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Title: Relationships between shelf temperatures, coastal sea level,

the coastal upwelling index, and English sole (Parophrys vetulus)

spawning activity off Oregon

Abstract approved: ___Redacted for privacy___
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The purpose of this study was to compile records of English sole
(Parophrys vetulus) spawning activity in Oregon waters and to attempt
to identify the environmental factors responsible for the control of
spawning.   A   subobjective was to determine whether statistical
relationships exist between Oregon coastal shelf temperatures, sea
level, and the upwelling index.

Spawning times for English sole in Oregon waters were estimated
for 13 years using data of adult female gonadal condition and surveys
of pelagic larvae and newly-settled benthic juveniles of known ages.
The breeding season of this species is extremely protracted and
variable. Most spawning occurs between September and April, with peak
spawning lasting 1-3 months within this period. Some spawning has been
documented to occur in all seasons of the year.

Data sets of barometric pressure, the upwelling index, photoperiod and continental shelf temperatures along the Oregon coast were obtained to examine possible interrelationships with the English sole spawning records. Because data of near-bottom temperature were not sufficiently complete, I investigated the relationships between the available sporadic records of temperature and two regularly measured variables, coastal sea level and the upwelling index. Monthly means of deep temperature at a moored current meter (Poinsettia), sea level at Newport, Oregon, and the coastal upwelling index at $45^{o}N$, $125^{o}W$ were found to be significantly ($P<0.05$) correlated over 1972-1974. Significant correlations were also found between both directly observed values and calculated anomalies of deep temperatures at two repeated hydrographic stations (NH-5 and NH-15), and monthly mean sea level at Neah Bay, Washington and the upwelling index at $45^{o}N$, $125^{o}W$ during 1959-1969. The geometric mean estimate of the functional regression best describes each linear relationship between variable pairs. Since the relationships between temperature and sea level were slightly stronger than those between temperature and the upwelling index, Neah Bay sea level data were used to generate time series of a bottom temperature index, which was then included into the environmental data set.

Of the environmental variables considered, shelf temperature dynamics (inferred from the relationship with Neah Bay sea level) appeared to best account for variations in English sole spawning activity. Three hypotheses about temperature control of spawning were

proposed and described by mathematical relationships. These relationships were incorporated into a simulation model, which was driven by time series of derived bottom temperature estimates. Hypotheses were parameterized and evaluated, based on the agreement between simulated and historical spawning records. The three hypotheses which collectively explained most of the variability in observed spawning are: (1) the rate of gonadal development is inversely related to summer bottom temperatures; (2) spawning is inhibited by temperatures below about 7.8 C; and (3) spawning is delayed by rapid increases in bottom temperature. The model can be used to simulate spawning activity for years of no empirical spawning records and can also be used in the design of laboratory experiments capable of validating the proposed hypotheses.

Relationships between Shelf Temperatures, Coastal Sea Level,
the Coastal Upwelling Index, and English sole (_Parophrys vetulus_)
Spawning Activity off Oregon

by

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William Gilbert constructed Fig. 1 and 4 of part II. Henry Pittock supplied the sea level data and Andrew Bakun provided recent values of the upwelling index. I am indebted to the following people who made part III possible by making their data available to me during the courses of their studies: Gary Hewitt, Earl Krygier, Joanne Laroche, Sally Richardson, William Pearcy, Andrew Rosenberg, Bruce Mundy and Katherine Myers.

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Relationships between Shelf Temperatures, Coastal Sea Level,

the Coastal Upwelling Index, and English sole (Parophrys vetulus)

Spawning Activity off Oregon

Introduction

The reproductive strategies utilized by a given species are
believed to be those which result in maximum reproductive success by
best ensuring that the young will encounter conditions favorable for
growth and survival. Annual variations in reproductive success (i.e.,
year-class strength) reflect deviations of those factors to which the
species' fecundity, reproductive strategies and survival are related.
Since reproductive success is an important component of fishery
productivity, investigations of this aspect constitute part of the
biological basis for the management of commercially important fish
stocks. In this regard studies of spawning activity and its
environmental control can be of value to the management of species with
variable spawning times. This is particularly true for those in which
year-class strength is determined by factors operating over a short
time period during the early stages of development. For these fishes
the spawning time partly determines whether the young will encounter
favorable conditions.

English sole, Parophrys vetulus, is a commercially important
species to the bottom trawl fisheries along the west coast of the
United States and Canada. The breeding season of this species is quite

protracted (Budd 1940; Harry 1959; Jow 1969) and variable (Laroche and Richardson 1979; Hayman and Tyler 1980). The spawning time may affect the survival rate of young English soles, because year-class strength appears to be largely determined by environmental conditions prevailing prior to spawning (Hayman and Tyler 1980) and during the early life history stages (Ketchen 1956). For this reason investigation of the variations in English sole spawning activity may lead to a better understanding of their recruitment process and to improved management.

The purpose of this study was three fold. The first objective was to compile records of English sole spawning activity in Oregon waters using data of gonadal condition from commercially caught females landed at Oregon ports, size distributions and known growth rates of pelagic larvae collected off the Oregon coast, and surveys of newly-settled juveniles in Yaquina Bay, Oregon. The second objective was to attempt to identify interrelationships between these spawning records and data of barometric pressure, the upwelling index, day length, and deep temperature on the Oregon continental shelf. Because deep temperature observations were not sufficiently complete, a third objective was to determine whether temperature is statistically related to two regularly measured variables (coastal sea level and the upwelling index), so that a continuous temperature index could be developed.

This thesis is comprised of two independent papers. The first is coauthored by Adriana Huyer and is designed to meet the third objective of this study. The second paper is coauthored by Albert V. Tyler and is directed towards the first two objectives.

The Relationships between Shelf Temperatures, Coastal Sea Level and the

Coastal Upwelling Index off Newport, Oregon

(Coauthor: Adriana Huyer)

Abstract

Sparse bottom temperature records have hampered studies dealing with demersal fish species living on the continental shelf along the northwest coast of North America. We investigated the relationships between deep temperatures on the Oregon continental shelf and two regularly measured variables, coastal sea level and the upwelling index. Monthly means of deep temperature at a moored current meter (Poinsettia), sea level at Newport, Oregon and the coastal upwelling index at 45^ON, 125^OW were found to be significantly ($P<0.05$) correlated over 1972-1974. Significant correlations were also found between both directly observed values and calculated anomalies of deep temperatures at two repeated hydrographic stations (NH-5 and NH-15), and monthly mean sea level at Neah Bay, Washington and the upwelling index at 45^ON, 125^OW during 1959-1969. Since the relationships between temperature and sea level were slightly stronger than those between temperature and the upwelling index, sea level is a more reliable deep temperature indicator. The geometric mean estimate of the functional regression best describes each linear relationship between variable pairs. The regression equations between temperature and sea level (or the upwelling index) and between their anomalies can be useful to

reveal bottom temperature dynamics during periods of sparse observations.

Introduction

Fishery stock-recruitment models must incorporate environmental factors in order to sufficiently account for year-class strength variations of many fish species. The most commonly considered physical factor is temperature, owing to its known effects on many physiological processes and its linkage to other factors such as salinity, currents and productivity. Temperature appears to significantly affect the recruitment success of numerous fishes (Ketchen 1956; Lett et al. 1975; Sutcliffe et al. 1977; and others). Temperature may act on reproductive success by controlling the amount of energy directed into growth and gonadal products in maturing adults. This control may be exercised directly through the physiological processes associated with growth (Warren and Davis 1967) and gonadogenesis (Weibe 1968) or indirectly through a linkage with food production (Bagenal 1967). Temperature variations may also influence spawning dates (de Vlaming 1972) and therefore the timing of eggs and larvae with fluctuating biotic and abiotic conditions. In addition temperature may regulate the survival of the young by influencing their food availability (Lett et al. 1975), growth (Zweifel and Lasker 1976) and duration of pelagic life (Ketchen 1956). For these reasons bottom temperatures can be very important to demersal fish species.

Unfortunately, sporadic bottom temperature records along the northwest coast of North America have impeded fishery correlation and simulation studies in this region. Therefore it would be advantageous to identify a regularly measured environmental factor which is well

correlated with deep temperatures on the continental shelf. Off Oregon surface temperatures are not representative of deep temperatures (at least not seasonally), in part because of the seasonal influences of coastal upwelling and the Columbia river plume (Huyer 1977). Previous studies have examined relationships between surface or near-surface temperatures and such factors as sea level, wind, atmospheric pressure and upwelling (Roden 1960; Bourke 1969; Fisher 1970; and others). To our knowledge no studies have found relationships between bottom or near-bottom shelf temperatures and these or other factors.

The apparent similarity between time series of coastal sea level and 40 m temperature at a current meter mooring located over the 100 m isobath off Newport, Oregon (Huyer and Smith 1978: Fig. 2) suggested to us that perhaps sea level might be a good index of bottom temperature. A temperature-sea level relationship would be useful because sea level measurements are readily available to researchers and are recorded at regular intervals. We also considered the possibility that deep temperatures are related to the coastal upwelling index (Bakun 1973; 1975), because this index is proportional to an important driving force in the Oregon oceanographic system, the alongshore wind stress. This index is already widely used in fishery and oceanographic studies in this region. Values of the upwelling index are available at regular intervals to provide information about upwelling system dynamics. The purpose of this study was to determine whether coastal sea level or the upwelling index can be used to infer near-bottom temperatures on the continental shelf off Oregon.

Description of Observations

We obtained a data set for the period 17 December 1972 through 2 April 1974 (Table 1), which included daily means of the 80 m temperature at a mid-shelf current meter mooring named Poinsettia (Fig. 1), the sea level at nearby Newport, Oregon and daily and monthly values of the coastal upwelling index at $45^{\circ}N$, $125^{\circ}W$. The current observations from this mooring and the simultaneous sea level data have been described by Huyer et al. (1979). The temperature at 80 m was recorded at intervals of 10 or 20 min, filtered to remove diurnal and shorter oscillations and reduced to 6-hourly values (4 per day). Sea level was recorded on an hourly basis, filtered to remove tides, adjusted for the inverted barometer effect and abridged to 6-hourly values. Using the 6-hourly records we calculated daily means of temperature and sea level (Fig. 2). Daily (Fig. 2) and monthly values of the upwelling index were reported by Bakun (1973; 1975). Since the computation of this index involves a nonlinear term (wind stress), monthly values (computed from monthly mean pressure fields) are not identical to the monthly means of the daily values (based on 6-hourly computations), although they are highly correlated (Bakun 1973).

A second data set spans June 1959 through November 1969 (Table 1) and includes observations of near-bottom temperatures from repeated hydrographic stations at NH-5 and NH-15 (Fig. 1), monthly means of hourly (not adjusted for atmospheric pressure) sea level at Neah Bay, Washington and monthly values of Bakun's upwelling index. The hydrographic stations were described by Huyer (1977). Temperature was

Table 1. Descriptions of oceanographic data used in this study.

Location	Observation	Total depth (m)	Sample depth (m)	Dates	Data Type	No. of values
Poinsettia (44°45′N, 124°17.5W)	Temperature*	100	80	17 Dec 72 – 2 Apr 74	Daily means	400
Newport, OR	Sea level[†]	–	–	17 Dec 72 – 2 Apr 74	Daily means	472
45°N 125°W	Upwelling index	–	–	17 Dec 72 – 2 Apr 74	Daily values	472
					Monthly values	17
NH-5 (44°39.1′N, 124°10.6′W)	Temperature	55	40 – 50	29 Jun 59 – 21 Nov 69	Approx. 8 per yr.	78
NH-15 (44°39.1′N, 124°27.4′W)	Temperature	100	60 – 90	29 Jun 59 – 21 Nov 69	Approx. 8 per yr.	82
Neah Bay, WA	Sea level[‡]	–	–	Jun 59 – Nov 69	Monthly means	126
45°N 125°W	Upwelling index	–	–	Jun 59 – Nov 69	Monthly values	126

*This record contains two gaps (23 March 1973 through 12 April 1973 and 25 June 1973 through 14 August 1973). These gaps were also placed into the sea level and upwelling records for all statistical analyses involving temperature and these other variables.

[†]Subtract 1.433 m from Newport sea level to refer to mean lower low water.

[‡]Subtract 0.701 m from Neah Bay sea level to refer to mean lower low water.

Figure 1. Location of stations Poinsettia (P), NH-5 and NH-15 in relation to Newport, Oregon and Neah Bay, Washington. This figure is a Lambert conformal conic projection made from the Juan de Fuca plate map, published by the Pacific Geoscience Center, Sidney, British Columbia.
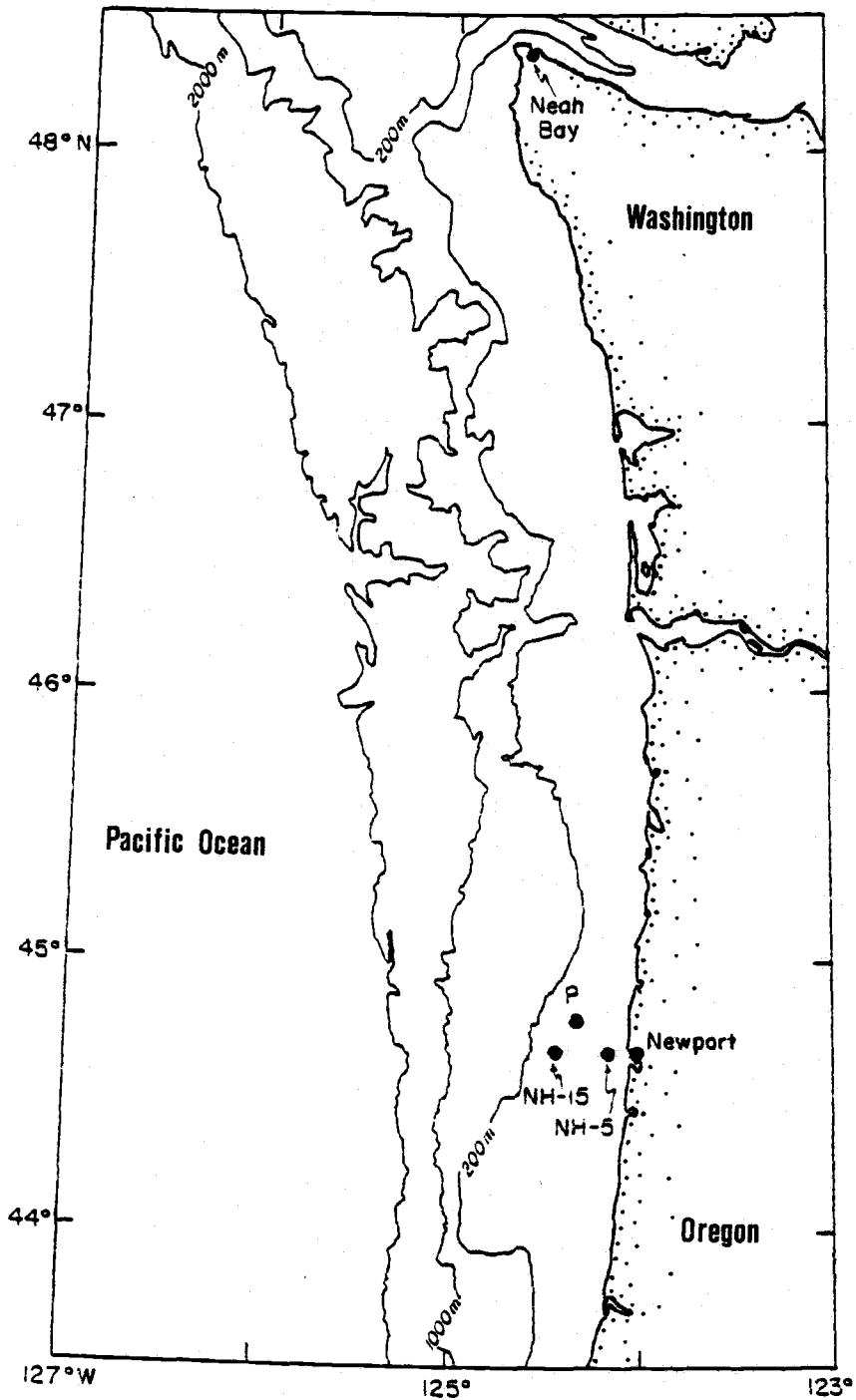
Figure 2.   Daily values of (a) 80 m temperature at station Poinsettia;
(b) Newport sea level; and (c) the upwelling index at   45°N, 125°W   for
16 December 1972 to 3 April 1974.
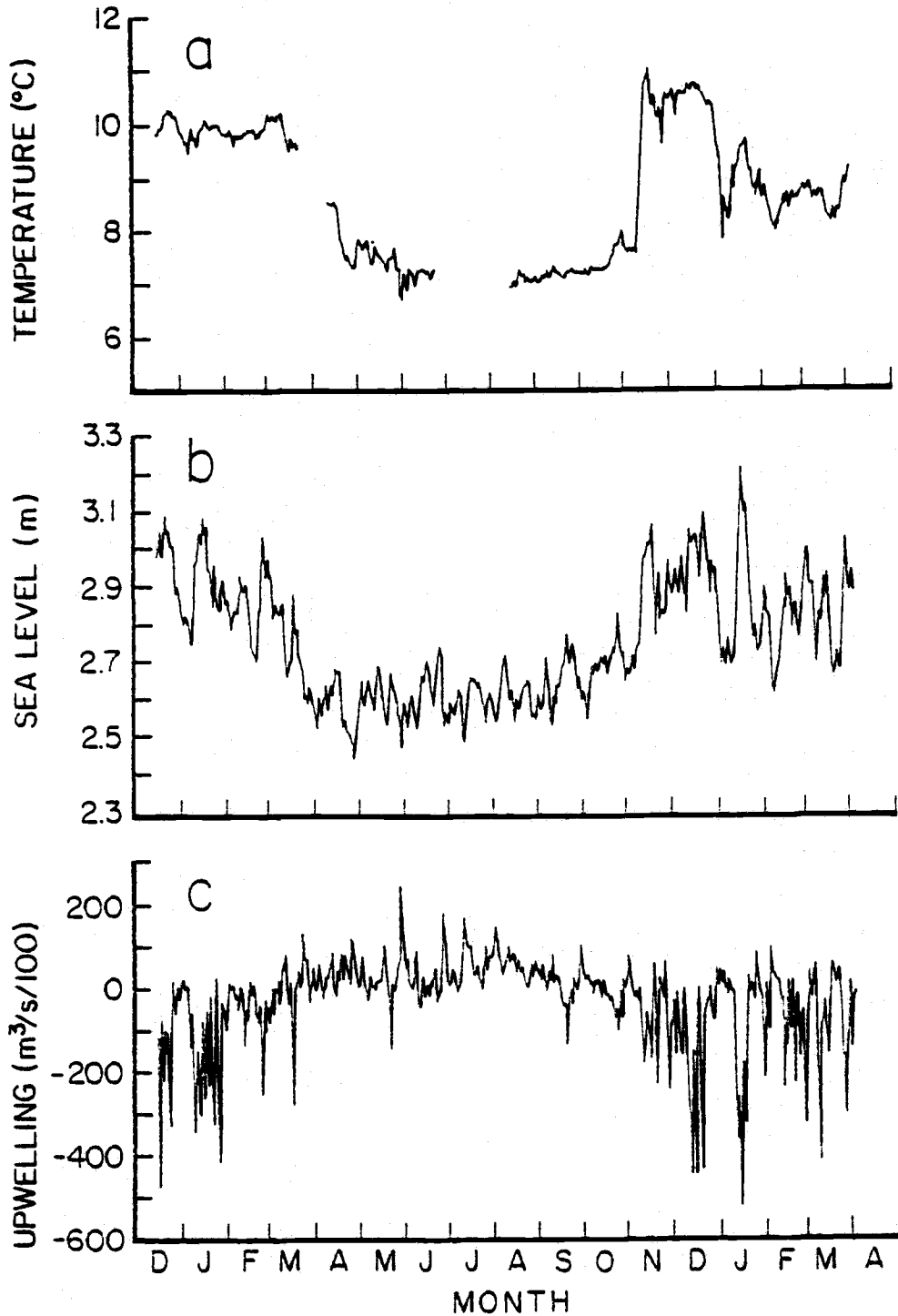
recorded an average of eight times per year at each station. When more than one observation was available for a given month, they were averaged. A total of six monthly values at each NH-5 and NH-15 are actually means of 2-4 observations.

Data Analysis

Time series plots (Fig. 2) and scatter diagrams (not shown) suggested the existence of linear relationships between Poinsettia deep temperature, Newport sea level and the upwelling index at $45^{\circ}N$, $125^{\circ}W$ for 1972-1974. To verify this we calculated simple linear correlation coefficients for daily and monthly mean values of the variables (Table 2). Since time series of each variable are autocorrelated, consecutive observations are not independent and the significance of these crosscorrelations cannot be determined by simply consulting standard statistical tables with $N_i - 2$ degrees of freedom, where N_i is the number of observations. In order to document statistical significance we could calculate normalized correlation coefficients (Sciremammano 1979) or adjust the number of degrees of freedom by first estimating the actual number of independent observations (Bayley and Hammersley 1946; Davis 1976). We chose the latter procedure and used the Bayley and Hammersley formulation because it is more conservative, i.e. results in fewer degrees of freedom. The Bayley and Hammersley formulation can be written as

$$n_i^* = \frac{N_i^2}{N_i + 2 \sum_{j=1}^{N_i - 1} (N_i - j) \, p \, (j \Delta t)^2} \quad (1)$$

where n_i^* is the number of independent observations estimated from the autocorrelation ($p_i(j \Delta t)$) at lag $j \cdot \Delta t$ of variable i for i=1,2. The number of degrees of freedom (DF) can then be taken as

$$DF = \min(n_1^*, n_2^*) - 2. \quad (2)$$

Table 2. Correlation coefficients (number of observations and degrees of freedom in parentheses) among daily and monthly means of 80 m temperature (T) at Poinsettia (P), sea level (SL) at Newport (NP) and the upwelling index (UI) at 45^ON, 125^OW.

a. Daily means

	SL(NP)	UI
UI	-0.6098(472,12)*	
T(P)	0.8046(400,12)**	-0.4040(400,12)

b. Monthly means

	SL(NP)	UI
UI	-0.8909(17,5)**	
T(P)	0.9085(15,5)**	-0.8255(15,5)*

*P<0.05
**P<0.02

In practice the summation in (1) is carried out for $j=1,2,...,K$, where K is some number large relative to the lag at which the autocorrelation becomes zero. We took K to be a value such that DF reached an asymptote.

Since the 80 m temperature series at Poinsettia has two gaps, it is not possible to calculate n_i^* for the entire temperature record. Over the longest noninterrupted period (15 August 1973 through 2 April 1974) the values of n_i^* calculated for the temperature and sea level records were nearly identical. Therefore we assumed the value of n_i^* for temperature over the entire record length (17 December 1972 through 2 April 1974) to be equal to the value of n_i^* calculated for sea level by Eq. (2).

Correlations among Poinsettia temperature, Newport sea level and the upwelling index (Table 2) were significant in all but one case at the 95% confidence level using tables of critical values of the correlation coefficient (Zar 1974: Table D.21). The exception (daily temperature versus upwelling) is not surprising because the short period upwelling index fluctuations are large relative to those of temperature, particularly during the winter months (Fig. 2a,c).

Observations at hydrographic stations made repeatedly (approximately 8 per year) at NH-5 and NH-15 (Fig. 1) between June 1959 and November 1969 allowed us to determine whether the associations suggested by the Poinsettia data remained true for longer time scales. For this time period, we had access to monthly mean sea level data from Neah Bay (the Newport sea level record does not start until 1967), and

monthly values of Bakun's upwelling index at 45^ON, 125^OW. Since short period deep temperature fluctuations are usually small (Fig. 2a), individual observations of temperature should generally be good approximations to the monthly means. On this basis we corresponded NH-5 and NH-15 temperature observations with monthly means of sea level and the upwelling index. Because lagged correlations on daily values during 1973 indicated that the upwelling index leads sea level by about 2 days and deep temperature by 5 days, no lagging of monthly means was necessary.

Scatter diagrams (not shown) again suggested linear relationships between monthly values of each variable pair. A significant ($P < 0.02$) positive correlation exists between temperature and sea level and significant negative correlations exist between these two variables and the coastal upwelling index (Table 3a). Degrees of freedom were calculated by the procedure used earlier. The conservatism of the Bayley and Hammersley (1946) formulation is reflected by the fact that there is approximately only one degree of freedom per year of data (Table 3a).

In order to eliminate the effect of seasonal cycles on the correlations, we first computed the long-term monthly means for each variable (Table 4). For temperature the long-term monthly means were estimated by averaging individual observations by month for the duration of the records (June 1959 - November 1969). For sea level and the upwelling index, a comparable period was chosen such that an equal number of values (11) were used for each month (June 1959 - May 1970).

Table 3. Correlation coefficients (number of observations and degrees of freedom in parentheses) between monthly observations of near-bottom temperatures (T) at NH-5 and NH-15 and monthly means of sea level (SL) at Neah Bay (NB) and the upwelling index (UI) at 45°N, 125°W over 1959-1969 for both the observed monthly means and the monthly anomalies.

a. Observed values

	SL(NB)	UI	T(NH-5)
UI	-0.8563(126,9)**		
T(NH-5)	0.7425(78,9)**	-0.7103(78,9)**	
T(NH-15)	0.7168(82,9)**	-0.6791(82,9)**	0.8579(78,9)**

b. Anomalies

	SL(NB)	UI	T(NH-5)
UI	-0.6198(126,65)**		
T(NH-5)	0.4662(78,65)**	-0.3432(78,65)**	
T(NH-15)	0.3544(82,65)**	-0.2428(82,65)*	0.7156(78,65)**

*$P<0.05$
**$P<0.02$

Table 4. Long-term means of temperature (^{o}C) observations, Neah Bay sea level (m) and the upwelling index (m^3/s/100 m of coastline) at 45°N, 125°W by month. Monthly means for temperature are based on observations during June 1959 - November 1969. Means for sea level and upwelling are based on a comparable period consisting of 11 values for each month (June 1959 - May 1970).

	T(NH- 5)	T(NH-15)	SL(NB)	UI
Jan	9.94	9.59	2.11	-92.55
Feb	9.12	9.49	2.07	-58.00
Mar	9.35	9.29	2.01	-19.73
Apr	8.89	8.73	1.93	12.45
May	8.43	8.72	1.88	39.73
Jun	7.49	7.78	1.86	57.00
Jul	7.19	7.60	1.85	84.36
Aug	7.43	7.52	1.89	52.55
Sep	7.69	7.76	1.92	20.82
Oct	10.10	9.05	2.00	-27.18
Nov	11.61	9.87	2.07	-65.82
Dec	10.68	10.26	2.13	-88.73
Annual mean	9.03	8.81	1.98	-7.09

We then subtracted these long-term monthly means from the observed values to obtain monthly anomalies. Simple linear correlations between all pairwise combinations of anomalies are significant at the 95% confidence level (Table 3b). The number of degrees of freedom between time series of anomalies is much higher than between absolutes, since the elimination of seasonal cycles reduces the autocorrelation of each time series.

Based on these results, it is reasonable to attempt to infer deep temperatures from either sea level or the upwelling index, but slightly more confidence would be placed upon those inferred from sea level. Although variables were not clearly definable as dependent or independent, we initially conducted simple linear regression analyses on the 1959-1969 records with temperature as the dependent variable and sea level or the upwelling index as the independent variable. However, we found these regressions to yield undesirable biases. Plots of time series (not shown) conspicuously revealed that at high sea levels (low upwelling index) inferred temperatures were considerably lower than observed temperatures and at low sea levels (high upwelling index) inferred temperatures were much higher than those observed. Reversal of dependent and independent variables resulted in the converse. This phenomenon exists since a regression of Y on X minimizes the sum of the squares of the vertical distances of the observations to the line, while a regression of X on Y minimizes the sum of squares of the horizontal distances of the points to the line.

To circumvent the obvious biases caused by either simple linear regressions, we computed the "geometric mean estimate of the functional regression", hereafter "GM regression", strongly advocated by Ricker (1973) particularly in situations in which variability due to natural causes outweighs that due to measurement. The GM regression yields a line which minimizes the sum of the products of the horizontal and vertical distances from each observation to the line, and is intermediate to the regressions of Y on X and X on Y. This regression equation is easily calculated from statistics normally provided by simple linear regression analyses (Ricker 1973). Computed GM regression equations are presented in Table 5 with approximate 95% confidence intervals for the slopes.

To visually demonstrate the utility of the relationship between temperature and sea level, plots were made of observed and inferred mean monthly near-bottom temperatures at NH-5 and NH-15 using Eq. (3) and (5), respectively (Fig. 3). A test of this relationship would be to use sea level to estimate temperature for a different time period. Since stations NH-15 and Poinsettia are close (15 km apart) and located over the same isobath (100 m), one would expect Eq. (5) (developed using data from 1959-1969) to reasonably estimate deep temperature at Poinsettia during 1972-1974. A plot (Fig. 4) of inferred monthly mean temperatures at NH-15 and observed monthly mean temperatures at Poinsettia indicates that this is the case. The average error is only 0.56 C, an error which should be acceptable for most purposes.

Table 5. Regression equations with 95% confidence intervals of the slopes between observations of temperature (^{o}C), sea level (m) and the upwelling index (m^3/s/100 m of coastline) based on 1959-1969 data for both the observed monthly means and the monthly mean anomalies.

a. Observed values

$$T(NH-5) = -15.8133 + (12.5108 \pm 2.1743) \times SL(NB) \qquad (3)$$
$$T(NH-5) = 8.8278 - (0.0228 \pm 0.0042) \times UI \qquad (4)$$
$$T(NH-15) = -9.1761 + (9.0841 \pm 1.6019) \times SL(NB) \qquad (5)$$
$$T(NH-15) = 8.6901 - (0.0168 \pm 0.0031) \times UI \qquad (6)$$
$$T(NH-15) = 2.2118 + (0.7294 \pm 0.0972) \times T(NH-5) \qquad (7)$$

b. Anomalies

$$T(NH-5) = -0.0863 + (10.6825 \pm 2.1659) \times SL(NB) \qquad (8)$$
$$T(NH-5) = -0.0319 - (0.0205 \pm 0.0044) \times UI \qquad (9)$$
$$T(NH-15) = -0.0213 + (8.7402 \pm 1.8257) \times SL(NB) \qquad (10)$$
$$T(NH-15) = -0.0010 - (0.0176 \pm 0.0038) \times UI \qquad (11)$$
$$T(NH-15) = 0.0000 + (0.8811 \pm 0.1411) \times T(NH-5) \qquad (12)$$

Figure 3.   Time series of observed (dots) and inferred (solid line) near-bottom temperature during 1959-1969 for (a) NH-5 and (b) NH-15 using Eqs. (3) and (5) of Table 5.
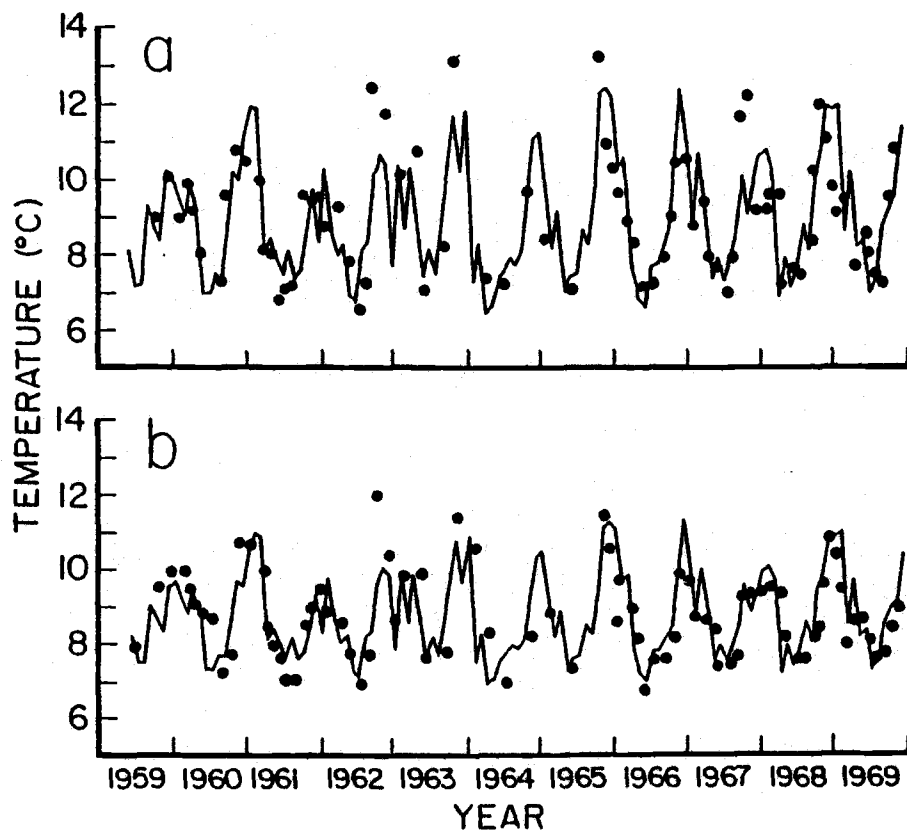
Figure 4. Inferred mean monthly temperature near the bottom at NH-15 from Neah Bay sea level using Eq. (5) (dashed line) and observed mean monthly temperature at Poinsettia (solid line) with ± 1 SD of the predicted (light stippled) and observed means (dark stippled). Monthly means and standard deviations of Poinsettia temperature are calculated using the full complement of daily values for each month except December 1972 (15 days), and five months in 1973: March (22 days), April (18 days), June (24 days), July (0 days) and August (17 days).
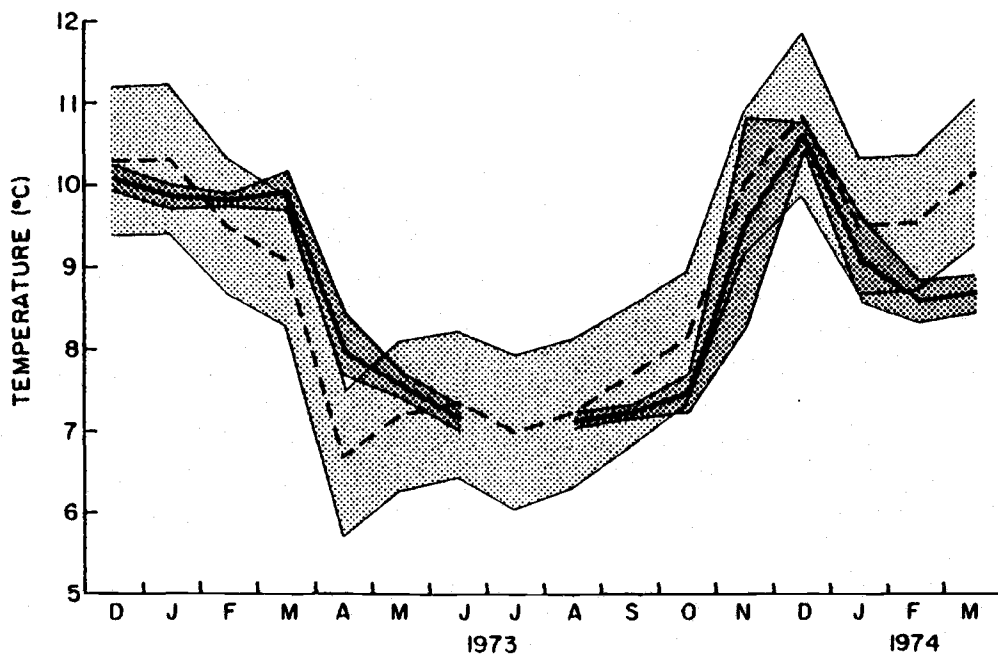
Discussion

Studies investigating the dynamics of marine demersal fishes have established a demand for long-term continuous bottom temperature records. Since such records are not usually available, we have attempted to meet this need by establishing relationships between near-bottom temperature (measured only sporadically) and other variables which are routinely measured on a continuing basis.

We found that near-bottom temperatures over the continental shelf off central Oregon are significantly correlated with coastal sea level, and also (though to a lesser extent) with the coastal upwelling index computed from the large scale wind field. Both of these correlations hold for monthly mean data. The correlation with sea level also holds for daily means of low-pass filtered sea level (i.e., with the diurnal and semi-diurnal tides removed from the sea level data before the daily means are computed). The correlation between temperature and the upwelling index does not hold on this shorter time scale. We also found significant correlations between the monthly anomalies of near-bottom temperature and those of sea level and the upwelling index. This correlation among anomalies indicates that the variables are actually correlated with each other, instead of only appearing to be correlated because they all have seasonal cycles.

The observed correlations were not entirely unexpected. Coastal upwelling is well known to affect shore temperatures along the Oregon coast, and one would naturally expect it to also affect the near-bottom temperatures over the inner continental shelf and perhaps over the

mid-shelf. Coastal sea level varies with the changing density field over the continental shelf and slope on both the longer (monthly mean) time scale (Reid and Mantyla 1976) and the shorter (days-to-weeks) time scale (Huyer et al. 1979). Since density is a function of temperature and salinity, one might expect near-bottom temperatures to be correlated with coastal sea level. Our results show that the bottom temperatures are actually better correlated with sea level than with Bakun's upwelling index.

We chose linear equations, termed GM regressions, to describe the relationships between variables (Table 5). Simple linear regression equations were not used due to biases which were particularly expressed at extreme values of each variable. For estimating monthly mean near-bottom temperature at NH-5 or NH-15, one should use the relationships with sea level: Eq. (3) or (5), respectively. Eq. (8) and (10) can be used for estimating monthly anomalies at these locations. The upwelling index is also useful to infer monthly values of temperature, particularly since gaps in the Neah Bay sea level record do exist in some years.

Although our quantitative results (the constants in Tables 4 and 5) are probably valid only for the locations from which they were derived (i.e., NH-5 and NH-15 over the continental shelf off Newport, Oregon), we expect the qualitative results to be more generally applicable. Anomalies of coastal sea level are coherent over long distances (Enfield and Allen 1980). Since near-bottom temperatures are correlated with sea level, anomalies of near-bottom temperature

probably also have high alongshore coherence. If so, the Neah Bay sea level will be a qualitative indicator of bottom temperatures over the shelf along much of Washington, Oregon, and perhaps northern California. Our quantitative results will certainly prove useful for simulation models of fisheries off central Oregon.

Influence of Physical Factors on the

English sole (Parophrys vetulus) Spawning Season

(Coauthor: Albert V. Tyler)

Abstract

Spawning times for English sole (Parophrys vetulus) in Oregon
waters were estimated for 13 years using data of adult female gonadal
condition and surveys of pelagic larvae and benthic juveniles of known
ages. The spawning season for this species is extremely protracted and
variable. Most spawning occurs between September and April, with peak
spawning lasting 1-3 months within this period. Some spawning has been
documented to occur in all seasons of the year.

Variations in the English sole spawning season appear to be
largely attributable to variations in a continental shelf temperature
index (developed from a relationship with Neah Bay sea level). Three
hypotheses about temperature control of spawning were proposed and
described by mathematical relationships. These relationships were
incorporated into a simulation model, which was driven by time series
of the bottom temperature index for those years in which spawning
records were available. Hypotheses were parameterized and evaluated,
based on the agreement between simulated and historical spawning
records. The three temperature hypotheses which collectively explained
much of the variablility in observed spawning are: (1) the rate of
gonadal development is inversely related to summer bottom temperatures;

(2) spawning is inhibited by temperatures below about 7.8 C; and (3) spawning is delayed by rapid increases in bottom temperature. The model can be used to simulate spawning activity for years of no empirical spawning records and can also be used in the design of laboratory experiments capable of validating the proposed hypotheses.

Introduction

Several general patterns in the reproductive strategies of marine fishes have been proposed by Qasim (1956), Cushing (1969;1975) and others. Fishes common to low latitudes or upwelling areas are often serial spawners and tend to have long and intermittent breeding seasons. In nonupwelling regions poleward of the subtropical convergences spring (and perhaps some fall) spawners generally breed only once per year over short (about three months) fixed seasons, while summer spawners tend to be intermediate in these characteristics.

The reproductive strategies utilized by a given species are believed to be those which result in maximum reproductive success by best ensuring that the young will encounter conditions favorable for growth and survival. Annual variations in reproductive success (i.e., year-class strength) reflect deviations of those factors to which the species' fecundity, reproductive strategies and survival are related.

Investigations of reproductive success constitute part of the biological basis for the management of commercially important fish stocks. In this regard studies of spawning activity and its environmental control can be of value to the management of species with variable spawning times. This is particularly true for those in which year-class strength is determined by factors operating over a short time period during the early stages of development. For these fishes the spawning time partly determines whether the young will encounter favorable conditions.

English sole, Parophrys vetulus, is a commercially important species to the bottom trawl fisheries along the west coast of the United States and Canada. The spawning strategy of this pleuronectid is consistent with at least one of the general patterns observed for fishes common to upwelling areas. While examination of ovaries suggests that individuals are not serial spawners (G. Hewitt, Oregon State University (OSU), pers. comm.), the breeding season of this species is quite protracted (Budd 1940; Harry 1959; Jow 1969) and variable (Laroche and Richardson 1979; Hayman and Tyler 1980). The spawning time may affect the survival rate of young English soles, because year-class strength appears to be largely determined by hydrographic events occurring prior to spawning (Hayman and Tyler 1980) and during the early stages of development (Ketchen 1956). For this reason investigation of the variations in English sole spawning activity may lead to a better understanding of their recruitment process and to improved management. The objectives of this study were to compile records of English sole spawning activity in Oregon waters and to attempt to identify the environmental factors which control the time of spawning.

Compilation of Spawning Times

Generally the most accurate procedure for the determination of teleost spawning times involves the examination of ovaries in a representative sample of adult females. Temporal variations in spawning intensity can be quantified using measures such as the proportion of females which are fully spawned (Harry 1959), gonadosomatic indices (Morse 1980) or the incidence of postovulatory follicles (Hunter and Goldberg 1980). Spawning times can also be back-calculated from larval or juvenile size composition data if the growth rates of these stages are accurately known. We had access to each of these types of data (Table 1) for the purpose of inferring past English sole spawning times.

The gonadal condition of adult P. vetulus females landed at Astoria (Fig. 1) was monitored by the Oregon Fish Commission, now the Oregon Department of Fish and Wildlife (ODFW), during 1947-1951 (Harry 1959). Since data have not been published on a year-by-year basis, we present them in Table 2. Ovaries were also sampled from individuals landed at Newport from October 1977 through February 1978 by Hewitt (1980). With these data, we used changes in the percentage of spent females between consecutive sampling dates as a measure of spawning activity.

Pelagic larval surveys were conducted along a transect off Yaquina Bay (Fig. 1) during June 1969 through August 1972 (Mundy MS; Richardson 1977; Richardson and Pearcy 1977), and along various transects between Cape Blanco and Astoria in March and April of 1972-1975 (Laroche and

Table 1. Sources of data used to infer English sole spawning times.

Method	Years	Source
Adult gonadal condition	1947-51	Harry (1959)
	1977-78	Hewitt (1980)
Planktonic larval surveys	1969-72	Mundy (MS)
	1971-72	Richardson (1977), Richardson and Pearcy (1977)
	1972-75	Laroche and Richardson (1979)
Benthic juvenile surveys	1970-72	Krygier and Pearcy (MS)
	1977-78	Myers (1980)
	1977-79	Krygier and Pearcy (MS) Rosenberg (1980)

Figure 1.   Location of data collection sites.   Data used in this study
came from gonads of females landed at Astoria and Newport, larval
surveys along transects between Astoria and Cape Blanco, and juvenile
surveys in Yaquina Bay.
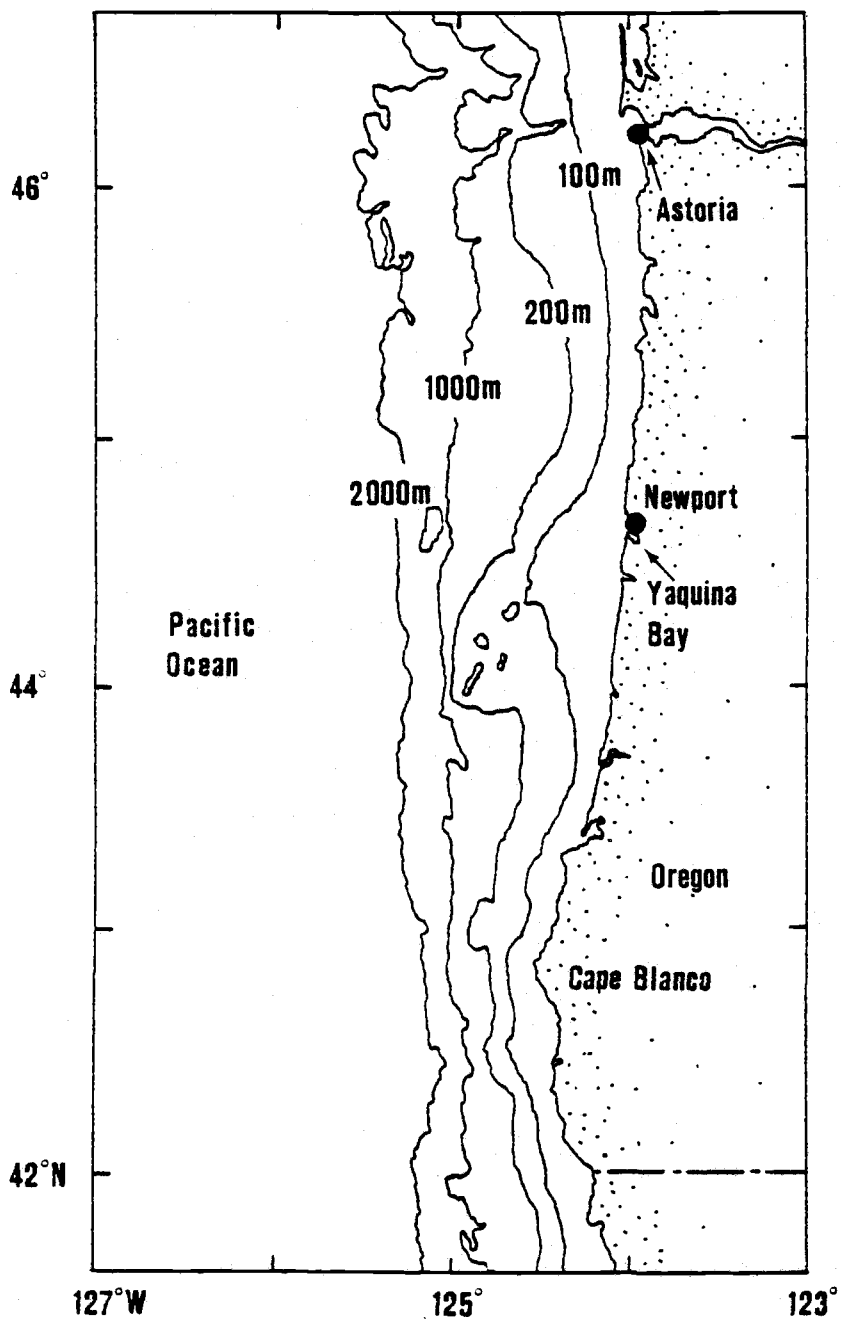
Table 2. Percentage of spent English sole females landed at Astoria on each sample date from ODFW data (Harry 1959).

Date	Sample Size	Percent Spent
18 JAN 1948*	374	59.0
18 MAR 1948	91	100.0
25 OCT 1948	9	0.0
10 NOV 1948	90	0.0
16 DEC 1948*	145	31.0
21 DEC 1948*	210	42.9
7 JAN 1949	167	59.9
14 JAN 1949	178	72.5
1 MAR 1949	67	95.5
8 MAR 1949	73	98.6
17 MAY 1949	99	99.0
18 NOV 1949	174	9.2
6 FEB 1950	141	80.9
5 APR 1950*	378	96.7
21 APR 1950*	112	95.7
18 NOV 1950*	722	16.0
19 DEC 1950*	255	43.1
1 JAN 1951	158	54.4
9 JAN 1951	62	69.4
31 JAN 1951	79	77.2

*Sample size and percentage of spent females represent averages for data obtained on several closely spaced collection dates.

Richardson 1979). Laroche and Richardson (1979) back-calculated English sole spawning times for several years based on the presence or absence of larvae in plankton samples and their estimates of larval growth rates. It is now known that these growth estimates are inaccurate and better ones have been obtained using improved aging techniques (Laroche et al. MS). With these revised growth rates we were able to back-calculate spawning times from reported larval size distributions. Due to the variability of ocean currents and of larval growth and survival rates, spawning dates calculated from small larvae are more accurate than those obtained from large larvae. For this reason spawning times which were inferred from larval size distributions were based primarily on the presence of newly-hatched larvae.

Juvenile English sole have been collected in Yaquina Bay by a number of studies. However these are of limited value for the back-calculation of spawning times due to the large variation in juvenile growth rates, particularly for individuals larger than about 25 mm standard length (SL) (Rosenberg 1980: Fig. 4). For this reason we considered only those juvenile surveys which appeared to adequately sample newly-settled juveniles, which are individuals of about 20 mm SL. Growth equations developed for both the pelagic (Laroche et al. MS) and benthic stages (Rosenberg 1980) of 0-age English soles show that individuals of this size average 2.5 months of age. The majority of 20 mm SL P. vetulus are 2-3 months old, while the youngest individual found of this size was 1.7 months old (Laroche et al. MS)

and the oldest was 6 months old (Rosenberg 1980).

Using each data type and inference procedure, we summarized English sole breeding activity in Oregon waters for 13 years (Fig. 2). Trends in spawning activity, particularly peak spawning times, are probably rather accurate, because inferences from different data sources were usually consistent. Certainly some errors exist due to the likelihood that all methods of data collection do not yield samples representative of the entire Oregon stock. When inconsistencies were encountered, we relied most upon inferences from data of adult gonadal condition, next upon newly-hatched larvae, and least upon older larvae or newly-settled juveniles. Because subjectivity cannot be entirely eliminated, we describe the bases for our conclusions in the Appendix.

Figure 2. Inferred spawning times for English sole using data of adult female gonadal condition and surveys of pelagic larvae and benthic juveniles. Spawning is indicated by a solid line and peak spawning is shown by the solid shaded areas. Stippled areas denote that data are inconclusive as to peak spawning times and dotted lines signify that data are inadequate for any spawning inferences.
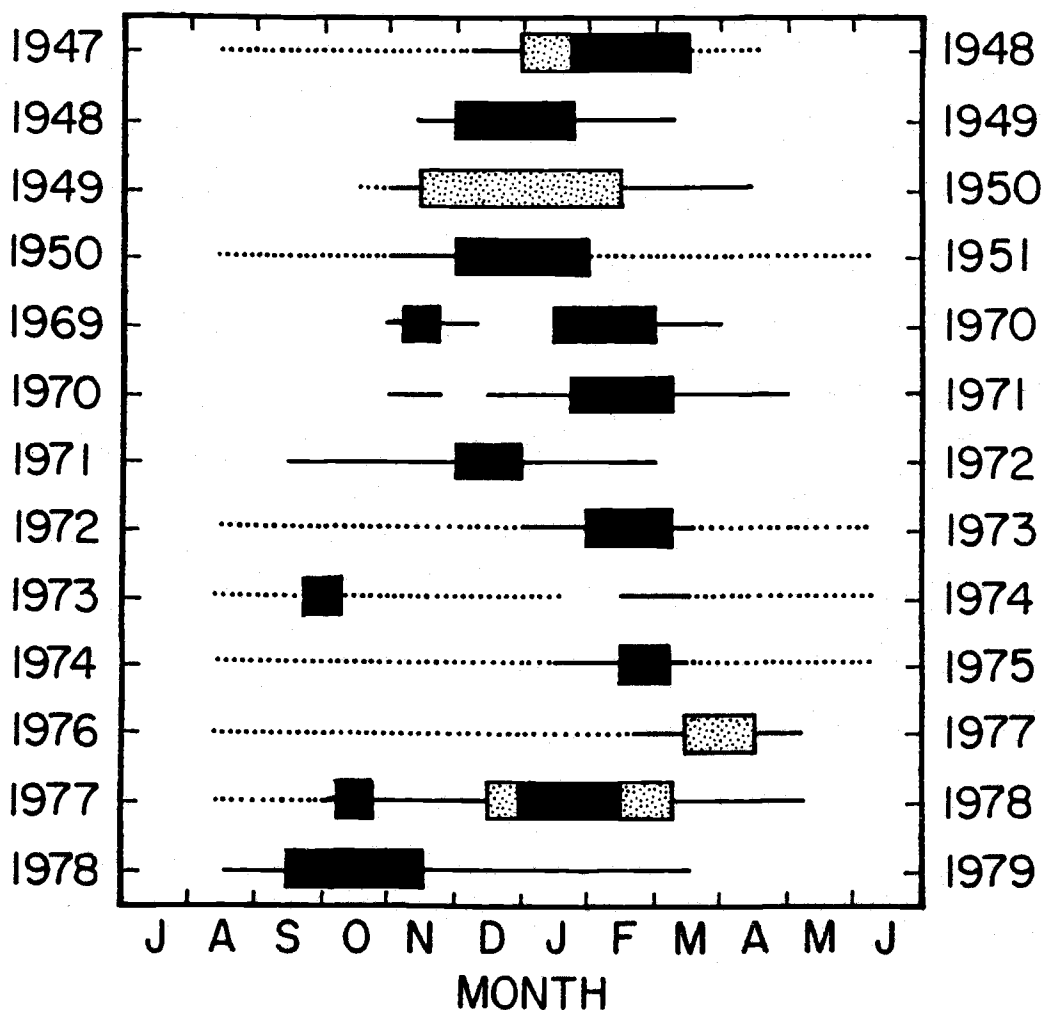
Development of Spawning Simulation Model

Exogenous factors which may be involved in the reproductive timing of marine fishes include photoperiod, temperature, salinity, ocean currents and food quantity and quality (Brett 1970). These variables may be classified into ultimate and proximate environmental factors (Sadleir 1973). Ultimate factors are those which control reproductive success through their effects on the survival and growth of the young, and influence spawning timing through evolutionary adaptation. These factors are often investigated by laboratory experiments dealing with egg and larval survival and by correlation or modelling studies involving time series of year-class strength and other fishery and environmental variables. Proximate factors are the environmental cues initiating gametogenesis and subsequent spawning behavior. Temperature and photoperiod have been found to be the principle proximate factors in most fishes (de Vlaming 1972). In addition, the grunion (Leuresthes tenuis) (Clarke 1925), threadfin (Polydactylus sexfilis) (May 1979), and many others (Johannes 1978) have spawning closely linked to lunar-driven tidal cycles.

We attempted to identify the proximate factors responsible for timing English sole reproduction by comparing the total annual range in magnitude of several environmental variables with their range of values over only those months in which spawning occurred (Table 3). For this purpose we had access to monthly mean data of barometric pressure at $46^{o}N$, $124^{o}W$, the coastal upwelling index at $45^{o}N$, $125^{o}W$ (Bakun 1973), an index of bottom temperature (derived from a relationship with sea

Table 3. Total range of values of barometric pressure,
daylength, and indices of upwelling and bottom temperature
over all months and over only those months in which
spawning occurred.

Factor	Total Range	Range during Spawning
Barometric Pressure 46°N, 124°W	1011.1-1027.0 mb	1012.3-1027.0 mb
Daylength 45°N	8.75-15.5 h	< 14.0 h
Upwelling Index 45°N, 125°W	-212 - +106 m^3/s/100 m	most < +3m^3/s/100 m
Bottom Temp. Index at NH-15 44°39.1′N, 124°27.4′W	6.60-11.19 C	most > 8.00 C

level) at a station (NH-15) over the 100 m isobath off Newport (Kruse
and Huyer MS), and bimonthly values of daylength at 45°N (Beck 1968).
We chose these variables because they were most likely to be related to
English sole reproductive cycling. As previously mentioned,
temperature and photoperiod are the common proximate timing factors of
other fishes. Upwelling could be important to English sole, due to its
relationships with variables such as food produciton, temperature and
current velocity. Barometric pressure could also be involved, because
it is related to local weather patterns. Comparisons suggested that
photoperiod, upwelling, and bottom temperature might be related to
reproduction, since spawning activity occurred only over a portion of
the total range of these variables (Table 3). Little spawning activity
occurred at daylengths greater than 14 h of light, which at 45°N
corresponds to the period spanning late April to late August. Possible
inhibition of spawning activity by cold temperatures is suggested not
only because most spawning seems to occur at temperatures greater than
8 C, but also since little spawning occurred at values of the upwelling
index greater than 3 m^3/s/100 m of coastline. We searched for other
associations such as correlations between the intensity of spawning and
the magnitudes of these variables, but no further relationships were
revealed.

Next we took a more analytical approach. Since English sole
spawning activity is so variable, it is improbable that photoperiod is
responsible for its interannual variation. Instead, shelf temperature
is most likely to be the primary proximate timing factor. In other

fishes temperature can have at least two regulatory effects on reproduction. It may control the rate of maturation (Hela and Laevastu 1961; Brett 1970; and others) or it may act as a releasing factor (Brett 1970; Hempel 1979; and others).

Laboratory experiments are commonly used to investigate the temperature control of spawning. However, since it is desirable to be able to account for the variable spawning activity of English soles in their natural environment, we attempted a different approach. First we suggested various hypotheses about temperature control of spawning and described them by mathematical relationships. Then we incorporated these relationships into a simulation model which could be driven by a time series of a bottom temperature index for those years in which empirically determined spawning times were available. This would allow us to determine whether spawning times simulated using the temperature hypotheses are consistent with the spawning times documented earlier. Since other physical factors are correlated with deep temperature (Kruse and Huyer MS), conclusions about these hypotheses cannot be made except to evaluate whether or not they are reasonable based on historical records of spawning activity and bottom temperature dynamics.

The first hypothesis considered is that temperature controls the rate of gametogenesis. Kreuz et al. (MS) found a negative correlation between annual variations in marginal interoperculum growth (an index of body growth) of young English soles and mean shelf temperature estimates during the growth season (summer). This implies an inverse

relationship between temperature and the somatic growth rate. We suggest that the gonadal development rate is also inversely related to temperature. A plot of annual English sole spawning records and an index of bottom temperatures during the summer prior to spawning (Fig. 3) does not reveal a close relationship, although the three earliest spawning seasons followed three of the four coldest summers. Even if maturation was solely temperature controlled, a plot of spawning time versus temperature would not reveal a close relationship if temperature must increase beyond a threshold or increase at a certain rate in order for spawning to be initiated. From trends in the dates of the start of peak spawning and the start of minor spawning, we proposed relationships between mean summer temperatures and the completion date of gonadal development for most individuals (Fig. 3, line a) and the most rapidly developing individuals (Fig. 3, line b).

We next considered a temperature threshold hypothesis suggested to us by Table 3. That is, we proposed that even if gonadal maturation was completed, spawning would not occur until temperature exceeded 8 C.

Both temperature hypotheses were incorporated into a FORTRAN computer model. Each month of simulation was divided into four subintervals of equal length. We assigned the estimated mean monthly temperature to the middle of each month. The temperature during any subinterval was estimated by linear interpolation between the values at the midpoints of successive months. We drove this model with records of the bottom temperature index and inferred the dates on which maturity would be completed (lines a and b of Fig. 3) and the dates

Figure 3. Relationship between Oregon English sole spawning records and the mean bottom temperature index for the summer (May-August) prior to spawning. Proposed relationships between mean summer temperature and the completion date of gonadal development for (a) most individuals and (b) the most rapidly developing individuals are also shown. A distinction is made between spawning (solid line), peak spawning (solid shaded areas) and probable peak spawning (stippled areas). A dotted line indicates no data.
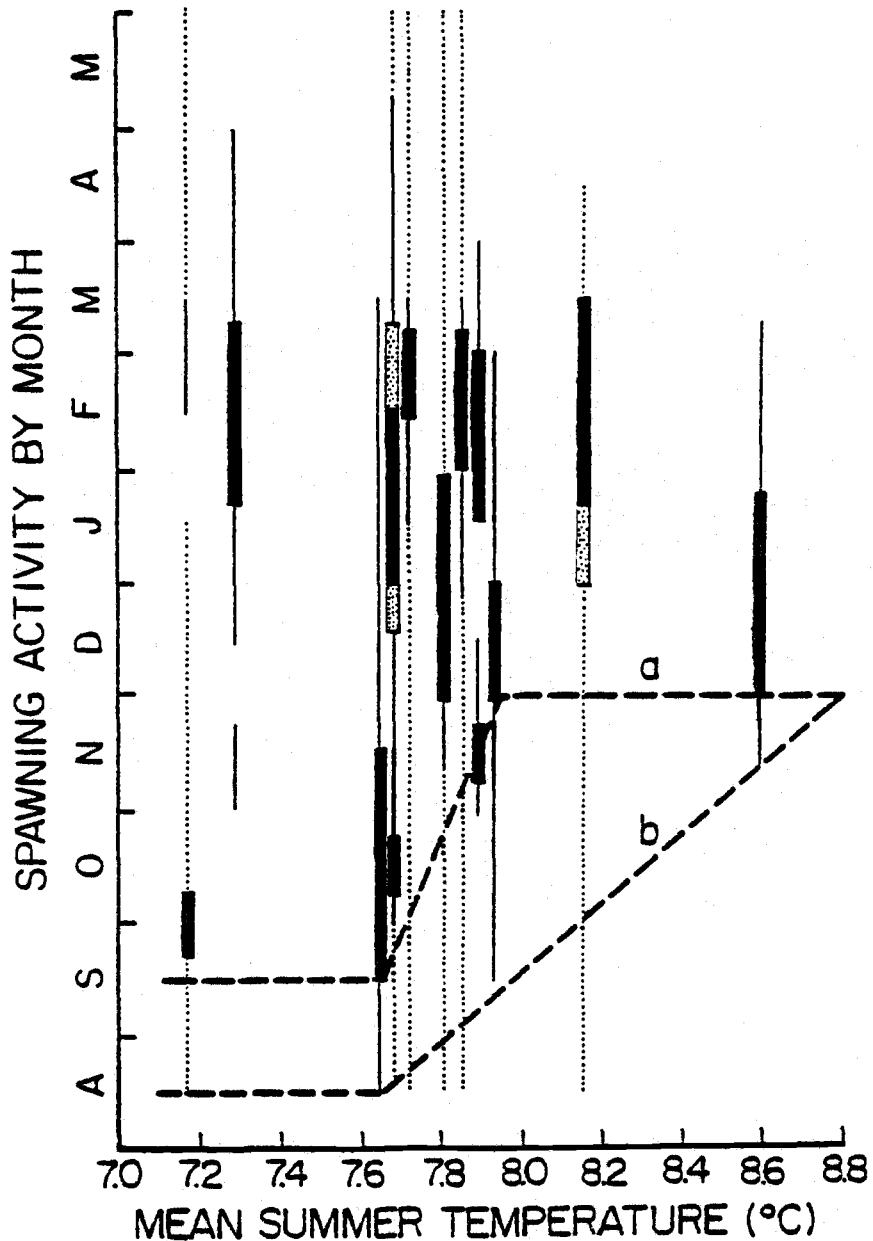
thereafter on which spawning would be started based on the warming of bottom temperatures above 8 C. The dates of spawning initiation inferred in this manner were generally in poor agreement with those inferred from empirical records described earlier. Adjustments to lines a and b or the temperature threshold did not significantly improve the correspondence. It became clear that either these hypotheses were not valid or else that the environmental control of English sole spawning was more complex.

We next recalled that the rate of change of temperature can significantly influence fish physiology and behavior. Reexamination of our data sets strongly suggested that when temperature increased rapidly (>0.95 C per month) just prior to the inferred completion time of gonadal maturation, spawning activity was delayed. For example, in 1947-1948 the calculated (using a of fig. 3) completion date of gonadal maturation for most individuals was early December. The temperature index increased 1.68 C between November and December, and peak spawning apparently did not occur until late January. Similar large temperature increases just prior to the calculated maturation completion dates occurred in other years (1950-1951, 1970-1971, 1972-1973, and 1974-1975) in which peak spawning did not start until sometime later than the maturation dates. Large temperature increases (1.36 C between November and December 1969 and 1.69 C between October and November 1977) also coincided with the only two documented interruptions in peak spawning activity. In general, the magnitude of the temperature increase (>0.95 C) and the number of these increases between several

consecutive months appear to be related to the duration of the delay. In all other years for which spawning data were available, peak spawning activity began near the calculated dates of completed gonadal development and pre-spawning temperatures increased less rapidly (<0.95 C per month). From this we constructed a third temperature hypothesis which includes these rate effects (Fig. 4).

All three temperature hypotheses were incorporated into a revised spawning model for which a flow chart is shown (Fig. 5). For expediency we have used shortened notation as follows: t - present date, t_c - completion date of gonadal development, $T(t)$ - present temperature, D_t - delay in spawning caused by a temperature increase from month $t-1$ to month t, and D - the actual delay expected considering temperature increases over the past several months. An equation such as $t = t+1$ is analogous to a FORTRAN assignment statement and replaces the present value of t with the value $t+1$. The model is run on a monthly basis, but spawning dates are interpolated to the precision of .25 months. In the model the question "Is spawning completed?" is answered in two ways. Peak spawning is completed if it has occurred for two months or if the date is later than early May. For spawning of lower intensity, spawning is completed if the present date is later than early May.

The spawning model including all three temperature hypotheses resulted in good agreement between simulated and observed starting dates of peak spawning. In fact, only minor changes in parameterization were necessary to achieve the best possible

Figure 4. Hypothesized relationship between the rate of increase in mean monthly temperature and the duration of the delay in the spawning time.
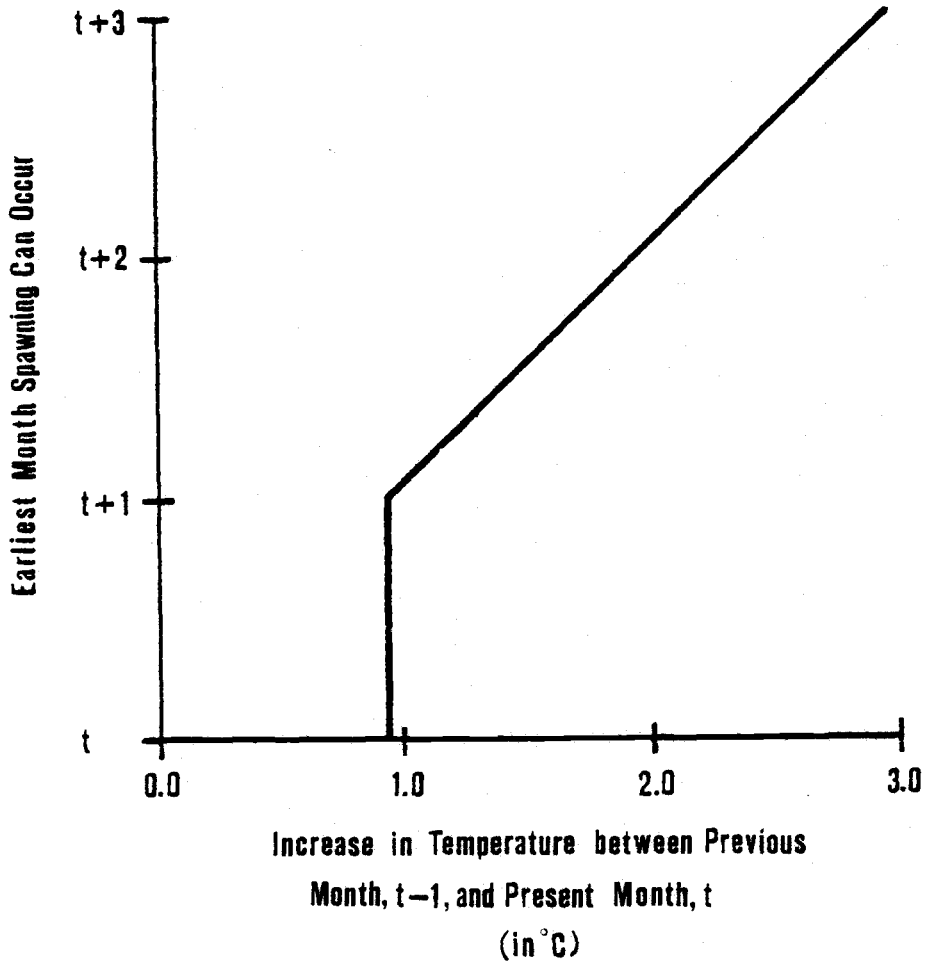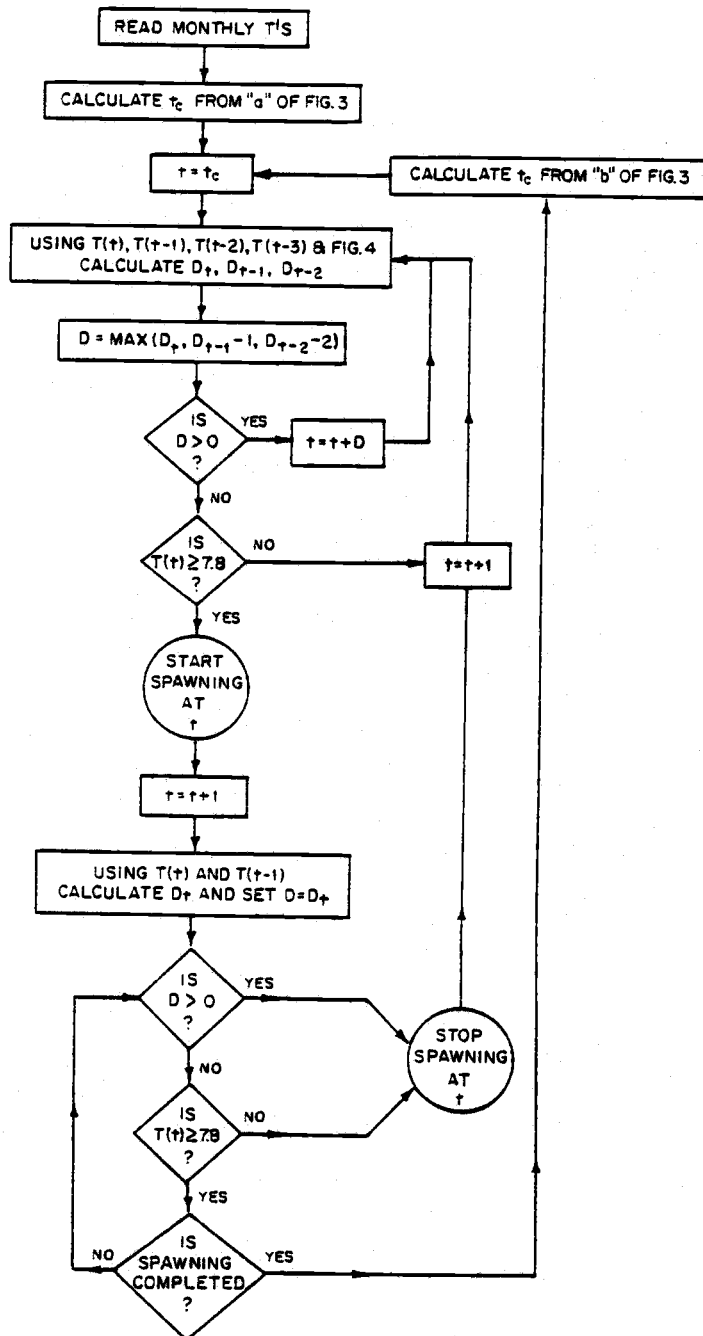
Figure 5. Flow chart of spawning simulation model. Terms are defined
in the text.

predictions from these hypotheses. By adding a constraint that peak spawning could last no longer than two months for any one spawning year (July to June), we could also account for the dates when peak spawning was terminated. The set of hypotheses yielding the best agreement between simulated and observed spawning activity (Fig. 6) were: (1) the earliest possible spawning time is given by b and the earliest possible peak spawning time is given by a in Fig. 3; (2) no spawning occurs below 7.8 C; and (3) spawning does not occur in a particular month if the mean monthly temperature increases by more than 0.95 C from the previous month. The length of the delay in spawning is linearly related to the rate of temperature increase (Fig. 4). Whether or not spawning actually occurs at this later time would again depend upon (2) and (3) and the current temperature. Rapid increases in temperature would also cause a cessation of spawning activity if spawning had already begun. In such a case spawning would restart later according to these same rules. We added the rule that if peak spawning is interrupted (by a large temperature rise), it would not begin again until one month later.

In our simulations we found that the maturation rate hypothesis (lines a and b of Fig. 3) set the limits to the earliest dates of spawning. The hypothesis about rapidly increasing temperatures was of primary importance as it frequently delayed or interrupted spawning. It also was responsible for the correct modelling of the apparent bimodal spawning activity in the 1969-1970 and 1977-1978 spawning seasons. The threshold hypothesis was usually responsible for

Figure 6.   Comparison between observed (O) spawning records and those
predicted (P) when all three temperature hypotheses are incorporated
into a simulation model driven with bottom temperature estimates. A
distinction is made between spawning (solid line), peak spawning (solid
shaded areas) and probable peak spawning (stippled areas). A dotted
line indicates no data.
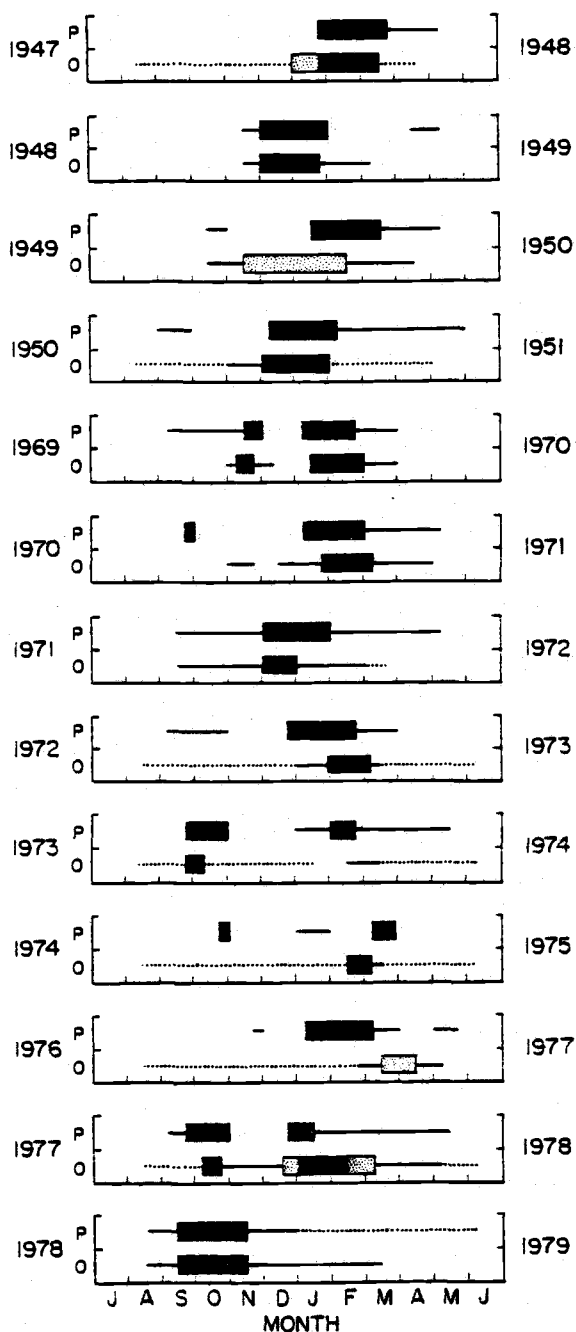
terminating spawning activity in the spring or summer.

Discussion

Off Oregon Parophrys vetulus spawn intermittently over an extended breeding season. We have extensively searched for the proximate factors regulating English sole reproductive cycling by comparing time series of spawning activity off Oregon and several environmental factors. Barometric pressure, which is related to weather patterns, seems to play no such role. Although day lengths greater than 14 h of light might preclude spawning or cue the initiation of gametogenesis, it does not appear that photoperiod can be used to explain large shifts in English sole spawning times. Spawning instead seems to be primarily accountable by bottom temperature dynamics (inferred from a relationship with Neah Bay sea level). Support is given to three hypotheses of temperature control, because they result in rather accurate simulation of spawning when incorporated into a computer model driven by records of a bottom temperature index (Fig. 6). However, since bottom temperature is correlated to other physical factors (Kruse and Huyer MS), it is possible that a simulation model incorporating hypotheses about roles of other factors in reproduction will also result in satisfactory spawning simulation. It is almost certain that other factors operate in concert with temperature to affect spawning control. To conclusively distinguish the effects of temperature from these other factors, laboratory experiments should be conducted.

It does seem reasonable that the rate of maturation is inversely related to the temperatures experienced during the summer (May-August). Gonadal development probably occurs during this time and it is known

that somatic growth is most rapid during this season of cool temperatures (Kreuz et al. MS). Negative correlations have previously been found between annual variations in marginal interoperculum growth in young English soles and mean summer bottom temperature estimates. In other species temperature has various effects on rates of gonadal development (de Vlaming 1972), sometimes having completely opposite effects on different stages of gametogenesis in any one species (Ahsan 1966; Weibe 1968). Since anomalies of bottom temperature and the coastal upwelling index are inversely related (Kruse and Huyer MS), colder summer temperatures and stronger upwelling may lead to greater primary and secondary production and increased availablity of English sole prey items, including polychaetes, amphipods, molluscs, ophiuroids and crustacea (Kravitz et al. 1977). Relationships between feeding and maturation rates have been identified in other fishes (Gross 1949; Kinne 1960; and others), so it is possible that food production operates with temperature to determine the maturation rates of English soles. In any case this species has presumably evolved physiological mechanisms providing for optimal somatic and gonadal growth at the environmental conditions existing during the summer (including cold temperatures), when productivity is high.

We also proposed that few or no P. vetulus spawn at temperatures colder than about 7.8 C. In some species such as Atlantic cod, Gadus morhua (Bigelow and Schroeder 1953) and mackerel, Scomber scombrus (Ware 1977; Lett 1978), a temperature threshold may be the primary determinant of spawning activity. Ahlstrom (1965) felt that

temperatures between 13-18 C were responsible for the time and length of the California sardine (Sardinops sagax) spawning season. Perhaps temperatures out of this range may operate by inhibiting production or release of hormones responsible for initiating breeding behavior.

Finally we hypothesized that increases in monthly mean bottom temperature greater than 0.95 C delay or interrupt spawning activity. The magnitude of the increase and the length of the delay are suggested to be linearly related. The mechanisms behind this response are not clear, although it is widely known that short-term deviations of temperature can produce physiological and behavioral changes in fishes. It is possible that English soles are physiologically stressed by relatively small increases in temperature, since adults experience temperature variations of 4 C or less over the course of the entire year (Huyer 1977; Kruse and Huyer MS). Rapid temperature increases might also alter English sole spawning migration patterns. Leggett and Whitney (1972) found that rising temperature accelerated upstream American shad (Alosa sapidissima) migration but that sudden increases could retard it. Alternatively, sharp increases in Oregon continental shelf temperatures may be associated with shifts in weather patterns and a general deterioration of the set of conditions required by English soles for spawning.

Before our hypothesized relationships between shelf temperatures and reproductive cycling are accepted, they should be validated through controlled laboratory experiments. However, in their present form they are certainly useful for simulating English sole spawning activity, as

we have shown. This is significant, because year-class strength appears to be largely determined by environmental conditions prevailing prior to spawning (Hayman and Tyler 1980) and during the early life history stages (Ketchen 1956). Thus our spawning model will be valuable to investigations of the mechanisms by which these physical factors operate. Once these mechanisms are understood, forecasts of English sole availability can be made in advance of recruitment and incorporated into future management strategies.

Conclusions

The first study presented here adds to our understanding of the oceanographic processes occurring along the Oregon coast. Although the relationships between deep temperatures, coastal sea level and Bakun's upwelling index are not totally unexpected, the statistical significance of these relationships is documented for the first time. It is felt that the relationship between sea level and temperature will be useful to researchers in need of regular shelf temperature estimates, particularly during periods of sporadic empirical records. In addition to being useful to the English sole spawning model, Albert Tyler and I have found this temperature index to be correlated to annual variations in the growth of young English soles and Dover soles (Microstomus pacificus). An understanding of such interactions between fishes and their environment should help managers to distinguish between those changes in fishery productivity related to fishing activity and those related to the environment.

The second part of this thesis contributes to our knowledge of English sole life history and perhaps of similar species living in the Oregon upwelling system. It is hoped that future studies can be conducted to validate the proposed hypotheses of temperature-controlled spawning and to assess the coupled effects of other factors, such as food availability and photoperiod. Predictions made from the spawning model developed here have already been valuable to an investigation of the English sole recruitment process conducted by myself and Albert Tyler.

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Appendix

Appendix. Spawning activity by season.

1947-1948

The gonadal condition of English sole females landed in Astoria were sampled by the ODFW during 1947-1951 (Harry 1959). We had access to the raw data collected during this time period (Table 2). No samples were obtained in 1947 and collections were made only in January and March of 1948. Approximately 40% of the total spawning activity occurred between mid-January and mid-March. Spawning was terminated by the middle of March.

1948-1949

Adult females landed in Astoria were sampled frequently during the 1948-1949 spawning season (Table 2). Spawning occurred between the middle of November and early March. The heaviest spawning period was from early December to late January.

1949-1950

Spawning began prior to the first sampling date in mid-November 1949 and terminated in about the middle of April 1950 (Table 2). Dates of peak spawning activity cannot be accurately determined, since no samples were taken in December or January. About 70% occurred sometime between mid-November and early February.

1950-1951

Gonadal condition during 1950-1951 was not sampled for the duration of the spawning season (Table 2). Approximately 16% of the females appear to have spawned prior to the first sampling in

mid-November 1950 and only 77% had spawned by the last sampling date, 31 January 1951. About 60% of the spawning activity occurred between the middle of November and late January.

1969-1970

Using revised growth estimates (Laroche et al. MS), collections of 2-3 mm SL English sole larvae (Mundy MS) show that the 1969-1970 spawning season began in early November 1969. Spawning appears to have stopped in mid-December, resumed in mid-January and finished completely by the end of March. Based on larval abundances, peaks in spawning intensity are indicated for mid-November 1969 and February 1970.

In 1970 juvenile surveys were also conducted in Yaquina Bay using beam trawls (Krygier and Pearcy MS). Individuals approximately 20 mm in length were collected in mid-January to early February. Allowing about 2-2.5 months to reach this length, this confirms spawning during the month of November. Juveniles of this age were also collected (and in greater abundance) from late March to late May, which indicates that additional heavy spawing occurred from mid-January through late March. However, we place more confidence in spawning inferred from larval data, which clearly shows spawning to be heavier in February than in March.

1970-1971

Small (2-3 mm SL) larvae first appeared in late December 1970 (Mundy MS), which means that spawning began in mid-December. Larval data (Mundy MS; Richardson 1977; Richardson and Pearcy 1977) also show

that spawning intensity increased many fold from late January through early March. Spawning activity seems to have stopped in late April, since 5-8 mm SL individuals were collected no later than May.

A survey using beam trawls in Yaquina Bay (Krygier and Pearcy MS) obtained a few juveniles less than 20 mm SL in mid-January 1971. This means that some spawning must have occurred in early to mid-November, contrary to the lack of such evidence from larval data. Significant numbers of small juveniles were obtained from late February through the end of June. Spawning times inferred from these later collections are essentially identical with those inferred from larval data. Since the greatest numbers of these young soles were observed between mid-March and mid-May, the peak spawning times inferred from both juvenile and larval data also closely agree.

1971-1972

Larval studies (Mundy MS; Richardson 1977; Richardson and Pearcy 1977) indicate that spawning began in mid-September 1971 and continued through late February 1972. Peak spawning activity appears to have been in December. Although no samples were taken in January or February 1972, heavy spawning likely did not occur during these months, since the numbers of 1-2 month old larvae collected in March were low.

Beam trawls (Krygier and Pearcy MS) first encountered juvenile fish less than 20 mm SL in late November. They were collected through early March when sampling was terminated. This suggests spawning from the middle of September 1971 through at least the end of January 1972. The greatest numbers of juveniles were taken from early to late

February, indicating peak spawning intensity in December. Thus juvenile data are highly supportive of conclusions drawn from larval samples.

1972-1973

Information regarding spawning for the 1972-1973 season is available from only one data source (Laroche and Richardson 1979). Larvae were surveyed using bongo tows during 17-29 March and 17-26 April 1973. Based on revised growth rates (Laroche et al. MS), the presence of larvae up to 20 mm SL in March samples indicated spawning activity from early January through March. No statement can be made about possible spawning prior to January. From the presence of very large numbers of 7-14 mm SL larvae in March samples and expected ages of these individuals (Laroche et al. MS), peak spawning is indicated for early February to early March. Spawning appears to have tapered off by late April, although it is possible that some spawning occurred after this last sample date.

1973-1974

Laroche and Richardson (1979) reported that large concentrations of running ripe and spent adults were found off the Oregon coast on 20 October 1973. Larval surveys were conducted only in the middle of March 1974 (Laroche and Richardson 1979). At this time newly-hatched soles were sparse and in the 2-8 mm SL size range. This indicates that minor spawning occurred from mid-February to mid-March and little or no spawning from at least mid-January to mid-February. The collection of two size groups of 0-age juveniles along the coast in 1974 also

suggested fall and winter-spring periods of spawning (Laroche and Holton 1979). Based on this information, it can be inferred that spawning was intense in early October, absent from mid-January to mid-February and minor from mid-February to mid-March.

1974-1975

Larvae were surveyed only on 14-16 March 1975 (Laroche and Richardson 1979), and large numbers were obtained on these dates. The presence of newly-hatched and 60 day old larvae indicated that spawning began at least by mid-February 1975 and continued at least through mid-March. The predominance of 8-25 day olds suggest a peak from mid-February to early March. No statement can be made about possible spawning prior to mid-January or after mid-March.

1976-1977

A juvenile sampling program (Krygier and Pearcy MS) was conducted in Yaquina Bay from 24 April to 2 July 1977. Individuals less than 20 mm SL were collected on all dates suggesting that spawning began at least by late February and continued through early May. The greatest numbers of larvae less than 20 mm SL collected during any sampling period were taken from 22 May to 4 June. This would suggest a peak in spawning during late March or early April. Due to the shortness of the sampling period, however, one cannot conclude that this would represent the peak spawning time over the entire season.

A beach seining program (Myers 1980) initiated in late June 1977, collected only very slight numbers of 19-22 mm fish. None were collected after late June indicating that spawning did not extend past

early May. No conclusion can be drawn about possible spawning prior to mid-January.

1977-1978

Hewitt (1980) sampled adult female gonads from October 1977 through March 1978. Based on the percentage of ripe stage III (the most advanced stage of ripeness) or spent females, his data show that spawning began at least by early October, continued moderately through January, and peaked strongly in February. Almost 95% of the females were spent by 1 March 1978.

Beam trawl samples (Rosenberg 1980; Krygier and Pearcy MS) of small juveniles in Yaquina Bay indicate spawning from mid-October through early April. Although trends are difficult to discern from these samples, spawning can be inferred to be intense in the middle to late October and heaviest in January.

Beach seine samples in Yaquina Bay (Myers 1980) first encountered individuals less than 20 mm SL om mid-December 1977 and collected them through late April 1978. A very small number were also obtained from late July to early August. This information implies that spawning occurred from early October through the end of February, with a minor amount in late May or so. A peak in spawning activity appears to have occurred from mid-December through early March.

Each of the 1977-1978 studies indicate similar spawning times. Clearly spawning began at least by early October and continued in varying intensity through early May. The precise dates for the start and finish of the major peak for this season are uncertain. However,

each study indicates heavy spawning in January and/or February.

1978-1979

Beach seine samples (Myers 1980) of small juveniles show that spawning began at least by mid-August 1978. Some fish less than 20 mm SL were caught as early as 28 October. Peak spawning appears to have occurred between mid-September and mid-October. Young soles were caught through the last sample date (10 December 1978).

Beam trawl samples (Rosenberg 1980; Krygier and Pearcy MS) indicate spawning to have occurred from early September and continued through mid-March. Peak spawning is indicated for mid-September through mid-November.

Both of these juvenile studies yield compatible inferences about spawning times. Using both, it seems that spawning began in mid-August, peaked from mid-September through mid-November and ended in mid-March.