

AN ABSTRACT OF THE THESIS OF

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Title: Environmental Fluctuation and Cohort Strength of Dover Sole
(Microstomus pacificus) and English Sole (Parophrys vetulus)

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Models were developed that described cohort strength of female Dover sole (Microstomus pacificus) and female English sole (Parophrys vetulus) in stocks off the Columbia River as functions of environmental variables. The environmental variables considered were those that could hypothetically influence spawning success or survival. They included a spawning power index, monthly mean measurements of different oceanographic and Columbia River factors, and short-term measurements of weather variability. Cohort strength was calculated by using Pope's cohort analysis.

For Dover sole, only upwelling in June and July, which may regulate food availability following yolk sac absorption, and offshore divergence the next December and January, which may regulate the location of larval settling, explained significant cohort strength variation. A model incorporating these two variables explained 64.7 percent of cohort variation. Although the Dover sole stocks were clumped around the Columbia River, it appeared that Columbia River

factors had less influence on recruitment than did these two oceanographic factors. Spawning power was also not significantly related to cohort strength over the range observed.

For English sole, the factors that were associated with the great success of the 1961 cohort were apparently unique to that cohort; thus, they could not be examined statistically. From data examined here, however, it appeared that unique weather variability, characterized by high storm frequency but low average wind speed, may have been partly responsible. For the other cohorts, variation in early fall (prespawning) values of upwelling, barometric pressure, and sea surface temperature explained 72.8 percent, 83.8 percent, and 49.0 percent, respectively, of the cohort variation. During upwelling these three factors are associated with bottom temperature; therefore, it was proposed that bottom temperature variation, which may regulate time of spawning or egg condition, was the factor most directly linked to English sole cohort strength. Colder bottom temperatures were associated with stronger cohorts.

Principal components of the environmental variables were derived and regressed against recruitment. The first two principal components explained 65.9 percent of the variation in Dover sole recruitment. For English sole, the third principal component explained 76.9 percent. Because many environmental variables probably influence recruitment, and because every environmental variable considered contributes to each principal component, models incorporating principal components could predict recruitment more accurately than models which include only one or two environmental variables.

Environmental Fluctuation and Cohort Strength of
Dover Sole (Microstomus pacificus) and
English Sole (Parophrys vetulus)

by

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ENVIRONMENTAL FLUCTUATION AND COHORT STRENGTH OF

DOVER SOLE (MICROSTOMUS PACIFICUS) AND

ENGLISH SOLE (PAROPHRYS VETULUS)

I. INTRODUCTION

The goal of this research was to determine the relation between environmental factors and variations in cohort strength, measured as female abundance, of Dover sole (Microstomus pacificus) and English sole (Parophrys vetulus) in PMFC Area 3A, the fishery off the Columbia River. In this analysis, it was important to determine whether cohort strength was most closely associated with ocean factors, spawning power, or Columbia River factors. Columbia River factors were included in this analysis because the Columbia River exerts a major influence on water properties in this area (Barnes et al. 1972; Small and Cross 1972), and because unpublished catch records, which show much higher catches of Dover and English sole near the mouth of the Columbia than elsewhere along the coast, imply a possible link between the Columbia River and flatfish abundance (A. V. Tyler, Oregon State University, pers. comm.).

Identifying the factors responsible for cohort strength variation can help in understanding the ecology of the fish, and can aid future yield predictions. In addition, in order to guard against recruitment failure and to manage for sustainable yield, information is required on whether cohort strength variation is influenced by variation in spawning power more strongly than by physical environmental variation.

The topic of relating measurements of environmental factors to cohort strength of fish has occupied researchers ever since Johan Hjort, a Norwegian biologist, noted that cohort strengths of fish may fluctuate greatly from year to year (Hjort 1926; May 1974). Correlations have been made between cohort strength of such fish as cod, plaice, salmon, herring, and scallops, and environmental factors such as sea surface temperature (Ketchen 1956; Rounsefell 1958), indices of water transport (Nelson et al. 1977; Parrish 1976), average components of wind velocity (Templeman 1972; Dickson et al. 1974), salinity, and river flow (Rounsefell 1949; Kingsbury et al. 1975). Correlation studies of this nature have not been done for Dover sole, but Ketchen (1956), working with English sole in Hecate Strait, British Columbia, found that colder December-May sea surface temperatures, which prolonged the pelagic life and northward transport of larvae (Alderdice and Forrester 1968), were associated with stronger cohorts.

These correlations are believed to reflect the influence of an environmental factor on food production, growth and predation, transport to suitable nurseries, or physical stress (hence, survival), during a critical period in the history of the cohort. In general, however, few predictions based on these past correlations have continued to predict future cohort strength, probably because the true relation between cohort strength and the environment involves more than one environmental factor, with success in different years being related to different factors (Ahlstrom 1965; Gulland 1965; Cushing 1974a).

To avoid some of the weaknesses common in many previous investigations, I considered more than one environmental parameter at a time by using multiple regression and principal components. Other refinements included an analysis of the effects of short-term variability in the environment, and the investigation of the role of spawning power. Development of the cohort strength variable is presented in Appendix I as a research paper that has been submitted to the Fishery Bulletin for publication. A short summary of the development of this variable is given now.

Cohort strength indices were calculated by two methods: by summing the catch per unit effort (CPUE) of each age group in a cohort (Ketchen and Forrester 1966), and by Pope's (1972) cohort analysis. The indices derived by each method were compared, and, where differences existed between the sets of indices, the relative validity of each set was assessed by both direct and indirect procedures. The direct procedure involved examining the magnitude of error likely to be associated with each method of calculation. The indirect procedure involved comparing the distinctness of plots of surplus production on stock size estimates that had been derived from each set of indices. The indices derived by Pope's method appeared to be more valid, and were used in the analysis of associations between environmental variation and cohort strength variation.

Before examining causes of cohort strength variation, I hypothesized mechanisms through which environmental factors might influence cohort strength. This required a review of both the physical environment in this area, and of the life histories of Dover and English sole.

II. REVIEW OF ABIOTIC AND BIOTIC FACTORS

Weather and Hydrography in the Region

PMFC Area 3A lies between 45°46' N and 47°20' N on the eastern border of the Northeastern Pacific (Figure 1 in Appendix I). The physical oceanography of this region has been described by several authors (Barnes et al. 1972; Fleming 1955; Dodimead et al. 1963; Uda 1963; Peterson 1972). The continental shelf is narrow, from 15 to 75 km wide, and breaks at a depth of about 200 m (McManus 1972). The continental slope is steep, so that water depth may be 200 m at a point 65 km offshore, and 1000 m at a point 10 km further offshore. The major surface currents originate from the West Wind Drift, which splits, at about the latitude of Cape Blanco (43°N), into the northward-flowing Alaska Gyre and the southward-flowing California Current. These currents lie over 300 km offshore. Inshore, the surface circulation is influenced by seasonal changes in the winds. In the winter, when the Aleutian low pressure system dominates the area, the winds come out of the south and surface transport is northward and onshore. In summer, the North Pacific high pressure system dominates; winds come out of the north and surface transport is southward and offshore (Barnes et al. 1972). Bottom currents deeper than 100 m are believed to move northward throughout most of the year (Huyer et al. 1975).

Two other features have major impacts on this area. One is coastal upwelling, in which northerly winds push surface waters

offshore, thereby drawing up cold, nutrient-rich deeper waters, which greatly enhance primary production. This process generally occurs within 15 km of the coast in spring and summer (Cushing 1971; Bakun 1973), so that surface and bottom temperatures over the continental shelf are colder in summer than in winter (Huyer et al. 1975). In winter, transport is generally onshore--a process sometimes called "downwelling."

The other feature is the Columbia River, which dilutes surface waters over a wide range, and carries nutrients, terrigenous sediments, and river plankton into the ocean. In the winter, the Columbia plume is a narrow band along the Washington Coast. By May and June, when discharge peaks, the plume extends like a broad tongue southwest from the river's mouth, and may dilute surface waters up to 800 km offshore (Barnes et al. 1972; Small and Cross 1972). In the summer, the river supplies major amounts of silicate to the adjacent ocean, and while it does not directly input much nitrate or phosphate, it does induce upwelling of these nutrients from deeper water into the photic layers. This nutrient input apparently enhances primary production in the plume (Conomos et al. 1972; Anderson 1972; Small and Curl 1972).

Early Life History of Dover Sole

Relating these physical oceanographic features to observed fluctuations in Dover sole cohort strength required knowledge of Dover sole life history. Unfortunately, this knowledge is incomplete,

and there is a particular lack of information on the early life history.

Fishery statistics indicate that throughout the summer females are generally found inshore of 200 m while males tend to stay in water deeper than 400 m (Demory 1975). Tagging studies show that in October and November, the females begin a spawning migration to join the males in water deeper than 400 m (Westrheim and Morgan 1963; Milburn 1966). Catches of gravid females indicate that spawning occurs from November until April, with the peak of spawning occurring from December to February (Hagerman 1952; Demory 1975). The eggs are pelagic and drift with the currents. Since the youngest larval stages are found from March through July, and abundance peaks in May and June (Pearcy et al. 1977), the time between spawning and yolk sac absorption for an individual fish is about 4 months. Dover sole larvae have been found from 2 km to 550 km offshore, but most of them range from 50 to 110 km offshore (Pearcy et al. 1977). Richardson and Pearcy (1977) characterized them as members of an "offshore species assemblage," where the division between "onshore" and "offshore" was between 28 km and 37 km offshore. The larvae are distributed vertically between the surface and 600 m, but most occur from the surface down to depths of 150 m. The larvae drift for several months, are capable of moving vertically, but are otherwise at the mercy of the currents. Before settling, the left eye migrates to the right side of the head, and the body flattens out. Newly settled juveniles (40 mm to 70 mm SL) first appear on the outer continental shelf and slope (60 to 70 km offshore) in water from 130 to

180 m deep in January and February (Demory 1971; Pearcy et al. 1977). This outer shelf area may be a nursery area. From there they move inshore and by May are found at depths of 20 to 100 m (Demory 1971). Thus, over a year may pass between spawning and the beginning of demersal life (Figure 1).

This picture is complicated, however, by the existence of larvae that do not settle in the first year. Significant percentages of large larvae, longer than 50 mm SL, are found throughout the year. Relatively more of these larvae occur offshore of 83 km. Pearcy et al. (1977) have hypothesized that Dover sole can arrest their own metamorphosis, delaying it until they find suitable bottom. If this is so, the large larvae would be those larvae that were unable to find suitable bottom in their first year, perhaps because they drifted too far offshore (offshore of 83 km water depths are generally greater than 1000 m, which is the depth of the oxygen minimum layer (Gross et al. 1972)). Juveniles that had been large larvae exhibit a distinctive scale pattern, and such fish are "extremely rare" in the benthic population (R. Demory, Oregon Dept. of Fish & Wildlife, pers. comm.). Since they are not rare in the larval population, it seems that most larvae that do not settle in the first year are condemned never to settle.

From this chronology of the early life history of Dover sole, it is worthwhile to extract possible critical periods. The months prior to the December-February spawning peak may be important, because adults in poor condition may produce poorer quality, or fewer eggs (Lett et al. 1975; Tyler and Dunn 1976). Survival rate during

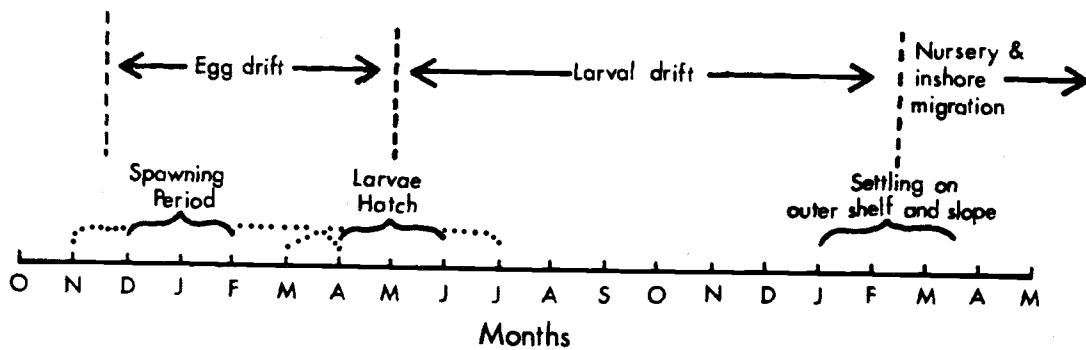


Figure 1. Time line showing important periods in early life history of Dover sole.

the egg stage is sometimes critical (Bannister et al. 1974; Pinus 1974; Saville et al. 1974), and this stage occurs from the spawning months until about June. Another critical period may be when larvae absorb their yolk sacs and feed for the first time (Hjort 1926). This occurs from April through July, with numbers of first-time feeders peaking in May and June. Larval drift continues until the fish settle. The suitability of the bottom on which they attempt to settle may help determine both nursery survival (Alderdice and Forrester 1968), and the percentage that are condemned to become large larvae. Thus, conditions during metamorphosis and settling, in December and January, may also be critical.

In all, it appears that critical periods for Dover sole may occur during a span of more than one year, from about October of the year before the cohort hatches, until May of the year following hatching.

Early Life History of English Sole

As with Dover sole, the life history of English sole is incompletely known. Although some reports state that English sole spawn mainly from December to February (Harry 1959; Barss 1976), recent egg and larval surveys, as well as times of appearance of recently metamorphosed juveniles, indicate that peak spawning may occur at varying times between October and March in different years (Richardson and Pearcy 1977; Laroche and Richardson MS). Spawning is believed to occur in water up to 100 meters deep, but analysis of catch-by-depth records (A. V. Tyler, O.S.U., unpub. data) indicates that some fish

are caught in much deeper water in the winter. It is not known whether these deep water fish are spawners.

The eggs hatch after about 100 hours (Barss 1976; Laroche and Richardson MS). Length frequency samples indicate that the larvae drift from 18 to 22 weeks before settling. During this time they are among the dominant fish larvae in Richardson and Percy's (1977) "on-shore species assemblage." Most larvae are found within 20 km of the coast but they occur out to at least 74 km. A significant percentage is found in the neuston, the top 17-1/2 cm of the water column, and these tend to be larger (median standard length = 15 to 20 mm in March) than those found deeper in the water column (median SL = 4 to 8 mm in March). When they reach a length of about 18 mm SL, the larvae metamorphose and settle (Laroche and Richardson MS). Their nursery area is in the coastal bays and estuaries and in shallow water along the open coast. They apparently migrate out of the estuaries after a year, and their range then overlaps that of the adult population (Demory 1971).

The large yearly variations in month of peak spawning make it difficult to determine possible critical months for English sole larval survival. Biological events do not occur in the same month each year, so that while a critical period may occur any time from about September of the calendar year preceding the cohort to July of that year, this period could vary from year to year. Unfortunately, the months of peak spawning and of subsequent developmental stages are not known for any cohort from 1955 to 1966. Thus, unless events during certain months are of such overriding importance that they

affect every developmental stage, it may be difficult to interpret the correlations between environmental conditions measured during the same months each year, and cohort strength.

III. METHODS

The indices of cohort strength, age 4 abundance of female English sole and age 6 or age 8 abundance of female Dover sole, were calculated by Pope's (1972) cohort analysis (Appendix I). This computation required data on the age and sex composition of the catch, average weight, total catch, and total effort. The age composition data (Appendix II and Appendix III) were obtained from Oregon Department of Fish and Wildlife (ODFW) reports (Demory 1966; Demory and Fredd 1966), and from unpublished ODFW market sampling records furnished by Robert L. Demory of ODFW. Sex composition and average weight data (Table 1 of Appendix I) were also obtained from ODFW market sampling records. Data on total landings (Table 1 of Appendix I) were obtained from annual ODFW Trawl Investigation Progress Reports, from an unpublished Pacific Marine Fisheries Commission (PMFC) Data Series, Bottom Fish Section, that was furnished by Jack Robinson of ODFW, and from personal communication with R. Dale Ward, Washington Department of Fisheries. I computed total effort (Table 1 of Appendix I) from unpublished log book data compiled by ODFW.

Only data on females were used, because the age composition data on males were questionable. Since males and females live in the same area and grow at about the same rate for the first several years of life (Demory 1975; Barss 1976), they should be subject to the same mortality rate. Therefore, a strong cohort of females should also be a strong cohort of males, and it should be valid to consider only females in this study.

To select the environmental factors included in this analysis, I hypothesized mechanisms by which different environmental factors might affect cohort strength, and those factors for which time-series data were available were selected for correlation with cohort strength (Table 1).

The goal of this study is construction of a multiple regression model that describes observed cohort strength as a function of a few significant environmental factors. Because there was, however, a large initial number of environmental factors, and of combinations of months that could constitute a "critical period," it was necessary first to reduce the number of independent variables to a manageable few by using the technique of "exploratory correlation" (Ricker 1975, p. 276). The basic procedure is to propose monthly or multi-month periods during which survival could be critical in deciding cohort strength, and then to correlate cohort strength with the value an environmental factor had during a proposed critical period. Correlations with cohort strength were found for each environmental factor and each proposed critical period. These correlations were done with the Statistical Interactive Programming System (SIPS) (Guthrie et al. 1973) on Oregon State University's CDC 3300 computer.

For each correlation that is significant at the 5% level, I tried to propose mechanisms through which the factor, acting at that time, might affect cohort strength. If no reasonable mechanism could be proposed, the correlation is regarded with suspicion. Factors with both a significant correlation with cohort strength, and a reasonable mechanism through which they might act, were chosen as independent

TABLE 1. ENVIRONMENTAL FACTORS USED IN THIS STUDY OF ENVIRONMENTAL INFLUENCES ON COHORT STRENGTH.

| <u>Environmental Factor</u> | <u>Place Where Measured</u> | <u>Years Covered</u> | <u>Source of Data</u> | |
|---|--|------------------------|---|---|
| <u>Oceanographic Factors</u> | | | | |
| Sea Surface Temperature | Between 44°N, 48°N, 124°N, 128°N, 124°W & 128°W | 1945-1972 | Pacific Environmental Group, NMFS, NOAA, Monterey, Calif. 93940 | |
| Barometric Pressure | 46°N 124°W, 46°N 125°W, Neah Bay, Washington | 1946-1972 1940-1962 | | |
| Offshore Transport (Upwelling) | 45°N 125°W | 1946-1972 | | |
| Meridional Ekman Transport | 46°N 125°W | 1946-1972 | | |
| Southerly and Westerly wind velocity | 46°N 124°W, 46°N 125°W | 1946-1972 | | |
| Offshore Divergence Index | 45°N 125°W | 1946-1972 | | |
| Upward speed into Ekman layer | 46°N 125°W | 1946-1972 | | |
| Mean Sea Level | Neah Bay, Washington | 1940-1969 | | |
| 4-to-6 hourly wind velocities | Columbia River Lightship | 1949-1967 | | National Climatic Center, Environmental Data Service, Asheville, North Carolina |
| Solar Radiation | Clatsop County Airport | 1953-1965 | | |
| <u>River Factors</u> | | | | |
| Columbia River Discharge | Astoria, Oregon | 1940-1972 | USGS Circular 550 | |
| Columbia River Discharge | The Dalles, Oregon | 1950-1972 | | |
| Dissolved Solid Load | The Dalles, Oregon | 1950-1972 | USGS Water Supply Papers | |
| Silicate Concentration | The Dalles, Oregon | 1950-1972 | | |
| Nitrate Concentration | The Dalles, Oregon | 1950-1972 | | |

variables in a multiple regression. The natural logarithm of cohort strength was the dependent variable in the multiple regression model. The model was built using STEPWISE, a procedure on the SIPS REGRESS subsystem, which brings one variable at a time into the model, such that the variable entering is the one that reduces residual sum of squares by the greatest amount. To insure that the most significant variables had entered the model first, I also used BACKSTEP, in which the variables that reduce residual variability the least are dropped from the model, one by one.

A principal components analysis was done on the independent variables used for the multiple regression. This was done on the CDC CYBER 73/14 computer with the Cooley and Lohnes (1971) programs CORREL, PRINCO, FSCOR, ROTATE, and COEFF. The most significant principle components were then used as independent variables in a least-squares multiple regression with the natural logarithm of cohort strength.

For the Dover sole cohorts 1953-1962, multiple regressions were done that included spawning power as an independent variable. Calculation of spawning power required data on fecundity and percentage maturity at length. Fecundity at length was determined by plotting a GM regression line (Ricker 1973) through Harry's (1959) fecundity-at-length data. The equation of the fitted line is: Fecundity = $-404075 + 10737 \times (\text{length in cm})$. Since Harry had no data for fish shorter than 44 cm, I estimated fecundity of smaller fish by drawing a smooth curve by eye through Hagerman's (1952) data for Dover sole off California. Because Dover sole off Oregon (Harry 1959) are about

60 percent as fecund as equal-length Dover sole off California, the fecundity values derived from Hagerman's data were multiplied by 0.60 to give the fecundity at length for the smaller fish. Maturity at length was taken directly from Harry's Figure 4 (Harry 1959, p. 8).

IV. DOVER SOLE

Single Correlations Between Environmental Factors
and Cohort StrengthPatterns in cohort strength

The indices of cohort strength that I used, age 6 female abundance (Appendix V), cover cohorts from 1945 through 1962. The Columbia River discharge and Neah Bay barometric pressure and sea level data series extended back to 1940 (Table 1). To make full use of these data series, I also determined the abundance of age 8 females, which covers the 1940 through 1962 cohorts, and I correlated age 8 abundance with each of these three factors. A comparison between age 6 and age 8 abundances shows that the two indices are in good agreement ($r=.823$, $P<.01$). The largest disagreements between age 6 and age 8 abundance concern the 1945 and 1946 year classes, from which large catches of age 6 and 7 fish were taken. Because more catch data was used to calculate the age 6 abundance, this index should be more reliable than the age 8 index.

In general, strong cohorts tended to follow strong cohorts and weak cohorts tended to follow weak cohorts. The correlation between the abundance of one cohort and the abundance of the next cohort was significant for both indices ($r=.56$, $P<.01$ for age 8; $r=.54$, $P<.05$ for age 6). In part, this was to be expected because the weather in one year was not independent of the weather the previous year. Thus, if cohort strength is related to weather factors, the abundances of consecutive cohorts should be related. However, some of this relation

is probably due to aging errors. For fish younger than 10, second readings of scales agree with first readings most of the time; through age 13, second readings are within one year of first readings about 85 percent of the time (Demory 1972). Nonetheless, there is some disagreement at all ages, so that a large cohort may inflate abundance estimates of adjacent cohorts. Cohort strength estimates may then represent moving averages of actual cohort strengths to some degree. The extent to which inaccurate aging affects the cohort strength indices is unknown, but there does seem to be sufficient variation between adjacent cohorts to justify assuming that the effect is small, and that relations between cohort strength and the environment are not obscured.

Critical periods

Dover sole begin spawning in the fall in water deeper than 400 m; eggs and larvae drift in the plankton for about a year; and they metamorphose and settle on the outer continental shelf in the winter and spring following the year of the cohort (Demory 1975; Pearcy and Richardson 1977). Assuming that cohort strength is determined by either spawning success, egg and larval survival, or by success in metamorphosing and settling on suitable nursery grounds, critical periods could occur from about September of the year before the cohort hatches until May of the year following hatching (Figure 1).

Sea surface temperature

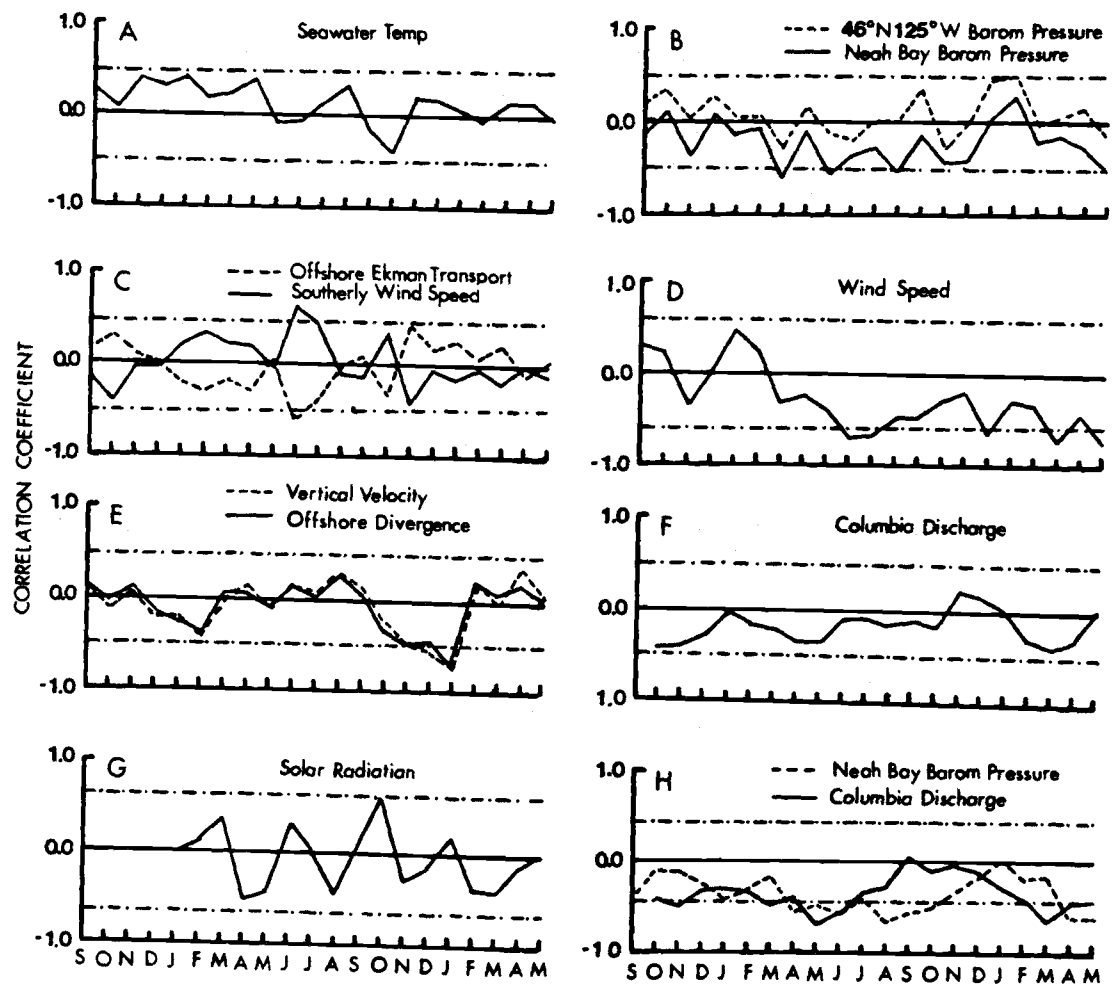
Temperature may influence cohort strength by affecting rates of egg and larval development, and of food and predator production.

Measurements of surface temperatures reported from ships at sea were compiled for 1° squares by the Pacific Environmental Group. The usefulness of these data for present purposes, however, is questionable. Many months had no observations, and few months had more than 10. Since these observations were taken at all times of the day and month, throughout areas of over 2000 square nautical miles, temperatures observed the same month varied considerably. Because 1° squares lacked sufficient numbers of observations, I partitioned the area between 44° N, 48° N, 124° W, and 128° W into two zones along the 126° W meridian, and pooled the observations within each zone. Given the quality of these data, all findings must be regarded with suspicion.

For the eastern (inshore) zone, in which most observations were taken near the mouth of the Columbia River, the correlation between cohort strength and temperature for the years 1946-1962 is generally positive, but in no case is the correlation significantly different from zero in any one month (Figure 2A). Analysis of combinations of months shows that during the period of spawning and egg drift, November through April, temperature is positively correlated with cohort strength ($r=+.55$, $P<.05$). Further analysis shows, however, that the significance of this correlation depends strongly on the 1949 cohort. That cohort was the weakest on record, and the winter of 1948-1949 was also the coldest on record, with average monthly temperatures more than 1°C colder than in other years (based on from 4 to 57 observations per month). For the less extreme years, however, there was no significant relation between winter temperatures and

Figure 2. Correlations between Dover sole cohort strength and environmental conditions measured each month from spawning through settling of a cohort. Dashed horizontal lines represent 95 percent significance level of correlation coefficients. Unless otherwise noted, cohort strength is age 6 female abundance.

- A. Between cohort strength and sea surface temperature in eastern (inshore) zone.
- B. Between cohort strength and barometric pressure at Neah Bay, Washington, and at 46° N 125° W.
- C. Between cohort strength and offshore Ekman Transport (upwelling) at 45° N 125° W, and southerly wind speed at 46° N 125° W.
- D. Between cohort strength and average wind speed at Columbia River lightship.
- E. Between cohort strength and upward velocity into Ekman Layer at 46° N 125° W, and offshore divergence at 45° N 125° W.
- F. Between cohort strength and Columbia River discharge at Astoria, Oregon.
- G. Cohort strength and average daily solar radiation at Clatsop County Airport, Astoria.
- H. Between age 8 female abundance and barometric pressure at Neah Bay, Washington, and Columbia River discharge at Astoria.



year class strength ($r=+.35$). Thus, it may be possible, if the 1949 relation was causal and not coincidental, that an extremely cold winter can have a negative effect on the cohort spawned that winter; however, more normal temperatures have no discernible impact.

Temperatures in the western (offshore) zone were not well correlated with cohort strength. There were fewer observations from this zone, and these observations were even more patchily distributed in time and space.

If temperature does affect survival, there is probably an optimal temperature, with survival dropping off as temperature increases or decreases. Thus, a relation between cohort strength and temperature might be hump-shaped, rather than linear. Further examination showed, however, that for no time period was there evidence of a hump-shaped relation between temperature and cohort strength.

Barometric pressure

Although it is difficult to envision how barometric pressure alone might affect the survival of an organism, it can be indirectly related to survival. Low pressure, for instance, is associated with southerly winds and storms, and it also affects sea level and coastal currents.

Records of monthly mean barometric pressure at 46° N 125° W (about 75 km WSW of the mouth of the Columbia), calculated by the Pacific Environmental Group from worldwide ship reports (Bakun 1973), are available from 1946-1976. The correlations show that cohort strength might be associated with the mean barometric pressure during

the time of settling (Figure 2B). The combined barometric pressures of the time-of-settling months December, January, and February have a higher correlation with cohort strength than any month alone ($r=+.61$, $P<.01$). The significance of this relation was difficult to interpret without examining other parameters that are related to barometric pressure.

Records of barometric pressure that go back to 1940 are available from Neah Bay, on the northwest tip of Washington, about 250 km north of 46° N 125° W. To include these six additional data points, I correlated Neah Bay barometric pressure with age 8 Dover sole abundance (Figure 2H).

The combined mean barometric pressures from the larval drift months of March through December have a highly significant negative correlation with age 8 abundance ($r=-.66$, $P<.001$). The correlation values for the years 1946-1962 at Neah Bay, however, were much different from those for the same years at 46° N 125° W (Figure 2B), indicating that the Neah Bay figures reflected only local pressure conditions, and were not related to conditions at 46° N 125° W. Since the fish actually live near 46° N 125° W, the significant March-October correlation with Neah Bay pressure may be coincidental.

Indices of north-south (meridional) transport

Although tagging studies have shown that adult migration is principally inshore-offshore (Milburn 1966; Westrheim and Morgan 1963), water transport in this region is primarily north-south. Yearly differences in transport may affect survival-related factors

such as suitability of bottom on which the fish settle. There are no long time-series measurements of surface currents in this area, but three indirect measurements of meridional transport are available: mean sea level, zonal (east-west) winds, and Ekman meridional transport.

Huyer et al. (1975) demonstrated that mean sea level seems to be associated with alongshore current strength--high mean sea level corresponds to strong northward flow, and low mean sea level corresponds to strong southward flow. Monthly mean sea level data from Neah Bay are available from 1940-1969. All correlations between cohort strength and mean monthly sea level are very low, indicating that alongshore current strength, as measured by sea level in Neah Bay, does not exert a noticeable influence on cohort strength.

Mean monthly values of westerly wind speeds and of northward Ekman transport, which are closely associated with each other through coriolis acceleration, were calculated for 46° N 125° W by using barometric pressure gradients (Bakun 1973). All correlations between cohort strength and monthly mean values of each of these parameters are not significant.

It would appear, therefore, that alongshore water movement considered alone has little relationship with cohort strength. This is not surprising, because the oceanic regime in this area changes little from north to south. The major changes occur from east to west.

Indices of east-west transport

The upwelling of cold, nutrient-rich deeper water, and the associated offshore transport of surface waters, have major effects on the environment in which Dover sole larvae live. Interestingly, although upwelling is known to enhance production greatly (Cushing 1971), production is not proportional to upwelling rate. In fact, recent modelling studies have shown that, because grazing is proportional to production rate and because residence time in the photic zone decreases with faster upwelling and offshore transport, slower upwelling and slower increases in production rate may cause greater total production (Cushing 1974; Wroblewski 1976; L. Small, OSU Dept. of Oceanography, pers. comm.).

The southerly component of surface winds and the westward, or offshore, component of Ekman transport, derived from barometric pressure data (Bakun 1973), are indices of upwelling. Correlations between cohort strength, and both upwelling indices are significant in June and July, at about the time yolk sac absorption is completed (Figure 2C). The signs of the correlation coefficients indicate that slower upwelling is associated with larger cohorts. Thus, some of the variation in cohort strength may be related to variations in food availability at the time of yolk sac absorption.

Average wind magnitude

An alternative hypothesis is that lower winds produce less physical damage to the eggs and larvae, thus increasing survival. To investigate this, I calculated monthly mean wind magnitude as the

average of all the wind speeds, regardless of wind direction, recorded that month at the Columbia River Lightship. The measurements have been made every 4 to 6 hours since 1949, but large gaps exist in the data series, principally in the years 1949, 1950, and 1954, and shorter gaps exist in other years.

The highest winds occurred during winter months when the eggs were vulnerable to physical shock. Since the correlations for these months are not only nonsignificant, but are also positive (Figure 2D), it would seem that variations in wind-induced physical pounding during the egg stage did not cause variations in cohort strength from 1949-1962. The significant correlation in late spring and summer is probably related to the effect of upwelling.

Average wind during the time of settling also seemed to be associated with cohort strength. Barometric pressure during the time of settling was also associated with cohort strength, and both factors are connected because low pressure systems produce storms and, hence, high winds.

Indices of offshore divergence

Transport of surface water is affected not only by surface currents and Ekman transport, but also by differences in the rate of Ekman transport from place to place. If the upwelling rate is higher inshore than it is offshore, surface waters converge (Figure 3a). This sets up a front that tends to confine the water to one area. Conversely, if upwelling is higher offshore than it is onshore, then surface waters diverge, so that inshore water is

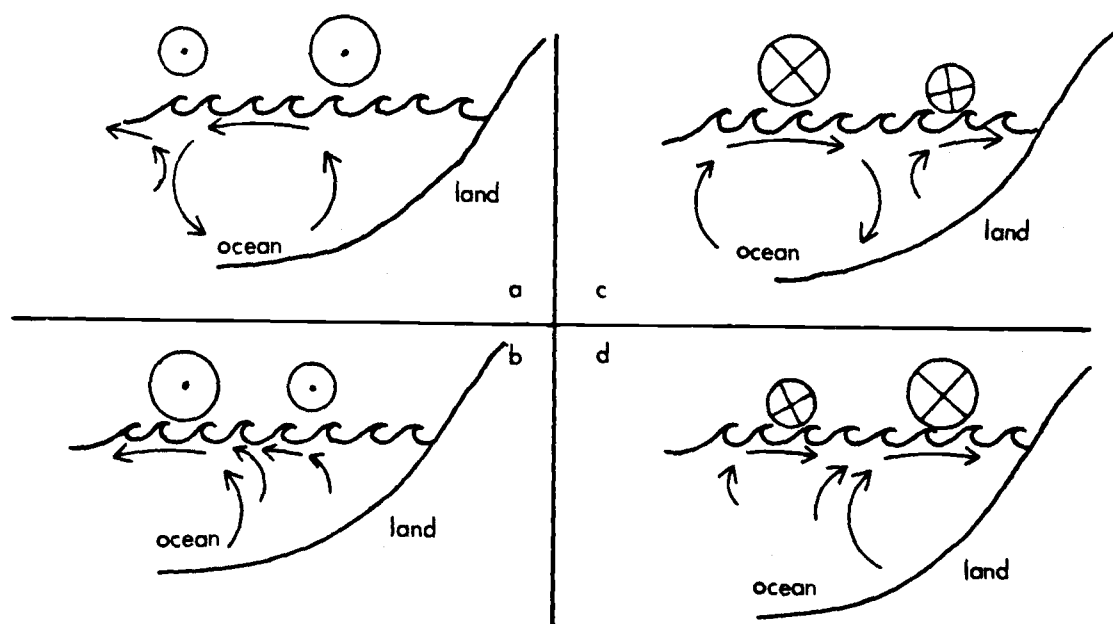


Figure 3. Schematic cross-section diagram of convergence (a and c) and divergence (b and d). Circles with dots inside represent wind coming out of paper. Circles with crosses inside represent wind going into page. Wind speed is proportional to diameter of circles, and arrows represent magnitude and direction of water transport.

continually carried farther offshore (Figure 3b). In winter, when southerly winds cause onshore transport, or "downwelling," the situation is reversed. In this case, higher downwelling offshore than inshore produces convergence, which confines offshore water to the offshore area (Figure 3c). Divergence results from higher downwelling inshore, and causes offshore water to be transported onshore (Figure 3d) (A. Bakun, Pacific Environmental Group, pers. comm.). The degree of divergence or convergence can affect the distribution of plankton, such as Dover sole eggs and larvae.

Bakun (1976) derived two very similar indices of offshore divergence: the offshore divergence index, which is the acceleration of surface transport at a point expressed as metric tons of water/km of coastline/sec²; and the calculated vertical velocity at which deeper water must rise to replace the surface water that had been displaced by divergence. A slightly different constant was used in calculating the vertical velocity index to account for latitudinal changes in the coriolis constant, but otherwise both indices measure nearly the same thing, and are highly correlated with each other. In this study I used the offshore divergence index calculated for 45° N 125° W and the vertical velocity calculated for 46° N 125° W.

For both indices, there is a highly significant correlation between cohort strength and convergence in December and January, just before and during settling (Figure 2E). The correlation is highest in January ($r=-.72$, $P<.001$ for the offshore divergence index; $r=-.73$, $P<.001$ for the vertical velocity). Convergence at this time could be important because Dover sole settle on a fairly narrow band on

the outer continental shelf, and any process which confines them to this area prior to settling might be beneficial. This correlation might be related to the average wind and barometric pressure correlations noted previously.

The Columbia River

The Columbia River discharge exerts a great direct influence on coastal waters, and is also an indirect index of other climatic factors such as storm frequency and precipitation. Records of discharge at the river mouth near Astoria, Oregon, have been kept since before 1940, so it is possible to correlate monthly discharge rates with Dover sole cohort strength measured both as age 8 abundance (Figure 2H) and as age 6 abundance (Figure 2F).

When expressed as age 8 abundance, the correlation between cohort strength and the combined April, May, and June discharge is highly significant ($r=-.68$, $P<.001$); however, when cohort strength is expressed as age 6 abundance the correlation with April-June discharge is nonsignificant ($r=-.34$). The apparent reason for this is that spring discharge in 1940, 1941, 1942, and 1944 was much lower than it was in any year between 1945 and 1962. Coincident with these low flows, the cohorts of 1940, 1941, and 1944 were larger as 8 year olds than any cohort through 1962. The age 6 index ignores these years and these cohorts. For both indices, the correlation between spring discharge and cohort strength for the years 1945-1962 is not significant. Therefore, it might be that extremely low flows were associated with strong cohorts but that more normal flows were

not related to cohort strength. This is somewhat surprising because river discharge is believed to enhance primary production (Conomos et al. 1972; Small and Curl 1972; Anderson 1972), which should benefit fish larvae, particularly following yolk sac absorption. If the relation indicated here was, in fact, causative, it may be that the river discharge did not have a direct effect, but rather it reflected earlier, more widespread, climatic conditions. Spring discharge is mainly derived from melting snow, which is deposited earlier in the winter. Thus, the low discharge in 1940-1944 means that the winter and spring were extremely mild and these mild conditions may have enhanced food production, or the decrease in violence may have increased egg survival. On the other hand, the success of the 1940, 1941, and 1944 cohorts may have been unrelated to Columbia discharge, and just happened to occur when discharge was low in spring. Unfortunately, most environmental data records do not go back to 1940, so it is not possible to investigate other environmental conditions that may have influenced the success of these cohorts. However, due to drought conditions, the Columbia discharge in 1976 and 1977 was also extremely low, and a test of this effect will be possible in a few years.

Cohort strength is also associated with Columbia discharge at the time of settling. The combined February, March, and April flows have correlations of $r = -.65$ ($P < .001$) with age 8 abundance and $r = -.52$ ($P < .05$) with age 6 abundance. Discharge at this time of year is influenced mainly by coastal storms, which are associated with low pressure systems and high average winds, two factors which also

have a significant correlation with cohort strength during the time of settling.

I also attempted to examine possible relations between cohort strength and the concentrations of certain constituents in Columbia River water. U.S. Geological Survey records back to 1951 give concentration (in parts per million) and load (in tons per day) of dissolved solids, silicate, and nitrate. Unfortunately for this study, these measurements were made near The Dalles, which is about 300 km upstream from the mouth, and is also upstream from two reservoirs and several major tributaries. Thus, water quality measurements made at this point may have had little relation to the water that actually reached the ocean. However, some significant correlations exist--for instance, the dissolved solid load during spawning is highly significant (for January, $r=-.79$, $P<.005$)--but this may only show that if enough factors are correlated, some are bound to be significant. It is possible that the chemical constituents of Columbia River water can affect Dover sole cohort strength, but adequate time-series measurements of these chemicals at the river mouth have not been made, and, except for sporadic research cruises, are not being made.

Solar radiation

Production blooms occur in the spring when the water column stabilizes and solar radiation increases (Riley 1942; Sverdrup 1953). Although there is some evidence that phytoplankton are capable of adapting to different levels of solar radiation, and that moderate

changes in solar radiation do not cause changes in production (Gilmartin 1964), it was still conceivable that variation in sunlight might affect production, and hence, cohort strength.

Monthly mean values of solar radiation (in Langleys) at the Clatsop County Airport, approximately 10 km southeast of the mouth of the Columbia, are available for the years 1953-1962 (Table 1). For no single month or combination of months is mean solar radiation significantly correlated to year class strength--in fact, some of the spring months, during which production blooms usually occur, are negatively correlated (Figure 2G). This does not prove that variation in solar radiation had no effect on variation in cohort strength, but it does indicate that for the years concerned, other factors were more important than solar radiation, measured some 10 km inland, acting alone.

Multiple Regression

Multiple regression shows how combinations of factors relate to variations in cohort strength, and which factors account for the most residual variation in the dependent variable--cohort strength. This information is unattainable with single correlations.

By analyzing the exploratory single correlations performed above, hypothetical relationships, and completeness of the data series, I chose 10 environmental factors as candidates for inclusion in a multiple regression model (Table 2). Since Ricker (1975, p. 274) pointed out that environmental factors probably act on a porportionate basis, rather than by adding or subtracting a fixed number to the

TABLE 2. ENVIRONMENTAL FACTORS USED IN MULTIPLE REGRESSION ON DOVER SOLE AND ENGLISH SOLE COHORT STRENGTH, t-VALUES OF THE MOST SIGNIFICANT REGRESSION COEFFICIENTS, AND CORRELATIONS BETWEEN EACH FACTOR AND THE FIRST THREE PRINCIPLE COMPONENTS.

| <u>Environmental Factor</u> | <u>Time Period</u> | <u>t-value of Regression Coefficient</u> | <u>Correlation with Principle Components</u> | | |
|--|--------------------|--|--|---------------|---------------|
| | | | <u>1st PC</u> | <u>2nd PC</u> | <u>3rd PC</u> |
| DOVER SOLE | | | | | |
| Upwelling | June of 1st yr | | .913 | .119 | -.071 |
| Offshore Divergence Index | Jan. of 2nd yr | | .112 | .857 | .221 |
| Columbia Discharge | Apr-June of 1st yr | | -.081 | .009 | .871 |
| Columbia Discharge | Feb-Apr of 2nd yr | | .780 | .156 | .054 |
| Northward Wind | June of 1st yr | 3.40 ** | -.941 | -.014 | .087 |
| Barometric Pressure at 46°N 125°W | Dec-Feb of 2nd yr | | -.769 | -.083 | -.218 |
| Barometric Pressure at Neah Bay, Washington | Mar-Oct of 1st yr | | .270 | .797 | -.354 |
| Sea Surface Temperature | Jan-Apr of 1st yr | 1.78 NS | -.133 | .031 | -.778 |
| Vertical Velocity into Ekman Layer | Jan of 2nd yr | -3.39 ** | .282 | .718 | .266 |
| Barometric Pressure at 46°N 125°W | Mar-Oct of 1st yr | | -.175 | .821 | -.287 |

TABLE 2. (Continued)

| <u>Environmental Factor</u> | <u>Time Period</u> | <u>t-value of Regression Coefficient</u> | <u>Correlation with Principle Components</u> | | |
|---|--------------------|--|--|---------------|---------------|
| | | | <u>1st PC</u> | <u>2nd PC</u> | <u>3rd PC</u> |
| ENGLISH SOLE | | | | | |
| Upwelling | Oct-Dec | -2.34 NS | .826 | .140 | -.077 |
| Upwelling | Jan-Mar | | .158 | -.887 | .176 |
| Vertical Velocity into Ekman Layer | May-July | | .369 | .686 | -.060 |
| Northward Wind | Sept-Oct | -2.05 NS | -.896 | -.088 | -.320 |
| Northward Ekman Transport | Jan-Mar | | .741 | -.239 | -.417 |
| Columbia Discharge | Feb-Mar | | .036 | .878 | .153 |
| Barometric Pressure | Sept-Oct | 5.07 ** | .110 | .040 | .941 |
| Average Wind Magnitude at Columbia Lightship | Apr-June | | -.392 | -.230 | .487 |

cohort strength for every unit change in a factor, the dependent variable used is the natural logarithm of cohort strength, measured as thousands of age 6 females.

In the stepwise regression, the first variable that entered the model was the vertical velocity into the Ekman layer in January at the time of settling:

$$\ln(R) = 8.17 - (6.69 \times 10^{-4}) X_1 \quad F = 10.11^{**} \quad \text{d.f.} = 1,15$$

where $\ln(R)$ is the natural logarithm of cohort strength, and X_1 is vertical velocity in cm/sec. This factor accounts for 40.3 percent of the observed variation in \ln (cohort strength). With the variability due to this measure of divergence removed, the factor that best accounts for the remaining variability is southerly wind speed in June:

$$\ln(R) = 8.33 - 5.60 \times 10^{-4} X_1 + 6.56 \times 10^{-3} X_2 \quad (1)$$

$$\text{Entering } F \text{ value} = 9.69^{**} \quad \text{d.f.} = 1,14$$

where X_2 is southerly wind speed in dm/sec. These two factors account for 64.7 percent of the observed variation. The next parameter that enters is sea surface temperature the first winter:

$$\ln(R) = 7.68 - 5.40 \times 10^{-4} X_1 + 6.66 \times 10^{-3} X_2 + 1.68 \times 10^{-2} X_3$$

$$\text{Entering } F \text{ value} = 3.18 \quad \text{d.f.} = 1,13$$

Where X_3 is temperature in $^{\circ}\text{C}$. These three factors account for 71.6 percent of the observed variation. However, the coefficient of X_3 ,

and of all variables that subsequently entered the model, is not significantly different from zero. This means that temperature the first winter may well have no relation to cohort strength, once the variability due to vertical velocity and southerly wind is accounted for. The backstep procedure yielded identical results: the last two variables remaining were vertical velocity and southerly wind. The coefficients of both of these variables are significantly different from zero (Table 2), indicating that there has been a relationship between changes in these factors and changes in cohort strength from 1946 to 1962. Equation (1) which describes this relation, has been a reasonably good predictor of cohort strength from 1946-1962, although the predictions are off for 1949 and 1960 (Figure 4). Because of the log transformation of cohort strength, for given values of vertical velocity and southerly wind, equation (1) estimates the geometric mean of the expected distribution of cohort strengths, which is lower than the arithmetic mean value (Ricker 1975, p. 274).

Principal Components

Cushing (1973, p. 144) pointed out that few models that explained cohort strength on the basis of one or two environmental factors, such as equation (1), ever continued to predict future cohort strengths with any accuracy. This might happen because the effect of a factor, such as Columbia discharge during hatching, may have been obscured by the effects of vertical velocity and southerly wind, but it still may have some influence on cohort strength, and in years

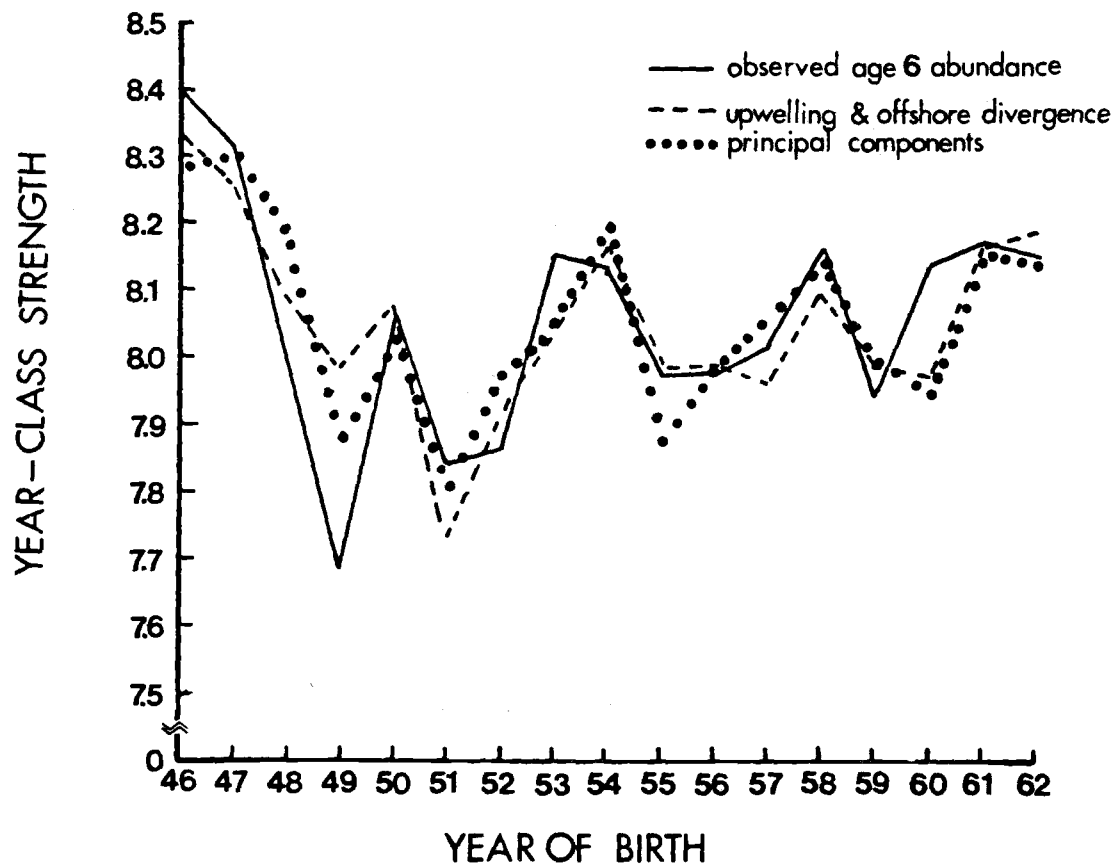


Figure 4. Comparison between natural logarithms of observed Dover sole cohort (year-class) strength, cohort strength as predicted from an upwelling and offshore divergence model (equation (1)), and cohort strength as predicted from a principle components model (equation (2)).

of abnormally low or high Columbia flow, that influence could be major. In such a year, a predictive model that does not account for Columbia discharge during hatching, such as equation (1), would give a poor estimate of recruitment. It may not be wise, however, to include this factor in the model, because there is a limit to the number of variables that can be included in a valid model.

One of the few models that has continued to predict recruitment is a correlation between Arcto-Norwegian cod recruitment and the width of pine tree rings near the spawning grounds (Cushing 1973, p. 145). In this case, the "environmental factor" (width of tree rings) is itself a combination of many environmental factors. In much the same way as the width of a pine tree ring represents a combination of many environmental factors, a principal component (Cooley and Lohnes 1971) can also represent a combination of many environmental factors.

A principal component is a variable constructed from a set of correlated independent variables such that the correlation between each principle component is zero and the variance in each is a maximum. If the independent variables are thought of as coordinate axes, and each data point is plotted on these axes, the first principle component would be a coordinate axis oriented to run through the longest axis of the data points and each subsequent principal component would be perpendicular to the first, and oriented to run through the next longest axis of the data points. For our purposes, a principal component can be thought of as a soup, into which different proportions of each environmental factor are mixed. The

proportion of each environmental factor in that soup can be found by correlating the factor with the principal component.

In a principal components analysis of the ten environmental factors listed in Table 2, the first three principal components accounted for 75 percent of the variation in these environmental factors. By disregarding the other seven principal components, the variability in ten factors was boiled down to only three variables. In the soup of the first principal component, correlations with the environmental factors (Table 2) show that its main ingredients are June upwelling, southerly wind in June, and Columbia flow and barometric pressure during settling. These environmental factors are therefore correlated with each other, but this need not mean, for instance, that high upwelling in June caused high Columbia River discharge the next February, March, and April. It does indicate some association, but analysis of the meteorological factors that may have caused this association is beyond the scope of this paper.

The main ingredients of the second principal component are vertical velocity and offshore divergence during settling, and barometric pressure at Neah Bay and 46° N 125° W the first summer. The third principal component is composed mainly of Columbia flow and sea temperature during hatching. In a multiple regression in which the natural log of cohort strength is the dependent variable and these three principal components are the independent variables, the first variable that enters the model is the first principal component, the one associated mainly with June upwelling and river flow or barometric pressure the next winter:

$$\ln(R) = 8.06 - (1.06 \times 10^{-1}) (PC1) \quad F = 9.42 ** \quad d.f. = 1,15$$

where PC1 is the first principal component. This model accounts for 38.6 percent of the variability in cohort strength. The second principal component enters next:

$$\ln(R) = 8.06 - (1.06 \times 10^{-1}) (PC1) - (8.91 \times 10^{-2}) (PC2) \quad (2)$$

$$\text{Entering } F \text{ value} = 11.22 ** \quad d.f. = 1,14$$

where PC2 is the second principal component. This model accounts for 65.9 percent of the variability in cohort strength. When the third principal component enters, its coefficient is not significantly different from zero, so that equation (2) best describes the relationship between the natural log of cohort strength and the principal components.

Equation (2) verifies what was shown in the multiple regression section above--that divergence at time of settling and wind speed at time of hatching/yolk sac absorption are major factors associated with resultant cohort strength. These two factors are not well correlated with each other, but act fairly independently. In addition, this analysis shows that factors such as river flow at the time of hatching are weakly associated with cohort strength for the time period considered.

The beauty of the principal components analysis, however, is that all 10 environmental factors contribute in some way to the prediction of cohort strength in model equation (2). No factor, not

even river flow during settling, is ignored, as it is in the multiple regression equation (1). Since it is likely that all these factors, as well as others not included, do affect cohort strength in varying degrees, equation (2) is probably a more realistic model than equation (1).

Cohort strength is also predicted reasonably well by equation (2) (Figure 4). By accounting for sea temperature, equation (2) predicts 1949 cohort strength more accurately than equation (1). Both models, however, are off in 1960.

The Effect of Spawning Power

Calculation of spawning power

All of the preceding analyses have ignored any possible effect parent stock size may have had on cohort strength. I now turn to the possibility that cohort strength may be related to the size of the spawning population.

Fecundity of Dover sole larger than 44 cm is a linear function of length (Harry 1959; Hagerman 1952), so that two populations with the same number of mature females may not produce the same number of eggs, if their length distributions differ. For this reason, egg production, rather than population size or biomass was used as the spawning power index (SPI).

Egg production for a group is the product of the number of females in the group, the proportion that are mature, and the average fecundity of each female. For Dover sole the data on fecundity and percentage maturity are given by length rather than by age (Harry

1959; Hagerman 1952). An age-length key could convert fecundity and percentage maturity by length to fecundity and percentage maturity by age, which would be easier quantities to work with, only if length at age did not change from year to year.

To test whether length at age varied by year, I analyzed the original age-length data from different years (Demory and Fredd 1966). In the first test, I compared the lengths of age 10 females in 1954 and 1960. In 1954 the average length of an age 10 female was 45.8 cm. In 1960 the average length was 41.8 cm. An analysis of variance shows that these two mean lengths are significantly different ($F=30.6$, $P<<.01$, $d.f.=1,95$). Thus, on the first trial it was shown that length at age is not necessarily constant from year to year. For this reason, I decided to calculate spawning power by length groups rather than by converting length to age and calculating by age groups.

To estimate the number of females in each length group, I multiplied the total number of mature females by the proportion of females in each length group. To determine the proportion of females in each length group, I divided the length-frequency in the landed catch (Demory 1966) by the mesh selection rate and the catch utilization rate, and then rescaled these to percentages. The mesh selection rates (percentage of each length group retained by the most commonly used net, a 4.7 inch single cod-end trawl) were obtained from ogives drawn by Best (1961). Catch utilization rates (percentage of each length group retained by the fishermen after being netted) were

determined by TenEyck and Demory (1975) and by methods described in Appendix I.

The total number of mature females in the population was derived from the numbers at age (Appendix V) that were calculated in Appendix I by cohort analysis (Pope 1972). I determined the mature female population as half of the age 7 females, plus all of the older females. Although some age 5 and 6 fish may have been mature, some age 8 and older fish may not have been, so this should have been a reasonable estimate.

The total egg production for each length group is the product of the number of females in that length group, the average fecundity for that length, and the proportion mature at that length. Summing for all length groups gives the SPI for that year. Figure 5 shows that the trend in spawning biomass (calculated in Appendix I) parallels that of SPI. Both were high in the early 1950s, but as the fishery developed and the number of older fish declined, so did the SPI and spawning biomass. They seem to have stabilized since 1964.

Relation between spawning power and cohort strength

I plotted cohort strength on spawning power, measured both as female biomass and egg production (Figure 6). The relation between cohort strength and female biomass is very nearly horizontal ($r = -.066$) and is not significantly different from zero. The relation between cohort strength and egg production, which should be a more precise index of spawning power, has a more pronounced negative slope ($r = -.371$) but is also not significantly different from zero. There

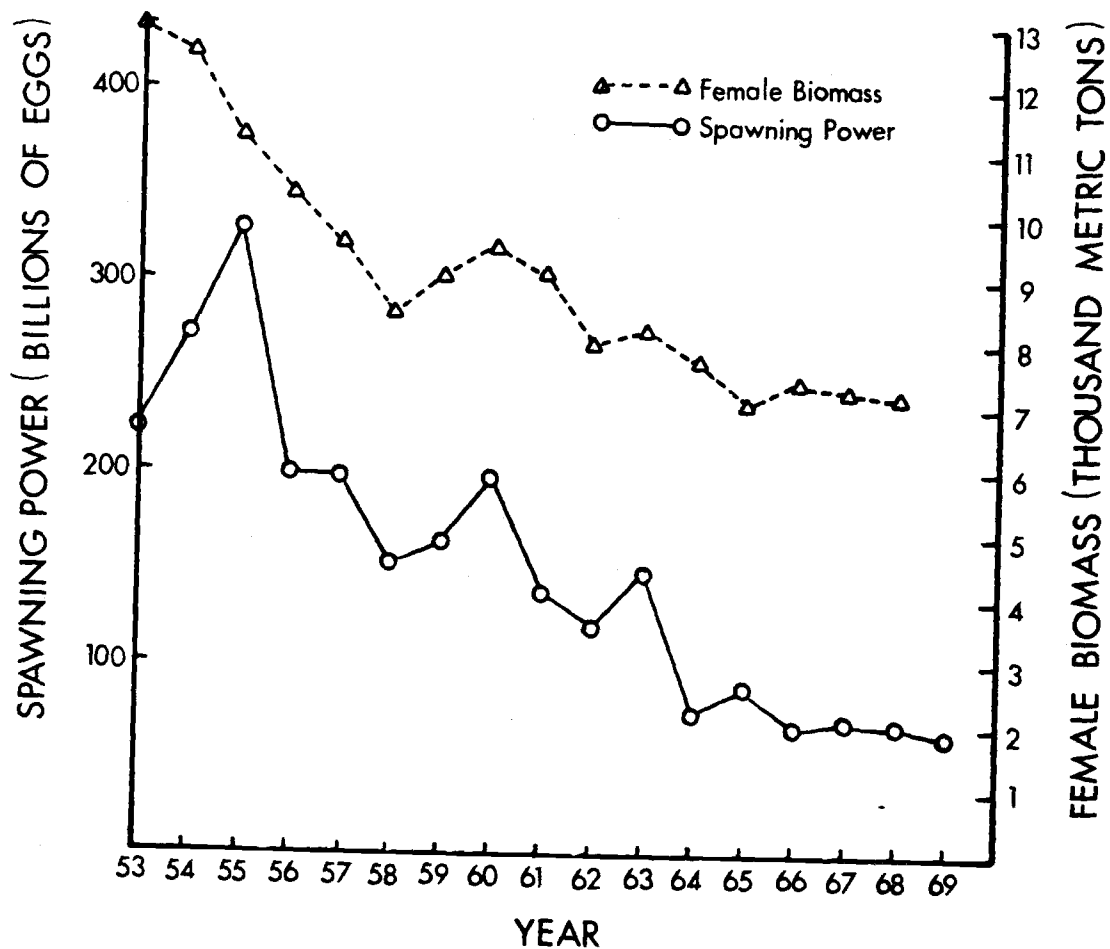


Figure 5. Dover sole spawning power in billions of eggs, and female biomass from 1953-1969.

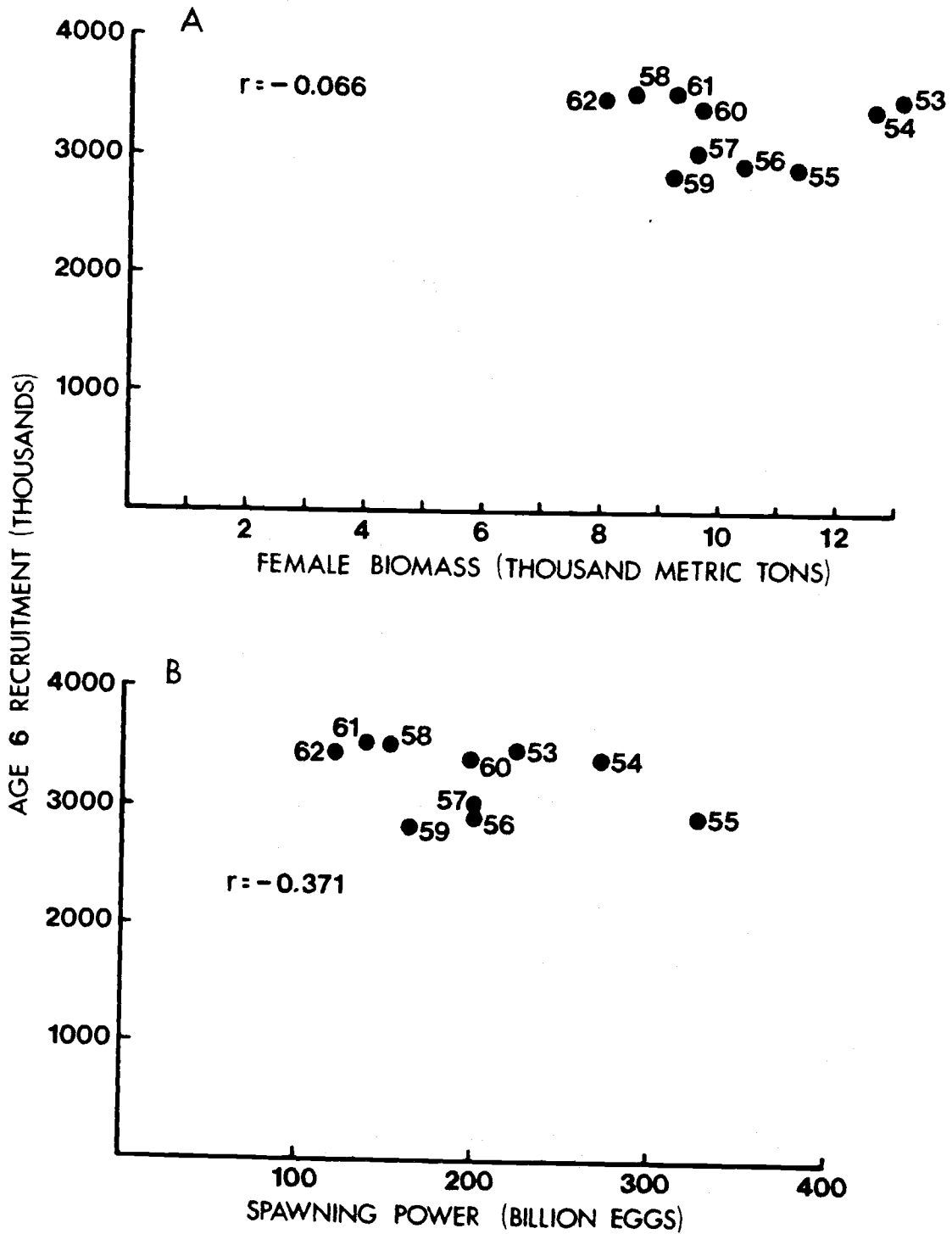


Figure 6. Spawner-recruit relations for Dover sole from 1953-1962. Top: Relation between female biomass and resultant cohort strength. Bottom: Relation between egg production and resultant cohort strength.

is also nothing in Figure 6 that ^{year 55} suggests a curvilinear relation or a Ricker-type recruitment curve. Thus, it seems that from 1953 to 1962 there was not a significant relation between cohort strength and spawning power. Since recruitment was remarkably stable during those years, perhaps a relationship might have been visible if the more variable recruitment of the 1940s is included in Figure 6. Spawning power, however, could not be calculated for those years. Spawning power declined after 1962, and cohort strength has not been calculated for these later years, but landing statistics give no evidence of any failure or great increase in cohort strength.

It is possible that a relationship between SPI and cohort strength did exist, but that effects of the environment obscured it. To test this, I used multiple regression to account for the variability due to environmental fluctuations, and tested whether SPI (as egg production) accounted for a significant amount of the remaining variation in cohort strength.

With SPI already in the model, I used the variables in Table 2 as the other independent variables in a stepwise regression. The first variable that entered the model was vertical velocity in January at the time of settling:

$$\ln(R) = 8.19 - 1.89 \times 10^{-13} (\text{SPI}) - 3.78 \times 10^{-4} X_1$$

$$F \text{ value for SPI} = 0.217 \quad \text{d.f.} = 1,7$$

where SPI is egg production and X_1 is vertical velocity in cm/sec.

However, in this model the coefficient of SPI is not significantly different from zero. The next variable to enter was June southerly wind:

$$\ln(R) = 8.26 - 1.22 \times 10^{-13} (\text{SPI}) - 4.63 \times 10^{-4} X_1 \\ + 2.77 \times 10^{-3} X_2$$

$$F \text{ value for SPI} = 0.097 \quad \text{d.f.} = 1,6$$

where X_2 is southerly wind in dm/sec.

Again, in this model, the coefficient of SPI is not significantly different from zero. In fact, no matter which environmental terms were included in the model, SPI did not explain a significant amount of the remaining variability.

Multiple regression with the principal components yielded similar results as with the other independent variables. Even when the variability due to the first two principal components is accounted for, SPI still does not account for a significant portion of the remainder. Thus, it seems that even with environmental effects accounted for, the range of SPI present from 1953 to 1962 was still not related to cohort strength, and equations (1) and (2) do not have to be modified to account for SPI.

V. ENGLISH SOLE

The cohort strength index for English sole was age 4 female abundance (Appendix VI). A striking feature is the great success of the 1961 cohort, a year which also produced large cohorts of Pacific hake (Merluccius productus) (Dark 1975) and Pacific Ocean perch (Sebastes alutus) (Gunderson et al. 1977). My estimates of cohort strength of Dover sole and English sole overlap from 1955-1962. During those eight years, their strengths were not significantly correlated ($r=+.378$), so it is possible that the mechanisms that affected English sole cohort strength differed from those that determined Dover sole cohort strength.

Single Correlations Between Environmental Factors and Cohort Strength

Critical periods

English sole may begin spawning in the fall preceding the year of the cohort in water less than 100 m deep; however, peak spawning has occurred as late as the next March (Pearcy and Richardson 1977; Laroche and Richardson MS). The larvae metamorphose and settle in shallow water about 5 months after spawning, so critical periods could occur from the September preceding the cohort year until August of the cohort year. However, biological events would not occur in the same months for each cohort.

Because the 1961 cohort was so much larger than the others, any environmental factor that had an extreme value between September 1960

and August 1961 would be significantly correlated to cohort strength, whether there is any true relation or not. Therefore, I also examined the relationship between those factors outstanding in 1961 and the strengths of all cohorts except 1961. If the relationship with the remaining 11 cohorts is not significant, then the effect of that factor should be viewed with extreme suspicion.

Sea surface temperature

For the eastern (inshore) zone, correlations between English sole cohort strength and temperatures are generally positive for winter months and negative for summer months, but only in the fall are they significant (Figure 7A). There is a weakly significant relation in October when the 1961 cohort is included. This relation is just nonsignificant ($r=-.651$) when the 1961 cohort was excluded. Combined September and October temperatures correlate significantly with cohort strength both with ($r=-.66$, $P<.05$) and without ($r=-.67$, $P<.05$) including the 1961 cohort. This relation may be linked to upwelling, since upwelling reduces surface temperatures.

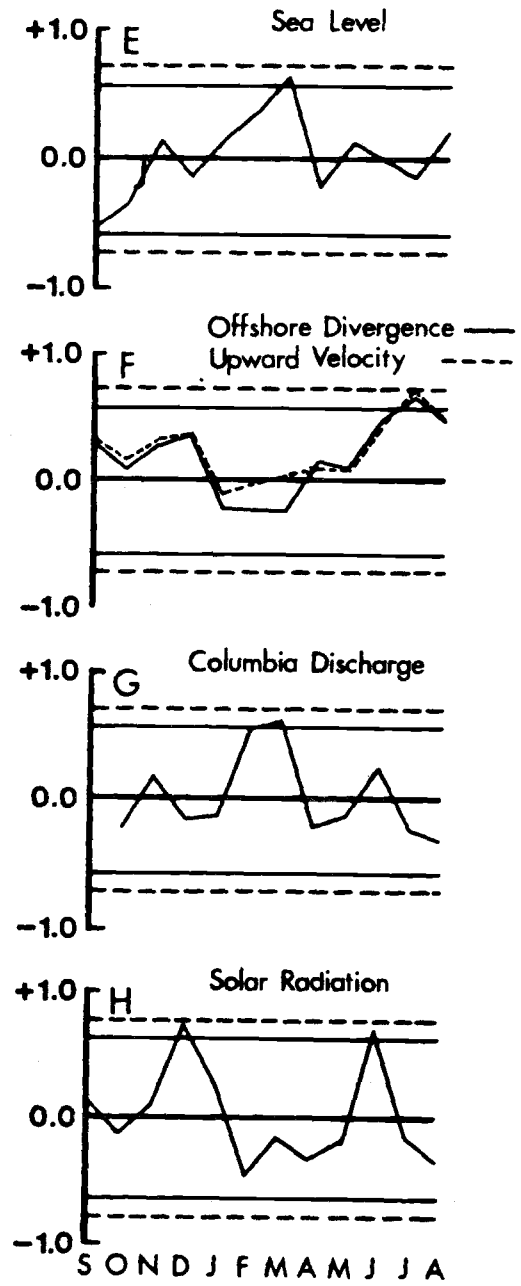
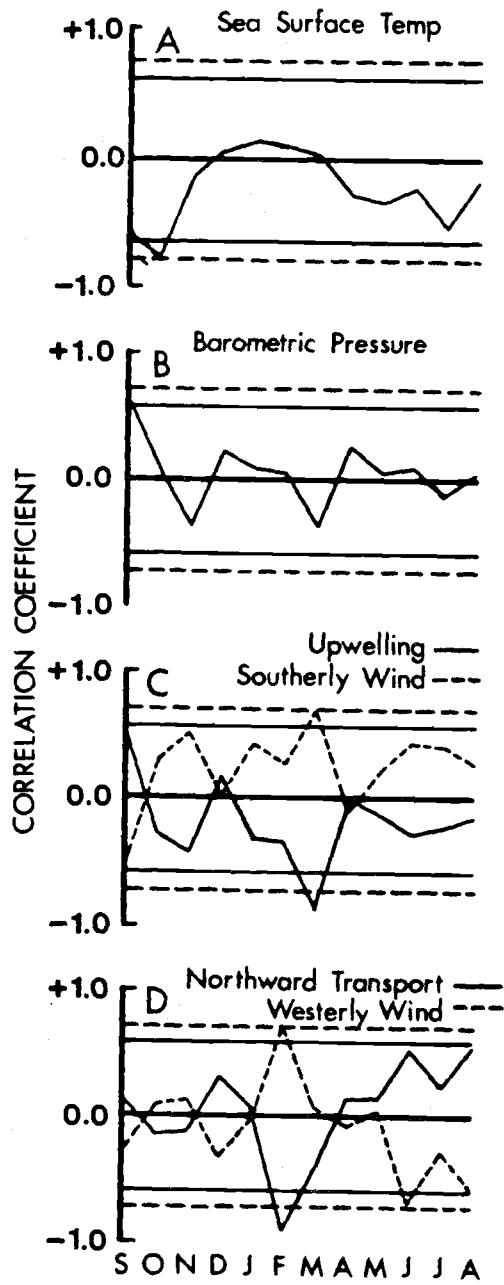
Temperatures in the western zone do not suggest a relationship with cohort strength. In neither zone is there suggestion of a hump-shaped relation. Because some data have been lost, each correlation represents a maximum of 10 data points.

Barometric pressure

For English sole, I correlated cohort strength with the mean barometric pressure calculated at 46° N 124° W, about 15 km due South of the mouth of the Columbia River (Figure 7B). Pressure in

Figure 7. Correlations between English sole cohort strength and environmental conditions measured each month from spawning through settling of a cohort. Solid horizontal lines represent 95 percent significance level of correlation coefficients, and dashed horizontal lines represent 99 percent significance level.

- A. Between cohort strength and sea surface temperature in the eastern (inshore) zone.
- B. Between cohort strength and barometric pressure at 46° N 124° W.
- C. Between cohort strength and upwelling at 45° N 125° W, and southerly wind speed at 46° N 124° W.
- D. Between cohort strength and northward Ekman Transport, and westerly wind speed at 46° N 124° W.
- E. Between cohort strength and sea level at Neah Bay, Washington.
- F. Between cohort strength and upward velocity into the Ekman Layer at 46° N 124° W, and offshore divergence at 45° N 125° W.
- G. Between cohort strength and Columbia River discharge at Astoria, Oregon.
- H. Between cohort strength and solar radiation at Clatsop County Airport, near Astoria.



September, which was either before or during the early part of spawning, is significantly correlated with cohort strength when the 1961 cohort is included ($r=+.650$, $P<.05$). Pressure was relatively high in September 1960 (1018.5 mb), but it was only slightly lower in September 1964, and the 1965 cohort was much smaller than the 1961 cohort. Thus, it would seem that the high barometric pressure in September 1960 cannot explain the success of the 1961 cohort by itself.

When the 1961 cohort is excluded from consideration, the strengths of the other 11 cohorts are highly significantly correlated with both September pressure ($r=+.847$, $P<.001$), and with combined September and October pressure ($r=+.90$, $P<.001$). The significance levels are very high, indicating that some kind of association between early fall pressure and the strength of those 11 cohorts is very likely. This association may not have been directly caused by barometric pressure, but rather it may have been linked to other environmental factors. There is a strong correlation between barometric pressure and sea surface temperature in September and October ($r=-.81$). These factors in turn may be related to upwelling and wind speed, because high pressure causes the northerly winds that induce upwelling.

Indices of east-west transport

Since the nursery for English sole juveniles is in shallow water, I hypothesized that onshore transport (downwelling) during time of settling may have benefitted cohort strength. Downwelling

in March 1961 was abnormally high, the 1961 cohort was unusually strong, and cohort strength is highly significantly correlated with the March values of both offshore transport at 45° N 125° W ($r=-.843$, $P<.001$) and mean southerly wind velocity at 46° N 124° W ($r=+.691$, $P<.01$) (Figure 7C). However, with 1961 data excluded, the correlations between these two factors and the 11 remaining cohorts are nonsignificant ($r=-.358$ for upwelling, and $r=+.210$ for southerly wind). Since these nonsignificant correlations indicate that east-west transport in March had no effect on the strength of these 11 cohorts, it is quite possible that the extreme downwelling in March 1961 also had no real effect on the 1961 cohort and merely happened to coincide with it.

With the 1961 cohort excluded, there is a significant correlation between cohort strength and east-west transport in September ($r=+.851$, $P<.001$ for upwelling, and $r=-.840$, $P<.01$ for southerly wind). Further analysis shows that southerly wind velocity in September is highly correlated with sea temperature ($r=+.72$) and with barometric pressure ($r=-.80$). Both September temperature and pressure are correlated to cohort strength, so there seems to be a link between these factors.

Indices of north-south transport

Tagging studies on English sole off the Columbia show that most fish stay in one area throughout their lives, but a small percentage of females undertake long north-south migrations (Barss 1976). Such migrations are an important part of spawning behavior of English sole

off British Columbia (Ketchen 1956), and therefore variation in north-south water movement may affect spawner success. Correlations between cohort strength and two indices of north-south transport--northward Ekman transport, and westerly wind speed--are high for February and June (Figure 7D). In 1961, north-south transport was abnormal in both months. However, with 1961 data excluded, the correlations between the strengths of the other 11 cohorts and north-south transport indices are all nonsignificant ($r=-.503$ for northward Ekman transport in February; $r=+.401$ for westerly wind speed in February; $r=+.268$ for northward Ekman transport in June; $r=-.305$ for westerly wind speed in June). Since this indicates that north-south transport had no significant effect on the strength of 11 cohorts, it is also possible that it had no real effect on the 1961 cohort, but merely coincided with it.

I got similar results from the correlations between sea level at Neah Bay and cohort strength. The correlation for March is significant (Figure 7E), and sea level was abnormally high in March 1961 as a result of high downwelling. With 1961 data excluded, however, sea level seems to have had no relation to the strengths of the other 11 cohorts ($r=-.028$), and this casts suspicion on any proposed connection between sea level and cohort strength in 1961.

Average wind magnitude

Correlations between cohort strength and monthly averages of winds measured at the Columbia River Lightship are not significant for any month or combination of months.

Indices of offshore divergence

In contrast to Dover sole, for which divergence seems to be important in determining cohort strength, there is little relation between English sole cohort strength and divergence indices (Figure 7F). There are significant correlations for July, but again, these correlations are nonsignificant with 1961 data excluded ($r=+.014$ for offshore divergence and $r=-.054$ for vertical velocity). Since the high divergence in July 1961 should have occurred after the bulk of settling was complete, it is unlikely that this divergence can explain the success of the 1961 cohort.

The Columbia River

Columbia River discharge in March is significantly correlated with cohort strength (Figure 7G). Again, however, with 1961 data excluded, March discharge had no significant effect on the 11 remaining cohorts ($r=+.036$). This casts suspicion on any proposal that the high flow in March 1961, or the abnormally stormy conditions which caused this high flow, were connected to the success of the 1961 cohort.

Concentrations of dissolved solids, silicate, and nitrate at The Dalles are not well correlated with cohort strength. This is not surprising, since these measurements may not even be related to the concentrations of these materials at the River's mouth.

Solar radiation

Cohort strength is significantly correlated with the solar radiation measured at Clatsop County Airport in December and June (Figure 7H). With the 1961 data excluded, however, these correlations are not significant ($r=+.027$ for December and $r=+.319$ for June).

Solar radiation was high in December 1960 and in June 1961, but it is doubtful whether the December value had much effect on the 1961 cohort's success, because this value (103 Langleys) could not have been high enough to affect production much. The June value (583 Langleys) may not explain the 1961 success itself, because slightly lower radiation values in other years did not produce comparable cohort successes.

Multiple Regression

The exploratory single correlations indicate that the factors that were abnormal in 1961 are not related to the strength of the other 11 cohorts, while the factors that are related to the strength of the other 11 cohorts were not extremely abnormal in 1961. Thus, it seems that the success of the 1961 cohort may have been determined by mechanisms different from those that regulated cohort strength in other years. Because including the high 1961 value in a multiple regression would obscure any relations between the environment and the strengths of other cohorts, I decided to exclude 1961 data from the multiple regressions. The eight environmental factors considered for multiple regression (Table 2) are those with

significant correlations with cohort strength, as well as those that reflected overall climatic conditions during several possible critical periods.

The first variable that entered the model was barometric pressure from September and October:

$$\ln(R) = 5.60 + (7.12 \times 10^{-3}) X_1 \quad (3)$$

Entering $F = 46.7$ ** d.f. = 1,9

where X_1 was combined pressures in (millibars $\times 10$) - 10,000.

This model accounts for 83.8 percent of the variability in cohort strength. No other variables reduce the cohort variability significantly, once the variation due to September-October pressure is accounted for, so only this one variable is significant in this "multiple" regression. Cohort strength as predicted by equation (3) is reasonably close to observed values for most years (Figure 8). However, it does not seem likely that barometric pressure alone can explain cohort variations. Associations between barometric pressure and the other factors considered in the multiple regression can be examined through principal components analysis.

Principal Components

I retained the first three principal components, which account for 74.9 percent of the environmental variation. The first principal component is composed primarily of upwelling from October to December, southerly wind in September and October, and northward Ekman transport

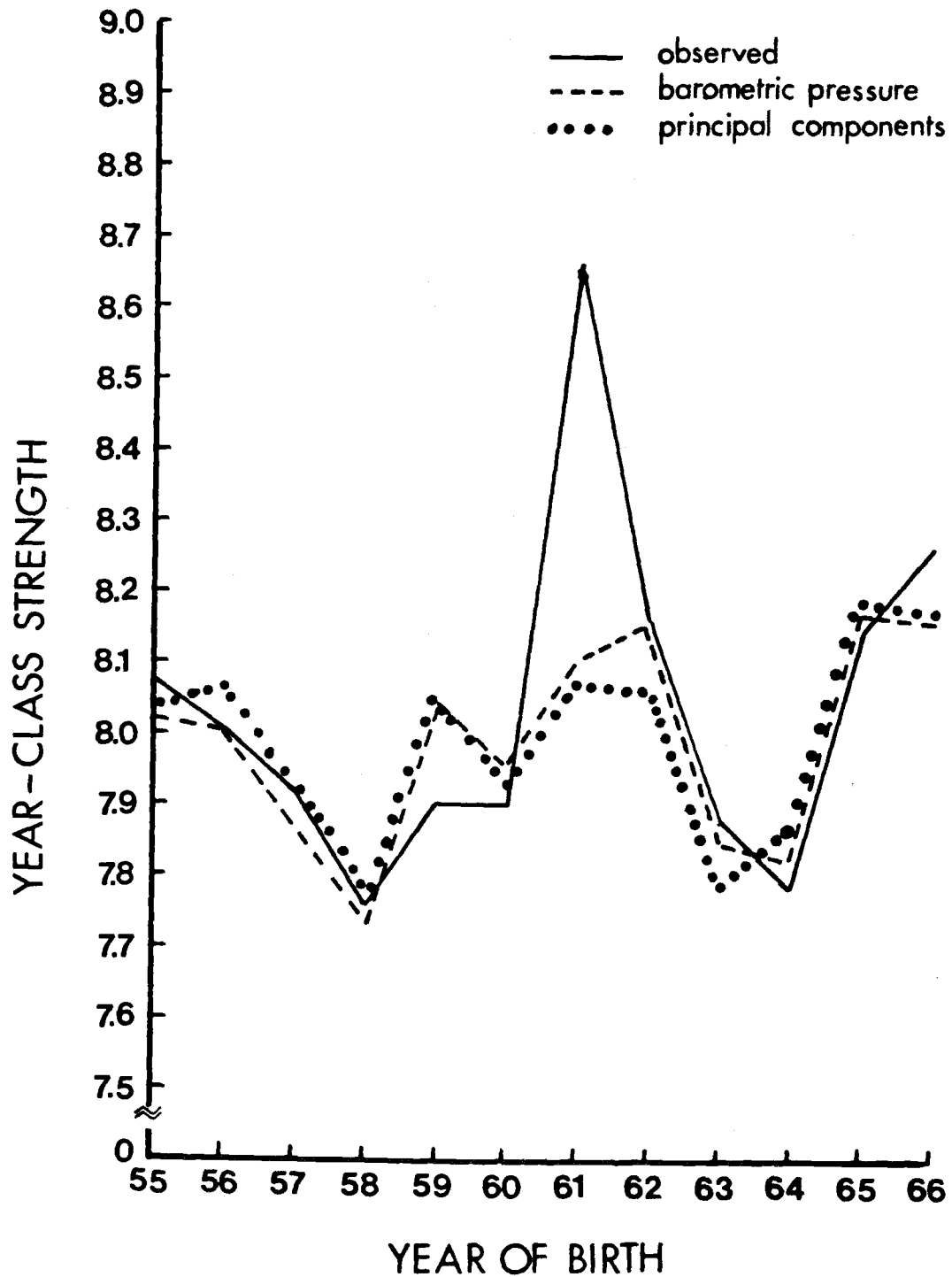


Figure 8. Comparison between natural logarithms of observed English sole cohort (year-class) strength, cohort strength as predicted from barometric pressure model (equation (3)), and cohort strength as predicted from principal components model (equation (4)).

from January to March. Upwelling from January to March, vertical velocity from May to July, and Columbia discharge in February and March are most closely associated with the second principal component, while barometric pressure in September and October is most closely related to the third (Table 2). In spite of the high correlation between pressure and southerly wind in September ($r=-.80$), differences in October cause these two factors to be related best to different principal components.

With the 1961 cohort excluded from consideration, the third principal component was the first variable that entered a multiple regression of cohort strength on principal components:

$$\ln(R) = 7.99 + (1.33 \times 10^{-1}) (PC3) \quad (4)$$

$$\text{Entering } F = 29.9 \quad ** \quad \text{d.f.} = 1,9$$

where PC3 is the third principal component.

This model accounts for 76.9 percent of the variability in cohort strength. Neither of the other principal components significantly reduce residual variability, so this model also includes only one variable. The model is a good predictor of cohort strength (Figure 8) and also it confirms the relation between cohort strength and September-October pressure that was shown by equation (3). It also acknowledges lesser effects of other factors such as average wind from April to June and northward Ekman transport from January to March. Since it is impossible to include more environmental factors in a principal component than there are data points, I would

need a longer data series before more environmental factors can be considered in the principal components. With more environmental factors included, a clearer picture of interactions between the environment and cohort strength can be obtained.

Spawning Power

Spawning power and resultant recruitment can only be calculated for three cohorts. This is not enough to permit analysis of possible effects of spawning power on cohort strength.

VI. THE EFFECT OF VARIABILITY

All of the environmental parameters analyzed to this point have been monthly averages. Cushing (1974) pointed out the importance of environmental variability on production, and concluded that short-term periods of variable weather were more productive than periods of unchanging conditions. To examine this possibility, I developed several indices which, I felt, reflect the degree of short-term change in the weather, and I correlated these indices with Dover and English sole cohort strength.

Changes in Wind Direction

Wroblewski (1976) and Cushing (1974) have indicated that slow, intermittent upwelling, a product of variable winds, is more productive than fast, continuous upwelling. I have shown that low winds in June were associated with strong Dover sole cohorts (Figure 2C). If months with low average winds were also months with more variable winds, then it might have been that wind variability, rather than average wind speed, was the factor most closely connected with cohort strength. To test this, I counted the number of times the wind direction changed from southerly to northerly in each 2 week period during the upwelling season, from April through August, and correlated this index of wind variability with cohort strength.

Dover sole cohort strength is not significantly correlated with the number of wind direction shifts during any time period. English sole cohort strength is significantly correlated to the number of

wind direction shifts from April 14-27 ($r=+.768$, $p<.01$) and from June 23-July 6 ($r=+.757$, $p<.01$); however, with 1961 excluded, the correlations between number of wind direction shifts and strength of the 11 remaining cohorts are not significant ($r=+.009$ for April 14-27 and $r=+.280$ for June 23-July 6). It is therefore quite possible that the number of wind direction shifts had no effect on cohort strength for either flatfish.

Possibly, the number of wind direction changes is poorly correlated with cohort strength because it is not an adequate measure of wind variability. It occurred to me that high winds that changed direction frequently exhibit more variability than do low winds that also change direction frequently. In that case perhaps a better index of wind variability would include average wind speed in a multiple regression of the form:

$$\ln(R) = b_0 + b_1 (\# \text{ wind shifts}) + b_2 (\text{average wind speed})$$

In the Dover sole model both regression coefficients for April 14-27 values are significantly different from zero:

$$\begin{aligned} \ln(R) = & 8.47 - (2.21 \times 10^{-2})(\# \text{ wind shifts}) \\ & - (2.99 \times 10^{-2})(\text{Avg wind speed}) \end{aligned} \quad (5)$$

If equation (5) illustrates a true causative relation, the signs of the regression coefficients imply that Dover sole benefit from low winds and low numbers of wind direction changes--in other words, a stable, less variable environment. I question the validity of

equation (5), however, because the April 14-27 model is the only one for which both coefficients are anywhere near significant. For a fish with a spawning periods as protracted as Dover sole, one would have expected a significant relation to overlap into adjacent 2 week periods.

For English sole, there is no 2 week period for which both coefficients in this measure of wind variability are significantly different from zero.

Storm Frequency

Storms might influence cohort strength negatively by physically damaging eggs and larvae, or positively by mixing nutrients into the photic zone, thereby enhancing production when calm returns (Smayda 1957; Gilmartin 1964). To test the effect of this factor, I correlated the number of times the wind speed rose above 24 knots each month with cohort strengths of Dover and English sole.

For Dover sole the correlations are generally positive the first winter and negative in summer, but none is significant. For English sole, February storm frequency is significantly correlated with cohort strength ($r=+.793$, $p<.01$); however, this is because of abnormally high storm frequency in February 1961. With 1961 excluded, the correlation is nearly zero ($r=-.060$), and this makes it less likely that storm frequency has much effect on cohort strength.

I calculated the maximum storm duration in each month, an index of violence, as the number of consecutive hours during which wind measurements remained greater than 24 knots. This index is also

poorly related to cohort strength for both Dover and English sole. This may be because the range of values did not vary much between years, generally on the order of only 1-1/2 to 2 days for each month.

Variability Expressed as Combinations of Variables

Rather than assuming that influences on cohort strength exerted during one time period are independent of influences exerted during other time periods, I considered the possibility that the influence of conditions in certain months is modified by conditions in succeeding months. For instance, high winter storm frequency may bring nutrients into the photic zone, but increased production and enhanced cohort strength may result from this only if the stormy winter is followed by a calm spring.

I tested this hypothesis by using average winter (January-March) wind speed and average spring (April-June or May-July) wind speeds as separate independent variables in a multiple regression on cohort strength. For neither Dover nor English sole, are any of the regression coefficients significant, which indicates that variation between average winter and spring wind speeds does not significantly affect cohort strength for either flatfish.

Reasoning that perhaps storm frequency is better related to nutrient mixing and spring production than is average wind speed, I repeated this multiple regression, but used winter and spring storm frequencies as the independent variables. The result, however, is similar to the average wind speed regressions: for neither fish does the multiple regression explain significant variability in cohort

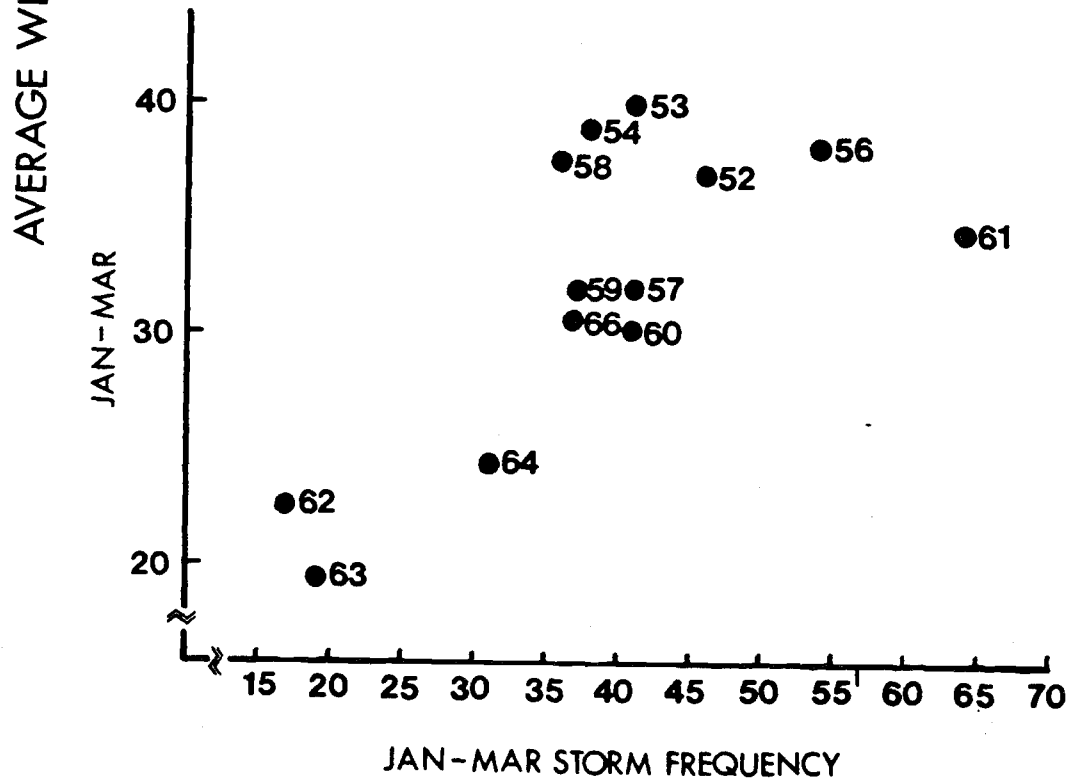
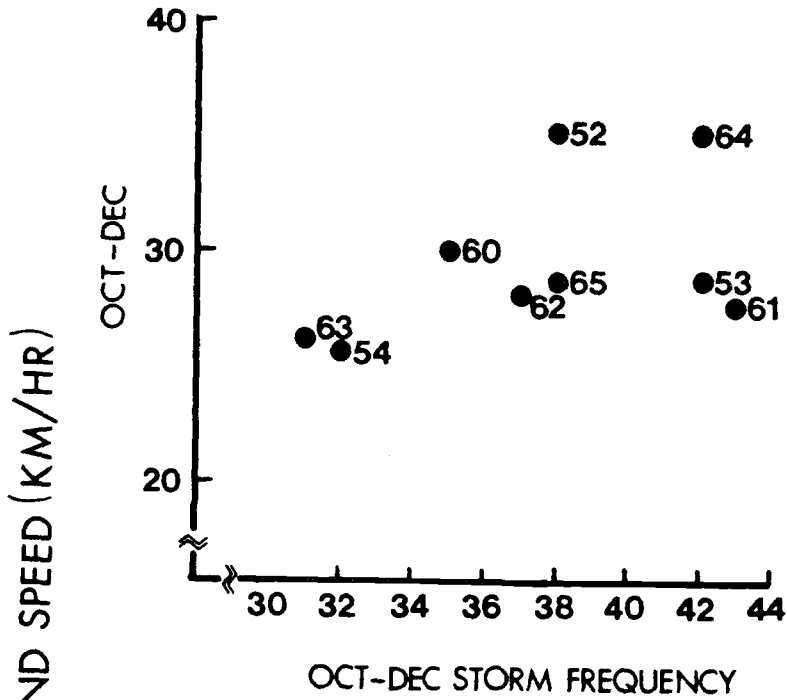
strength, again indicating that cohort strength variation is not accounted for by the combined effects of relative winter and spring roughness.

One problem with these multiple regressions might be that production cycles are shorter than the 3 month periods examined above. Since it is more likely that increases in production result from only a few days of rough weather followed by a few days of calm weather (Smayda 1957), the 3 month averages used above would not be very meaningful, unless the 3 month averages are correlated to the frequency of these short-term changes that increase production. I could not measure the frequency of these production-inducing short-term changes directly because it is not known how long the rough and calm periods should be, nor how rough or calm they should be, before production would increase. Instead, I tried to find an index, derived from monthly averages, that might be correlated to the relative frequency of these production-inducing short-term changes. For this purpose, I tried combining average wind speed and storm frequency as separate independent terms in a multiple regression on cohort strength. I used these two factors because I thought that if a period had a high storm frequency but low average winds, this would imply that calm had prevailed during most of that period, but there had been frequent breaks in that calm. This would have been a highly variable condition, favorable for production blooms. Conversely, high average winds and low storm frequency over a long term would imply that winds had been high almost continually--an invariable condition.

Before doing the multiple regressions, I tested whether there had been sufficient year-to-year differences in the wind speed:storm frequency ratio to justify doing the regressions. To see this, I plotted the average wind speed on the storm frequency during the same time interval, by year (Figure 9). The time intervals considered are only October-December and January-March, because after March, upwelling begins and storms are less important for mixing nutrients into the photic zone. Both plots show that wind speed and storm frequency are correlated; however, there does seem to be sufficient year-to-year differences in their ratio to justify doing the regressions. Further analysis of these plots shows that for the October-December periods the autumns of 1952 and 1960 were unusual in having low average winds and high storm frequency, and therefore, seem to have had highly variable conditions (Figure 9, Top). In the January-March plot (Figure 9, Bottom), it can be seen that the winter of 1953 had fairly high average winds with low storm frequency, or fairly invariable conditions; however, variability remained high in the winter of 1961. This is suggestive, because the English sole cohort spawned in the fall of 1960 and winter of 1961 was the biggest on record, and this period experienced unusually high variability.

The results of the regressions of cohort strength on wind speed and storm frequency are somewhat inconclusive, partly because there are gaps in the lightship data, so that each regression has only 5 to 10 data points. For Dover sole, there is no time interval for which both regression coefficients are significant, indicating that weather

Figure 9. Top: October-December average wind plotted against number of storms from October through December in each year. Bottom: January-March average wind plotted against number of storms from January through March in each year. Numbers on plots identify the year of the cohort spawned during the period represented.



variability, as measured here, has little effect on Dover sole cohort success. For English sole, both regression coefficients are highly significant in a model that includes variables from the October-December (early spawning) period:

$$\ln(R) = 8.31 - (8.47 \times 10^{-2})(\text{avg. wind}) + (1.01 \times 10^{-1})(\# \text{ storms})$$

$$F = 39.9 ** \quad \text{d.f.} = 2,3$$

The signs of the coefficients indicate that low average winds and high storm frequency benefit cohort strength, as would be expected in our hypothesis. However, only six cohorts are represented in this model. Excluding the 1961 year class makes the model nonsignificant ($F=13.5$), but with only five data points, it is difficult to conclude that variability in weather does not affect cohort strength. Adding to the model September-October barometric pressure, which has been shown to be related to cohort strength, only reduces the number of degrees of freedom and further obscures any relationship between variability in the weather and cohort strength. A longer data series would be required for further examination of possible relations between weather variability and cohort strength.

VII. DISCUSSION

In this study, I assumed that cohort strength of Dover and English sole is already determined before the juvenile stage; therefore, juvenile abundance on nurseries should be related to cohort strength. However, studies on Atlantic cod (Lett et al. 1975) and plaice (Steele and Edwards 1970) indicate that survival during the nursery period, which is related to predator and prey densities, is more important in determining cohort strength than survival during the pelagic phase. While nursery survival could indeed affect recruitment of Dover or English sole, there are no time-series data available for factors that might affect nursery survival.

Regardless of whether cohort strength is related to nursery survival, my analysis does indicate that Dover sole cohort strength is not related to spawning power over the range of spawning power present from 1953-1962. This independence between spawning power and recruitment has been noted for other flatfish such as halibut, plaice, and petrale sole (Cushing 1973, pp. 89-113). Cushing's conclusion, that "for flatfish, recruitment may possibly be considered as independent of stock over the exploited range" (Cushing 1973, p. 97), is supported by my Dover sole results. This case with flatfish is in contrast to recent findings concerning California mackerel (Scomber japonicus) a pelagic fish, for which Parrish (1976) used methods similar to those used here, and found that cohort strength is related to spawning biomass, in spite of a strong relationship between cohort strength and water transport factors.

An implication of the nearly-horizontal relationship between recruitment and spawning biomass (Figure 6, Top), is that as biomass increases and recruitment remains constant, a greater proportion of the recruitment is required to replace the spawning biomass. Thus, the excess recruitment, or surplus production, would decrease as biomass increases. Plots in Appendix I of Dover sole surplus production on biomass do indeed show that surplus production decreases as biomass increases. Since extrapolation of this surplus production curve indicates that surplus production would increase with further biomass reduction, it is possible that the spawning biomass could be reduced further without causing any reduction in present recruitment levels. Extrapolation beyond the historical data, however, has its risks.

Since spawning power is not related to variations in Dover sole cohort strength, over the range of spawning power tested, observed variations may be due to environmental conditions that modify survival rates. Although adult stocks are clumped around the mouth of the Columbia River, my analysis indicates that oceanographic, rather than river-related factors are most strongly related to cohort strength. I have indicated that food availability, a function of upwelling, after yolk sac absorption, might affect cohort strength. Published laboratory studies confirm the importance of food availability to young fry. If plaice and herring are not fed immediately after yolk sac absorption, their swimming ability declines, decreasing their ability to catch food that does happen by, and they starve (May 1974). Cushing (1974b) noted that larvae that have

difficulty swimming cannot avoid predators, so that if less food is present and growth rate is slower, predation is higher. While food availability may be the mechanism through which early summer winds are related to cohort strength, this cannot be proven without studies which relate food concentration, larval growth and survival, and Dover sole cohort strength.

The other factor that seems strongly related to Dover sole cohort strength is offshore divergence/convergence at time of settling. Convergence, which set up fronts that prevent inshore transport of larvae at time of settling, is associated with large cohorts. But why should it be advantageous to settle on the outer continental shelf, particularly since juveniles move inshore anyway after a few months?

The reason may be linked to differences between the inner and outer shelf environments as related to the food or physiological requirements of recently-settled juveniles. The benthic environment of the outer shelf where the larvae settle is different from the inshore region to which they migrate. Sediment is coarser inshore. North of the Columbia, at a depth of about 60 m, and south of the Columbia at a depth of 80-150 m, the sand grades into silt and mud (McManus 1972; Harmon 1972). Coincident with the decrease in sediment size, the concentration of organic carbon in the sediment and the salinity of the bottom water increases, while temperature and oxygen concentrations decrease (Gross et al. 1972). Benthic species compositions differ from the inner shelf to the outer shelf and slope. Studies show that the inner shelf epifauna and infauna are

composed mostly of gastropods, filter feeding amphipods, and, to a lesser extent, bivalves, while the outer shelf is dominated by ophiuroids, echinoids, shrimps, crabs, and deposit feeding polychaetes (Harmon 1972). There is some indication that benthic biomass is higher on the outer shelf and upper slope than it is on the inner shelf (Carey 1972). The significance that these differences have on the distribution of Dover sole juveniles is unknown, but there seems to be some adaptive advantage for Dover sole to settle on the outer shelf, and then after a period of growth, to move to the inner shelf. Whether the reasons are physiological, or related to food size, type, or abundance, it seems that processes that transport larvae inshore, so that they settle on the inner shelf, are not associated with strong cohorts. This being the case, it seems that the degree of convergence or divergence should not be as important as the existence of either convergence or divergence. In fact, when only the years of divergence are considered, the slope in a plot of cohort strength on degree of divergence is not significantly different from zero ($F=3.65$, $d.f.=1,12$). Since, however, the divergence index is a monthly average, and months with a low divergence value probably have some periods of convergence during which settling larvae might be confined to the outer shelf, the index still might have some predictive power for models such as equation (1). A more precise index might measure the relative proportions of convergence periods and divergence periods during settling.

I have mentioned advantages of using principal components in predictive models, but there is a practical problem. One cannot go

out in the field and measure a principal component. Imbrie and Kipp (1971), working with marine sediments, devised a method which incorporated principal components into a model that reconstructed ancient climate conditions. Their procedure, applied to equation (2) would be to measure each of the 10 environmental factors used to derive the principal components, standardize their measures, weight the standardized measures by the correlations between the factors and each principal component (Table 2), and substitute the weighted measure into equation (2):

$$\begin{aligned} \ln(R) = & 8.06 - (1.06 \times 10^{-1}) [(.913)(\text{standardized June upwelling}) \\ & + (.112)(\text{standardized Offshore Divergence}) + \dots + (-.175) \\ & (\text{standardized Mar-Oct Barom Pressure})] - (8.91 \times 10^{-2}) \\ & [(.119)(\text{standardized June upwelling}) + \dots + (.821) \\ & (\text{standardized Mar-Oct Barom Pressure})] \end{aligned}$$

Once the prediction has been made, the principal components should be recalculated to include the new environmental measurements. Then the predictive model should be revised to account for any changes in the correlations between the environmental factors and the principal components. With a sufficiently long data series, changes should be minor, barring a major climatic change.

This procedure seems straightforward and logical, but has not been used widely. It should have potential use in fisheries for predicting cohort strength because it incorporates many environmental variables, rather than just one or two. When constructing a predictive model from a relatively short data series, scientists are usually

faced with the choice of either including all potentially important factors, and possibly including some extraneous factors that may invalidate the model, or of limiting the number of variables, and possibly leaving out important factors. With principal components, however, it is possible, with a relatively short data series, to build a model that has only a few variables, but still accounts for all potentially important factors.

Of course, the model will be more valid if the factors incorporated in the principal component are, in fact, all of the important ones. In the case of English sole, the principal components model (equation (4)) explains less cohort strength variation than does the barometric pressure model (equation (3)), possibly because factors that have nothing to do with cohort strength may be incorporated in the principal component, and this may obscure its relation with cohort strength. This may also be why the principal components model for Dover sole (equation (2)), explains only slightly more variation in cohort strength than does the divergence/upwelling model (equation (1)). Future work with principal components should focus on determining which environmental factors are the best ones to include when constructing predictive models.

Cohort strength of English sole is apparently affected by factors different from those affecting Dover sole, which is not unexpected, because young English sole live in a more inshore environment than Dover sole. I could not identify the factors responsible for the success of the 1961 cohort, because my analysis indicates that the factors that caused this success were different from the factors

regulating cohort size in every other year. Several factors were abnormal in 1961, such as northward transport in February, downwelling in March, solar radiation in June, and the unique combination of high storm frequency and relatively low average winds throughout the winter, but it is impossible to tell whether the co-occurrence of any of these abnormal conditions and the 1961 cohort was merely chance. Perhaps the unique combination of storm frequency and wind speed in the winter of 1960-1961 may have enhanced winter food production, but this is not known, because Anderson's (1964) production measurements, the only ones done in this area during 1961, were designed to compare seasonal, and not yearly, differences. Without comparative production studies during years of similar cohort success, it will be difficult to identify the factors responsible for the great 1961 success.

Analysis of factors that regulated the strength of the 11 remaining cohorts is more straightforward. Cohort strength seems to be related to sea temperature, upwelling, and barometric pressure in the early fall, prior to spawning. If the relation is causal, it should therefore affect the spawners rather than the eggs or larvae. Since the spawners would probably be affected more by factors that modify their sea bottom environment than by surface events, these factors would have to be linked to some factor in the bottom environment. My analysis shows that during upwelling, barometric pressure, upwelling, and surface temperatures are correlated with each other. Huyer (1977) showed that the bottom temperatures over the continental shelf are inversely proportional to the rate of upwelling. Therefore,

bottom temperatures must also be related to barometric pressure and surface temperature, although, because of thermal inertia, the surface temperature would reflect the bottom temperature with a days or weeks lag, rather than present bottom temperature. If bottom temperature is the factor in the bottom environment that affects spawner success, then this thermal inertia would explain why October sea temperature is better correlated to cohort strength than September sea temperature.

Conceivably, bottom temperatures could regulate the rate of egg maturation and the time of spawning. Although Cushing (1969) pointed out that time of peak spawning for some cold-water fish, such as plaice and herring, is genetically fixed and may vary by only a few days each year, environmental cues may also modify time of spawning for some fish. For instance, spawning may be induced in sticklebacks by raising the water temperature (Marshall 1966, p. 250).

The limited information available on English sole suggests that spawning may be delayed until bottom water warms up following the cessation of upwelling. In 1969, a year of moderate September upwelling, with upwelling ceasing in late September, 3 mm SL larvae were first found in November. In 1970, a year of strong September upwelling, with upwelling ceasing in October, 3 mm SL larvae were first found in December. In 1971, a year of weak upwelling, with upwelling ceasing in August, 4 mm SL larvae were first found in October (B. Mundy, O.S.U. School of Oceanography, pers. comm.). Evidence indicates that peak spawning times for the 1970-1975 year classes occurred around November 1969, January 1971, October 1971,

January 1973, the fall of 1973, and early 1975 (Olson and Pratt 1973; Laroche and Richardson MS), and in general the peak spawning time was later when upwelling in September was higher. Although these observations are not definitive, they are consistent with the hypothesis that English sole do not spawn until the bottom water warms up.

Since bottom temperature is apparently related to cohort strength, this implies that delayed spawning benefits cohort strength. This may be because larvae spawned in the fall have to endure the low productivity of late fall and early winter, while winter-spawned larvae avoid this obstacle. There are no data relating time of spawning and cohort strength, but the 1973 and 1975 cohorts, which were probably spawned in winter, were abundant on larval surveys in those years. This does not necessarily mean, however, that those cohorts will be strong, because there are no data that relate larval abundance to subsequent cohort strength.

An alternative explanation for the wide variation in time of spawning for English sole is that there is more than one spawning population. If Cushing's (1969) assertion is true, that time of spawning should not vary, and there are, for instance, fall spawning and winter spawning populations, then peak spawning might vary because one population is low while the other is high. A two-population hypothesis gets some support from the observation that the frequency of larvae in the plankton seems to follow a bimodal distribution over a season (Laroche and Richardson 1977). Tyler and Dunn (1976) showed that whether or not a fish spawns is dependent on its physical condition, so that females would not necessarily spawn every year. Thus,

even though up to 10 age groups may be present in the spawning population, it is conceivable that spawning biomass could be high one year and low the next.

If this is the situation, then I should change my interpretation of how the environment influences cohort strength. The two-population hypothesis might indicate that the success of the 1961 cohort was due to success of both the fall and winter populations, possibly as a result of variable conditions and high food production in both fall and winter. The effect of bottom temperature in early fall might have been to regulate egg quality or food production for the fall spawners, and maturation rate for the winter spawners.

Understanding the relation between environment and cohort strength requires us to learn whether there is more than one spawning population of English sole. Determining whether there is more than one spawning population also has important management implications, and studies of peak spawning times, ovary development, stage of maturity in catch samples, serology, and meristics should be undertaken. Understanding the relation between the environment and cohort strength also requires further studies of larval and juvenile population dynamics, species interactions, physiological (including energy budget) requirements, and effects of population density on fecundity and spawning power. Finally, environmental and fishery data must continue to be collected.

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APPENDICES

APPENDIX I

A COMPARISON BETWEEN COHORT ANALYSIS AND
CATCH PER UNIT EFFORT AS INDICES OF YEAR-CLASS STRENGTH
OF DOVER SOLE (MICROSTOMUS PACIFICUS) AND
ENGLISH SOLE (PAROPHRYS VETULUS)¹

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ABSTRACT

Year-class strength of Dover sole (Microstomus pacificus) and English sole (Parophrys vetulus) was calculated by summing the catch per unit effort (CPUE) of each age group in a year-class. Because of fluctuating market demand and the difficulties inherent in assigning effort by species in a multi-species fishery, there were questions about the validity of the CPUE data. For comparison, year-class strength was also calculated by Pope's cohort analysis, using natural mortality rates calculated as 0.20 for Dover and 0.30 for English sole, and catchability coefficients calculated as 3.5×10^{-5} /boat-hr for Dover and 7.4×10^{-5} /boat-hr for English sole.

For Dover sole, both year-class strength indices show similar general trends--strong year classes in the early and mid-1940s, declining recruitment in the late 1940s and early 1950s, and an increase in strength up to 1962; however, the indices differ in detail and are not significantly correlated.

Slow development of the Dover fishery allows application of the Schaefer yield model. Resulting surplus production estimates are more closely related to biomass estimates based on cohort analysis than to fishing effort. For this reason, and also because of the relative robustness of cohort analysis, we feel that year-class strength changes are better determined by cohort analysis than by CPUE.

The plot of surplus production on biomass suggests a maximum sustainable yield of about 1300 metric tons, which is well above recent yields.

The two English sole year-class strength indices, unlike those of Dover sole, are highly correlated with each other. They both show extraordinary success in 1961, but no long-term trends in recruitment. A Schaefer model was not applied because of the short data series.

INTRODUCTION

The purpose of this report is to compare year-class strength indices derived from catch per unit effort (CPUE) data with those derived from cohort analysis for two species of flatfish, the Dover sole (Microstomus pacificus) and the English sole (Parophrys vetulus), which are abundant in PMFC Area 3A (Figure 1).

Both indices have previously been used to measure year-class strength (Ketchen and Forrester 1966; Pinhorn 1972), and they have been compared with each other (Garrod 1975), but the relative validity of each index has not been analyzed. As accurate measurement of recruitment becomes more necessary in fishery management, it becomes more important to know the strengths and limitations of the different methods of measuring recruitment. In this study, we tested the validity of each Dover sole index by deriving estimates of stock size from each index, and then comparing plots of surplus production on the estimates of stock size.

Historically, year-class strength in Area 3A has been measured by CPUE, because these data were readily available. However, Ketchen and Forrester (1966: p. 94, 105) pointed out that such indices of year-class strength can be biased by fluctuations in effort and catchability, and that these biases can be partly overcome by using, as the index of year-class strength, the total catch from each year class, or virtual population (Fry 1947).

Virtual populations, however, are also subject to bias under conditions of fluctuating effort (Bishop 1959), and correcting for

this bias by incorporating Baranov's catch equation (Ricker 1975: p. 13) into the virtual population analysis requires use of unwieldy iterations (Paloheimo 1958; Pope 1972). Pope's (1972) cohort analysis computes year-class strength without requiring iterations, and it uses only catch at age data, one estimate of population size, and an estimate of natural mortality, thus circumventing the biases noted by Ketchen and Forrester (1966) in indices of year-class strength computed from CPUE. Because of these differences, we decided to compare the historical CPUE-based indices of year-class strength with indices derived from Pope's cohort analysis.

Studies of this type should be done on closed stocks of fish. It is likely that the Dover stock fished in the region off the Columbia River is separate from the concentrations fished farther north or south. Unpublished maps of commercial catches and research cruise surveys by the Oregon Department of Fish and Wildlife (O.D.F.W.) show that Dover sole abundance drops off 30 miles to the north and south of Columbia River. Tagging studies in the area indicate that Dover sole migrate inshore and offshore, but generally don't move north or south (Westrheim and Morgan 1963; Milburn 1966). English sole catches, however, are scattered along the coast, and there is no evidence that the Area 3A fish form a distinct stock.

COLLECTION AND MODIFICATION OF DATA

Catch and Effort Data

Catch and effort statistics for PMFC Area 3A have been collected from logbooks of participating fishing vessels and compiled for Dover

sole since 1948 and for English sole since 1959 (Table 1). PMFC areas, however, were not designated until 1956. The catch totals listed for 1948 through 1955 represent the landings at Westport and Ilwaco in Washington, plus the landings classified as "North" or "local" at Astoria, Oregon. The area covered by these landings is roughly the same as the current Area 3A (R. D. Ward, Washington Department of Fisheries, pers. comm.). Because PMFC Area 2D was incorporated into Area 3A in 1962, the figures for the years 1956 through 1961, are the combined Area 2D and 3A totals. The landing statistics for subsequent years are Area 3A figures.

Because fishing effort may be applied simultaneously to several species in a multi-species fishery such as this, it is difficult to assign an effort figure to one specific species. The effort expended on incidental catches of Dover sole should not be counted as effort on Dover sole, but it is difficult to define an "incidental catch."

To deal with this problem of assigning effort to species, ODFW has established the criterion that if a species comprises at least 29 percent of a landing, then the catch of that species is a "significant catch," and all effort on that trip is counted as effort on that species. The result of this definition is that a substantial percentage of the catch of Dover and English sole each year is considered incidental. This percentage varies from year to year. For Dover sole, the incidental percentage varied from 6.5 percent in 1950 up to 77 percent in 1957, and generally ranged between 40 and 60 percent. While this variation does not necessarily affect the validity of the CPUE as an index of abundance, it can give a false impression of the

intensity of the fishery if measured effort is considered alone. Therefore, for purposes that require consideration of effort alone we define the concept of the "equivalent effort." This rescales the measured effort to approximate the amount of effort that the fish actually experience, assuming constant catchability, and is determined by increasing the measured effort by the ratio of total catch to significant catch,

$$f^* = f \cdot C_t / C_s \quad (1)$$

where f^* is equivalent effort, f is measured effort in boat-hours, C_t is total catch, and C_s is significant catch (Table 1).

Comparison between equivalent effort on Dover sole with that on English sole each year since 1959 shows that effort on one species does not parallel effort on the other ($r=+.30$ NS, $P>.05$, $d.f.=15$); thus, it has been possible to concentrate on one species without catching the other.

Age Distribution Data

Since 1948, ODFW personnel have sampled trawl landings in Astoria to obtain data on length, weight, sex, age, and maturity. These data form the basis for the analysis of year-class strength.

Dover sole samples taken in 1948, and from 1951 through 1956, were aged by reading otoliths. Subsequently, they were aged by scale readings (Demory 1972). Scales from older fish are difficult to read. Second readings may disagree with first readings by up to 3 years. In addition, males, which live in deeper water and grow more slowly than

females, are extremely difficult to age. Tagging has shown that males frequently do not lay down annuli (Demory 1972). For these reasons, only female Dover sole younger than 14 years old will be considered in calculations of year class strength. Because males and females inhabit the same area and grow at about the same rate for about the first 6 years of life, they should be subject to the same mortality. A strong year class of females, therefore, would also have been a strong year class for males, obviating the need to interpret data for males.

The Dover sole samples were usually taken from May through September; however, the fishery continues to operate through the winter. Since the winter fishery generally operates in deeper waters to which the older fish have made a spawning migration (Alverson 1960; Demory 1975), we explored the possibility that the winter catch could be composed of a higher percentage of older fish than our May-September age composition samples. For data from 1967 and 1970, the only two years in which winter samples were taken, a Kolmogorov-Smirnov test (Tate and Clelland 1957) showed that the age distribution of the winter catch was not, in fact, significantly different from that of the summer catch. This was possibly because most fishing boats remained inshore until well after the beginning of the spawning migration; thus, in early winter the age distribution of the catch was skewed toward younger fish than the summer catch, while later in winter the age distribution was skewed toward older fish (Hayman 1978: Appendix). Over the entire winter the two trends apparently balanced out, so that the overall winter age distribution did not

differ significantly from the summer distribution. In this case, the May-September age composition data can justifiably be considered representative of the entire year.

Age samples of Dover sole were not taken in 1949 and 1950. To estimate the percentage of the 1940, 1941, and 1942 year-classes in the catch in these years, catch curves were constructed in which a constant rate of total mortality was assumed from the modal age (age 8) onward. We plotted the natural logarithm of the CPUE of each age older than 7 against age, for each of these three year-classes. From these three catch curves, we interpolated the CPUEs of the age 9 and 10 Dover sole from the 1940 year-class, the age 8 and 9 fish from the 1941 year-class, and the age 8 members of the 1942 year-class. Dividing these CPUEs by the total female CPUE in 1949 or 1950 estimated the proportion of age 8 and 9 Dover sole in the 1949 catch, and of age 8, 9, and 10 Dover sole in the 1950 catch. Although these may be rather crude approximations, they do not seem to be out of line with the figures for other years.

The age composition data (Hayman 1978: Appendix) show that over the years, older fish have made up an increasingly smaller percentage of the catch. Because of this, mean landed fish weight has decreased. This is the normal fishing-up process, and it appears that the average weight has stabilized in recent years.

English sole were sampled throughout each year since 1948, but age determinations were made only from 1959 through 1975. They were aged with an age-length key from 1959 through 1965, and subsequently they were aged from interopercle readings. Repeatability of

interopercle readings is almost 100 percent. No age samples were taken in 1962, and the age composition that year was estimated using the catch curve method described previously. Because female English sole constitute nearly the entire catch, only females are considered in calculations of year-class strength.

Catch Utilization

The catch at age each year can be calculated from the age distribution of the catch (Hayman 1978: Appendix) and from total landings (Table 1). However, this is only the catch at age of the landed catch, and not all of the fish that are caught are actually landed. Dover sole and English sole that are judged by eye to be too small for processing are discarded at sea. Although these fish aren't sampled in the landings, they should still be counted when calculating the age distribution of the catch because most of them are dead after discarding.

TenEyck and Demory (1975) determined the proportion of Dover and English sole of each age that was retained by fishermen (utilization rate) in 1974. However, in earlier years the rates may have been different. The only data available from which earlier utilization rates can be derived is a comparison of the length frequencies of Dover sole caught at sea to those in the landed catch between 1950 and 1961 (Demory and Fredd 1973: Figure 1).

To derive utilization rates from this data, we set the minimum length of 100 percent utilization at the same value as that found by TenEyck and Demory (1975). This length was 43 cm, the average length

of age 11 Dover sole. Fish in the 43 cm length group comprised 4.9 percent of the total at-sea catch from 1950-1961, and 6.7 percent of the total landed catch. Since the number of 43 cm fish caught at sea equalled the number of 43 cm fish landed, it is possible to compute algebraically the proportion of the total 1950-1961 catch discarded:

$$.049 \times (\text{total at-sea catch}) = .067 \times ((\text{total at-sea catch}) - (\text{total discarded})) \quad (2)$$

From this, the total discard rate of the 1950-1961 catch, without respect to size, was 27 percent of the total at-sea catch; therefore, the total landed catch was 73 percent of the at-sea catch. We derived length-specific discard rates (d_L) by setting the at-sea catch of each length group equal to the landed catch plus the discards:

$$\text{Pct}_s \times C_s = (\text{Pct}_L \times 0.73 \times C_s) + d_L \quad (3)$$

where Pct_s and Pct_L are the proportions of that length in the at-sea and landed catch, respectively, d_L is the number of discards of that length and C_s is the total at-sea catch, which if set at 100 results in d_L being expressed on a percentage basis. The length-specific utilization rate (u_L) is then:

$$u_L = 1 - d_L / (\text{Pct}_s \times C_s) \quad (4)$$

These rates (Table 2) seem to indicate that fishermen are currently retaining higher percentages of small fish than they had previously, but differences in rates are fairly small.

Although no data on utilization rates were available for the years 1962-1973, we assigned the 1974 utilization rates (TenEyck and Demory 1975) to these years because the age distribution data indicate that, beginning in 1962, there was an increase in the percentage of smaller Dover sole, age 6, 7, and 8 in the catch, and the 1974 utilization rates show higher utilization of these younger fish. Actually, catch utilization rates probably did not abruptly change between 1961 and 1962 because the utilization rates vary from year to year and even from haul to haul, and long-term changes should be gradual, unless there is a sudden change in gear, fish distribution and size, or market conditions. Nonetheless, some dividing line had to be drawn, and it was drawn between 1961 and 1962.

Dividing landings at age by the age-specific, time-period-specific, utilization rate gives the at-sea catch at age that was used in calculating year-class strength.

THE YEAR-CLASS STRENGTH INDICES

Sum-of-CPUE

Using the methods of Ketchen and Forrester (1966: p. 95-104), we took the sum of CPUEs of each age of a year-class to get an index of year class strength for that year class. This method of year class strength calculation will be referred to as the "sum-of-CPUE method."

Because we could not interpolate the percentage composition of Dover sole younger than age 8 in the 1949 or 1950 catch, we could not include fish younger than 8 in calculations of year-class strength

that required data from those 2 years. Since younger fish do comprise a significant percentage of the catch, we derived two sum-of-CPUE indices for Dover sole; one summed the CPUE of ages 6 through 13 and considered only data taken after 1950; the other used data from 1948-1975, but only summed the CPUE of ages 8 through 13. These indices are not independent of each other and are highly correlated for the 1945-1962 year classes ($r=+.938$, $p<.001$). Except for the 1945 and 1946 year-classes, from which large numbers of age 6 and 7 fish were caught, the trends in the two indices are identical (Figure 2A).

Dover sole year-class strength was highest in the early 1940s and it declined fairly steadily to a minimum in 1952, then rose again, reaching a second peak in 1961. There seem to be no signs of recruitment failures, such as those that plagued the Pacific sardine and mackerel fisheries. On the whole, recruitment appears to have been fairly stable over the years. Such stability has also been noted for similarly fecund flatfishes, such as plaice (Cushing 1973: p. 97).

We calculated English sole year-class strength as the sum of the CPUEs of age 4 through 9 fish. Although English sole can be aged accurately to ages greater than 9 years, each additional age included would remove another year-class from consideration. As it was, this time series covered only 12 year classes (Figure 2B). For this period, 1955-1966, there seem to be no discernible trends in year-class strength. The more recent year-classes were smaller, but there is no indication of recruitment failure. The 1961 year class was extraordinarily large, and produced record catches when it

entered the fishery in 1966. Interestingly, 1961 also produced strong year classes of other species such as hake (Merluccius productus) and Pacific Ocean perch (Sebastes alutus) (Dark 1975; Gunderson et al. 1977).

The estimates of year-class strength are valid only if the CPUE data are accurate, or at least consistent, from year to year. For the Area 3A fishery, however, the data may not be consistent. When used to compare abundance in different years, CPUE has inherent inaccuracies due to failure to account for changes in catchability resulting from gear improvement and changes in fish distribution or growth. In addition, the sum-of-CPUE method does not make allowances for fluctuations in effort, which cause fluctuations in total mortality rates. Year-classes that experience high fishing mortality during their younger, more abundant years, could have a smaller average population size, and hence smaller CPUE, than year classes that experience less fishing mortality during their most abundant years. Because of this, one year class may have a smaller sum-of-CPUE index than another, initially less abundant, year class (Ketchen and Forrester 1966: p. 94).

If the actual desired target species is not abundant enough to make up 29 percent of a landing, effort would be ignored and CPUE would overestimate this species' true abundance (Parrish et al. 1975). Also, market conditions have always limited the amount of Dover and English sole that the fishermen can keep. If the market limits for a species are reached on the first tow, all subsequent tows would be directed at other species, and if the first species is caught, it

would be dumped overboard. Then, when the catch is landed, if the first species accounts for 29 percent of the landing, all towing effort for the entire trip counts as effort directed against that species. This underestimates the abundance of that species and causes yearly fluctuations in the CPUE that are related to market conditions, rather than to species abundance.

Comparison between the CPUE at different ages in the same year class indicates that these deficiencies in the sum-of-CPUE method may have biased the calculations of year class strength. It would be expected that if, for example, the age 9 CPUE is high for a year class, then the age 10 CPUE should also be high for that same year class. However, this was not necessarily the case (Figure 3). For Dover sole the correlation between age 9 and age 10 abundance, as measured by CPUE, is not statistically significant ($r=+.375$, $P>.05$, $d.f.=25$). Similarly, when the CPUE of age 4 through 6 English sole is compared with that of age 7 through 9 English sole, the correlation is also not statistically significant ($r=+.243$, $d.f.=10$). This lack of agreement between CPUEs within the same year classes indicates that these CPUE figures are very rough indices of abundance, and hence, poor estimators of year class strength. For these reasons, it was felt that the year-class strength figures might be improved by using a method of calculation that requires minimum use of effort statistics, such as cohort analysis.

Cohort Analysis

Pope's (1972) method of cohort analysis requires only catch-at-age data, a value of natural mortality (M), and an estimate of population size at an older age. Basically, what is assumed in Pope's approximation is that the entire catch each year is taken at one instant midway through the year. This approximation, for values of $M < 0.3$ and $F < 1.2$, is within 4 percent of those given by Baranov's equation, $C = F \cdot A \cdot N / Z$, where C is catch in numbers, N is initial population size, F is instantaneous fishing mortality rate, A is proportional total mortality rate, and Z is instantaneous total mortality rate (Pope 1972).

To find M , we used values of instantaneous fishing mortality (F) that had been obtained from ODFW tagging studies, and subtracted them from catch-curve estimates of instantaneous total mortality (Z).

An F on Dover sole of about 0.13 during the 1966-1970 period (Demory and Fredd 1973) was estimated from a tagging study begun in 1964 (Milburn 1966). This F was not classified according to sex, and since, in summer, females are generally found inshore where the fishery is the most intense, females would be expected to have a higher F than males. This was confirmed, because limited data on sex composition of tagged fish (Milburn 1966) indicated that a higher percentage of tagged females were recaptured than tagged males. However, since 70 to 80 percent of the tagged fish were females, the value 0.13 does essentially reflect the fishing mortality on females. To

accommodate the effect males likely had on this figure, we increased the estimate of F for females to 0.15.

To find Z for the same time period, we found the total catch of each age group from 1966-1970 and constructed a catch curve. We combined catches at age over several years in catch curves because this tends to smooth out year-class variation somewhat. After correcting for age-specific utilization rates, we plotted the natural logarithm of the catches at each fully recruited age (age 10 to 13) against age. The slope of the line, which is an estimate of Z, is 0.334. Subtracting the estimate of F (0.15) from 0.334 gives a natural mortality rate of 0.184, which rounds off to M=0.2. This value of M is consistent with the Dover sole lifespan of more than 20 years, and with previous mortality estimates (Demory and Fredd 1973).

For English sole of age 6 to 9, the Z estimated by catch curve for 1971-1974 was 0.494. From research cruise data, Demory et al. (1976) estimated the exploitation rate (E) on English sole in PMFC Area 3A during the 1971-1974 period as E=0.156. By definition, $E=C/N$, where C is the numerical catch and N is the initial number of fish in the population. Since from Baranov,

$$C = N \cdot \frac{F}{Z} \cdot (1 - e^{-Z}) \quad (5)$$

rearranging and substituting gives,

$$F = E [Z / (1 - e^{-Z})] \quad (6)$$

or $F = 0.20$ for English sole in 1971-1974. Subtracting 0.20 from the estimate of Z (0.494) and rounding off gives a natural mortality rate of 0.3 for female English sole. This value of M is also consistent with the English sole lifespan of slightly less than 20 years.

We also tried to estimate M using a linear regression of Z on effort (Ricker 1975: p. 169), in which Z was estimated using both CPUE (Paloheimo 1961) and virtual populations (Fry 1949; Bishop 1959). These estimates of M , however, were unsatisfactory--confidence limits were extremely wide and estimates were often negative. Thus, the catch curve values were used in the cohort analysis.

We believe that these values are reasonably accurate. Great precision, however, is not critical as long as the natural mortality rate of adult fish has remained fairly constant over the years, because then the error in M would affect all year classes to the same degree and their relative strengths would not vary.

To start the cohort analysis, it is necessary to have an estimate of numbers of fish (N) at an advanced age, in this case at age 13 for Dover sole and at age 9 for English sole. Pope (1972) showed that it is not critical that this initial estimate be precise, because as the cohort analysis is carried forward over successively younger ages, the calculated number at age converges on the true value of number at age. Nevertheless, we used our best estimate of starting N .

An estimate of number at age can be made if F is known for that age. Since $Z = F + M$, F can be substituted into Baranov's catch equation to solve for N . Thus, we needed to know F for age 13 Dover sole and

for age 9 English sole for each year. Since $F = q \times f^*$ where f^* is equivalent effort in boat-hours, we could get a rough estimate of F each year by multiplying q by the equivalent effort that year. Substituting this F and that year's catch of age 13 Dover sole or age 9 English sole into the Baranov equation gives a rough estimate of the number of age 13 Dover sole or age 9 English sole in the population that year. Unfortunately, this procedure required us to use the effort data, which we had sought to avoid using in the cohort analysis. Our use of the effort data makes this step a weak link in the comparison of the two methods, but since the estimated year-class strength does converge toward the true value as more ages are considered, the inaccuracy that the effort data confers on the starting values of N should have minimal effect on the final year-class strength figures. Furthermore, because the effort data only directly affects the numerical estimate of the oldest age-group, it should have less impact on the cohort analysis year-class strengths than it did on the sum-of-CPUE year-class strengths, where effort was intimately linked with abundance indices for all age-groups.

For the period 1966-1970, an F of 0.15 has been calculated for female Dover sole. Dividing this F by the average equivalent effort over that period (Table 1) gives a catchability coefficient (q) of 3.5×10^{-5} per boat-hr. For the period 1970-1974, F for English sole is 0.20. Dividing by average equivalent effort from that period gives $q = 7.4 \times 10^{-5}$ per boat-hr.

Using these values of catch at age, M , and numbers of age 13 Dover sole and age 9 English sole, we used Pope's equation to derive

year class strength figures. As with the sum-of-CPUE method, we computed two indices for Dover sole; age 8 abundance and age 6 abundance (Figure 2A). These two indices are highly correlated ($r=+.823$, $p<.01$), and, like the sum-of-CPUE indices, the 1945 and 1946 year classes were relatively stronger at age 6 because they contributed substantially to the catch as 6 and 7 year olds. These indices show strong year classes in the early 1940s, a decline to a minimum in 1949, and a gradual increase in recruitment into the early 1960s. Overall, recruitment has been fairly stable.

The index of English sole year-class strength was age 4 abundance, as determined by catches of ages 4 through 9 fish. The most notable feature of this time series (Figure 2B) is the strong year class in 1961. Otherwise there have been no discernible trends in year-class strength.

Comparison of Year-Class Strength Indices

One possible source of bias in both calculations of year-class strength is that we assumed constant catchability (q). Gear improvement, however, may have enhanced catchability in later years. On the other hand, fluctuations in market conditions, which can cause varying proportions of the catch to be landed, may have obscured any increase in q caused by gear improvement. Further analysis showed that the latter appeared to be the case: calculated q fluctuated without trend both for Dover and English sole (Figure 4).

To show this, we computed fishing mortality (F) each year (Hayman 1978: Appendix) and divided it by equivalent effort to get

q each year. F was determined by directly calculating total mortality rate (Z) of fully recruited ages from the cohort analysis numbers at age data (Hayman 1978: Appendix), and subtracting the natural mortality rate (M) from this Z. Since we used a constant q to initiate the cohort analysis, this method of calculating q dampens fluctuations in q; however, trends, if they exist, should still be apparent. The q's calculated in Figure 4 fluctuate widely with no clear upward trend. This indicates that q may be more strongly affected by market conditions than by gear improvement, and that the assumption of constant catchability does not introduce artificial trends into the year-class strength time series (Figure 2).

For Dover sole, the year-class strength indices derived from cohort analysis do not, in general, agree very well with the sum-of-CPUE indices. The cohort analysis age 8 recruitment indices are not significantly correlated with the age 8 sum-of-CPUE indices for the year classes 1943-1962 ($r=+.215$, d.f.=18) (Figure 2A). Similarly, the age 6 cohort analysis year-class strengths are not significantly correlated with the age 6 sum-of-CPUE year class strengths ($r=+.408$, d.f.=16). Major disagreements between these indices concern the relative strengths of the 1947, 1953, 1956, and 1958 year classes.

Since the fishery developed slowly and has been essentially in equilibrium for about 30 years the relative validity of the cohort analysis indices vs. the effort-based index can be compared by plotting surplus production against either biomass or the effort measure. If application of the model is valid, then the scatter of points should describe a hump that intersects the origin (Ricker 1975: p.

316), or, if the range of either biomass or effort is not wide enough to cover both the ascending and descending arms of the hump, the scatter should be close to linear. Effort itself should be an index of biomass, because fishing effort exerts a direct influence on equilibrium population size; hence, population size should be inversely proportional to fishing effort over the previous years (Ricker 1975: p. 328). To maximize the number of data points, but still to allow for the effect of effort in previous years on current population size, we used a 5-year running average of equivalent effort as an index of stock size. To estimate each year's biomass from the cohort analysis, we summed the estimates, derived from cohort analysis, of numbers at age 6 to 13, and estimated the population older than 13 by multiplying the number of fully recruited (age 10 through 13) Dover sole by the ratio of older-than-13 fish to age-10-through-13 fish in the age distribution samples. Summing for all ages estimated population size each year. We multiplied this total by average weight per fish (Table 1) to get total biomass each year. The surplus production in one year was estimated as the change in biomass from that year to the next year, plus the yield that year.

The resultant surplus production plots for females seem to be the high biomass limb of the curve (Figure 5). The scatter of surplus production on average effort shows a wide scatter of points and an insignificant correlation between surplus production and average effort ($r = -.296$, $P > .05$, $d.f. = 13$). The scatter of surplus production on biomass shows a higher, but still insignificant, correlation ($r = -.484$, $P > .05$, $d.f. = 13$). However, considering that surplus

production models do not account for fluctuations in recruitment, caused by environmental fluctuations, and that surplus production arises both from growth, which is a function of current biomass, and recruitment, which is a function of biomass several years past, the correlation between surplus production and biomass is surprisingly close to being significant ($P_{.05} = +.51$), and is especially good when compared to other published surplus production plots (Ricker 1975: p. 324). Nonetheless, the negative surplus production values in some years indicate a decrease in biomass beyond what the fishery extracted, and this may be due partly to decreased recruitment.

A hump-shaped curve, fitted by eye through the plot of surplus production on biomass (Figure 5A), shows that the carrying capacity should be about 10 thousand metric tons. The maximum yield should then be taken at a biomass of about half of the carrying capacity, or 5000 metric tons. This yield, which is only a crude approximation, would be about 1300 metric tons. The average female yield for 1971-1975 was 475 metric tons, and the most recently estimated female biomass, that of 1967, was well above 5000 metric tons, so it seems that the fishery could sustain increased effort.

In the case of English sole, in contrast, the cohort analysis indices and the sum-of-CPUE indices are in close agreement over all the year classes ($r = +.90$, d.f.=10, $P < .001$) (Figure 2B). Even if 1961 is disregarded, the correlation is high ($r = +.61$, d.f.=9, $P < .05$). Thus, it appears that for the English sole year classes considered, both indices estimated comparable year class strengths.

We did not compare the validity of the different indices by doing a surplus production model for English sole, because the shorter time series would not have allowed sufficient data points.

DISCUSSION

Both methods of calculating year-class strength are susceptible to error. Factors mentioned here that bias the sum-of-CPUE indices include fluctuations in catchability and effort. A possibly more critical source of bias arises from the difficulty in defining effort in this multi-species fishery. The 29 percent threshold used here may underestimate declines in species abundance (Ketchen and Forrester 1966: p. 63). More important, it creates a CPUE index that is heavily influenced by market demand, rather than by species abundance, and this has apparently caused the situation in which the abundances of different ages within a year class are not correlated with each other. Ketchen and Forrester's (1966) petrale sole sum-of-CPUE indices for different ages within the same year class were more highly correlated ($r=+.88$, $d.f.=12$), possibly because they didn't use a set threshold for measuring effort. In their analysis, they counted all catches which landed petrale sole, but they made adjustments for years during which petrale sole was more likely to be caught incidentally. Perhaps a similarly flexible threshold would help remove some of the bias in CPUE introduced by market fluctuations.

Cohort analysis is not free of error, either. Error exists in catch sampling, in aging, in the selection of the initial population size, and in the approximation that all fish are caught midway through

the year. The error due to catch sampling and aging, however, is common to both cohort analysis and sum-of-CPUE, and should not contribute to making one index more reliable than the other. The initial population size was selected by assuming q stayed constant, which it didn't, and by using the same effort data as the sum-of-CPUE method. This error, however, affects the estimates of numbers only in the oldest age group, and when brought forward by cohort analysis to younger ages, the error in numbers at age diminishes (Pope 1972).

By confining the catch to one instant during the season, Pope's equation makes the approximation that:

$$(F + M) \cdot (1 - e^{-F}) / [F \cdot (1 - e^{-(F+M)})] = e^{M/2} \quad (7)$$

(Pope 1972). For $F=0.50$ and $M=0.30$, the highest rates found here, equation (7) says that: $1.14=1.16$, which is an error of less than 2 percent. Thus, it seems that the error in cohort analysis is either: (1) shared in common with sum-of-CPUE, with an equal effect on both indices; (2) shared in common, but with a bigger effect on sum-of-CPUE; or (3) not shared, but with an insignificant effect on the cohort analysis indices.

The conclusion indicated by this listing of sources of error is that while cohort analysis can also be biased, it seems that sum-of-CPUE indices are more susceptible to error. The comparison of surplus production models bear this out. In instances where the two year-class strength indices disagree, therefore, the cohort analysis index is probably the more accurate.

The two indices do not disagree over English sole year-class strength, however, which indicates that CPUE seems to be a valid abundance index for English sole. Why should it be valid for English sole, but not Dover? One reason might be that English sole fetches a higher ex-vessel price and is preferred by processors, so that market conditions may restrict the Dover sole catch more than the English sole catch (J. Bergeron, OSU Marine Extension, pers. comm.). In this case, the English sole catch should reflect abundance, whereas the Dover sole catch would reflect market limitations more. Discussions with fishermen indicate that they also prefer to catch English sole, because Dover catches are often heavily contaminated with Arrowtooth flounder and require much labor to sort. In addition, Dover sole concentrations tend to disperse during fishing, while English sole do not, so that English sole catches would be less influenced by previous tows. Furthermore, while most vessels in the Astoria fleet are capable of fishing the entire range of English sole concentrations, fewer are equipped to fish the deeper concentrations of Dover sole, so that Dover sole landings may often come from the fringes of the population, particularly since Dover are often caught incidental to petrale sole. The CPUE at the fringes does not necessarily reflect the abundance of the whole population (Parrish et al. 1975). Alverson (1960) points out that CPUE of Dover sole in winter increases greatly with depth, and is much higher than summer CPUE at any depth; thus, CPUE is greatly affected by how much deep-water trawling the weather permits. CPUE for English sole would be less affected by this factor. A final difference might be that English

sole have a higher natural mortality rate; and therefore, the older age groups comprise a smaller percentage of the catch. Since these older fish compound the error in sum-of-CPUE under conditions of fluctuating effort, they would contribute less error to the English sole indices than to the Dover indices. Because of these differences, it seems that the errors that afflict CPUE figures for Dover sole are less important for English sole.

Although this study has shown deficiencies in CPUE data for Dover sole, these data must still be collected because, unlike cohort analysis, they can provide current information on the status of stocks. Clearly, however, refinements are needed before CPUE data can be used with much confidence. Some refinements might include listing target species and market limits in logbooks, and using a more flexible threshold to define a significant landing.

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TABLE 1. PMFC AREA 3A CATCH, EFFORT AND CPUE STATISTICS FOR DOVER SOLE AND ENGLISH SOLE.

| Year | <u>Dover sole</u> | | | | | | |
|------|------------------------------|---|-------------------------------|--------------------------------------|------------------------------------|------------------------|-------------------------------|
| | Total Catch (Metric tons) | Sig- nifi- cant Catch (Metric tons) | Measured Effort (Hours) | Equi- valent Effort (Hours) | Percent Females by Weight | Avg. Weight (kg) | CPUE (Num- bers/ hr) |
| 1948 | 1338 | 973 | 3383 | 4653 | 61.7 | .78 | 227 |
| 1949 | 1115 | 969 | 3183 | 3660 | 66.9 | .83 | 245 |
| 1950 | 2160 | 2018 | 6541 | 7002 | 63.6 | .77 | 256 |
| 1951 | 2130 | 1292 | 4726 | 7789 | 64.0 | .75 | 233 |
| 1952 | 1843 | 810 | 3922 | 8929 | 64.7 | .75 | 177 |
| 1953 | 753 | 379 | 1684 | 3349 | 65.4 | .80 | 184 |
| 1954 | 1337 | 425 | 1812 | 5696 | 75.3 | .80 | 221 |
| 1955 | 1227 | 544 | 2726 | 6145 | 70.7 | .81 | 174 |
| 1956 | 849 | 371 | 2144 | 4912 | 63.0 | .78 | 139 |
| 1957 | 1182 | 274 | 1344 | 5810 | 69.0 | .78 | 180 |
| 1958 | 816 | 366 | 1859 | 4146 | 71.8 | .73 | 193 |
| 1959 | 886 | 499 | 2607 | 4633 | 72.4 | .77 | 181 |
| 1960 | 1010 | 614 | 3626 | 5967 | 74.9 | .83 | 152 |
| 1961 | 795 | 352 | 2503 | 5659 | 69.6 | .74 | 131 |
| 1962 | 867 | 268 | 1779 | 5758 | 77.0 | .73 | 158 |
| 1963 | 1121 | 549 | 3874 | 7916 | 75.3 | .74 | 144 |
| 1964 | 1002 | 361 | 2765 | 7687 | 70.3 | .68 | 135 |
| 1965 | 667 | 276 | 1700 | 4108 | 66.0 | .68 | 160 |
| 1966 | 766 | 475 | 2374 | 3827 | 71.3 | .62 | 229 |
| 1967 | 709 | 515 | 3066 | 4215 | 70.4 | .64 | 185 |
| 1968 | 695 | 420 | 2956 | 4896 | 75.4 | .58 | 188 |
| 1969 | 698 | 450 | 2933 | 4539 | 71.8 | .55 | 206 |
| 1970 | 716 | 403 | 2818 | 5014 | 73.2 | .61 | 172 |
| 1971 | 587 | 297 | 2171 | 4288 | 83.5 | .67 | 175 |
| 1972 | 811 | 463 | 2709 | 4739 | 69.6 | .64 | 182 |
| 1973 | 512 | 233 | 1333 | 2933 | 71.0 | .59 | 230 |
| 1974 | 712 | 319 | 2156 | 4817 | 77.0 | .61 | 205 |
| 1975 | 648 | 353 | 2480 | 4550 | 63.3 | .64 | 142 |

TABLE 1. (Continued)

| Year | <u>English sole</u> | | | | | | |
|------|------------------------------------|--|-------------------------------|--------------------------------------|------------------------------------|------------------------|-------------------------------|
| | Total Catch (Metric tons) | Sig- nifi- cant Catch (Metric tons) | Measured Effort (Hours) | Equi- valent Effort (Hours) | Percent Females by Weight | Avg. Weight (kg) | CPUE (Num- bers/ hr) |
| 1959 | 606 | 606 | 3755 | 3755 | 99.2 | .48 | 340 |
| 1960 | 761 | 738 | 4421 | 4558 | 100.0 | .43 | 387 |
| 1961 | 582 | 582 | 4693 | 4693 | 100.0 | .47 | 263 |
| 1962 | 660 | 640 | 5076 | 5238 | 96.2 | .49 | 249 |
| 1963 | 575 | 567 | 4830 | 4888 | 91.5 | .49 | 217 |
| 1964 | 419 | 410 | 3003 | 3015 | 83.5 | .45 | 251 |
| 1965 | 440 | 435 | 2520 | 2548 | 88.9 | .43 | 356 |
| 1966 | 1100 | 1100 | 4829 | 4833 | 91.1 | .46 | 453 |
| 1967 | 572 | 561 | 3494 | 3584 | 93.3 | .49 | 306 |
| 1968 | 456 | 450 | 3546 | 3592 | 91.7 | .47 | 249 |
| 1969 | 439 | 210 | 1849 | 3854 | 89.4 | .45 | 224 |
| 1970 | 362 | 338 | 3008 | 3207 | 85.4 | .45 | 214 |
| 1971 | 313 | 287 | 2953 | 3222 | 90.7 | .43 | 204 |
| 1972 | 376 | 327 | 2054 | 2365 | 89.8 | .45 | 315 |
| 1973 | 364 | 304 | 2567 | 3073 | 94.0 | .42 | 264 |
| 1974 | 295 | 295 | 2044 | 2044 | 94.4 | .44 | 310 |
| 1975 | 303 | 85 | 598 | 2145 | 93.8 | .44 | 302 |

TABLE 2. CATCH UTILIZATION RATES BY AGE FOR DOVER SOLE AND ENGLISH SOLE FROM PMFC AREA 3A. DOVER SOLE RATES FOR 1962-1975 AND ENGLISH SOLE RATES ARE FROM TENNEYCK AND DEMORY (1975). DOVER SOLE RATES FOR 1948-1961 WERE COMPUTED BY METHODS DESCRIBED IN TEXT.

| <u>Age</u> | <u>Percent of Dover Sole Uti- lized by Age 1948- 1961</u> | <u>Percent of Dover Sole Uti- lized by Age 1962- 1975</u> | <u>Percent of English Sole Utilized by Age</u> |
|------------|---|---|--|
| 4 | | | 61 |
| 5 | | | 79 |
| 6 | 12 | 32 | 89 |
| 7 | 38 | 52 | 93.5 |
| 8 | 67 | 79 | 96 |
| 9 | 86 | 94.5 | 97 |
| 10 | 97 | 99 | |
| 11 | 100 | 100 | |
| 12 | 100 | 100 | |
| 13 | 100 | 100 | |

FIGURE CAPTIONS

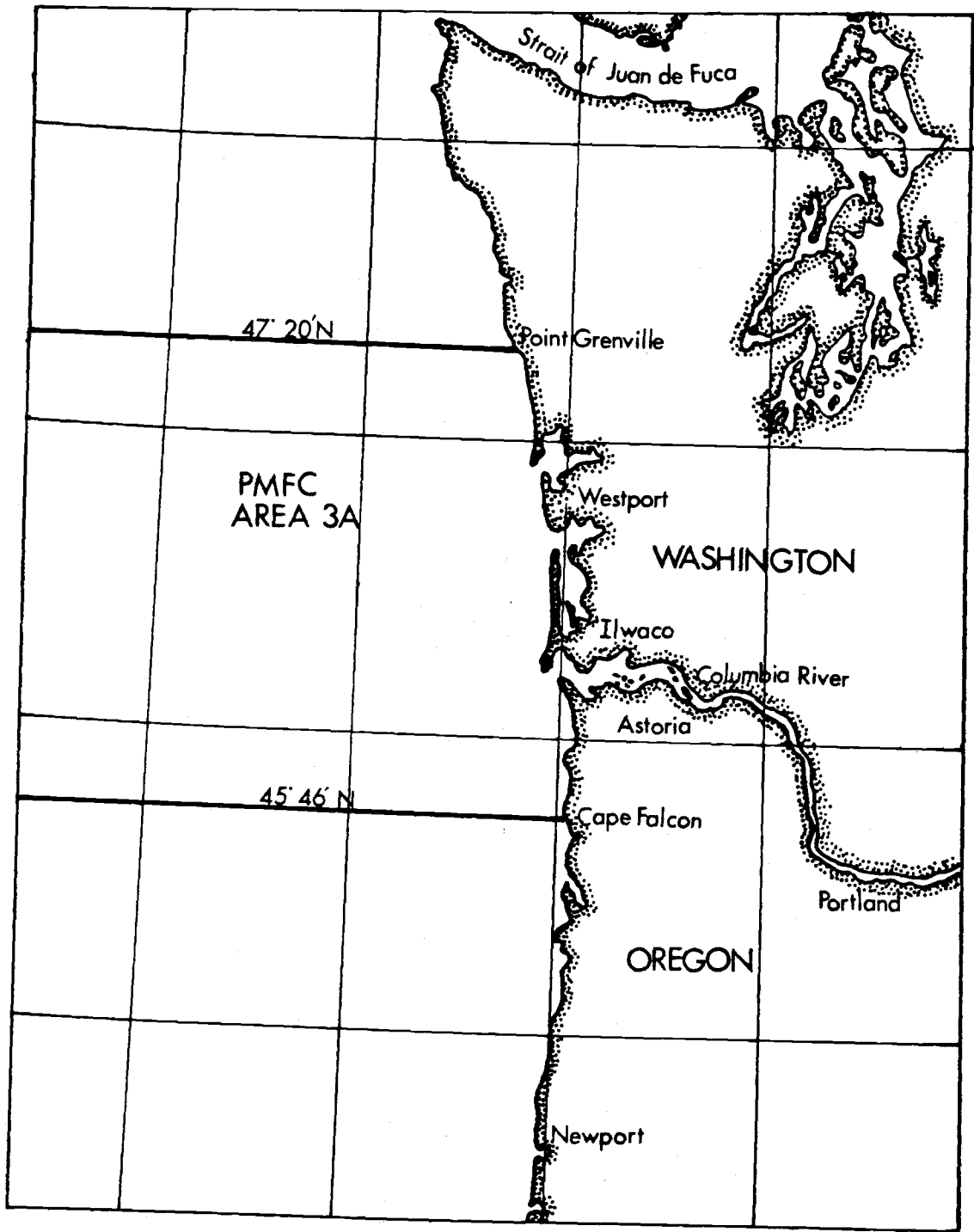
Figure 1. Location of PMFC Area 3A.

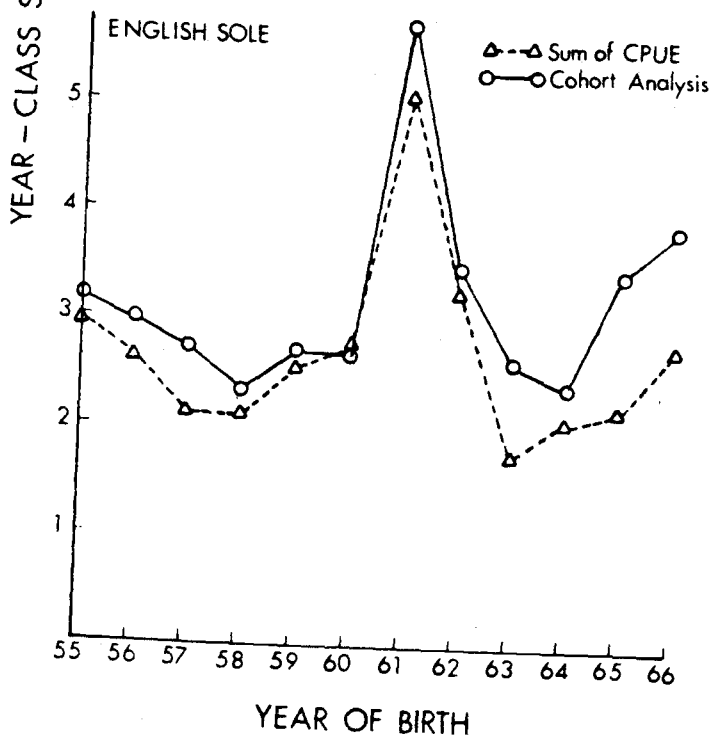
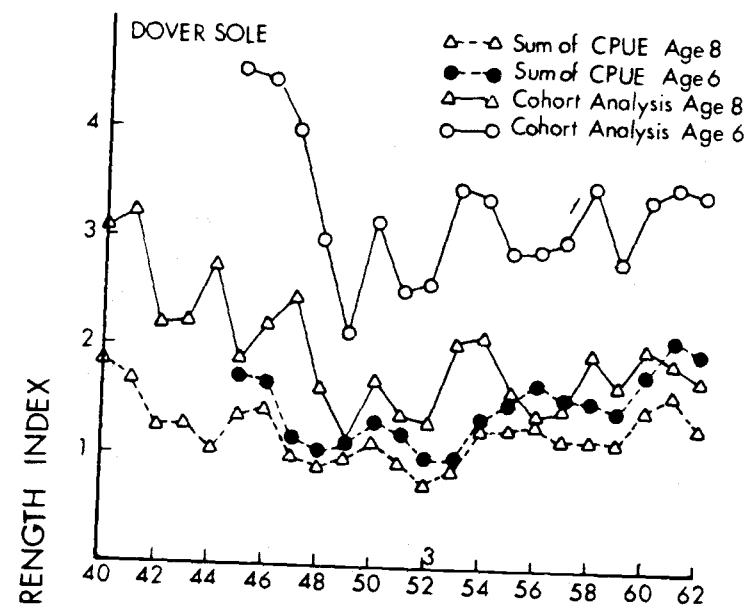
Figure 2. Indices of year class strength of Dover sole (top) and English sole (bottom). Sum-of-CPUE indices (dashed lines) are in hundreds of females per significant boat-hr. Cohort analysis indices (solid lines) are in millions of females.

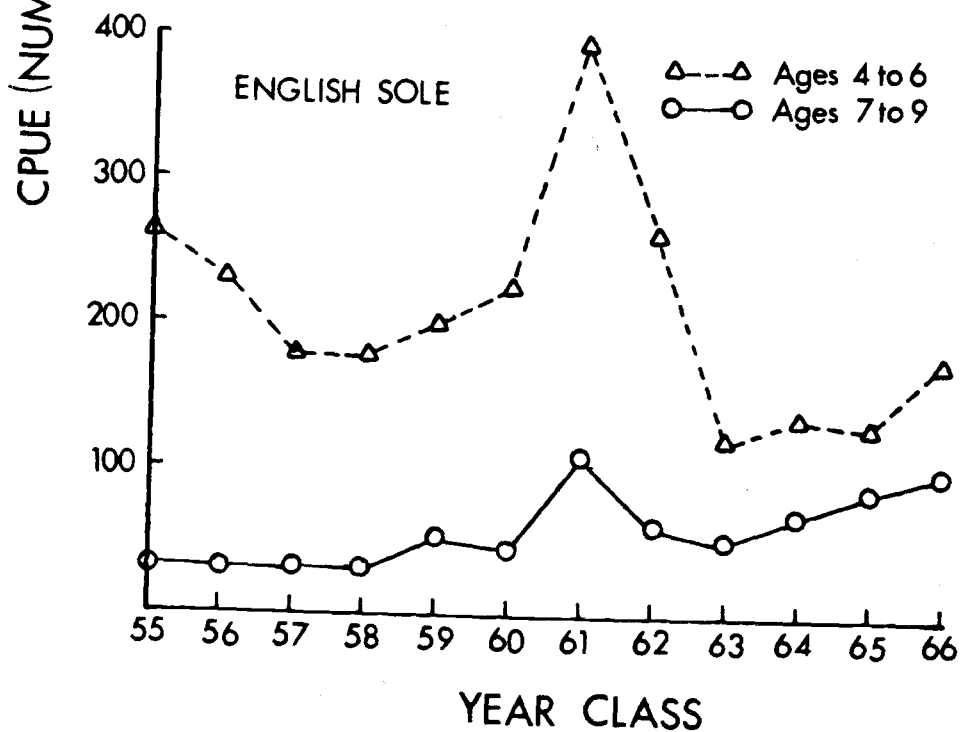
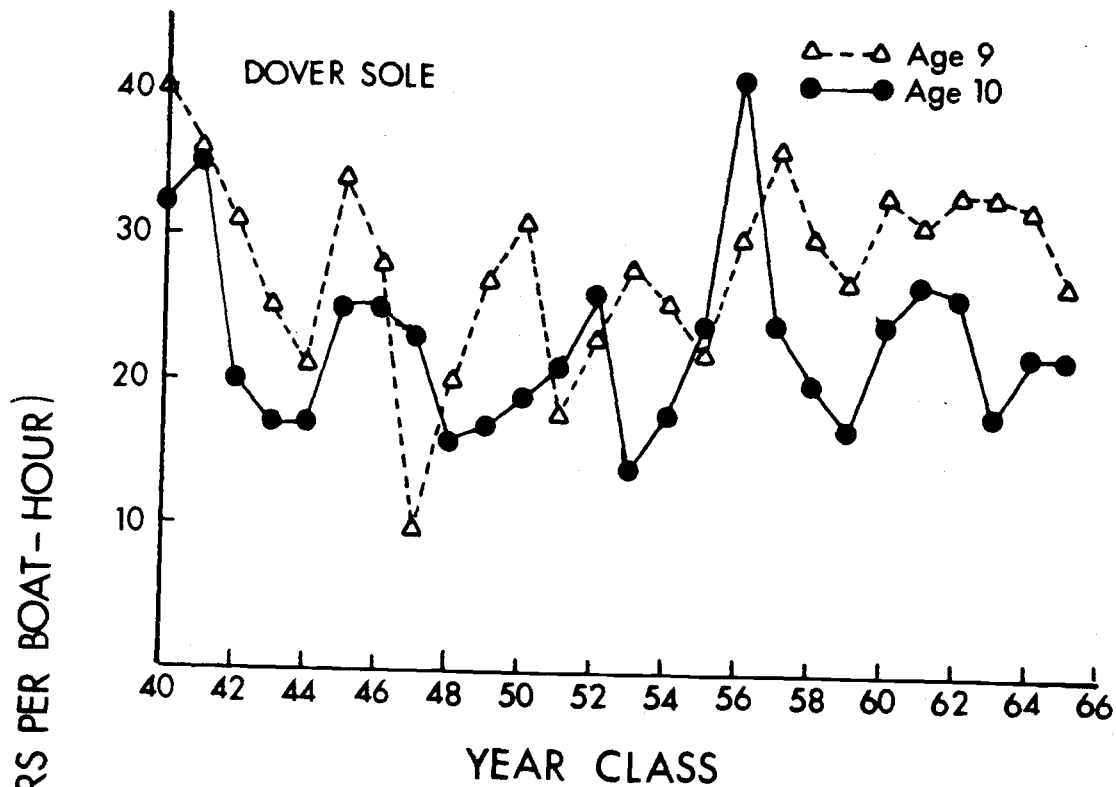
Figure 3. Top: Comparison between age 9 and age 10 CPUE abundance indices for each Dover sole year class from 1940-1966. Correlation is poor ($r=+.375$). Bottom: Combined CPUEs of ages 4 to 6 English sole compared with combined CPUEs of ages 7 through 9 English sole for each year class from 1955-1966. Age 4 to 6 CPUE was higher for year classes 1955-1960 than for 1963-1966. Opposite is true of age 7 to 9 CPUE, resulting in poor correlation between the two abundance indices ($r=+.243$).

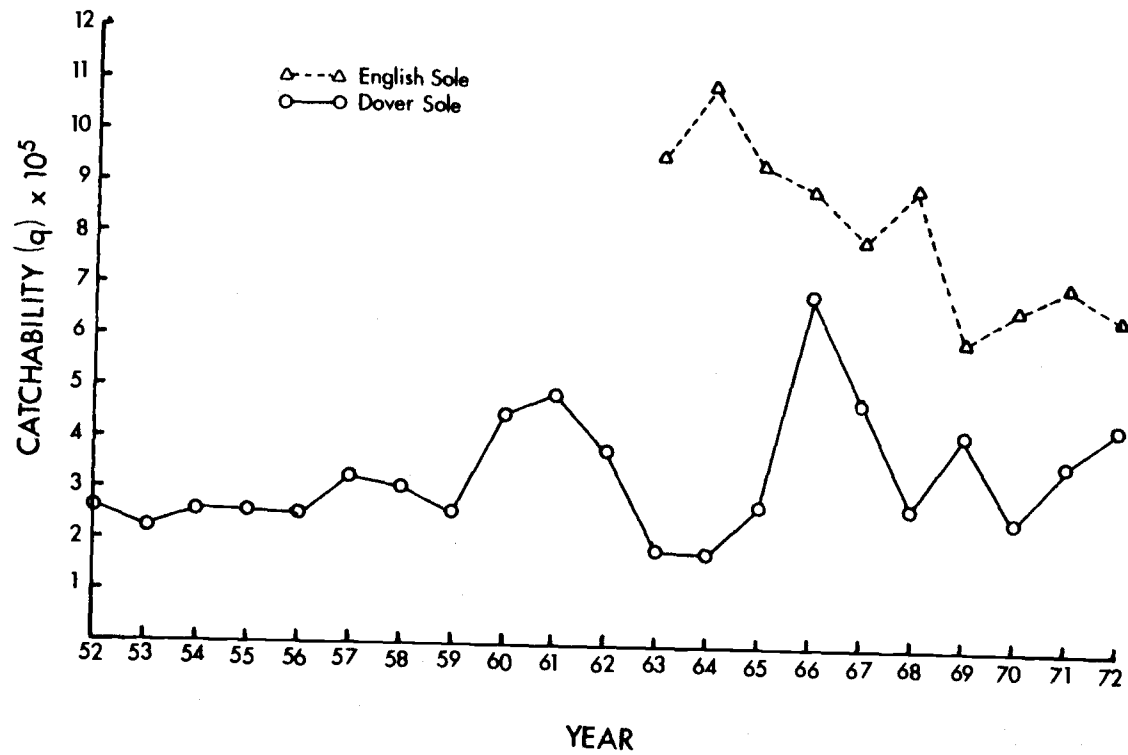
Figure 4. Yearly catchability coefficients (q) from 1952-1972 for Dover sole and from 1963-1972 for English sole. For neither fishery is there a marked upward trend, which would be expected if gear improvement had had a dominating influence on catchability.

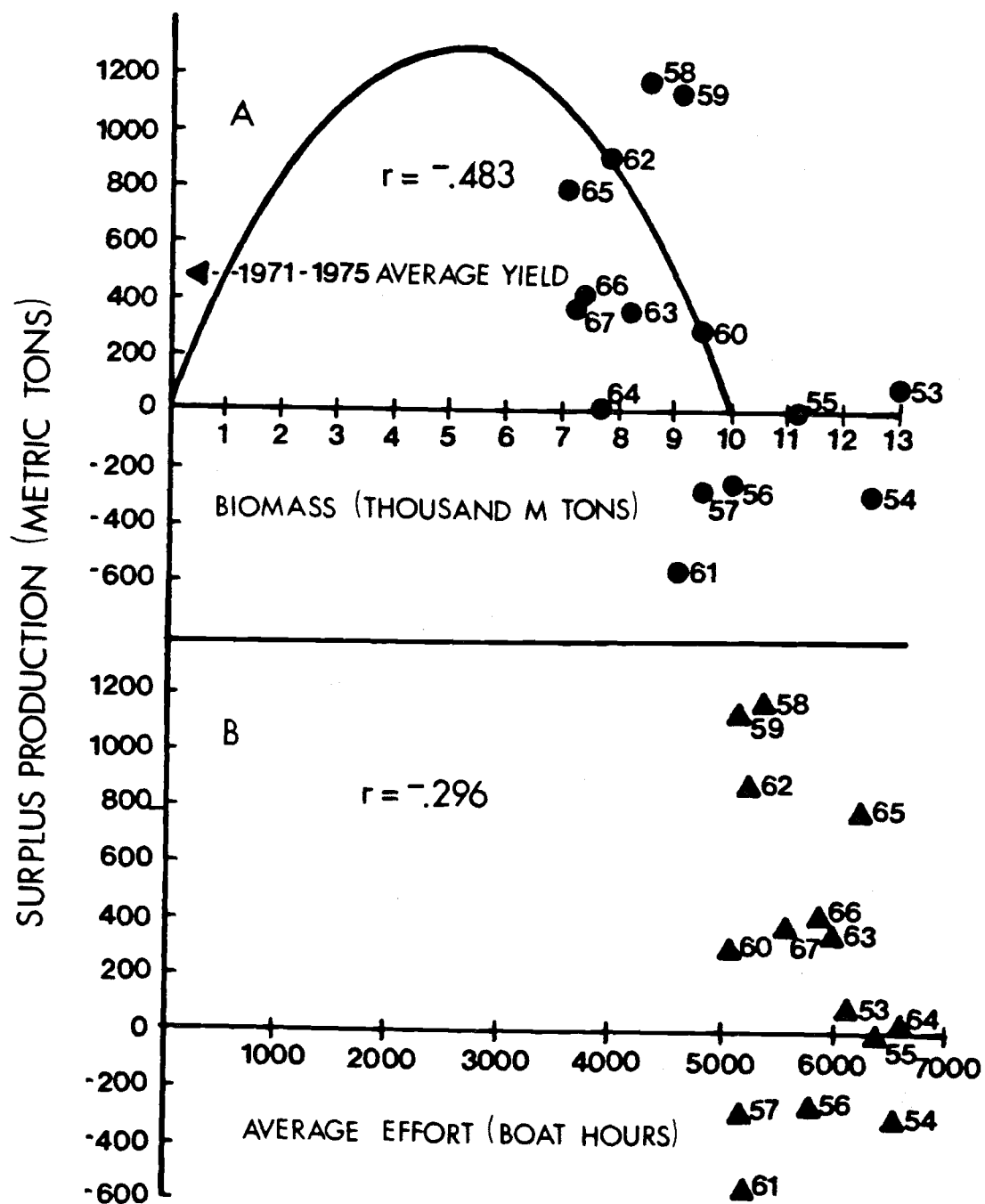
Figure 5. Top: Surplus production of female Dover sole plotted on biomass of age 6 and older females for each year from 1953-1967. Parabola fitted through origin and points by eye. Bottom: Surplus production against equivalent effort averaged over the five preceding years.











APPENDIX II.

AGE COMPOSITION OF FEMALE DOVER SOLE IN PMFC AREA 3A
LANDINGS 1948-1975 (IN PERCENT)

| Year | 4 | 5 | 6 | 7 | 8 | Age 9 | 10 | 11 | 12 | 13 | 13+ |
|------|-----|-----|------|------|------|----------|------|------|------|------|------|
| 1948 | | 0.3 | 4.5 | 17.8 | 19.2 | 18.5 | 12.9 | 7.3 | 5.9 | 3.8 | 9.4 |
| 1949 | | | | | 18.4 | 16.3 | | | | | |
| 1950 | | | | | 14.5 | 14.1 | 12.5 | | | | |
| 1951 | 0.2 | 0.7 | 5.7 | 7.6 | 16.8 | 13.3 | 15.0 | 14.2 | 10.7 | 6.3 | 9.6 |
| 1952 | | | 7.0 | 14.1 | 11.0 | 14.3 | 11.0 | 10.3 | 12.2 | 6.6 | 13.6 |
| 1953 | 0.2 | 0.3 | 2.2 | 5.8 | 12.6 | 11.3 | 9.3 | 6.8 | 8.6 | 6.8 | 36.1 |
| 1954 | | 1.7 | 3.1 | 5.8 | 14.1 | 15.4 | 7.9 | 10.6 | 8.1 | 7.9 | 25.4 |
| 1955 | | 0.2 | 2.6 | 5.5 | 5.3 | 15.9 | 14.5 | 10.4 | 7.2 | 4.6 | 33.8 |
| 1956 | | | 5.5 | 6.8 | 6.5 | 7.4 | 17.8 | 15.2 | 7.1 | 6.4 | 27.2 |
| 1957 | | | 1.8 | 6.6 | 6.2 | 10.9 | 12.8 | 14.6 | 13.9 | 10.9 | 22.0 |
| 1958 | 0.4 | 1.3 | 4.8 | 10.1 | 14.0 | 14.0 | 8.3 | 13.6 | 12.7 | 3.5 | 17.0 |
| 1959 | 0.3 | 0.3 | 3.9 | 8.2 | 17.4 | 17.4 | 9.5 | 8.6 | 7.6 | 5.3 | 21.3 |
| 1960 | | | | 2.5 | 4.9 | 11.7 | 12.5 | 15.8 | 13.6 | 11.7 | 27.3 |
| 1961 | | | 2.1 | 7.6 | 10.7 | 17.3 | 16.3 | 15.2 | 11.8 | 6.6 | 12.4 |
| 1962 | | 1.3 | 6.0 | 13.2 | 22.4 | 17.7 | 16.7 | 10.1 | 6.0 | 1.6 | 5.1 |
| 1963 | 0.3 | 1.8 | 7.8 | 20.4 | 24.3 | 18.0 | 9.9 | 5.4 | 5.4 | 5.4 | 6.6 |
| 1964 | | 1.4 | 9.0 | 19.0 | 22.4 | 16.0 | 13.7 | 7.8 | 3.9 | 3.4 | 3.6 |
| 1965 | | 2.4 | 6.1 | 13.8 | 19.9 | 19.2 | 15.3 | 9.2 | 5.6 | 4.1 | 4.3 |
| 1966 | | 0.3 | 2.3 | 8.4 | 15.6 | 15.5 | 17.7 | 11.5 | 9.7 | 6.1 | 12.9 |
| 1967 | 0.1 | 0.3 | 6.5 | 14.7 | 19.5 | 16.4 | 12.9 | 9.4 | 7.7 | 5.9 | 6.4 |
| 1968 | | 1.1 | 11.6 | 21.1 | 22.6 | 14.4 | 10.7 | 7.4 | 4.8 | 2.9 | 3.4 |
| 1969 | 0.1 | 1.9 | 10.5 | 22.1 | 26.2 | 16.2 | 8.3 | 5.3 | 3.8 | 2.2 | 3.5 |
| 1970 | 0.1 | 0.5 | 5.0 | 13.3 | 18.2 | 13.2 | 13.7 | 8.1 | 6.2 | 4.5 | 12.2 |
| 1971 | | 0.2 | 0.9 | 7.0 | 13.9 | 19.1 | 15.7 | 13.7 | 8.7 | 7.8 | 9.0 |
| 1972 | | 0.2 | 2.6 | 9.8 | 12.2 | 18.1 | 14.1 | 16.3 | 9.2 | 5.0 | 12.6 |
| 1973 | | 1.2 | 8.6 | 15.1 | 16.4 | 15.2 | 8.4 | 9.4 | 6.7 | 5.0 | 14.1 |
| 1974 | | 0.6 | 3.2 | 16.8 | 20.8 | 14.2 | 12.0 | 9.0 | 8.5 | 4.5 | 11.2 |
| 1975 | | 0.3 | 3.8 | 12.3 | 17.1 | 17.9 | 15.3 | 10.2 | 10.2 | 6.1 | 6.8 |

APPENDIX III

PERCENTAGE AGE COMPOSITION OF FEMALE ENGLISH SOLE IN PMFC AREA 3A LANDINGS, 1959-1975

| <u>Year</u> | <u>2</u> | <u>3</u> | <u>4</u> | <u>5</u> | <u>6</u> | <u>7</u> | Age <u>8</u> | <u>9</u> | <u>10</u> | <u>11</u> | <u>12</u> | <u>13</u> | <u>13+</u> |
|-------------|----------|----------|----------|----------|----------|----------|-----------------|----------|-----------|-----------|-----------|-----------|------------|
| 1959 | 0.3 | 5.6 | 19.9 | 33.6 | 24.7 | 7.6 | 3.5 | 2.1 | 1.8 | 0.8 | 0.1 | 0.1 | |
| 1960 | 1.1 | 9.3 | 24.9 | 34.0 | 20.6 | 5.1 | 2.1 | 1.3 | 1.1 | 0.5 | 0.1 | 0.1 | |
| 1961 | 0.1 | 5.3 | 20.7 | 35.4 | 24.3 | 6.6 | 3.0 | 1.9 | 1.6 | 1.0 | 0.1 | 0.1 | |
| 1962 | | | 20.9 | 29.7 | 16.8 | 8.8 | 5.2 | 0.8 | | | | | |
| 1963 | 0.2 | 5.3 | 20.6 | 31.3 | 23.3 | 8.5 | 3.0 | 3.4 | 3.4 | 0.9 | | | |
| 1964 | 0.6 | 7.3 | 21.5 | 33.4 | 23.4 | 6.8 | 3.0 | 1.7 | 1.5 | 0.7 | 0.1 | | |
| 1965 | 0.7 | 9.5 | 26.0 | 32.9 | 20.3 | 5.0 | 2.2 | 1.4 | 1.2 | 0.7 | 0.1 | | |
| 1966 | 0.4 | 4.0 | 26.9 | 43.6 | 12.2 | 7.5 | 1.9 | 1.7 | 1.3 | 0.7 | | | 0.1 |
| 1967 | 0.3 | 5.1 | 15.6 | 29.1 | 34.6 | 7.5 | 3.8 | 1.7 | 1.1 | 0.9 | 0.2 | 0.1 | 0.1 |
| 1968 | 0.2 | 5.1 | 15.4 | 17.8 | 21.2 | 27.0 | 7.0 | 3.3 | 1.4 | 0.9 | 0.5 | 0.1 | 0.1 |
| 1969 | 0.1 | 8.0 | 18.5 | 25.1 | 13.2 | 16.4 | 11.9 | 3.5 | 2.0 | 0.6 | 0.5 | 0.3 | 0.1 |
| 1970 | | 4.6 | 17.2 | 23.5 | 20.4 | 12.6 | 8.9 | 7.8 | 3.0 | 1.3 | 0.5 | 0.3 | 0.1 |
| 1971 | | 3.5 | 14.5 | 34.6 | 20.3 | 12.6 | 4.6 | 3.7 | 3.9 | 1.4 | | 0.6 | 0.4 |
| 1972 | | 1.2 | 10.8 | 21.7 | 22.3 | 13.7 | 11.2 | 5.4 | 3.7 | 4.9 | 1.3 | 1.1 | 0.2 |
| 1973 | | 6.9 | 18.5 | 29.1 | 16.7 | 15.3 | 6.9 | 3.7 | 1.2 | 1.1 | 0.3 | 0.2 | |
| 1974 | | 2.8 | 18.1 | 21.6 | 24.2 | 11.3 | 10.3 | 8.2 | 3.1 | 1.9 | 0.5 | 0.7 | 0.3 |
| 1975 | | 1.8 | 9.5 | 24.6 | 22.6 | 15.8 | 8.6 | 9.2 | 3.7 | 1.5 | 1.3 | 0.4 | 0.9 |

APPENDIX IV

KOLMOGOROV-SMIRNOV TEST OF DIFFERENCE BETWEEN MAY-SEPTEMBER DOVER SOLE AGE DISTRIBUTIONS AND AGE DISTRIBUTIONS IN OCTOBER 1967 (TOP), APRIL 1970 (MIDDLE), AND WINTER 1967 (BOTTOM).

(Columns 2 and 4 list the percentage of Dover sole of that age or younger in each seasonal age distribution. Column 5 lists the absolute difference between columns 2 and 4. The highest number in column 5 (underlined) is the measure of the significance of the difference between the two distributions.)

| Age | 1 Percent Each Age in Summer Catch | 2 Cumulative Percent in Summer | 3 Percent Each Age in Winter Catch | 4 Cumulative Percent in Winter | 5 Difference Between Cumulative Percentages |
|---|--|--|--|--|---|
| May-September 1967 vs. October 1967 (N=335) | | | | | |
| 5 | 0.4 | 0.4 | 1.5 | 1.5 | 1.1 |
| 6 | 6.5 | 6.9 | 11.3 | 12.8 | 5.9 |
| 7 | 14.7 | 21.6 | 25.7 | 38.5 | 16.9 |
| 8 | 19.5 | 41.1 | 23.9 | 62.4 | 21.3 |
| 9 | 16.4 | 57.5 | 17.6 | 80.0 | <u>22.5**</u> |
| 10 | 12.9 | 70.4 | 8.4 | 88.4 | <u>18.0</u> |
| 11 | 9.4 | 79.8 | 5.7 | 94.1 | 14.3 |
| 12 | 7.7 | 87.5 | 2.1 | 96.2 | 8.7 |
| 13 | 5.9 | 93.4 | 2.7 | 98.9 | 5.5 |
| 13+ | 6.4 | 100.0 | 1.1 | 100.0 | 0.0 |
| May-September 1970 vs. April 1970 (N=269) | | | | | |
| 5 | 0.6 | 0.6 | 1.5 | 1.5 | 0.9 |
| 6 | 5.0 | 5.6 | 1.9 | 3.4 | 2.2 |
| 7 | 13.3 | 18.9 | 8.2 | 11.6 | 7.3 |
| 8 | 18.2 | 37.1 | 12.6 | 24.2 | 12.9 |
| 9 | 13.2 | 55.3 | 18.6 | 42.8 | 12.5 |
| 10 | 13.7 | 69.0 | 12.6 | 55.4 | <u>13.6*</u> |
| 11 | 8.1 | 77.1 | 16.6 | 72.0 | <u>5.1</u> |
| 12 | 6.2 | 83.3 | 10.0 | 82.0 | 1.3 |
| 13 | 4.5 | 87.8 | 5.6 | 87.6 | 0.2 |
| 13+ | 12.2 | 100.0 | 12.4 | 100.0 | 0.0 |

| <u>Age</u> | <u>1</u> Percent Each Age in Summer Catch | <u>2</u> Cumulative Percent in Summer | <u>3</u> Percent Each Age in Winter Catch | <u>4</u> Cumulative Percent in Winter | <u>5</u> Difference Between Cumulative Percentages |
|--|---|---|---|---|--|
| May-September 1967 vs. January-April and October-December 1967 (N=508) | | | | | |
| 5 | 0.4 | 0.4 | 1.0 | 1.0 | 0.6 |
| 6 | 6.5 | 6.9 | 7.7 | 8.7 | 1.8 |
| 7 | 14.7 | 21.6 | 17.7 | 26.4 | <u>4.8</u> NS |
| 8 | 19.5 | 41.1 | 18.9 | 45.3 | 4.2 |
| 9 | 16.4 | 57.5 | 15.6 | 60.9 | 3.4 |
| 10 | 12.9 | 70.4 | 11.8 | 72.7 | 2.3 |
| 11 | 9.4 | 79.8 | 9.4 | 82.1 | 2.3 |
| 12 | 7.7 | 87.5 | 6.7 | 88.8 | 1.3 |
| 13 | 5.9 | 93.4 | 5.1 | 93.9 | 0.5 |
| 13+ | 6.4 | 100.0 | 6.1 | 100.0 | 0.0 |

APPENDIX V

NUMBERS AT AGE (IN THOUSANDS) OF EACH COHORT OF DOVER SOLE FEMALES IN PMFC AREA 3A FROM 1940 COHORT TO 1962 COHORT. CALCULATED BY METHOD OF POPE (1972).

| Cohort | Age | | | | | | | |
|--------|------|------|------|------|------|------|-----|-----|
| | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 1940 | | | 3074 | 2242 | 1682 | 1168 | 724 | 418 |
| 1941 | | | 3237 | 2427 | 1721 | 1156 | 799 | 606 |
| 1942 | | | 2197 | 1448 | 932 | 601 | 454 | 279 |
| 1943 | | | 2239 | 1423 | 927 | 705 | 456 | 304 |
| 1944 | | | 2754 | 2019 | 1580 | 1201 | 883 | 679 |
| 1945 | 4553 | 2950 | 1883 | 1437 | 972 | 651 | 439 | 229 |
| 1946 | 4445 | 2803 | 2210 | 1569 | 1106 | 792 | 511 | 326 |
| 1947 | 4063 | 3224 | 2466 | 1942 | 1537 | 1134 | 830 | 622 |
| 1948 | 3001 | 2162 | 1630 | 1275 | 924 | 695 | 504 | 300 |
| 1949 | 2154 | 1554 | 1162 | 864 | 589 | 408 | 204 | 88 |
| 1950 | 3170 | 2313 | 1730 | 1265 | 882 | 616 | 402 | 280 |
| 1951 | 2543 | 1940 | 1396 | 946 | 663 | 429 | 269 | 164 |
| 1952 | 2611 | 1847 | 1349 | 1044 | 720 | 450 | 313 | 220 |
| 1953 | 3487 | 2609 | 2082 | 1597 | 1153 | 841 | 615 | 471 |
| 1954 | 3407 | 2789 | 2149 | 1526 | 1053 | 732 | 545 | 369 |
| 1955 | 2906 | 2262 | 1643 | 1027 | 682 | 468 | 291 | 184 |
| 1956 | 2921 | 2237 | 1426 | 902 | 618 | 364 | 232 | 150 |
| 1957 | 3035 | 2233 | 1486 | 1068 | 744 | 517 | 363 | 265 |
| 1958 | 3521 | 2619 | 1988 | 1470 | 1081 | 797 | 608 | 450 |
| 1959 | 2835 | 2209 | 1680 | 1201 | 858 | 633 | 455 | 315 |
| 1960 | 3411 | 2736 | 2040 | 1435 | 1034 | 738 | 514 | 348 |
| 1961 | 3539 | 2754 | 1921 | 1299 | 913 | 643 | 397 | 288 |
| 1962 | 3469 | 2542 | 1731 | 1237 | 879 | 607 | 445 | 295 |

APPENDIX VI

NUMBERS AT AGE (IN THOUSANDS) OF EACH COHORT OF ENGLISH SOLE FEMALES
IN PMFC AREA 3A FROM 1955 COHORT TO 1966 COHORT. CALCULATED BY METHOD
OF POPE (1972)

| <u>Cohort</u> | <u>Age</u> | | | | | |
|---------------|------------|----------|----------|----------|----------|----------|
| | <u>4</u> | <u>5</u> | <u>6</u> | <u>7</u> | <u>8</u> | <u>9</u> |
| 1955 | 3200 | 2020 | 842 | 334 | 142 | 76 |
| 1956 | 2987 | 1592 | 704 | 309 | 146 | 88 |
| 1957 | 2738 | 1668 | 814 | 363 | 222 | 146 |
| 1958 | 2332 | 1343 | 633 | 297 | 178 | 95 |
| 1959 | 2700 | 1691 | 977 | 546 | 253 | 150 |
| 1960 | 2690 | 1763 | 980 | 468 | 271 | 145 |
| 1961 | 5742 | 3921 | 1865 | 1015 | 529 | 300 |
| 1962 | 3496 | 1759 | 956 | 524 | 258 | 136 |
| 1963 | 2635 | 1711 | 1093 | 700 | 438 | 298 |
| 1964 | 2401 | 1584 | 937 | 558 | 337 | 175 |
| 1965 | 3450 | 2330 | 1550 | 1019 | 661 | 440 |
| 1966 | 3874 | 2703 | 1755 | 1139 | 730 | 482 |

APPENDIX VII

INSTANTANEOUS FISHING MORTALITY RATE BY AGE FOR FEMALE DOVER SOLE IN PMFC AREA 3A FROM 1952-1972. CALCULATED FROM NUMBERS AT AGE (APPENDIX V)

| Year | Age | | | | | | | | \bar{F} by Year for Ages 10-13 |
|--|------|------|------|------|------|------|------|------|--|
| | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | |
| 1952 | .261 | .249 | .110 | .229 | .240 | .170 | .350 | | .237 |
| 1953 | .031 | .038 | .071 | .045 | .073 | .080 | .076 | .117 | .076 |
| 1954 | .128 | .068 | .142 | .191 | .075 | .235 | .286 | .199 | .147 |
| 1955 | .126 | .082 | .039 | .150 | .200 | .108 | .206 | .215 | .158 |
| 1956 | .115 | .091 | .046 | .034 | .134 | .193 | .063 | .172 | .124 |
| 1957 | .070 | .090 | .096 | .122 | .104 | .239 | .453 | .203 | .190 |
| 1958 | .146 | .129 | .113 | .183 | .086 | .112 | .249 | .145 | .128 |
| 1959 | .090 | .114 | .189 | .160 | .167 | .122 | .089 | .162 | .121 |
| 1960 | .000 | .026 | .056 | .156 | .159 | .494 | .317 | .209 | .271 |
| 1961 | .051 | .061 | .065 | .172 | .234 | .226 | .645 | .198 | .278 |
| 1962 | .067 | .120 | .142 | .125 | .269 | .270 | .162 | .202 | .221 |
| 1963 | .107 | .250 | .270 | .171 | .116 | .164 | .293 | .277 | .150 |
| 1964 | .096 | .207 | .258 | .209 | .163 | .112 | .154 | .269 | .142 |
| 1965 | .050 | .076 | .180 | .177 | .178 | .095 | .068 | .144 | .113 |
| 1966 | .021 | .074 | .101 | .162 | .330 | .273 | .190 | .134 | .265 |
| 1967 | .051 | .093 | .135 | .107 | .164 | .252 | .259 | .148 | .205 |
| 1968 | .111 | .160 | .152 | .136 | .106 | .155 | .233 | .171 | .135 |
| 1969 | | .185 | .191 | .128 | .104 | .069 | .112 | .159 | .192 |
| 1970 | | | .136 | .152 | .137 | .130 | .102 | .175 | .126 |
| 1971 | | | | .141 | .151 | .162 | .167 | .150 | .158 |
| 1972 | | | | | .171 | .282 | .190 | .166 | .209 |
| \bar{F} by age (1952- 1968) | .089 | .113 | .124 | .149 | .165 | .175 | .200 | .185 | .174 |

APPENDIX VIII

INSTANTANEOUS FISHING MORTALITY RATE BY AGE FOR FEMALE ENGLISH SOLE IN PMFC AREA 3A FROM 1963-1972. CALCULATED FROM NUMBERS AT AGE (APPENDIX VI)

| Year | Age | | | | | | F by Year for Ages 6-9 |
|--------------------------------|------|------|------|------|------|------|------------------------------------|
| | 4 | 5 | 6 | 7 | 8 | 9 | |
| 1963 | .168 | .453 | .506 | .451 | .318 | | .471 |
| 1964 | .123 | .249 | .456 | .194 | .209 | .223 | .332 |
| 1965 | .081 | .237 | .283 | .211 | .115 | .189 | .242 |
| 1966 | .387 | .443 | .439 | .468 | .332 | .358 | .436 |
| 1967 | .132 | .310 | .308 | .246 | .222 | .265 | .288 |
| 1968 | .116 | .147 | .300 | .352 | .329 | .266 | .327 |
| 1969 | .092 | .225 | .147 | .410 | .267 | .285 | .234 |
| 1970 | .060 | .108 | .218 | .167 | .339 | .237 | .215 |
| 1971 | | .132 | .119 | .204 | .087 | .238 | .231 |
| 1972 | | | .132 | .133 | .356 | .175 | .154 |
| F by age (1963- 1970) | .145 | .256 | .308 | .300 | .246 | .258 | .293 |