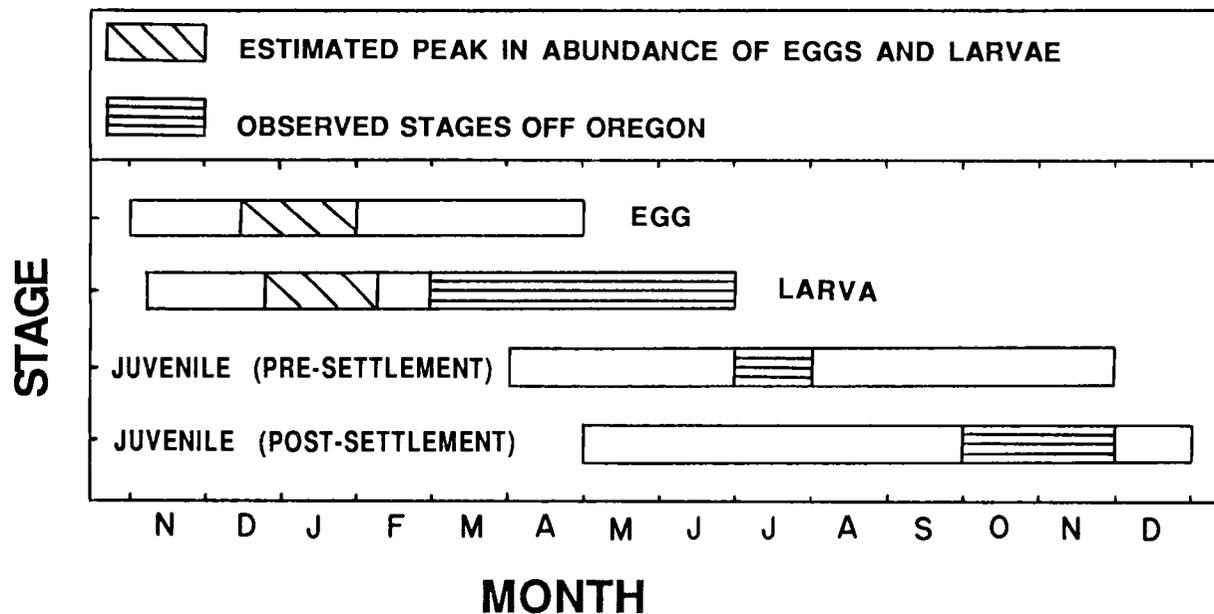


Figure II.1. Estimated duration of early life stages of petrale sole from the beginning of the spawning period to the time in which most age-0 juveniles have been found settled in continental shelf areas off Oregon. (Based on: Cleaver 1949, Harry 1959, Best 1963, Porter 1964, Ketchen and Forrester 1966, Alderdice and Forrester 1971, Gregory and Jow 1976, and Pearcy et al. 1977).

Table II.2. Number of petrale sole larvae per tow for different depth ranges and their corresponding relative abundance. Samples are from Isaacs-Kidd midwater trawls off Oregon from 1963 to 1976. Individuals were vulnerable from March to June. (Relative abundance in the larger depth ranges is overestimated since depth of tow was directly related to filtered volume, W. G. Pearcy, pers. comm. 1992).

Depth Range (m)	Number of Tows ^(a,b) (NT)	Number of Larva ^b (NL)	Relative abundance 100 * (NL / NT)
0 - 50	72	11	15.27
0 - 100	23	1	4.35
0 - 150	59	4	6.78
0 - 200	145	10	6.89
0 - 250	27	2	7.41
0 - 1000	117	1	0.85
0 - 1500	51	3	5.88

^a Based on cumulative tows from surface to each depth.

^b Data collected by W. G. Pearcy, and furnished by D. F. Markle (Oregon State University, Corvallis, OR).

Table II.3. Mean total length of petrale sole larvae by month of capture and distance from shore. Based on available Isaacs Kidd midwater trawl and bongo net collections off Oregon from 1961 to 1976. n: number of individuals collected using 0.571 mm mesh size. (Original data were furnished by W. G. Pearcy, Oregon State University).

Month	Mean Total Length (mm)		
	Distance from Shore (km)		
	(0 - 50) ^a	(51 - 100) ^b	(101 - 306) ^c
March n	23.5 2	20.0 1	13.0 1
April n	- 0	18.3 10	- 0
May n	21.7 4	20.2 11	20.7 4
June n	24.0 5	22.6 3	23.3 3

^{a, b, c} The respective mean Julian days of sample collections were: 145, 129 and 141.

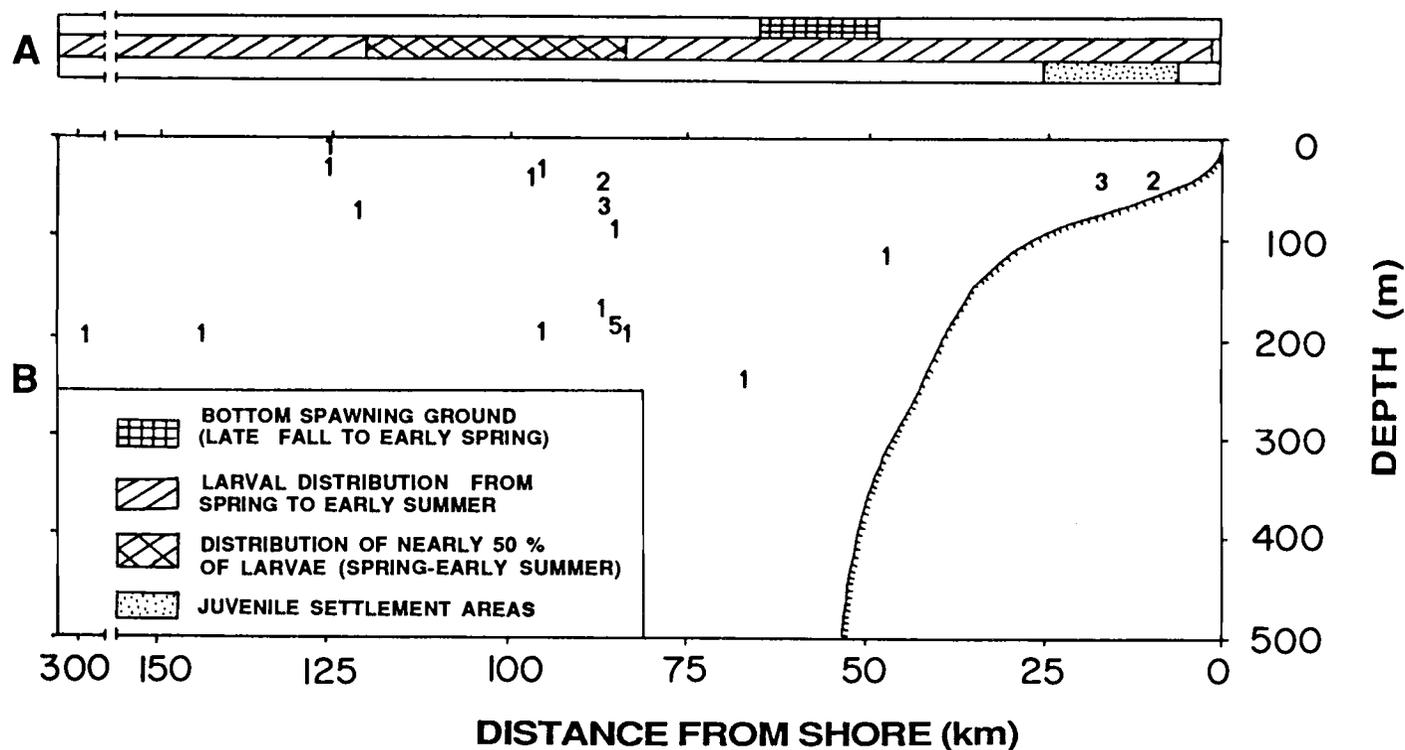


Figure II.2. A: Cross-shore distribution of spawning areas, larvae and juvenile settlement areas of petrale sole in relation to the distance from shore shown in part B (Based on references for Figure II.1).
 B: Location of each number shows the maximum depth of Isaacs Kidd midwater tows containing the attendant number of petrale sole larvae off Oregon. Tows retrieved under 500 m of depth to the surface containing four larvae collected between 80 and 160 km off the coast are not shown. (Based on data collected from 1963 to 1976 by W. G. Percy, Oregon State University).

Forrester (1971) for petrale sole off British Columbia, the scarcity of larvae in nearshore areas off Oregon could be explained by:

i) predominant sampling toward large larvae during the winter period of spawning and onshore transport, ii) offshore distribution of spawning grounds, and iii) offshore advection of larvae from spring to summer.

The first explanation is supported by the use of relatively large mesh sizes (0.571 mm) at the cod-end of Isaacs Kidd midwater trawls (Pearcy et al. 1977). On the other hand, the stenohaline condition of petrale sole could further explain why larval and juvenile stages have not been found in estuaries or shallow waters along the Northeast Pacific.

Based on the narrow nearshore distribution of post-settlement juveniles, it is conceivable that younger stages in offshore areas may not contribute to the recruitment after the spring transition.

Although some of the individuals in offshore areas could return to nearshore areas later on (e.g., through active migration in summer, or inshore advection the next fall), no evidence exists for such mechanisms.

Despite that alongshore gradients in depth and bottom composition off Oregon are minimal when compared to cross-shore variations (see Kulm 1977), alongshore coastal flow is the dominant transport process off Oregon (Huyer et al. 1975). Thus, cross-shore and alongshore interannual variations in coastal transport, as well as temperature and salinity fluctuations (Ketchen and Forrester 1966, Alderdice and Forrester 1971) could influence the recruitment of petrale sole off Oregon and Washington.

Even considering the reduced sampling of small larvae in ichthyoplankton surveys, the remarkable scarcity of larvae and juvenile stages of petrale sole in relation to other fishes (e.g., Demory 1971, Pearcy et al. 1977), suggests that the potential for intraspecific density-dependence can be comparatively lower for this species. However, this and other conceivable factors affecting recruitment strength need further evaluation.

Spawner-Recruit Variations

To examine if variations in parental spawning biomass of petrale sole may have affected subsequent recruitment strength for available years, the YCS index from 1970 to 1977 was divided by potential egg production and compared with attendant changes in YCS (Figure II.3). Since trends of YCS per parent egg were similar to YCS indices, the effect of spawning biomass on subsequent recruitment strength seem to be minimal. YCS was also compared to potential egg production to determine if any spawner-recruit relation could be detected. For original series, negative trends between YCS and potential egg production were observed for year-classes 1970 to 1977 (area 2B: $r = -0.81$, $P < 0.05$; area 3A: $r = -0.57$, $P < 0.20$; Figure II.4). These inverse patterns suggested that the YCS decline in the early 1970's was not linked to a decline of parental-stock size. Although these inverse trends could be considered part of a spawner-recruit relation for high values of parental stock size (e.g., Ricker 1954), the attendant filtered series were inconsistent with such relation (area 2B: $r = 0.21$, $P > 0.20$; area 3A: $r = 0.07$ respectively, $P > 0.20$; Figure II.5). Thus, over the years considered, opposite trends between recruitment of petrale sole and parental egg production seem to be their only common feature.

Environmental-YCS Fluctuations (1959-1977)

Alongshore Transport Indices:

1- Mean Sea Level Height

The highest (and lowest) mean sea level off Oregon correspond approximately to the periods of strongest northward (and southward) coastal flow (Huyer et al. 1975). Thus, although the highest and lowest long-term mean sea level values from 1959 to 1977 occurred in winter and summer respectively (Appendix II.2), a positive sea level anomaly in a given season should indicate a higher (lower) than average northward (southward) transport. The highest correlations between YCS

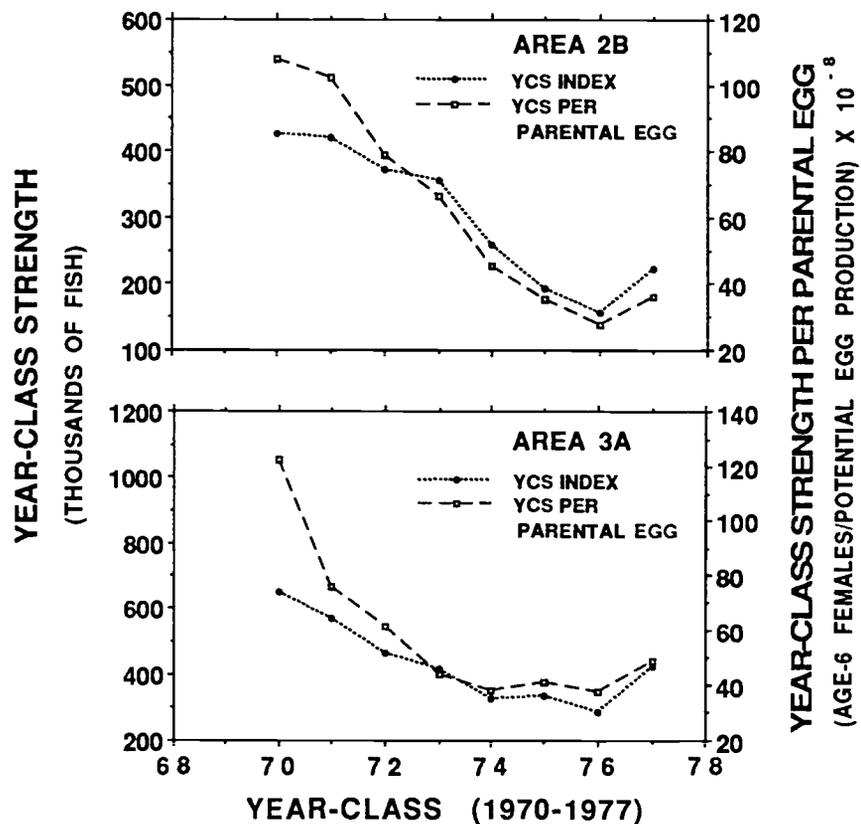


Figure II.3. Comparison between YCS indices of petrale sole and the attendant number of fish reaching age 6 per parental egg in PSMFC areas 2B and 3A. (Cohorts considered in YCS indices were born from 1970 to 1977).

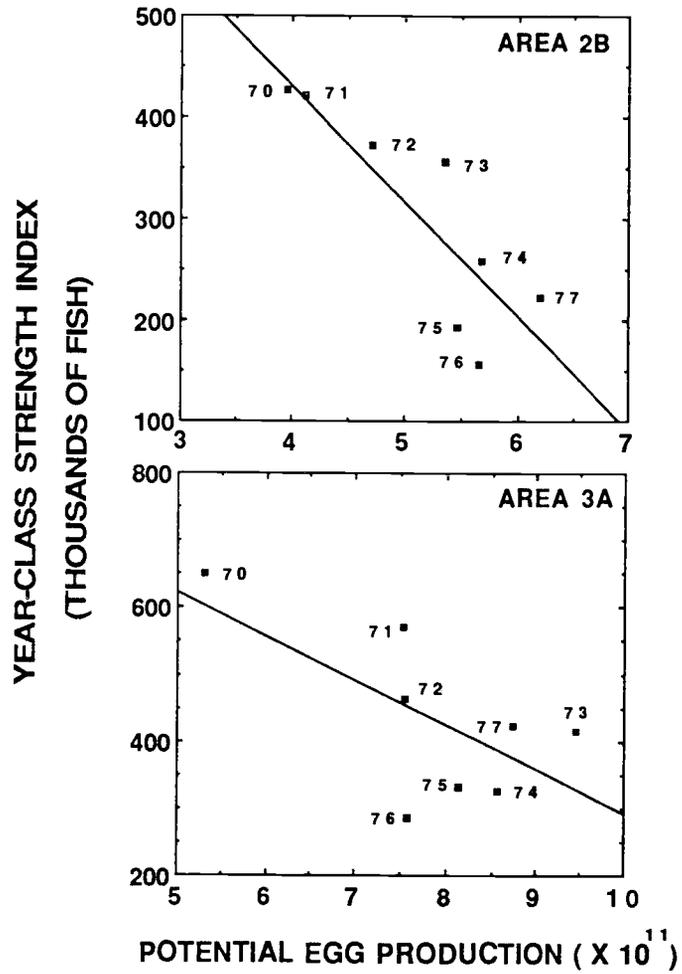


Figure II.4. Variation of YCS of petrale sole for cohorts born from 1970 to 1977 in relation to potential parental egg production in PSMFC areas 2B and 3A.

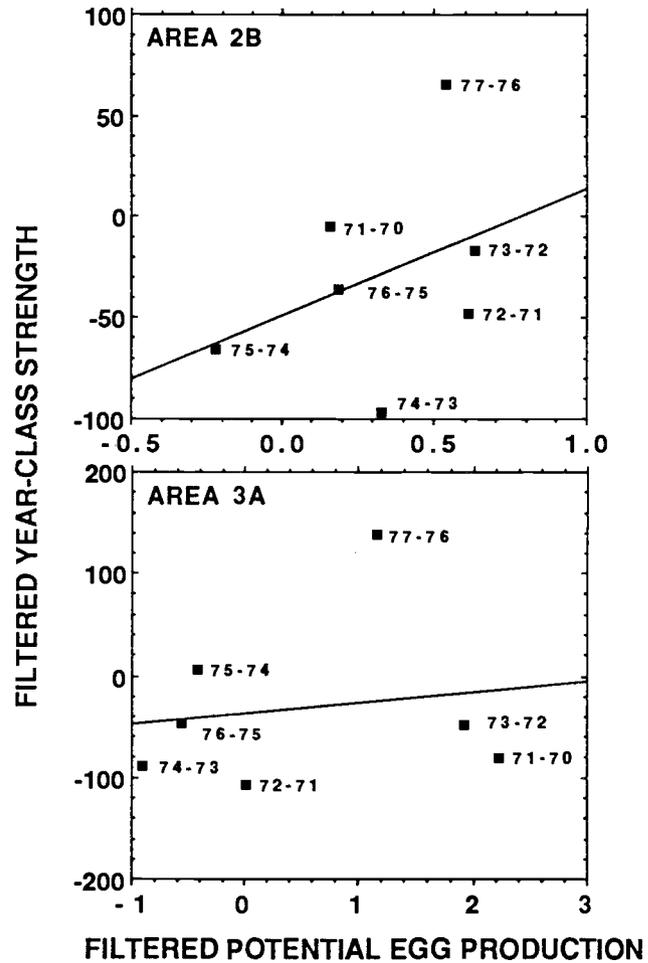


Figure II.5. Variation between filtered values of YCS of petrale sole and potential parental egg production in PSMFC areas 2B and 3A. (Cohorts considered are those from Figure II.4).

and mean sea level occurred in winter for both areas (Figure II.6.A). Correlations for attendant filtered series showed lower but still positive correlations for winter (Figure II.7.A). Thus, recruitment strength seems to be consistent with low and high frequency variations of nearshore northward transport in winter.

2- Northward Ekman Transport

This index indicates the alongshore flow of surface mixed layers driven by wind stress. Off the Northeast Pacific coast, Ekman transport appears to be most important in the upper 20 to 30 m (Parrish et al. 1981). Contrary to the nearshore transport inferred from sea level height, the four long-term seasonal means 1959-1977 of this index indicated predominant negative northward transport (i.e., southward transport) of surface waters in more offshore areas (45° N 125° W, Appendix II.2). Although no correlations between northward Ekman transport and YCS were found for original data (Figure II.6.B), filtered series suggested a positive association for both winter and summer indices (Figure II.7.B).

3- Northward Sverdrup transport

This index measures alongshore transport over the entire water column by adding geostrophic flow to Ekman transport. For non winter seasons, the long-term seasonal means 1959-1977 of this index showed southward transport of waters at 45° N 125° W (Appendix II.2). With the exception of correlations for spring in both areas, and for fall in area 3A, positive but low associations between YCS and northward Sverdrup transport were suggested. This pattern was observed for both original and filtered series (Figures II.6.C and II.7.C, respectively). Thus, northward Sverdrup transport for winter also support the positive association between YCS and northward transport suggested from sea level.

Offshore Ekman Transport

Long term seasonal means 1959 to 1977 of this index indicated

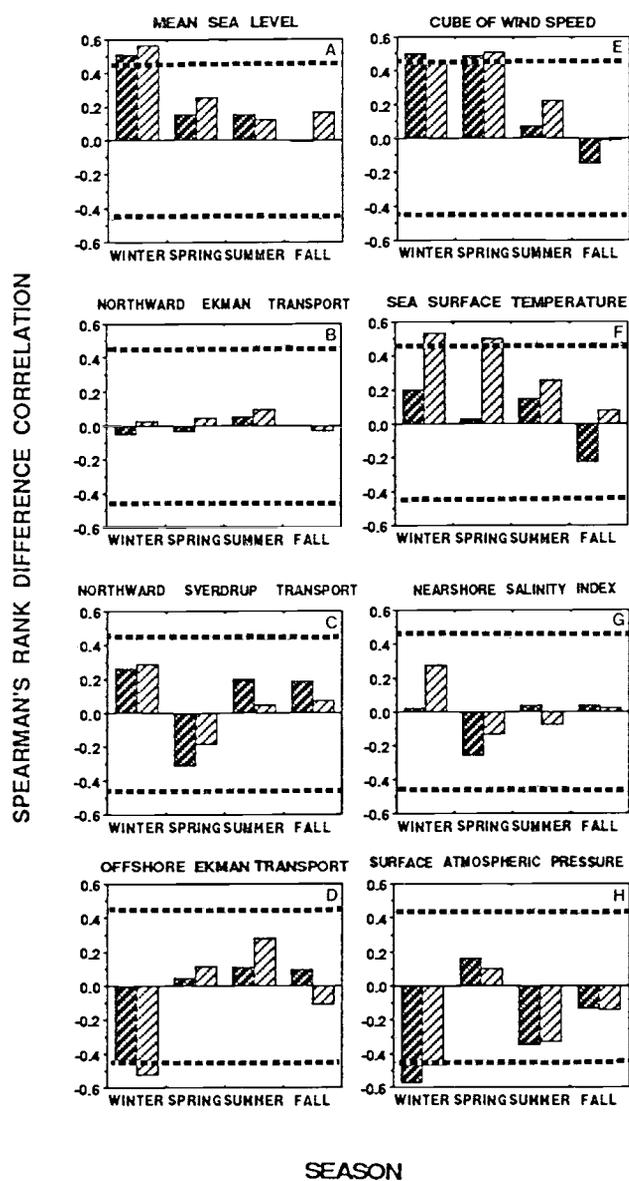


Figure II.6. Spearman's correlations between YCS indices of petrale sole and seasonal averages of environmental factors (Table II.1) lagged to the first year of life. Correlation for cohorts 1959 to 1977 are compared for PSMFC areas 2B (dark bar) and 3A (light bar). Dashed lines correspond to $P = 0.05$ for individual correlations (see Methods).

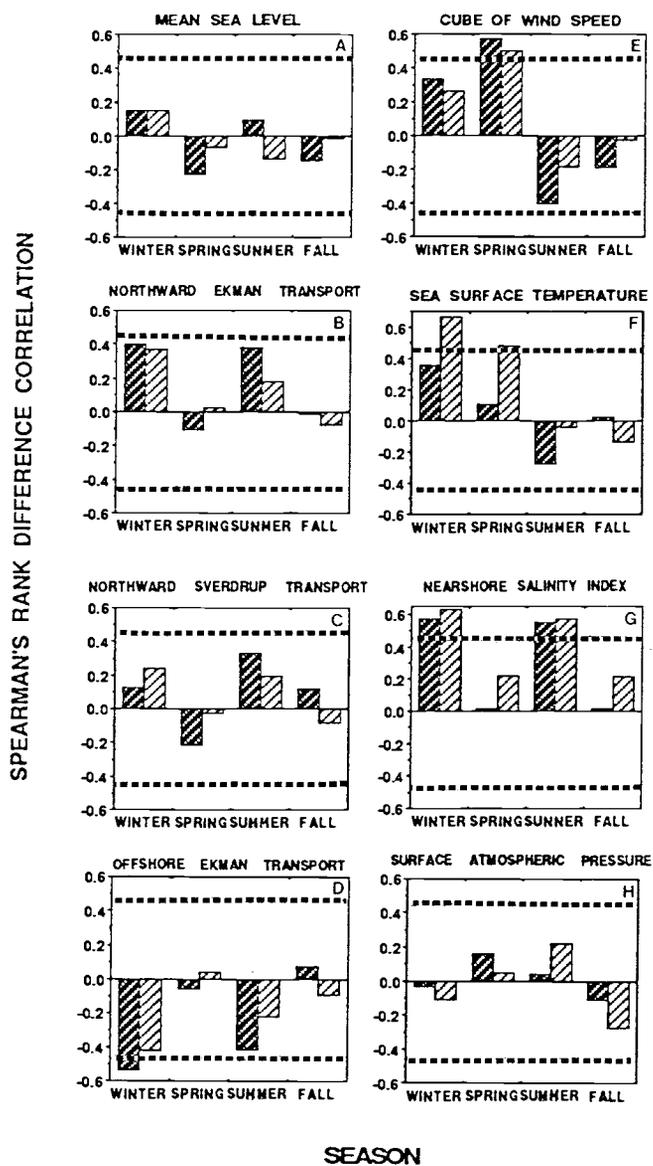


Figure II.7. Spearman's correlations between filtered YCS indices of petrale sole and filtered seasonal averages of environmental factors (Table II.1) lagged to the first year of life. Bars and dashed lines correspond to those of Figure II.6.

average offshore transport of surface waters and upwelling from spring to summer, which is followed by onshore transport and downwelling from fall to winter (Appendix II.2). Consistent negative correlations between YCS and winter offshore Ekman transport were observed for actual and filtered data in both areas (Figures II.6.D and II.7.D, respectively). Although offshore Ekman transport during spring and summer could also be negatively related to recruitment in petrale sole, such association was only suggested from summer filtered series. Thus, high onshore transport during winter could favor YCS of petrale sole due to reduced offshore advection of eggs and larvae.

Cube of Wind Speed

This index reflects the turbulence transferred to the sea surface by the wind (Niiler and Kraus 1977). Thus, it could also be associated with the vertical distribution of fish larvae and their food supply (e.g., Lasker 1981, Wroblewsky et al. 1989). Although cube of wind speed was correlated with YCS for winter and spring (Figures II.6.E, II.7.E), a more detailed analysis for these seasons revealed that the previous correlations were largely explained by onshore Ekman transport during winter and early spring. This interpretation is supported by the fact that northeastward winds during winter and early spring tend to favor onshore advection of early life stages. Moreover, correlations for spring vanish in both areas when March is excluded from the analyses. Thus, cube of wind speed only appears to magnify the positive effect of onshore Ekman transport on YCS.

Water Properties:

1- Sea Surface Temperature

Long-term seasonal means of sea surface temperature from 1959 to 1977 increased from winter through summer and decreased in fall (Appendix II.2). Correlations for original and filtered series showed high positive values for area 3A for winter and spring (Figures II.6.F and II.7.F, respectively). For area 2B, attendant correlations for original series were much lower. Yet, filtered series for winter

temperature and YCS in area 2B also suggested a positive effect of temperature on recruitment.

2- Nearshore Salinity Index

Although long-term salinity anomalies off Oregon and Washington have been compiled for available years (Landry et al. 1989), the number of salinity observations has varied greatly throughout the studied period. In spite of this, it is conceivable that early survival in petrale sole could be affected by salinity variation caused by water outflow from the Columbia River. A proxy for salinity in the present study was based on observations of water density at constant temperature available at Columbia River Estuary (Table II.1). This river accounts for nearly 77 % of the drainage between San Francisco Bay and the Strait of Juan de Fuca (Budinger et al., 1964). Although the effluent generally flows northward off Washington during winter and southward off Oregon during summer (Hickey 1979-a), significant spatial variations have been detected over intervals as short as three days (Hickey 1979-b).

Positive relations between YCS of petrale sole and the winter salinity index were suggested for area 3A both from original and filtered series (Figures II.6.G and II.7.G, respectively). The lower attendant relation for original series in area 2B could be due in part to its greater distance from the Columbia River. Moreover, the difference of YCS-salinity relations between both areas suggests that large-scale salinity changes (e.g., due to coastal upwelling or alongshore transport), could be less important on YCS of petrale sole than those caused by the Columbia River in area 3A.

Surface Atmospheric Pressure

Seasonal variations in nearshore transport, and water properties are largely forced by atmospheric circulation around the North Pacific High and Aleutian Low atmospheric pressure systems (Huyer 1977, Huyer 1983). Thus, this index integrates many of the factors which could explain YCS variations of petrale sole. High negative correlations

between YCS and winter sea surface pressure were evident in both areas (Figure II.6.H). Yet, the fact that these correlations were not consistent with filtered series (Figure II.7.H), suggests that similar averages of surface atmospheric pressure can induce different response on particular oceanographic factors, which may ultimately affect recruitment strength.

Effects of the Spring Transition on YCS

To ascertain if the timing of the spring transition could influence recruitment strength of petrale sole, Spearman's correlations between YCS and the week of the spring transition were computed. Only small positive associations were suggested in both areas (area 2B: $r = 0.27$, area 3A: $r = 0.22$; $P > 0.20$; Figure II.8), and inconsistent negative correlations were obtained from attendant filtered series (area 2B: $r = -0.18$, area 3A: $r = -0.32$; $P > 0.20$; Figure II.9). Thus, although extreme variations in the timing of the spring transition could affect YCS of petrale sole, other factors seem to disrupt high frequency associations. This interpretation was also supported when correlating YCS from 1958 to 1977 with the month in which the average offshore Ekman transport changed from negative to positive. In this case there was not even indication of positive association for actual or filtered series in both areas ($r < 0.05$, $P > 0.20$). Yet, offshore Ekman transport values for March, a period of predominant onshore transport, showed a remarkable correspondence with YCS in both studied areas. This suggested that recruitment of petrale sole could greatly depend on unusually low offshore advection of eggs and larvae during early spring, following the spawning peak, and prior to the spring transition. Hence, unless a delay in the spring transition is associated with unusually high onshore transport in early spring, its timing appears to be largely unrelated to the recruitment strength of petrale sole off Oregon and Washington.

Environmental-YCS Series

The more consistent relations between YCS and environmental factors were further considered for analyzing temporal fluctuations

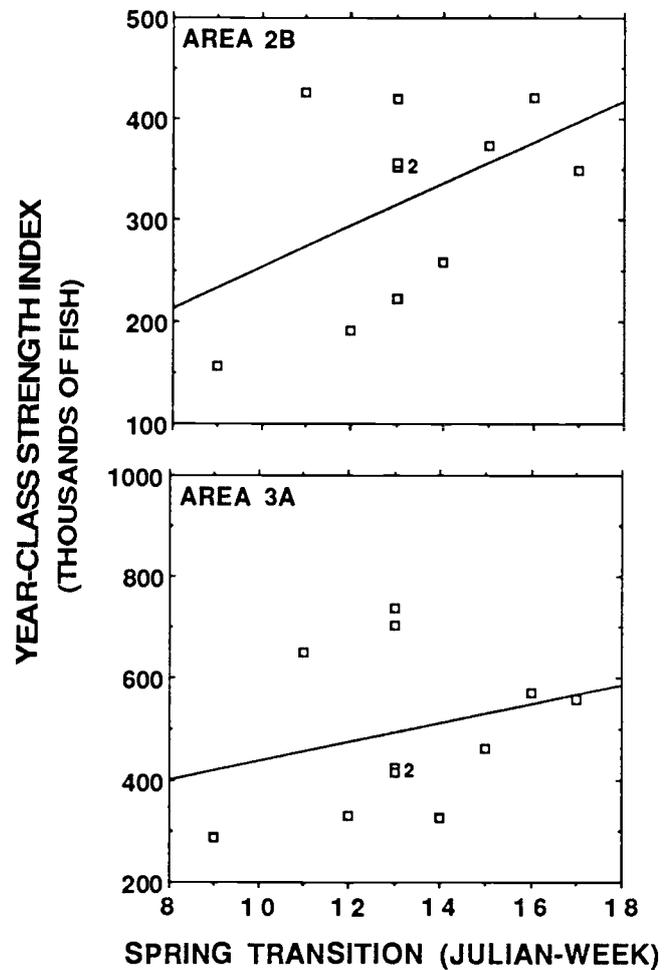


Figure II.8. Variation of YCS for petrale sole in PSMFC areas 2B and 3A in relation to the estimated week in which the spring transition occurred. Comparisons were made for year-classes born from 1967 to 1977.

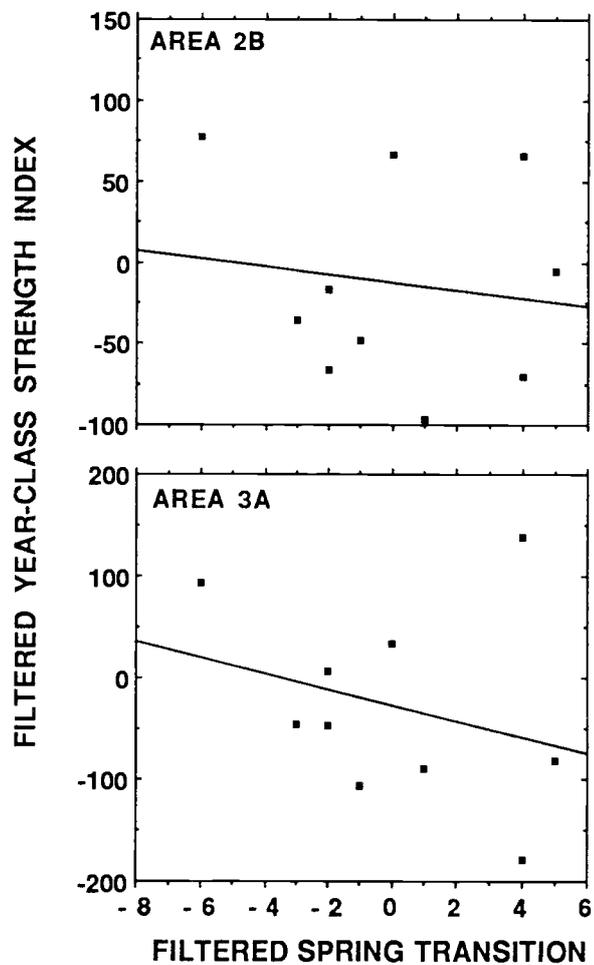


Figure II.9. Filtered values of YCS for petrale sole in PSMFC areas 2B and 3A in relation to the week of the year in which the spring transition occurred. (Based on the same years used in Figure II.8).

from the long-term mean 1958-1977, and for determining the best fitted regressions of YCS on environmental factors. Offshore Ekman transport appeared to be the main factor associated with YCS of petrale sole in areas 2B and 3A. This relation was more clearly seen for winter onshore Ekman transport (i.e., negative offshore Ekman transport) anomalies computed from January through March, instead of December through February (Figure II.10). Years 1958 and 1961 showed the largest positive anomalies in onshore Ekman transport from 1958 to 1977. Yet, unlike 1961, 1958 was not associated with correspondingly larger positive YCS anomalies, particularly for area 2B.

Other anomalies for indices such as nearshore salinity, winter and spring sea surface temperatures and winter sea level height also appeared to be consistently correlated with YCS anomalies in area 3A. In area 2B however, only onshore Ekman transport and sea level height showed high associations with YCS. Excepting for the salinity index, both mean sea surface temperatures (winter and spring) and mean sea level for winter showed large anomalies during El Niño year 1958. However, low frequency variations of these environmental indices were similar to those seen for Ekman transport anomalies (Figure II.11).

It must be pointed out that a positive association between the salinity index and the sea surface temperatures during winter was consistent with Spearman's correlations between winter salinity anomalies off Oregon-Washington (Landry et al. 1989) and winter sea surface temperature indices for both areas (area 2B: $r = 0.48$, $P < 0.06$; and area 3A: $r = 0.51$, $P < 0.05$; $n = 16$). Thus, besides of the Columbia River, a potential YCS-salinity relation in area 3A could also be explained by variations in the northward flow of the Davidson Current during winter.

The relation between YCS on January-March offshore Ekman transport anomalies were best described by second-order polynomials (Figure II.12). Associations between YCS and winter sea level height anomalies in areas 2B and 3A (Figure II.13), as well as between YCS and winter sea surface temperature in area 3A (Figure II.14), were also described by second-order polynomial regressions. Although a very

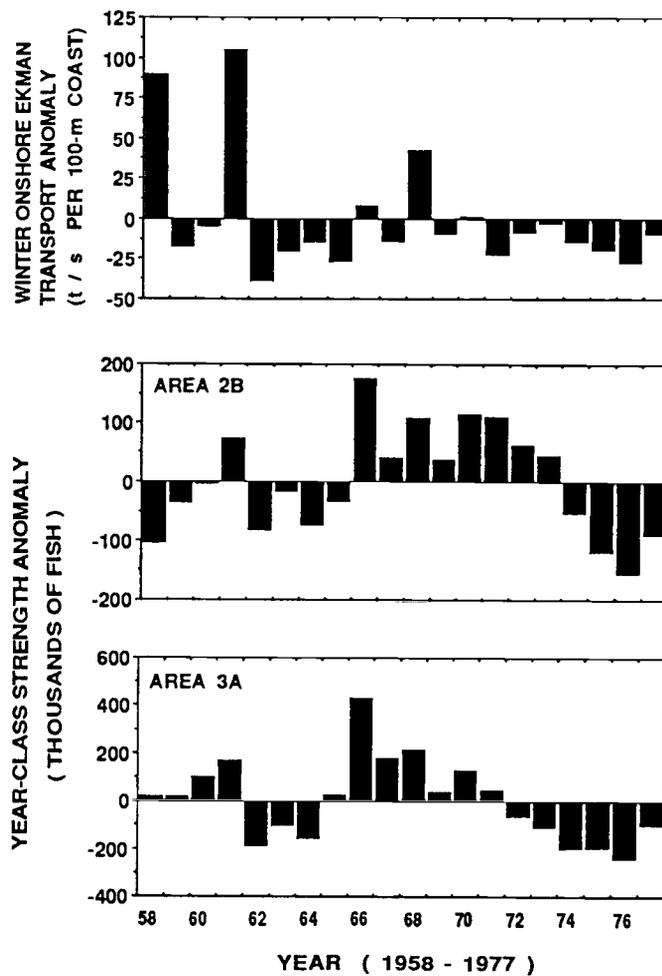


Figure II.10. Anomalies for mean onshore Ekman transport off Oregon (January to March), and for YCS of petrale sole in PSMFC areas 2B and 3A. (Values computed from the long-term mean 1958-1977).

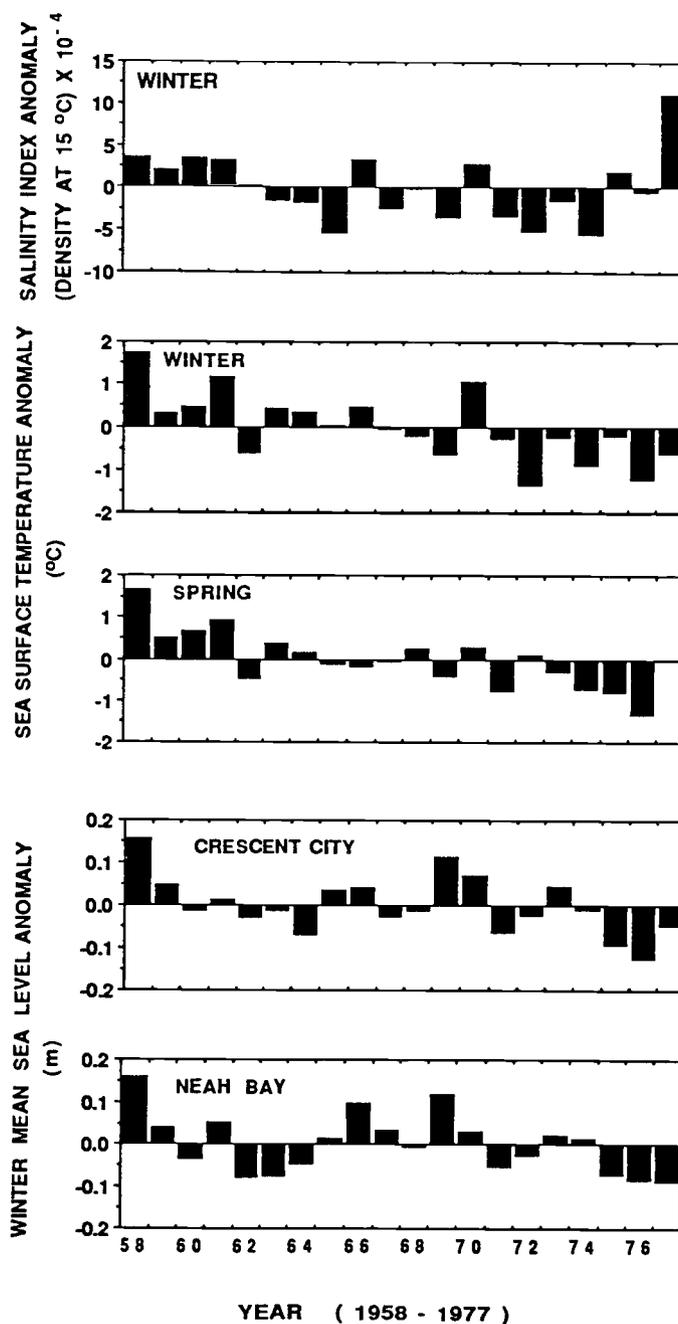


Figure II.11. Winter anomalies for the Columbia River salinity index, for sea level height (Crescent City and Neah Bay), and for winter and spring sea surface temperature anomalies off Oregon-Washington (used for PSMFC area 3A). Values based on the long-term mean 1958-1977. (Locations for environmental indices are shown in Table II.1).

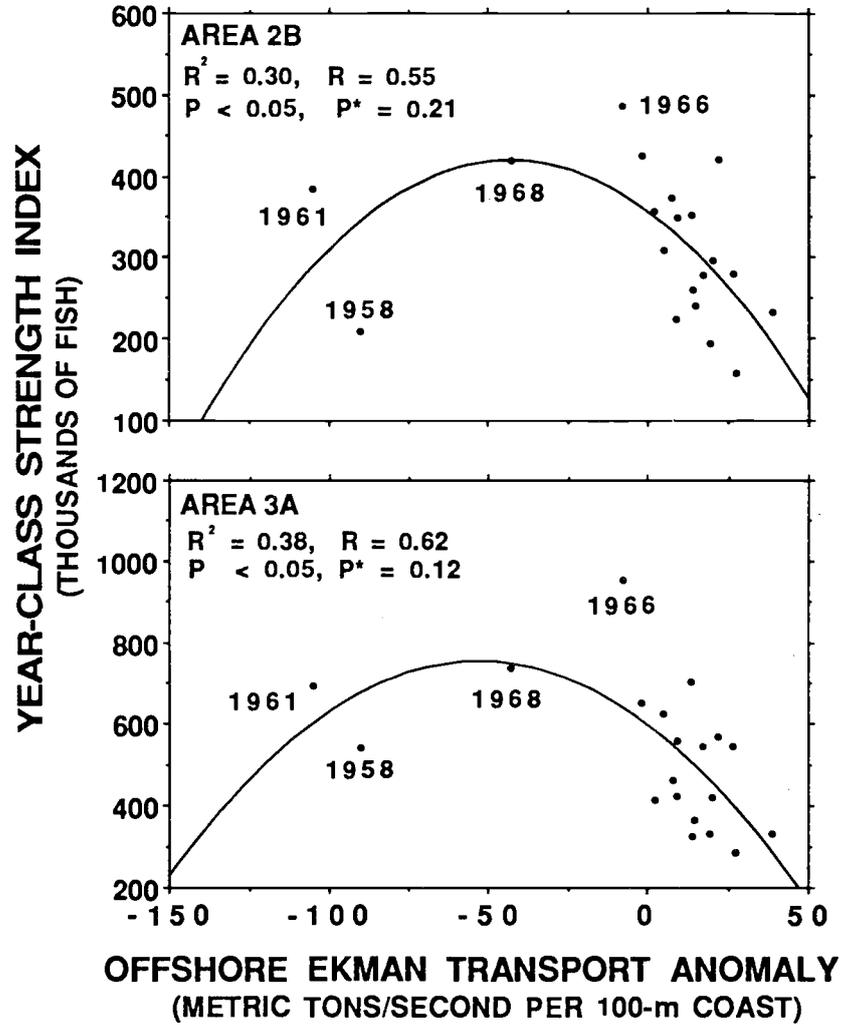


Figure II.12. Relations between YCS of petrale sole in PSMFC areas 2B and 3A and mean offshore Ekman transport anomaly off Oregon from January to March. P^* is the adjusted P-value for autocorrelation. (Regression parameters are shown in Table II.4).

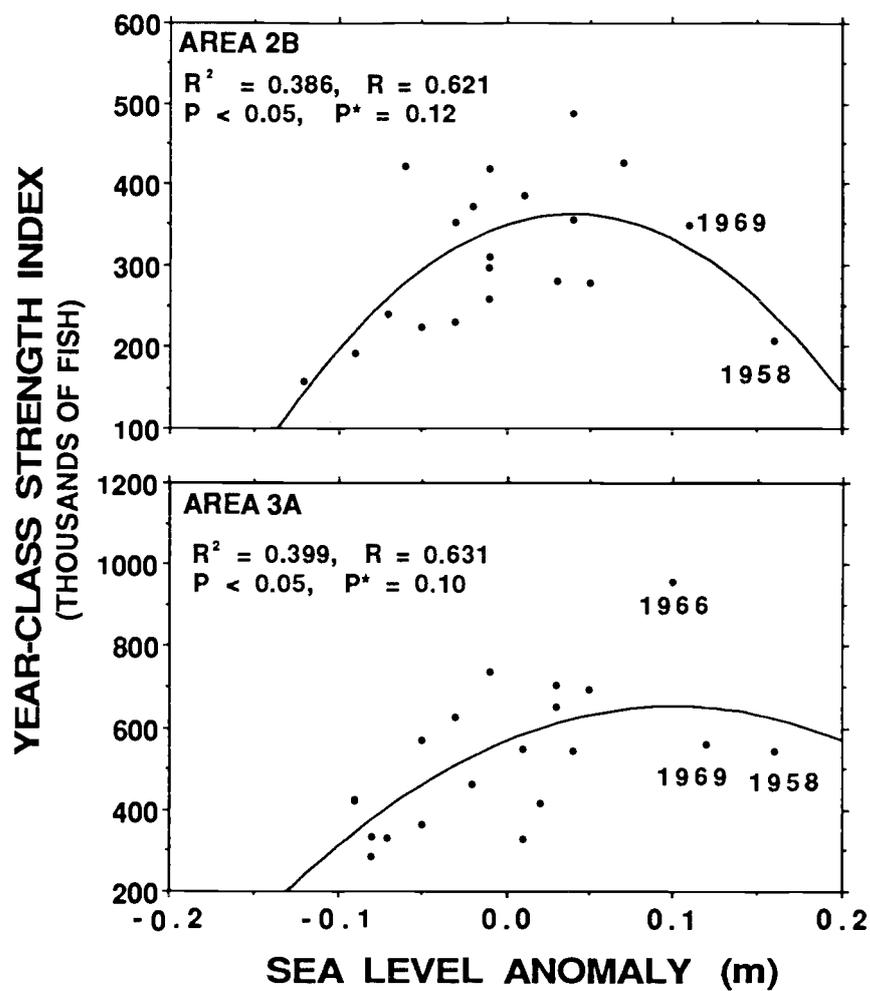


Figure II.13. Relations between YCS of petrale sole in PSMFC areas 2B and 3A and winter mean sea level anomaly for Neah Bay and Crescent City respectively. (P^* is the adjusted P-value for autocorrelation. Regression parameters are shown in Table II.4).

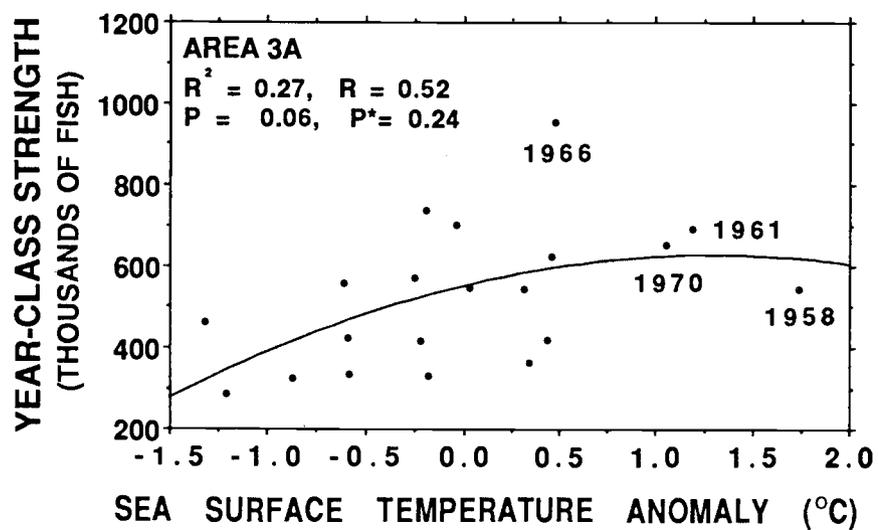


Figure II.14. Relation between YCS of petrale sole in PSMFC area 3A and mean winter sea surface temperature anomaly off Oregon-Washington (December-February). P^* is the adjusted P-value for autocorrelation (Regression parameters are shown in Table II.4).

similar association between YCS in area 3A and spring sea surface temperature was evident, it was less clear than in the case of winter temperature. Excepting for year 1958, and for other two or three years with large environmental anomalies (Figures II.12 to II.14), a common feature in these regressions is the nearly linear association for most of the studied period.

Polynomial regressions for individual environmental factors explained less than 50 % of the YCS variation in each area. For area 2B, regressions including offshore Ekman transport and sea level accounted for nearly 55 % of the YCS from 1958 to 1977. Over the same period in area 3A, these two environmental factors plus sea surface temperature explained about 65 % of the YCS variation (Figure II.15). Although conventional significance levels of correlation coefficients for polynomial regressions were small ($P \leq 0.06$), the presence of autocorrelated series of YCS and environmental factors reduced the number of independent observations from 20 to 12 and increased adjusted P-values (P^* , Table II.4). Predictably, due to the strong dependence of significance values on the number of observations and independent variables, adjusted P-values levels do not negate the existence of functional relations between recruitment of petrale sole and the previous environmental factors. Yet, the difference between unadjusted and adjusted P-values indicates that a larger number of observations is needed to better evaluate the fitted relations.

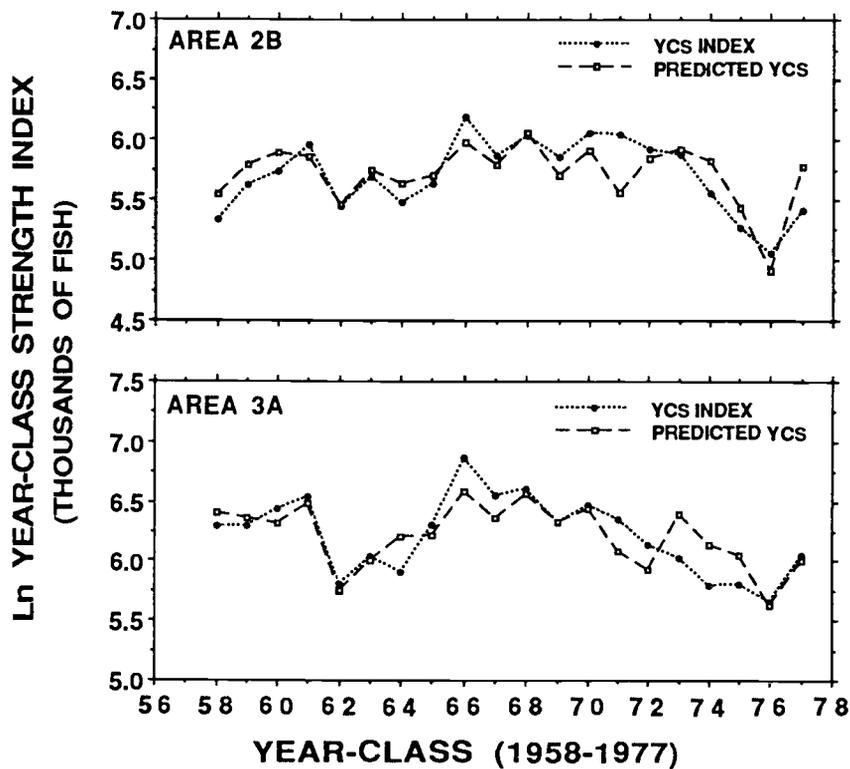


Figure II.15. Log-transformed estimated and predicted YCS for petrale sole. PSMFC area 2B: prediction based on anomalies of offshore Ekman transport and sea level and their attendant squared values. PSMFC area 3A: predicted values are based on anomalies of offshore Ekman transport, sea level and sea surface temperature and their attendant squared values. (Regression parameters are shown in Table II.4).

Table II.4. Regressions of YCS for petrale sole on environmental anomalies. YCS in thousands of females attaining age-6 in PSMFC areas 2B and 3A (cohorts born from 1958 to 1977). Environmental anomalies are based on the 1958-1977 long-term mean. Me: offshore Ekman transport anomaly (Jan.- March), SL: mean sea level anomaly (Dec.-Feb.), SST: sea surface temperature anomaly (Dec.- Feb.).

AREA	REGRESSION MODEL	R ²	R	P ^a	P ^{a,b}
YCS on Me and Me ²					
2B:	YCS = 357.02245 - 2.91211 Me - 0.03403 Me ²	0.302	0.550	< 0.05	0.21
3A:	YCS = 576.01523 - 4.30347 Me - 0.03910 Me ²	0.381	0.617	< 0.05	0.12
YCS on SL and SL ²					
2B:	YCS = 347.01575 + 625.33140 SL - 8103.14874 SL ²	0.386	0.621	< 0.05	0.12
3A:	YCS = 565.15954 + 1686.40186 SL - 8512.45238 SL ²	0.399	0.631	< 0.05	0.10
YCS on SST and SST ²					
3A:	YCS = 550.44591 + 116.83381 SST - 44.96999 SST ²	0.270	0.520	0.06	0.24
YCS on Me, Me ² , SL and SL ²					
2B:	YCS = 377.93250 - 2.37122 Me - 0.02546 Me ² + 346.42807 SL - 7477.85987 SL ²	0.549	0.741	< 0.05	0.20
3A:	YCS = 608.34903 - 3.85461 Me - 0.03778 Me ² + 1104.26907 SL - 7115.58430 SL ²	0.508	0.713	< 0.05	0.24
Ln (YCS) on Me, Me ² , SL, SL ² , SST and SST ² ^c					
3A:	Ln (YCS) = 6.41148 - 0.00679 Me - 6X10 ⁻⁵ Me ² + 1.95846 SL - 9.00662 SL ² + 0.10693 SST - 0.13208 SST ²	0.648	0.805	< 0.05	0.34

^a P probability based on the total number of observations (n = 20)

^b P^a probability based on the estimated number of independent observations (n^a = 12)

^c Back-transformed to YCS: R² = 0.667, r = 0.816, P < 0.05, P^a = 0.31

Discussion

From 55 % to 65 % of the recruitment variations of petrale sole in this study were correlated with oceanographic conditions from winter to early spring, period in which egg and larval stages of this species appear to be most abundant (Figure II.1). For most year-classes born in the 1970's, these environmental-recruitment relations were consistent with decreasing trends in YCS. Such trends could partially explain the reported decline of commercial catch rates in this species from the late 1970's to the middle 1980's (Section I). Moreover, considering the high correspondence between autocorrelated series of environmental factors and YCS of petrale sole in this study (Figures II.10 and II.11), it would be unreasonable to assume constant or random recruitment in harvest models.

Excluding the unusual environmental anomalies, particularly years 1958 and in a lower extent 1961, most of the data could have been better fitted by simple linear regressions using only half of the independent variables (i.e., excluding squared variables in Table II.4). Hence, adjusted P-values for a narrower model scope should have been closer to conventional significance levels. These results are supported by those obtained for petrale sole off British Columbia (Ketchen and Forrester 1966, Alderdice and Forrester 1971). Thus, the present work tends to confirm the presumed recruitment dependence of petrale sole on northeastward transport and sea surface temperature during winter. Although the relation between salinity and YCS in both areas was not high enough to be included in regression models, such association was strongly suggested from Spearman's correlation analyses (Figures II.6.G. and II.7.G). Thus, salinity and temperature seem to affect YCS of petrale sole at smaller spatial scales than offshore-alongshore transport.

Besides of the potential errors in determining spawner-recruit relations (e.g., Walters and Ludwig 1981, Rothschild and Fogarty 1989), a critical assumption for establishing such relations is that density-

independent survival variations at early life stages can be neglected when compared with variations in spawning biomass. Such assumption appears inconsistent with the results obtained in the present study, as well as with scale analysis of factors affecting survival of fish larvae in upwelling regions (Sharp 1980), or with the role of postlarval stages on recruitment variations (Sissenwine 1984, Peterman and Bradford 1987).

Although series of potential egg production were only available to investigate spawner-recruit relations for year-classes born from 1970 to 1977, such cohorts showed the largest YCS decline over the 20-year studied period. Spawner-recruit relations neither have been detected for petrale sole in other areas (Ketchen and Forrester 1966), nor in most of the studied flatfish (Cushing 1971, Roff 1981).

The present study tends to support the view that larval stage and egg production in fishes are the two major sources of population variability and stability respectively (Rothschild et al. 1989). To reconcile the stabilizing role of egg production with the sudden collapse of some fisheries, the latter authors further postulated that more than one stability level in egg production could exist. If such is the case, potential spawner-recruit relations could be detected over periods involving several stability levels.

Based on correlations for original and filtered series, offshore Ekman transport seems to be more related to recruitment strength of petrale sole than alongshore transport, sea surface temperature or salinity variations. Yet, the fact that these factors reflect interrelated oceanographic processes (Huyer 1977, Kruse and Huyer 1983) makes it difficult to compare their relative contributions to YCS variations. For example, onshore Ekman transport tends to cause high sea level and sinking of isotherms along the coast, and the attendant upward slope of the sea surface toward the coast could then force poleward coastal transport. Thus, 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. Moreover, northward Sverdrup

transport and offshore Ekman transport are respectively related to vertical transport driven both by wind-stress curl during winter and wind-stress during spring and summer. Thus, horizontal transport should also induce upward transport of nutrients and affect production of upper ocean layers where petrale larvae tend to concentrate.

In the Northeast Pacific ocean, besides of El Niño 1957-58, the 1940-41 and 1982-83 events appear to have been so far the only ones producing major sea level rise in the twentieth century (Cannon et al. 1985). Thus, a correspondingly higher winter onshore transport during those El Niño events may have partially offset adverse environmental effects on the recruitment of petrale sole. Although YCS series in the present study were only available until 1977, two unusual changes during El Niño event 1982-83 support this counteracting mechanism, the first one is a lower overall density of zooplankton in spring and summer 1983, about 30 % of that in non El Niño years (Miller et al. 1985), which may have resulted in lower feeding, growth and survival of petrale sole larvae. A mechanism for reduced food production available to larvae could be the sinking of the nutricline in response to strong northward transport (William G. Percy, Oregon State University, Corvallis, OR, pers. comm. 1992). The second change is the inshore advection of the typical offshore ichthyoplankton group off Oregon, also reported by Miller et al. (1985), which could have increased larval retention into juvenile settlement areas.

The anomalously high onshore transport for two non-El Niño events, 1961 and 1968, did not appear to have induced a correspondingly higher recruitment (Figure II.12). In those two years, high onshore Ekman transport also may have reduced larval retention or food production in the studied recruitment areas, which is supported by higher northward transport (Figure II.13). Moreover, optimum temperatures for viable petrale sole larvae in laboratory (6-7 °C, Alderdice and Forrester 1971) are lower than winter temperatures associated with higher than average YCS off British Columbia (mean sea surface temperature > 8 °C, Ketchen and Forrester 1966) or off

Washington-Oregon (Mean sea surface temperature $> 9^{\circ}\text{C}$). Thus, suboptimal sea surface temperatures associated with high onshore surface transport could also contribute to the parabolic relations between YCS and offshore Ekman transport (or sea level) in areas 2B and 3A. On the other hand, it has also been suggested that northward advection of organisms during El Niño events could also increase the predation on fish larvae (Bailey and Incze, 1985). Yet, this increased predation of fish larvae could also occur during non-El Niño years characterized by unusually high northward transport.

If winter northward advection of eggs and larvae were not compensated by subsequent southward advection, or by a southward spawning migration, the maintenance of separate spawning groups of petrale sole could not be explained by inshore winter transport alone. Although southward larval advection during spring may contribute in part to maintain segregation between subpopulations, a southward pre-spawning migration by a portion of the mature fish could also counteract for the winter northward drift of early life stages. Such inference is based on the observed northeastward post-spawning migration of an important fraction of the spawners tagged in areas 2B and 3A (DiDonato and Pasquale 1970, Oregon Fish Commission 1970), as well as from other spawning grounds (Alverson and Chatwin 1957, Best 1963, Pedersen 1975-b). In the previous three studies, a referred "homing" tendency of mature fish to particular spawning grounds is consistent with the model of fish stock unit for temperate cyclones (Cushing 1975).

Although the environmental factors considered in this study appeared normal during 1959, Bailey and Incze (1985) indicated that years 1958 and 1959 coincided with weak recruitment in at least six northeast Pacific fish stocks living near the species's southern limit. In contrast, they reported that six stocks living in the species's northern range of distribution, including petrale sole off Canada, showed at least one strong year-class in the period 1958-59. They suggested that the simultaneous observed increase in sea temperature

and zooplankton biomass in northern areas may have favored growth and feeding of fish larvae. Conversely, they indicated that substantial decrease of zooplankton biomass in the southern range could have been linked to poor recruitment in such areas. These previous patterns are consistent both with: i) North-south differences in recruitment of Northeast Pacific fishes, presumably influenced by inverse fluctuations between the California and the Alaska currents (Chelton 1984, Hollowed and Wooster 1992), and ii) with strong YCS associated with warmer temperatures in the poleward range of the species's distribution, and with attendant inverse relations at the equatorward species's range (e.g., Cushing 1982, Bailey and Incze 1985, Frank 1991).

Although positive relations between temperature and recruitment for petrale sole appear to exist at least off British Columbia (Ketchen and Forrester 1966), and for most of the studied period off Washington and Northern Oregon (area 3A), only a small positive correlation was found off Central-South Oregon (area 2B); (Figures II.6.F and II.7.F). Thus, despite the proximity between areas 3A and 2B, the higher temperature-YCS association for Area 3A in relation to Area 2B is consistent with temperature differences between recruitment areas (Appendix II.2), and with the previous latitudinal effect of temperature on recruitment strength.

For petrale sole off British Columbia, Ketchen and Forrester (1966) reported strong year classes in the early 1940's, which coincided with high sea surface temperatures in relation to temperatures dating back to at least 1915. Based on a strong 1958 cohort, and a warming period not observed since the early 1940's, these authors also suggested a recruitment increase for petrale sole from the late 1950's to the early 1960's, which is also consistent with the results obtained for areas 2B and 3A in the present study.

No clear recruitment response can be inferred for southern subpopulations of petrale sole from available data. For example, the latitudinal effect of temperature in other fishes suggests a negative YCS-temperature relation for the southern range of petrale sole. Yet,

considering the extremely low winter onshore Ekman transport off California (Bakun 1973), and the narrower continental shelf off California in relation to northern locations (Heezen and Tharp 1982), it can alternatively be deduced that high onshore advection of larvae (i.e., downwelling) could be associated with high YCS, and consequently with high sea surface temperatures.

The December-January spawning peak for petrale sole off Oregon-Washington does not only appear to be an adaptation to favor advection of larvae toward juvenile settlement areas. For example, an earlier spawning peak (e.g., October-November) could increase larval retention into north nearshore areas in relation to areas normally occupied by each subpopulation. Yet, earlier spawning peak could also reduce larval growth and survival due to lower winter temperatures and food supply for larvae. Such possibilities are suggested by: i) a March-April peak of phytoplankton production at these latitudes (Landry et al., 1989), ii) lower zooplankton abundance for winter in relation to spring (Peterson and Miller 1977), and iii) lower sea surface temperatures for winter than for spring (Appendix II.2).

The fact that winter and spring cube of wind speed and YCS showed no curvilinear relation also support the idea that these factors were spuriously correlated. Husby and Nelson (1982) hypothesized that reproductive strategies in fish could reflect adaptation to "optimum" levels or frequencies of turbulence levels. Although such relations can not be discarded for petrale sole, interannual variation in primary and secondary production may not be high enough to override the effects of advection and temperature on recruitment strength. For example, although positive associations between primary production and usable solar radiation have been reported during winter and spring off Oregon (Small et al. 1972), no corresponding variation between YCS of petrale sole and mean usable radiation for winter or spring were observed from available solar radiation estimates in coastal locations close to area 2B (U.S. Weather Bureau, 1961 to 1964) and area 3A (U.S. Weather Bureau 1958 to 1964).

Although a nearly ten-fold 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 could be generally limited by zooplankton production. (Figures II.6.D, II.7.D). On the other hand, no relations between recruitment and the frequencies of storms and upwelling events -- both presumably related to food production -- were reported for two other flatfishes in Area 3A (Hayman and Tyler 1980).

In addition to potential differences between actual and estimated YCS indices, many other physico-chemical and biological factors, or processes, and temporal-spatial scales could contribute to the non-explained variation of predicted YCS estimates. Other reasons for the uncertainty of recruitment predictions have included: i) spurious correlations (Gulland 1953), ii) interannual change in the relative order of importance of forcing factors (Ahlstrom 1965), and iii) lack of simultaneous consideration of density-dependent and density-independent factors (Sissenwine 1984). Thus, the main contribution of the present regression models may be to identify those factors which appear to be the most related to YCS variations during the studied period.

Strong cohorts for petrale sole off Oregon in the 1960's (e.g., 1961, 1966 and 1968) were also detected from surveys in other flatfishes (Demory et al. 1976). In particular, year-class 1961 was strong in nearly 85 % of 13 groundfishes and in about 52 % of 31 fish stocks from the Northeast Pacific (Hollowed et al. 1987). The latter authors also reported a synchrony between strong onshore transport, high sea level and depressed isotherms during the winters 1961, 1970 and 1977 with attendant, and adjacent, strong cohorts in groundfish stocks. Which is also consistent with YCS generally stronger than average for petrale sole in the present study. The extremely high onshore Ekman transport in winter 1961 (Figure II.12) suggests that high inshore advection of early life stages could have been the main

forcing factor for the high recruitment in most of these species.

The similar autocorrelation pattern of environmental and YCS series in this study, points out the need for long-term recruitment-environmental research. Substantially more conceptual and practical understanding on fish recruitment variations could be gained from multi-disciplinary research goals (e.g., Jackson 1981, Wooster and Bailey 1989) and from the use of in situ and remote sensing methods (e.g., Laurs 1983, Dickey 1988).

III. SUMMARY AND CONCLUSIONS

Relative abundance of petrale sole based on standardized and non standardized catch rates showed a substantial decline from the late 1970's to the middle 1980's in Pacific States Marine Fisheries Commission areas 2B and 3A. For area 2B, a small increase in abundance after the middle 1980's appeared to have persisted at least until 1989. This suggested a larger decrease in the number of fish from Willapa Deep than from Heceta Bank spawning grounds during the 1980's.

The present YCS indices based on female petrale sole are also representative for males as recruitment fluctuations inferred from younger fish were the same for both sexes. Relative YCS indices indicated that year-classes born in 1961, 1966, 1968, 1970 and 1971 were comparatively stronger during the period 1960 to 1971. Despite the age underestimation in males over 8 years old using the surface aging method of otoliths (W. H. Barss, ODFW, unpublished information), the present relative YCS indices using only female petrale sole agreed with those obtained by Demory et al. (1976) from the combined age frequency for both sexes.

YCS indices for female petrale sole based on Summed-CPUE indices for ages (6 + 7) and cohort analyses for age-6 tended to be significantly associated in areas 2B and 3A ($r \geq 0.45$, $P \leq 0.06$). Yet, survey data indicated that year to year recruitment fluctuations were better reflected in cohort analyses indices.

Cohort analyses indicated that YCS of year-classes born from 1962 to 1965 and from 1973 to 1977 tended to be intermediate to weak. A declining trend of YCS in the first half of the 1970's in areas 2B and 3A was supported by Summed-CPUE indices, and it was consistent with a subsequent decline of standardized and non-standardized catch rates when those cohorts entered the fishery in the late 1970's. Moreover, as revealed by an increase of fishing mortality and by a decrease of YCS for cohorts born in the 1970's, the increase of fishing effort in the late 1970's may have further enhanced the decline in abundance of petrale sole in areas 2B and 3A.

The inverse pattern between potential egg production and recruitment strength for cohorts 1970 to 1977 was inconsistent with attendant first-differenced series. Thus, a lack of spawner-recruit relation for petrale sole in areas 2B and 3A within the range of parent-stock sizes examined is supported by studies in petrale sole off British Columbia and Washington (Ketchen and Forrester 1966, Pedersen 1975-a), and in the most investigated flatfishes (e.g., Cushing 1971, Cushing 1973, Roff 1981).

Vertical distribution of petrale sole larvae appeared to be largely restricted to waters in the upper 50 m over the continental slope and continental shelf off Oregon. Moreover, petrale sole larvae (or pre-settlement juveniles) found in areas close to spawning grounds (50-100 km offshore), generally showed a smaller average size than individual collected in nearshore or offshore areas. Such difference in size could be due to growth of early life stages during periods of onshore advection (winter to early spring), and offshore advection (middle-spring to summer). The presence of settlement areas of juveniles on the continental shelf, in relation to spawning grounds on the continental slope, strongly suggested that recruitment may be favored by onshore advection of pre-settlement stages. Yet, the fact that the predominant transport off Oregon is alongshore, and that this is also associated with cross-shelf transport imply that recruitment may also depend on northward advection. On the other hand, the stenoplastic condition of eggs and larvae of petrale sole to temperature and salinity (Alderdice and Forrester 1971) could also be related to YCS of petrale sole off Oregon and Washington.

The effect of YCS variations of petrale sole on the fishery appeared to be more associated with low-frequency recruitment fluctuations than to year-to-year variations. The non-random recruitment variation seems to have substantially affected catch rates of petrale sole in areas 2B and 3A from the late 1970's to at least the middle 1980's. Similar autocorrelation patterns between YCS in areas 2B and 3A with environmental factors (January-March mean onshore Ekman transport and December-February mean sea level for both areas, and

December-February mean sea surface temperature and salinity index in area 3A), strongly suggested that recruitment variations for petrale sole off Oregon and Washington may be largely forced by winter and early spring oceanographic conditions. These results support the hypothesized effect of the previous environmental factors on the recruitment for petrale sole off British Columbia (Ketchen and Forrester 1966, Alderdice and Forrester 1971). Thus, adjusted significance values of the correlations obtained from regression analyses (Table II.4) could approach those of conventional significance values if more years were included in the analyses.

Although most of the recruitment fluctuations of petrale sole off Oregon and Washington seemed to be linearly associated with offshore Ekman transport and sea level in areas 2B and 3A, as well as to temperature and salinity in area 3A, some unusually large environmental anomalies, particularly those present during El Niño year 1958 and during the non-El Niño year 1961, appeared to have caused large departures from linear relations between YCS and environmental factors. The positive association between onshore Ekman transport and sea level during winter could explain in part the parabolic regressions of YCS on offshore Ekman transport and sea level. By this association, the highest recruitment levels of petrale sole into areas 2B and 3A could depend on moderately high onshore advection of eggs and larvae during winter and early spring. Since winter onshore Ekman transport is correlated with northward transport, it is probable that unusually high onshore transport could cause excessive advection of eggs and larvae away from inshore recruitment areas used by each subpopulation. Yet, under El Niño years a reduction of food supply for petrale sole larvae could also offset the attendant increase in onshore transport. Other factors such as suboptimal temperatures and salinities for petrale sole eggs and larvae (Alderdice and Forrester 1971) and a potential increase in predators of fish larvae (e.g., Bailey and Incze 1985) could also reduce YCS during years of unusually high onshore transport.

The timing of the spring transition appears to be relevant to the

recruitment of petrale sole only if a delay in such transition is associated with high onshore Ekman transport. In particular, high values of onshore Ekman transport during March, month usually preceding the spring transition, seem to be highly associated with YCS of petrale sole in areas 2B and 3A.

A southward decrease in the positive temperature-YCS relation for petrale sole from waters off British Columbia (Ketchen and Forrester 1966) to waters off Central-Southern Oregon (Section II) is consistent with positive (or negative) temperature-recruitment relation in the poleward (or equatorward) distribution range of several species of fish (e.g., Cushing 1982, Bailey and Incze 1984). Yet, although it is conceivable that the recruitment of petrale sole could be negatively correlated with temperature in its southern range of distribution, onshore Ekman transport (and attendant warmer temperatures) could also favor YCS.

Nearly 55 % of the YCS variation of petrale sole in area 2B from 1958 to 1977 was explained by a regression model based on an index of mean offshore Ekman transport from January to March, and an index of northward transport (sea level anomalies from December to February). For area 3A, a regression model based on the previous indices plus sea surface temperature anomalies from December to February accounted for about 65 % of the YCS variation. These results strongly suggested that recruitment variations of petrale sole off Oregon and Washington may have been more determined by oceanographic conditions affecting survival and/or distribution of egg and larval stages than by parental spawning biomass. Large-scale recruitment patterns for petrale sole appear to be greatly controlled by cross-shelf and alongshore coastal transport. Yet, temperature and salinity also seem to be associated with recruitment strength at smaller spatial scales.

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V. APPENDICES

Appendix I.1. Mean total (center) length by age group of female petrale sole landed in PSMFC area 2B, and number of fish used for age estimations (n). Period 1982 to 1989 (no samples were collected in 1984). Age estimates for 1987 and part of 1986 were provided by ODFW. Age structure for other years in this table was obtained as part of this study.

Year	Age Group										
	3	4	5	6	7	8	9	10	11	12	13+
	Mean Total Length (cm)										
1982	29.0	32.6	35.0	36.8	40.4	42.6	43.9	45.5	45.4	50.2	53.6
n	1	10	35	44	31	37	21	20	13	17	45
1983	--	33.2	38.3	39.0	40.3	41.4	43.5	43.3	47.1	46.4	52.7
n	0	5	12	23	18	26	29	18	14	12	47
1985	--	31.4	33.0	37.8	38.5	40.8	43.9	46.0	47.1	49.0	50.1
n	0	8	18	28	20	29	14	15	14	10	15
1986	28.0	32.2	32.9	33.4	38.3	42.3	43.5	45.1	45.8	45.5	49.3
n	1	20	46	35	50	35	24	9	4	2	3
1987	--	35.0	33.5	34.9	38.3	36.5	43.8	46.3	48.0	47.0	--
n	0	11	13	34	19	19	6	4	1	1	0
1988	--	27.0	36.5	38.7	40.4	40.8	43.4	44.9	43.4	43.3	--
n	0	1	2	11	23	25	11	9	5	3	0
1989	--	33.0	33.7	34.1	35.1	38.6	39.7	43.7	45.7	50.0	43.5
n	0	2	31	60	33	29	17	9	3	2	2

Appendix I.2. Mean total (center) length by age group of female petrale sole landed in PSMFC area 3A, and number of fish used for age estimations (n). Period 1982 to 1989 (no samples were collected in 1983-84). Age estimates for 1987 and part of 1986 were provided by ODFW. Age structure for other years in this table was obtained as part of the present study.

Year	Age Group										
	3	4	5	6	7	8	9	10	11	12	13+
	Mean Total Length (cm)										
1982	--	34.1	35.3	38.2	39.8	42.5	43.7	51.7	47.0	50.0	52.9
n	0	14	31	25	28	11	10	3	10	6	15
1985	--	32.9	35.2	38.4	40.7	42.0	45.4	39.3	45.0	46.5	48.8
n	0	7	51	54	48	25	11	6	6	2	6
1986	29.0	34.6	37.5	41.6	44.9	46.4	49.1	49.8	51.5	53.8	53.8
n	1	27	39	36	60	46	22	12	11	5	3
1987	--	36.5	38.9	39.9	42.4	44.8	47.0	40.0	--	--	56.0
n	0	17	42	34	26	16	3	1	0	0	1
1988	--	31.2	35.8	39.0	42.1	44.9	48.0	48.9	50.0	--	51.0
n	0	20	40	46	31	14	9	8	4	0	1
1989	--	30.8	34.2	37.0	41.0	42.2	45.5	48.3	47.0	--	51.0
n	0	11	62	68	42	17	6	3	2	0	1

Appendix I.3. Standardized values of landings (C), fishing effort (f) and catch rates (C/f) of petrale sole in PSMFC statistical area 2B up to 420 m of depth. C_o and f_o are respectively the partial landings and attendant effort of the Oregon fleet obtained from fishermen logbooks. Also shown are the proportions of total Oregon landings and effort for petrale sole catches up to 420 m of depth and the weight proportion of females in landings. (C_o , f_o , C, f and WP_f were defined in methods by equations 1 and 2).

Year	C_o Oregon Landings (tons)	f_o Oregon Effort (days) ^a	Proportion of landings under 420 m ^b	Proportion of effort under 420 m ^b	C Total Landings (tons)	f Total Effort (days)	C / f Catch rates (tons/day)	WP_f Female weight proportion in landings
1966	108	97	1.00	1.00	109	98	1.12	0.78
1967	65	88	1.00	1.00	97	131	0.74	0.61
1968	89	103	0.99	0.98	108	125	0.86	0.68
1969	119	170	0.97	0.94	141	201	0.70	0.65
1970	155	157	0.86	0.88	230	234	0.98	0.76
1971	189	258	0.95	0.94	229	314	0.73	0.65
1972	241	248	0.92	0.91	249	257	0.97	0.54
1973	138	206	0.90	0.90	198	295	0.67	0.55
1974	280	206	0.93	0.93	280	206	1.36	0.55
1975	427	263	0.93	0.93	427	263	1.63	0.51
1976	286	322	0.97	0.96	331	373	0.89	0.55 ^c
1977	201	201	0.98	0.99	269	269	1.00	0.60 ^d
1978	236	238	0.98	0.97	351	353	0.99	0.63
1979	291	276	0.97	0.95	431	409	1.05	0.66
1980	95	128	0.98	0.91	252	340	0.74	0.77
1981	179	296	0.99	0.96	323	534	0.60	0.77
1982	190	351	0.97	0.94	310	571	0.54	0.58
1983	129	241	0.94	0.92	320	600	0.53	0.71
1984	58	132	0.94	0.87	166	378	0.44	0.71 ^c
1985	69	159	0.93	0.87	173	397	0.43	0.75 ^d
1986	65	77	0.98	0.91	246	293	0.84	0.74
1987	151	304	0.89	0.84	198	397	0.50	0.77
1988	124	239	0.83	0.75	226	435	0.52	0.73
1989	132	224	0.87	0.71	234	399	0.59	0.71

a: Values for 1966, 1974 and 1975 are regression estimates of Oregon effort on total effort.

b: Values for 1966 are assumed to be those of 1967. Estimate for 1974-75 is the mean of 1973 and 1976.

c: Based on mean proportion for adjacent years.

d: Based on mean weight of fish for this year and the mean number of fish sampled the 6 adjacent years.

Appendix I.4. Standardized values of landings (C), fishing effort (f) and catch rates (C/f) of petrale sole in PSMFC statistical area 3A up to 420 m of depth. C_o and f_o are respectively the partial landings and attendant effort of the Oregon fleet obtained from fishermen logbooks. Also shown are the proportions of total Oregon landings and effort for petrale sole catches up to 420 m of depth and the weight proportion of females in landings. (C_o , f_o , C, f and WP_f were defined in methods by equations 1 and 2).

Year	C_o Oregon Landings (tons)	f_o Oregon Effort (days) ^a	Proportion of landings under 420 m ^b	Proportion of effort under 420 m ^b	C Total Landings (tons)	f Total Effort (days)	C / f Catch rates (tons/day)	WP_f Female weight proportion in landings
1966	475	360	1.00	1.00	478	362	1.32	0.62
1967	484	363	1.00	1.00	524	394	1.33	0.71
1968	366	350	1.00	1.00	373	357	1.05	0.72
1969	402	385	1.00	1.00	435	416	1.05	0.68
1970	412	342	0.99	0.99	412	342	1.20	0.71
1971	570	373	0.97	0.98	570	373	1.53	0.67
1972	489	335	0.97	0.99	489	335	1.46	0.64
1973	482	338	0.99	0.97	522	366	1.43	0.68
1974	607	332	0.99	0.98	791	433	1.83	0.48
1975	400	308	0.99	0.98	555	428	1.30	0.64
1976	290	234	0.99	0.99	486	392	1.24	0.67 ^d
1977	307	246	0.99	0.99	489	392	1.25	0.60
1978	292	299	0.99	0.99	667	685	0.97	0.62
1979	255	399	0.99	0.99	657	1030	0.64	0.67
1980	205	347	1.00	0.99	696	1177	0.59	0.65
1981	220	311	0.99	0.98	464	658	0.71	0.70
1982	179	274	0.99	0.98	489	747	0.66	0.72 ^d
1983	178	248	0.96	0.96	524	730	0.72	0.66 ^c
1984	171	285	0.98	0.97	420	700	0.60	0.72
1985	70	150	0.97	0.96	314	674	0.47	0.64
1986	85	82	0.95	0.95	294	285	1.03	0.64
1987	169	216	0.97	0.97	561	716	0.78	0.58
1988	137	236	0.92	0.93	447	770	0.58	0.61
1989	130	290	0.94	0.87	450	1006	0.45	0.59

a: Values for 1966, 1974 and 1975 are regression estimates of Oregon effort on total effort.

b: Values for 1966 are assumed to be those of 1967. Estimate for 1974-75 is the mean of 1973 and 1976.

c: Based on mean proportion for adjacent years.

d: Based on mean weight of fish for this year and the mean number of fish sampled the 6 adjacent years.

Appendix I.5. Numbers of female petrale sole (thousands) landed in PSMFC area 2B from 1966 to 1989. Values include all fishing depths and are not corrected for discard rates.

Year	Age Groups											Total
	3	4	5	6	7	8	9	10	11	12	13+	
Thousands of Fish												
1966	0	0	2	17	32	24	10	12	8	3	3	111
1967	0	1	6	13	23	15	7	6	4	2	1	78
1968	0	0	5	10	29	28	14	7	2	2	2	101
1969	0	0	6	17	21	29	24	15	8	4	1	125
1970	0	1	10	41	62	64	47	43	10	6	6	290
1971	0	9	34	29	29	18	20	28	8	9	5	190
1972	2	23	23	33	39	27	19	14	8	9	10	206
1973	1	5	12	15	24	21	13	12	10	13	17	144
1974	1	14	6	33	36	30	23	13	24	6	36	221
1975	1	8	51	58	65	37	29	18	8	6	1	282
1976 ^a	2	9	51	53	51	44	21	16	6	7	2	263
1977	2	9	46	44	36	22	22	9	5	2	2	201
1978	2	12	21	42	56	46	25	24	10	10	10	259
1979	5	41	58	46	63	47	29	23	11	10	23	356
1980	1	20	25	37	37	31	19	19	15	9	18	231
1981	1	18	36	30	31	26	20	18	15	12	53	260
1982	1	7	23	29	21	24	14	13	9	11	30	181
1983	0	5	13	24	19	27	31	19	15	13	50	215
1984 ^a	1	9	16	15	24	15	18	19	12	7	27	164
1985	0	7	16	25	18	26	13	14	13	9	14	156
1986	1	25	56	43	61	43	29	11	5	2	4	281
1987	1	24	31	85	61	57	12	9	1	2	3	288
1988	0	3	8	29	65	61	27	22	15	8	0	239
1989	1	4	55	107	59	52	30	16	5	4	4	335

a: Estimates based on catch curves and age frequencies of individual cohorts.

Appendix I.6. Numbers of female petrale sole (thousands) landed in PSMFC area 3A from 1966 to 1989. Values include all fishing depths and are not corrected for fishing depth.

Year	Age Groups											Total
	3	4	5	6	7	8	9	10	11	12	13+	
Thousands of Fish												
1966	0	0	8	61	86	58	44	33	27	12	21	350
1967	0	3	14	69	120	81	56	33	19	17	17	430
1968	0	3	18	28	61	82	45	25	20	10	10	302
1969	0	7	45	59	40	76	53	28	16	10	9	342
1970	0	1	26	56	62	34	45	45	26	9	12	317
1971	4	87	195	88	53	24	32	34	9	3	6	535
1972	4	29	72	117	58	41	26	19	20	6	9	401
1973	4	32	96	78	95	61	33	32	13	15	24	482
1974	3	8	24	48	84	79	48	38	24	16	24	395
1975	2	6	50	77	83	73	53	15	7	6	11	382
1976	0	6	15	44	96	69	43	12	11	0	0	297
1977	2	21	47	88	98	54	30	12	9	1	3	365
1978	0	49	20	58	58	63	60	37	31	15	27	419
1979	2	18	91	123	95	63	46	29	23	21	24	536
1980	8	56	63	76	41	39	21	23	14	29	54	424
1981	4	28	57	60	46	23	10	11	12	10	51	312
1982	1	36	80	64	72	28	26	8	26	15	39	394
1983 ^a	2	26	73	111	65	54	22	24	10	11	27	426
1984 ^b	0	3	38	80	101	44	21	9	15	9	9	328
1985	0	9	65	69	61	32	14	8	8	3	8	277
1986	1	19	27	25	42	32	15	8	8	3	2	182
1987	1	73	125	103	60	45	10	2	1	1	2	422
1988	1	43	86	99	66	30	19	17	9	1	2	372
1989	1	22	125	137	85	34	12	6	4	1	2	429

a: Values based on catch curves and age frequencies of individual cohorts.

b: Values based on 1984 length frequency and 1982-85 age-length key.

Appendix I.7. Mean total (center) length of female petrale sole observed in PSMFC area 2B and 3A from commercial landings, and calculated by combining survey data for fish under age-9 with commercial landings for ages 9 to 13.

Age	Observed Total Length (cm)		Calculated Total Length (cm)	
	Area 2B	Area 3A	Area 2B	Area 3A
2	-	-	19.9	19.7
3	28.8	32.2	24.3	24.1
4	37.2	33.6	27.9	27.9
5	37.1	35.5	31.1	31.2
6	39.2	37.7	33.9	34.3
7	40.7	40.0	36.6	37.0
8	41.8	41.9	39.0	39.6
9	43.7	43.7	41.3	42.0
10	45.0	45.4	43.5	44.3
11	46.5	46.7	45.5	46.5
12	49.0	49.1	47.5	48.6
13	49.3	50.2	49.4	50.6

Appendix II.1.

Spawning Period and Early Life History of Petrale Sole

Spawning has been detected as early as November off the Southern-Washington to Northern-Oregon coast, with a peak from December through January, and is almost completed by March (Harry 1959). For the Northern California-Southern Oregon coast the spawning also appears to be close to the previous period (Porter 1964). Personal unpublished observations of maturity in petrale sole from late November 1990 through late January 1991 in areas 2B and 3A are consistent with an onset and peak in spawning for November and December-January respectively. Spawning along the British Columbia and California coast is restricted from late fall to early spring (Cleave 1949, Ketchen and Forrester 1966, Best 1963), but it appears to start at least one month earlier off California than off British Columbia. Despite this latitudinal trend, a rather specific timing in the spawning peak of petrale sole off Oregon and Washington was observed in different years.

Incubation period for petrale sole under different temperature-salinity conditions has ranged from 6.2 to 13.5 days (Alderdice and Forrester 1971). In the same study, starved larvae increased from an average size of 2.84 mm total length (TL) from the time of hatching to about 5.6 mm TL until the time of yolk absorption, which occurred 10 to 16.5 days later. Petrale sole larvae off Oregon have been collected from March through June (Pearcy et al. 1977).

Despite the substantial sampling effort using midwater trawls and plankton tows in the Northeast Pacific coast, the latter authors only reported a total of 52 collected larvae in this species. This fact could also explain the unclear temporal progression of larval stages reported by Pearcy et al. (1977). However, these latter authors indicated that the younger larval stage sampled (c.a. 10-15 mm standard length, SL) was caught only in March and April and the older stage (c.a. 20-21 mm SL) was only collected in June. They characterized this latter stage as larvae having the left eye fully on the right side. The description of the previous stage of petrale sole is similar to

that given for two individuals (21-22 mm TL) caught in April off Centerville, California (Porter 1964). These two fish were collected between c.a. 13 to 24 m off of the bottom in waters 46 to 55 m of depth. Despite their small size, Porter (1964) showed substantial evidence that these individuals were juveniles.

Post-settlement juveniles along the Northeast Pacific coast have only been found since late spring. Ketchen and Forrester (1966) reported 14 juveniles (8 - 9 cm, presumably TL) collected off British Columbia at depths ranging from 18 to 90 m from May through August.

Off San Francisco and Northern California, Gregory and Jow (1976) found 13 fish between 7.1 - 10 cm TL. With a single exception, all these were age-0 fish. These juveniles were caught from 38 to 73 m depth from September to October. On the other hand, Gregory and Jow (1976) reported a length range from 7.9 to 13.6 cm TL for one year-old fish. Thus, as predicted from the spawning peak, it is likely that most of these fish were born in winter. This conclusion is also supported by observations of Pearcy et al. (1977) off Oregon. The latter authors reported 28 juveniles age-0 juveniles (6.2 - 10.7 cm TL) from October to November between 64 to 82 m of depth.

Pearcy et al. (1977) suggested that metamorphosis of petrale sole may occur during the fall of their first year, when fish have been found settled on the inner continental shelf off Oregon. However, considering the attendant earlier onset of spawning of petrale sole in southern areas, plus the finding of settled juveniles off British Columbia as early as May, and through August, it is conceivable that juvenile settlement off Oregon and California could start earlier than off British Columbia. Thus, in areas south off British Columbia it is likely that metamorphosis in a morphological sense could begin at least from March for individuals of at least 2.0 cm TL. Post-settlement could start as early as May for juveniles of at least 6.2 cm TL. Yet, the peak in occurrence for pre-settlement and post-settlement juveniles could be summer and fall respectively.

Although no studies on feeding habits are available for this

species during its first year of life, older juveniles could eat similar prey found in adult fish. Euphausiids, shrimps and fishes are the food items more frequently reported in the diet of adult petrale sole (Cleaver 1949, Ketchen and Forrester 1966, Kravitz et al. 1977).

Appendix II.2. Long-term seasonal means (1959-1977) of environmental indices used in exploratory correlation analyses. (Geographical locations and sources for environmental indices are shown in Table II.1).

Environmental Index	Season			
	Winter	Spring	Summer	Fall
Mean Sea Level ^a				
Area 2B	2.09	1.93	1.88	1.98
Area 3A	2.33	2.19	2.25	2.29
Northward Ekman Transport ^b				
Areas 2B and 3A	-26.09	-20.02	-14.24	-10.69
Northward Sverdrup Transport ^c				
Areas 2B and 3A	18.43	-117.43	-200.35	-15.63
Offshore Ekman Transport ^d				
Areas 2B and 3A	-72.31	9.97	61.28	-19.71
Cube of Wind Speed ^e				
Areas 2B and 3A	155.16	46.17	104.99	53.31
Sea Surface Temperature ^f				
Area 2B	10.40	10.73	13.67	13.22
Area 3A	9.38	10.16	13.85	12.87
Nearshore Salinity Index ^g				
Areas 2B, 3A	9984.63	9990.12	10102.03	9999.48
Surface Atmospheric Pressure ^h				
Areas 2B and 3A	1017.60	1018.56	1018.58	1017.17

^a Meters.

^b Value x 10 = metric tons per second per kilometer.

^c Value x 100 = metric tons per second per kilometer.

^d Metric tons per second per 100-meter of coast width.

^e (meters/second)³

^f Value = Celsius degrees.

^g Value / 10000 = water density (grams/cm³) at 15 °C.

^h Millibars.