

AN ABSTRACT OF THE THESIS OF

Gordon Henry Kruse for the degree of Doctor of Philosophy
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Title: A Simulation Model of English sole (Parophrys vetulus)
Recruitment Mechanisms.

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Albert V. Tyler

A computer simulation model was constructed to investigate the operation of several hypotheses in English sole year-class formation. The model was constructed using the best available information on the species' life history and oceanographic environment. We investigated hypotheses about (1) fecundity related to bottom temperatures, (2) egg hatch success related to surface temperatures, (3) advective loss related to winds, (4) stress mortality related to storms, and (5) starvation related to primary productivity. The hypotheses were translated into functional relationships which could be logically switched on or off in our model. We then evaluated them based on the correlation between observed (from cohort analysis) and simulated recruitment, when the model was driven by time series of fishery and physical data. Results indicated that mechanical stress due to storms or starvation linked to general primary production cannot account for significant variance in recruitment. Stock size, age structure and individual fecundity could account for about 12% of the variance. A complete model with population egg production, egg hatch success and transport could account for 53% of the variation; hatch success and transport appear to contribute equally. Curve-fitting procedures

could have been adopted which would have led to accounting for 80% or so of the variation in recruitment. However, curve-fitting was not our purpose. We attempted to determine whether specific hypotheses conform to observation, not whether observation could be made to match hypotheses.

English sole spawning seasonality appears adapted to minimize the combined mortalities associated with hatching and transport. Because spawning is partly cued by the warming of shelf waters, egg releases tend to be timed to match periods of onshore transport coincident with increased bottom temperatures. Onshore transport not only carries young toward coastal nursery areas, but also may increase the availability of appendicularians, the principal larval prey. A coherent theory of the English sole recruitment process is presented.

The model predicts a series of above average year classes for 1971-1976. When data becomes available to estimate the sizes of these cohorts, the predictions will be useful to evaluate further our hypotheses about the recruitment process. In particular, the role of the hypothesized fecundity-temperature relationship should become much clearer; stock and fecundity (as indexed by temperature) patterns are coincident over the period of validation, but opposite over the period of prediction.

A Simulation Model of English sole
(Parophrys vetulus) Recruitment Mechanisms

by
Gordon H. Kruse

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Redacted for privacy

Head of Department of Fisheries and Wildlife

Redacted for privacy

Dean of Graduate School

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PREFACE

This thesis is written in manuscript format. The manuscript, which will be submitted for publication, lacks an extensive literature review and a discourse on the significance of this work to my other research at Oregon State University. I treat both of these topics in the section, "Discussion of thesis with regard to English sole biology, environment and fishery production." Dr. Albert V. Tyler of Oregon State University (now at the Pacific Biological Station, Nanaimo, BC) coauthored the manuscript forming the body of this thesis.

A SIMULATION MODEL OF ENGLISH SOLE
(PAROPHRYS VETULUS) RECRUITMENT MECHANISMS

INTRODUCTION

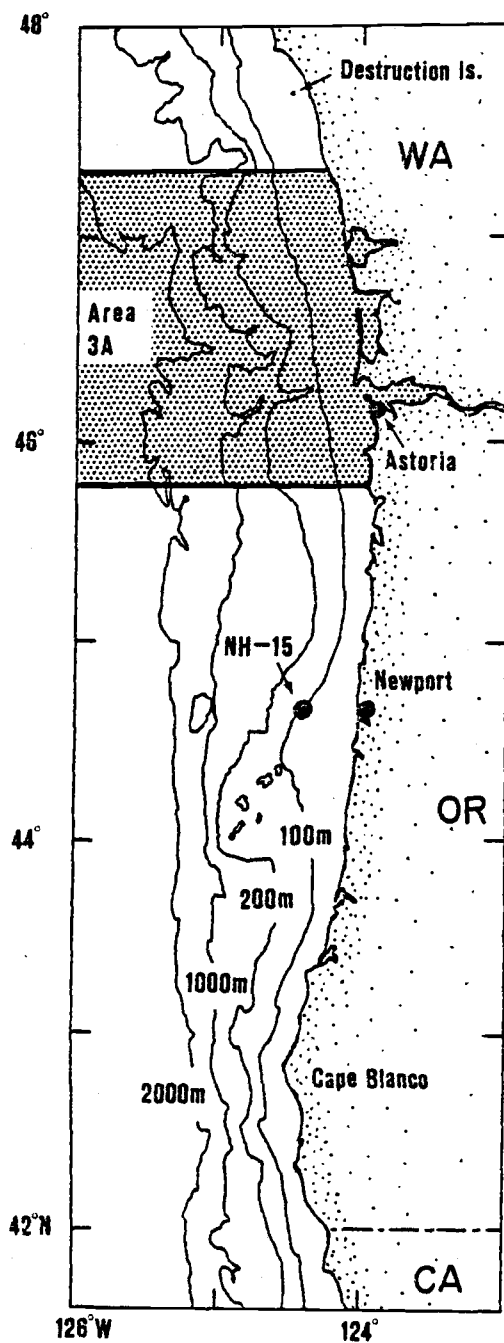
The objective of this study was to identify the mechanisms responsible for English sole (Parophrys vetulus) year-class formation in Pacific Marine Fisheries Commission (PMFC) Area 3A (Fig. 1). Correlations have been established between English sole cohort strength and environmental factors for stocks in Oregon (Hayman and Tyler 1980) and British Columbia (Ketchen 1956). Underlying cause and effect relationships have been suggested but remain uncertain. An understanding of these mechanisms could facilitate better prediction and management of English sole production.

Hayman et al. (1980) quantified English sole recruitment strength variations for Area 3A. Hayman and Tyler (1980) conducted a correlation study using this record and time series of various environmental factors. Variations in year-class strength were found to be positively correlated with both barometric pressure and the coastal upwelling index (Bakun 1973) during the September and October prior to spawning. Hayman and Tyler speculated that higher fall barometric pressure and upwelling were related to colder bottom temperatures which might delay spawning. They further reasoned that delayed spawning led to a better match of larval and prey abundances, a recruitment mechanism which has been proposed for several species (Cushing 1972).

In Hecate Strait, British Columbia, Ketchen (1956) found English sole cohort strength to be inversely related to winter sea surface

Figure 1. The location of Pacific Marine Fisheries Commission (PMFC) Area 3A, the region where English sole catch and effort statistics were obtained.

Figure 1.



temperatures; he obtained the best correlations with temperature averaged over January through March. Ketchen had reasoned that colder temperatures prolonged the pelagic stage and allowed for increased northward transport from spawning grounds to the nursery areas. This is consistent with laboratory experiments in which temperature and hatch time were found to be positively related (Alderdice and Forrester 1968; Ketchen 1956). As further support Alderdice (Pacific Biological Station, pers. comm.) found January surface temperature at Triple Island and coastal sea level (an index of northward transport) to account for much of the recruitment variation in British Columbia. Intermediate temperatures and sea levels resulted in the strongest year classes. In Oregon Hayman and Tyler (1980) did not find recruitment to be related to surface temperatures, but did find positive correlations with onshore transport (negative of upwelling in Fig. 6 of Hayman and Tyler 1980) during January through March.

Both Ketchen (1956) and Hayman and Tyler (1980) used correlation analyses. A number of problems are associated with the use of simple correlations to investigate recruitment mechanisms. Factors often operate simultaneously and in complex ways such that correlations would not reveal their true importance. The assumption of linearity is often unsatisfied, as in the case of sea level and temperature relations to recruitment found by Alderdice. Such curvilinear relationships may be transparent to correlation analysis. Timing can also be an important consideration and is often overlooked. For example the English sole spawning season is so variable (Kruse and Tyler 1983) that the pelagic stage may span different seasons in

different years. Larvae may occur primarily in the autumn of one year or the spring of another (Laroche and Richardson 1979). Thus a correlation between year-class strength and environmental conditions using physical factors for fixed months each year may not reveal true survival mechanisms operating during the sole's pelagic stage.

We have constructed a mechanistic model (RECRU) which eliminated many of the limitations of correlation studies. This model includes factor interactions, sequential events and nonlinearities. We investigated possible causes of year-class strength fluctuations based on the agreement between recruitment observed from cohort analysis (Pope 1972) and recruitment simulated from the model, driven by historical records of biotic and abiotic factors.

METHODS

We assembled a selection of hypotheses about possible mechanisms of year class formation based on our understanding about the English sole's life history and ocean environment. We limited our modelling approach to those hypotheses dealing with factors for which empirical data sets exist. Furthermore, only those mechanisms operating during gonadal maturation or during the pelagic egg and larval stage were explored, because of the promise shown by Ketchen (1956), Alderdice (Pacific Biological Station, pers. comm.) and Hayman and Tyler (1980). We do not imply that mechanisms operating after settling, are inconsequential to recruitment variations. The following mechanisms were hypothesized to be potentially important in the English sole recruitment process: (1) population egg production is related to stock age structure, age-specific maturity, and age- and temperature-dependent fecundity; (2) surface temperature determines egg hatching success; (3) survival is related to transport of eggs and larvae from offshore spawning grounds to coastal nursery areas by ocean currents; (4) storm-generated shear causes mortality of eggs and larvae; and (5) food availability causes starvation during the larval stage (Fig. 2 and 3, as will be discussed below).

Hypotheses about these factors were expressed as functional relationships, translated into FORTRAN statements, and programmed in a manner such that their possible individual or collective roles could be investigated. The model is driven by time series of biotic and abiotic variables (Table 1). Corresponding to factors (1) - (5)

Figure 2. Possible components and processes associated with English sole cohort formation through their effects on adult reproduction and early life survival. Relationships a through j appear in Fig. 3.

Figure 2.

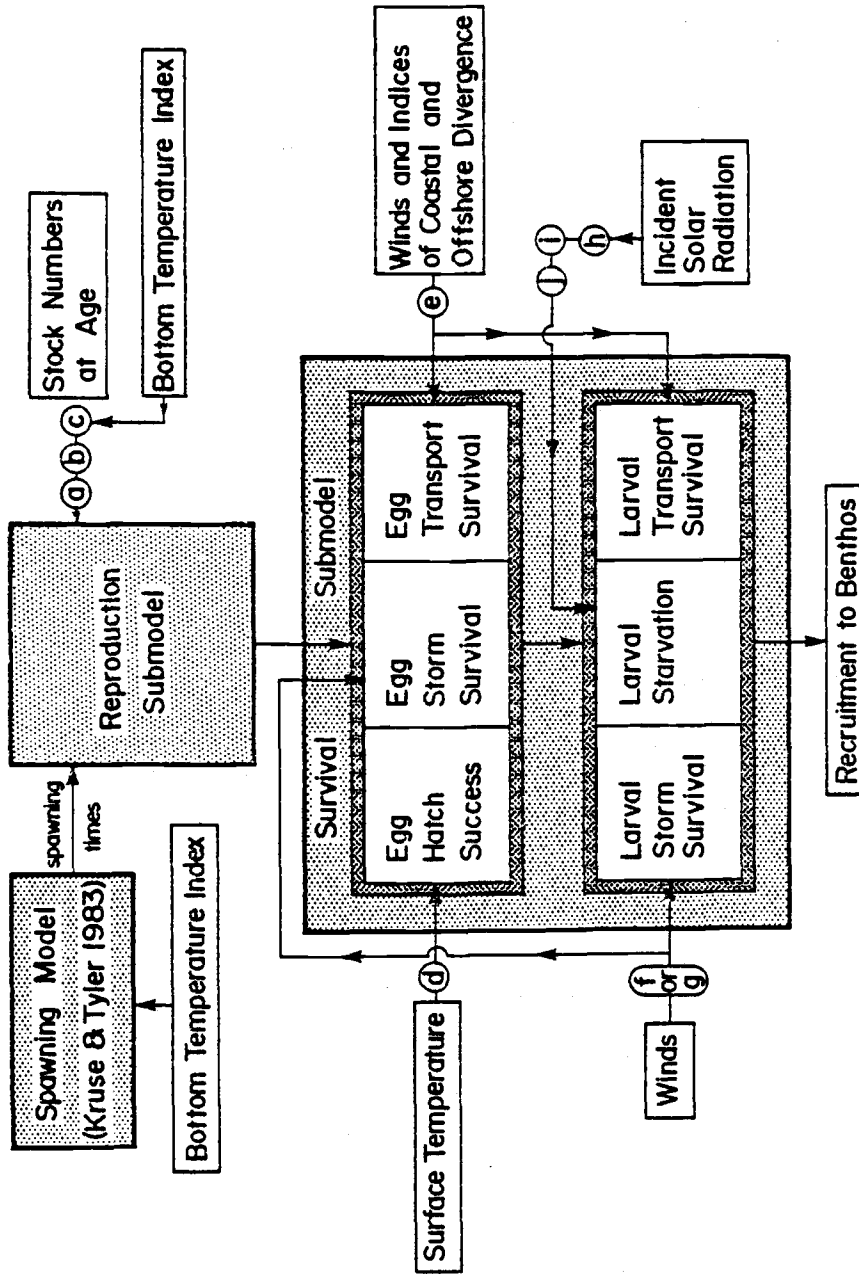


Figure 3. Relationships used in Fig. 2.

Figure 3.

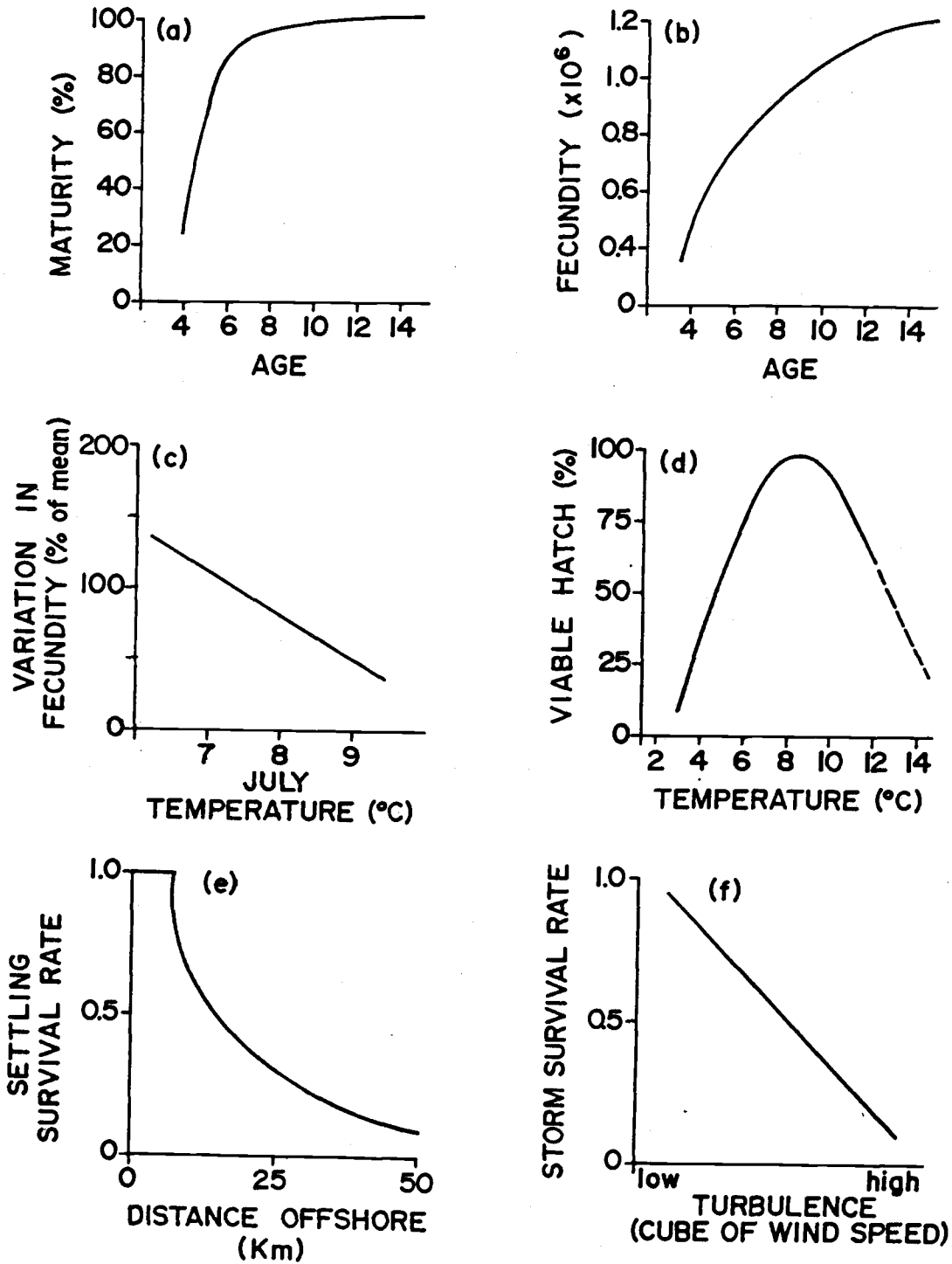


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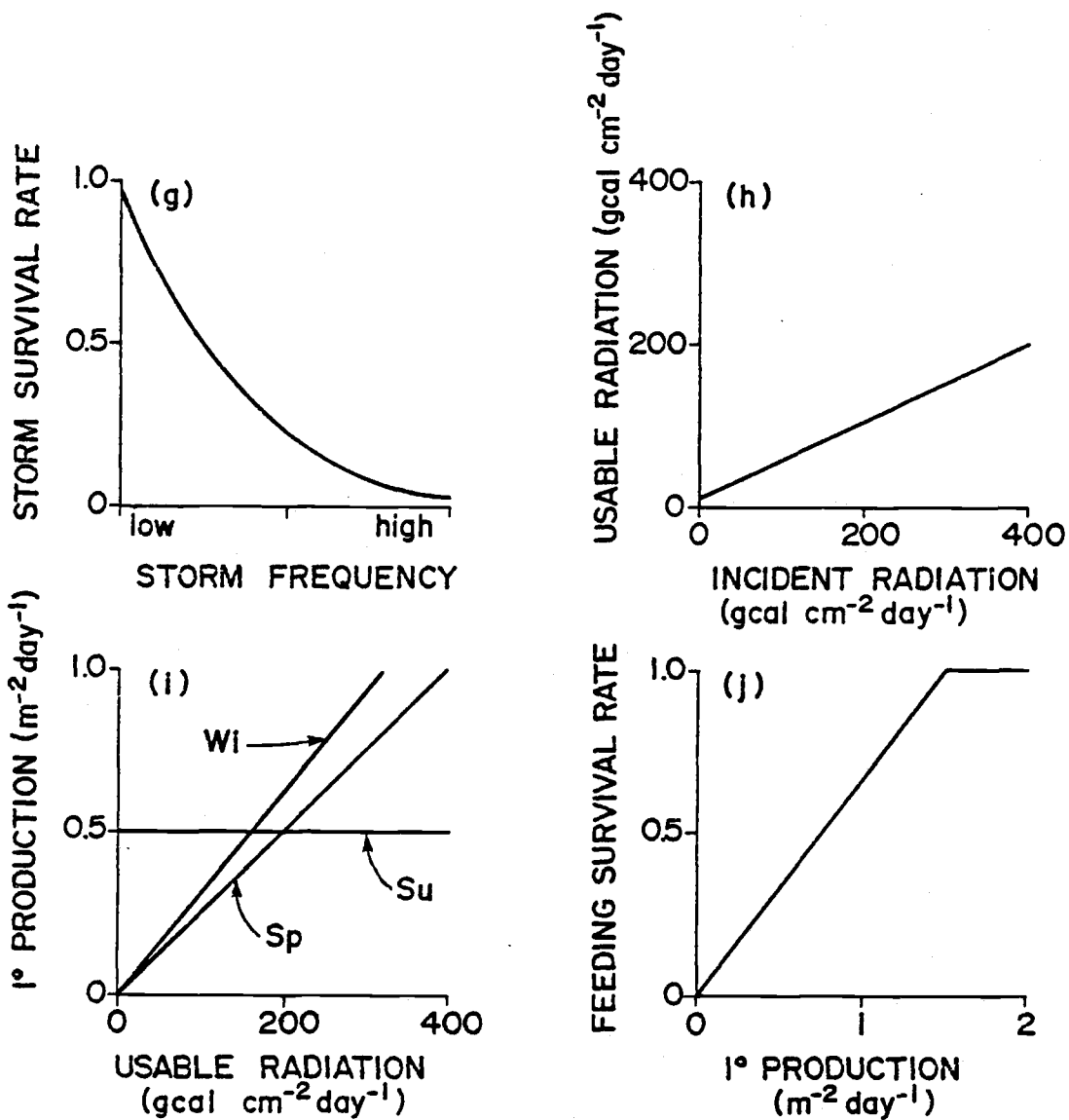


Table 1. Data used in recruitment model (RECRU). Values for environmental data are monthly means, except Columbia River lightship winds which were recorded every 4-6 h. Fishery data are annual averages.

Data	Location	Years	Source
a. Environmental Data			
Bottom temperature index	Station NH-15 (see Fig. 1, this report)	1954-1977	Kruse and Huyer (1983)
Sea surface temperature	44-46° N, 124-125° W	"	Douglas McLain NOAA, NMFS Pacific Environ. Group Monterey, CA
Northward and eastward wind speed	46° N, 124° W	"	Andrew Bakun (same address)
Coastal upwelling and offshore diverg. indices	45° N, 125° W	"	"
Incident solar radiation	Clatsop Co. Airport near Astoria (Fig. 1)	1954-1965	National Climatic Center Environmental Data Service Asheville, NC
Wind velocity	Columbia River lightship	1954-1972	"
b. Fishery Data			
Female E. Sole landings, effort, percentage of females in the catch (by weight), average weight per female and catch age composition	PMFC Area 3A (Fig. 1)	1959-1977	Robert Demory Oregon Dept. Fish & Wildlife Marine Regional Office Newport, OR

above, these include (1) stock numbers-at-age calculated using fishery data from PMFC AREA 3A, (2) monthly mean sea surface temperature for the area bounded by 44-46° N and 124-125° W, (3) monthly mean wind components at 46° N, 125° W and indices of coastal upwelling and offshore divergence at 45° N, 125° W, (4) hourly wind speed at the Columbia River lightship or monthly mean wind speed at 46° N, 124° W, and (5) monthly mean incident solar radiation near Astoria. Based on the degree of agreement between simulated and observed recruitment, conclusions were made about possible operation of each mechanism in the recruitment process. The correlation coefficient, r , between the two records was used as a measure of the agreement between them.

External to the model, we calculated the time series of observed recruitment strength and stock age structure. We chose age-4 female numbers, calculated by Pope's (1972) cohort analysis, as our index of observed recruitment. The fishery takes very few males and so it is not possible to develop meaningful statistics for them. Because some fishery statistics have been recalculated by the Oregon Department of Fish and Wildlife (ODFW), we chose not to use the cohort results of Hayman et al. (1980). Instead, T. Hayden (OSU, pers. comm.) and one of us (GHK) updated the fishery statistics (Table 2 and 3) and estimated numbers-at-age (Table 4) using the same methodology of Hayman et al. (1980). We make a distinction between landings as target species (at least 29% of the catch by weight) and total landings (Table 2), because English soles are also caught incidentally in fisheries directed toward other species. The catch of English soles resulting from a unit of effort directed toward them would be

Table 2. Total landings (t), landings as target species (t), effort (h), percent females in catch by weight, and average female weight (kg) for English soles caught in Pacific Marine Fisheries Commission Area 3A.

Year	Total landings	Landings as target species	Effort (f)	Percent females by weight	Average female weight
1959	606	601	3755	0.992	0.48
1960	761	738	4421	1.000	0.43
1961	583	583	4693	1.000	0.47
1962	660	616	5076	0.962	0.49
1963	575	519	4830	0.915	0.49
1964	419	342	3003	0.835	0.45
1965	440	387	2520	0.889	0.43
1966	1100	1002	4829	0.911	0.46
1967	572	523	3494	0.933	0.49
1968	456	413	3543	0.917	0.47
1969	439	384	3771	0.894	0.45
1970	362	289	3018	0.854	0.45
1971	313	260	2925	0.907	0.43
1972	376	294	2057	0.898	0.45
1973	363	286	2576	0.940	0.42
1974	296	213	1569	0.944	0.44
1975	372	284	2755	0.938	0.44
1976	921	671	4097	0.930	0.44
1977	371	288	2541	0.930	0.44
1978	718	564	3586	0.930	0.36
1979	697	490	7132	0.930	0.54

Table 3. Proportionate age composition of landed female English soles caught in Pacific Marine Fisheries Commission Area 3A.

Year	Age												
	2	3	4	5	6	7	8	9	10	11	12	13	>13
1959	0.003	0.056	0.199	0.336	0.247	0.076	0.035	0.021	0.018	0.008	0.001	0.001	0.000
1960	0.011	0.093	0.249	0.340	0.206	0.051	0.210	0.013	0.011	0.005	0.001	0.001	0.000
1961	0.001	0.053	0.207	0.354	0.243	0.066	0.030	0.019	0.016	0.010	0.001	0.001	0.000
1962	0.000	0.000	0.209	0.297	0.168	0.088	0.052	0.008	0.000	0.000	0.000	0.000	0.000
1963	0.002	0.053	0.206	0.313	0.233	0.085	0.030	0.034	0.034	0.009	0.000	0.000	0.000
1964	0.006	0.073	0.215	0.334	0.234	0.068	0.030	0.017	0.015	0.007	0.001	0.000	0.000
1965	0.007	0.095	0.260	0.329	0.203	0.050	0.022	0.014	0.012	0.007	0.001	0.000	0.000
1966	0.004	0.040	0.269	0.436	0.122	0.075	0.019	0.017	0.013	0.007	0.000	0.000	0.001
1967	0.003	0.051	0.156	0.291	0.346	0.075	0.038	0.017	0.011	0.009	0.002	0.001	0.001
1968	0.002	0.051	0.154	0.178	0.212	0.270	0.070	0.033	0.014	0.009	0.005	0.001	0.001
1969	0.001	0.080	0.185	0.251	0.132	0.164	0.119	0.035	0.020	0.006	0.005	0.003	0.001
1970	0.000	0.046	0.172	0.235	0.204	0.126	0.089	0.078	0.030	0.013	0.005	0.003	0.001
1971	0.000	0.035	0.145	0.346	0.203	0.126	0.046	0.037	0.039	0.014	0.000	0.006	0.004
1972	0.000	0.012	0.108	0.217	0.223	0.137	0.112	0.054	0.370	0.049	0.013	0.011	0.002
1973	0.000	0.069	0.185	0.291	0.167	0.153	0.069	0.037	0.012	0.011	0.003	0.002	0.000
1974	0.000	0.028	0.181	0.216	0.242	0.113	0.103	0.082	0.031	0.019	0.005	0.007	0.003
1975	0.000	0.018	0.095	0.246	0.226	0.158	0.086	0.092	0.037	0.015	0.013	0.004	0.009
1976	0.000	0.028	0.170	0.290	0.180	0.150	0.100	0.075	0.032	0.018	0.012	0.004	0.000
1977	0.004	0.054	0.170	0.194	0.176	0.161	0.101	0.045	0.035	0.033	0.016	0.004	0.007
1978	0.000	0.014	0.069	0.231	0.209	0.177	0.170	0.077	0.031	0.008	0.008	0.003	0.003
1979	0.001	0.008	0.099	0.224	0.254	0.186	0.096	0.064	0.039	0.019	0.005	0.002	0.002

Table 4. Numbers at age (in thousands) of female English soles in Pacific Marine Fisheries Commission Area 3A, calculated by the method of Pope (1972).

Year	Age					
	4	5	6	7	8	9
1955	3208	2025	845	335	143	77
1956	2995	1597	705	312	147	88
1957	2743	1670	818	364	221	146
1958	2345	1355	638	297	178	95
1959	2711	1696	974	543	252	149
1960	2698	1763	980	469	272	146
1961	5724	3907	1859	1013	529	299
1962	3494	1761	960	528	260	138
1963	2643	1719	1101	704	442	300
1964	2406	1589	939	560	338	175
1965	3449	2328	1549	1018	659	438
1966	3466	2401	1530	972	605	390
1967	3728	2626	1768	1179	807	538
1968	3080	2167	1348	850	516	208
1969	5001	3493	2438	1635	942	627
1970	3891	2721	1806	999	624	179

different from that expected from effort directed toward another species with a different geographical distribution. Catch and effort statistics in the English sole-directed fishery are most appropriate and were used in the cohort analysis. See Hayman et al. (1980) for more details.

There is little overlap between the stock and recruitment records, so we could not directly estimate a stock-recruit relationship. Instead, we used another method to reconstruct the stock. First we reconstructed the stock age frequencies. The age structure of the catch does not approximate that of the stock, because trawlers do not catch fish of all sizes at the same rate. Additionally, fishermen commonly discard small individuals. We converted length-specific catch rates (Best 1961) and discard rates (TenEyck and Demory 1974) to the form of age-specific rates using mean size-at-age (TenEyck and Demory 1975). We estimated what the landed catch-at-age would have been if the gear had caught all ages equally and if fishermen did not throw back young fish. This "adjusted catch" was calculated for each age and year by multiplying the actual total landings as target species by the age frequencies in the landed catch, and dividing by the catch and utilization rates (frequencies) at age. The age frequencies in the stock were then taken to be the same as those in the adjusted catch.

Next we estimated total stock size. This was done using the Baranov catch equation

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

where \underline{N} is total numbers of females in the stock, \underline{C} is total adjusted catch (numbers of females), \underline{F} is instantaneous fishing mortality and \underline{Z}

is the sum of instantaneous fishing and natural mortalities. We set $Z = 0.494$, as estimated by Hayman et al. (1980). The equation

$$F = q \cdot f \quad (2)$$

was used to estimate F by year, where f is the effort (in h) directed toward English sole as a target species and q is 7.4×10^{-5} per boat-h (Hayman et al. 1980). Using annual values of f and C and mean estimates of the other parameters, we calculated N for each year using eq. (1) and (2). The age frequencies of the stock were then used to estimate stock numbers at each age.

The major disadvantage of using this method of stock reconstruction is that it is more sensitive than cohort analysis to errors in the estimates of f and the age frequencies in the catch. Samples of age composition of the English sole catch are not always representative of the stock. For example, in 1962 no individuals older than age-9 were present in catch samples, but in 1963 ages up through 11 were represented. This problem seems to be restricted to individuals older than age-9 and is less prevalent after 1969. We do not feel that this poses a significant problem to our analysis. But to reduce such errors, we suggest that future recruitment studies use cohort analysis for generating both stock and recruit numbers, as the time series of fishery statistics become longer.

THE MODEL

System Definition and General Structure

The system considered here is that which includes all subsystems responsible for regulating English sole cohort size off Oregon. These subsystems include ecological, oceanographic and meteorological components which operate at various levels or stages of the life cycle. We constructed a simplified version or model of the real system, which includes only those processes perceived to be most consequential to English soles. The model can be manageable by selecting reasonable physical and conceptual limitations.

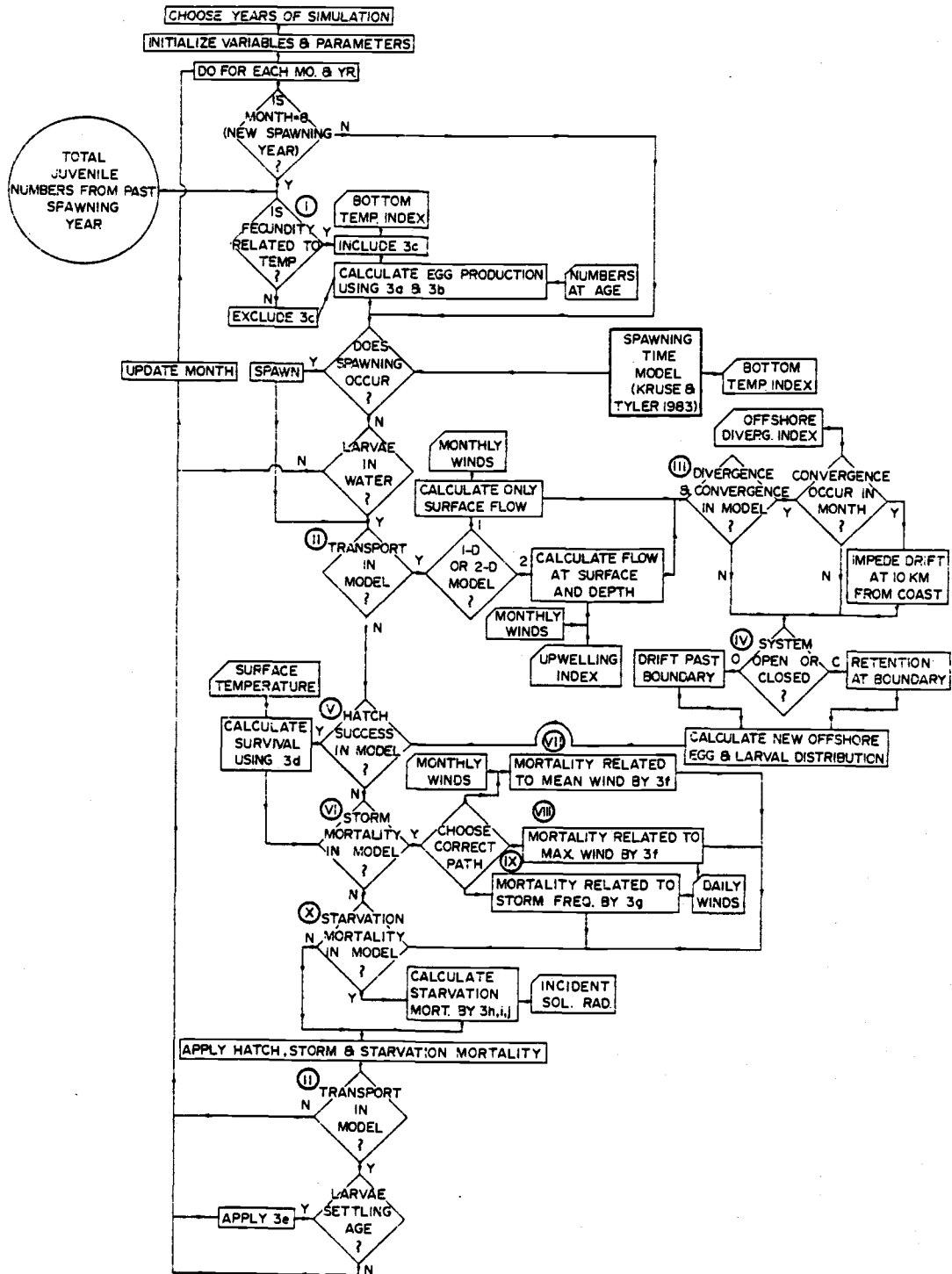
Physically, our model system is bounded by the geographical limits of the English sole off Oregon. The coastline forms the eastern boundary, but a western boundary is less obvious. Adults spawn as far as 30 km offshore (as will be shown), and larvae have been collected as far as 74 km from the coastline (Richardson and Pearcy 1977). The "Oregon" stock extends latitudinally from the vicinity of Destruction Island ($47^{\circ} 41' N$) to Cape Blanco ($42^{\circ} 50' N$) (Robert Demory, Oregon Department of Fish and Wildlife, ODFW, pers. comm.). Not only have tagging studies and trawl surveys (Demory et al. 1976) indicated a rather continuous distribution from the Columbia River to over 100 km south, no significant difference in growth exists for individuals landed at Astoria ($46^{\circ} 22' N$) or Coos Bay ($43^{\circ} 22' N$) (Kreuz et al. 1982). Maps of bathymetry and surface sediments (Byrne and Panshin 1977) imply that a lack of suitable substrate and a narrow shelf near Cape Blanco may account for the southern boundary. The northern

boundary is less clearly established, and present tagging studies (Golden et al. 1979) may result in a northward extension of the range. Thus, the fishery data from Area 3A (Fig. 1) used in our study include samples from only a portion of the region inhabited by the Oregon - southern Washington stock of English soles. However, due to migration and mixing we feel that Area 3A fishery statistics likely constitute reasonably representative samples from the entire stock.

We perceived the natural system to be composed of two classes of processes: those affecting reproduction and those affecting survival to recruitment (Fig. 2 and 3). The former class includes the influence of stock size and structure on population egg production and the influence of environmental effects on individual fecundity and spawning seasonality. The latter class includes environmental effects on egg and larval survival. Accordingly, our computer model is divided into two major components: the reproduction and early life survival submodels (Fig. 4 to be discussed in detail later). In overview, the reproduction submodel handles considerations of spawning time, egg production and spawning geography. Another model (Kruse and Tyler 1983) provides estimates of spawning times to the reproduction submodel based on bottom temperatures. Egg production is calculated from adult population dynamics (derived from fishery statistics) and from mean maturity and fecundity by age, with an option for temperature-dependent fecundity. The early life submodel treats young soles only with regard to mortalities during their residence in the water column. These include egg hatching mortality related to surface

Figure 4. Flow chart of our computer simulation model (RECRU) of the English sole recruitment process. Explanation in text.

Figure 4.



temperatures, advection and storm mortality related to winds, and starvation related to solar radiation through primary production.

Spawning

Processes leading to the recruitment of English soles commence with gonad maturation. Three aspects of spawning activity may influence the strength of the resulting cohort: population egg production, the location of spawning areas relative to ocean currents and nursery areas, and spawning times. Most recruitment studies only consider the first of these. We chose to treat all three, because for English soles there is reason to suspect that geography with respect to currents (Ketchen 1956) and timing (Kruse and Tyler 1983) are also of considerable consequence to recruitment.

In Oregon the English sole stock biomass may not be a good index of total egg production. The population lacks a stable age distribution due to the sporadic occurrence of large cohorts. Fluctuations in age structure are consequential to population egg production, because fecundity and maturity are strongly size-specific (Harry 1959). No Oregon females less than about 26 cm are mature and 100% maturity is reached at 36 cm. Mature females of length 30 and 43 cm produce an average of 3×10^5 and 1.5×10^6 ova, respectively.

We incorporated fecundity, maturity, and variations in the age structure of the stock into estimates of total population egg (PEP) using the equation

$$PEP(t) = P(a,t) \cdot FEC(a,t) \cdot N(a,t) \quad (3)$$

where $P(a,t)$, $FEC(a,t)$, and $N(a,t)$ are the percentage of mature

females, the average fecundity, and the total number of females, respectively, at each age a (4, 5, ..., 13, 13+) in year t . $N(a,t)$ was calculated using eq. (1) and (2), as discussed earlier. We used simple linear regression on data presented by Harry (1959) to determine the fecundity-length relation

$$FEC = 0.0004558 \cdot L^{3.6097} \quad (4)$$

where FEC is the mean total number of ova per female and L is the total length in mm. Length-specific maturity (Harry 1959) and fecundity (eq. 4) were converted to age-specific rates (Fig. 2a and b, respectively) using mean length-at-age (TenEyck and Demory 1975).

Data do not exist to examine interannual variability in the maturity and fecundity schedules. We chose to treat maturity to be time-invariant, i.e. $P(a,t) = P(a)$. However, we suspect that age-specific fecundity and growth are directly related. Given fecundity-length (eq. 4) and weight-length relationships (Smith and Nitsos 1969), it can be shown that the English sole fecundity-weight relation is nearly linear. We felt it also probable that interannual variations in fecundity and weight at age are also nearly linear. This became our first hypothesis in the model. We used annual values of adjusted length increment at age-1 (Kreuz et al. 1982) and the weight-length relationship of Smith and Nitsos (1969) to calculate the annual variation or anomaly in weight as a proportion of the long-term mean $[PWT(t)]$ over 1961-1974. Because the time series of empirical growth was shorter than we needed for our model, we utilized a strong negative correlation (Kreuz et al. 1982) between interannual variations of growth and the bottom temperature index (Table 1) to

generate proxy data. This inverse relation between growth and temperature is supported by laboratory experiments (Williams 1974). Using linear regression we defined the following relationship

$$PWT(t) = 4.1335 - 0.4118 \cdot BT(t) \quad (5)$$

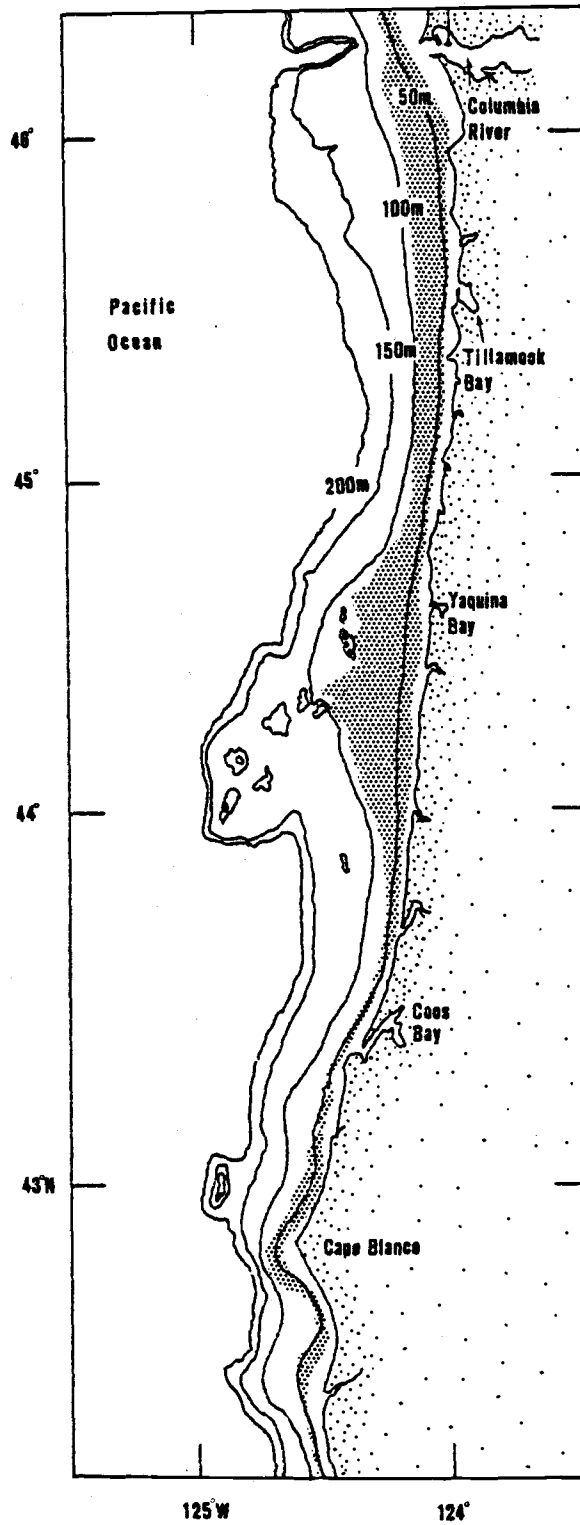
where BT(t) is the June bottom temperature index for year t. We hypothesized fecundity-at-age and weight-at-age to vary by the same proportion each year. Thus, fecundity, FEC(a,t), was taken to be a function of age and annual variations in shelf temperature.

The location of spawning areas must be included in our model, if egg and larval advection is to be investigated as an important process in the Parophrys vetulus early life history. These areas seem to have two characteristics in common. They have sand or mixed sand-mud sediment, because adults occur almost exclusively over these bottoms (Barss 1976). They also appear to be largely restricted to depths of about 35-90 m (Barss 1976; Hewitt 1980; and Ketchen 1956). Using these two criteria and maps with sediment distribution and isobaths (Byrne and Panshin 1977), we determined the area available to English soles for spawning (Fig. 5). Inferences about English sole spawning areas from larval surveys (Laroche and Richardson 1979), collection of ripe adult females (Harry 1959; Hewitt 1980) and analysis of winter catch distributions (Alverson 1960; Hewitt 1980) are consistent with Fig. 5. However, in the future a study should be conducted to completely describe English sole spawning areas empirically.

Because we considered only onshore-offshore (not alongshore) advection of eggs and larvae in our model, we condensed Fig. 5 into an average offshore profile of spawning intensity. Using Fig. 5 we made

Figure 5. Areas available to English sole spawning along the Oregon coast based on the distribution of sand or mixed sand-mud sediment between 35-90 m from Byrne and Panshin (1977).

Figure 5.

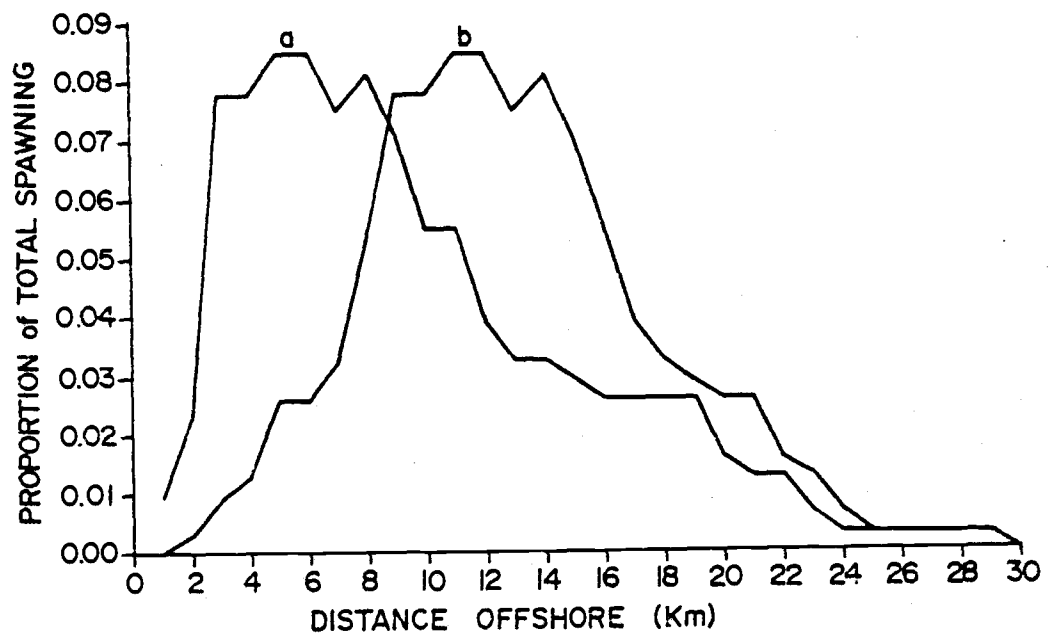


a total of 30 transects, one at every 15 km from 42° 09' N to 46° 18' N. Each transect was divided into 1 km intervals, and we tallied the number of transects along which spawning area was available at each interval. The count for each interval was divided by the total count for all intervals to yield a coastwise index of relative spawning intensity with distance offshore (Fig. 6a). We have assumed an even distribution of spawners throughout the available spawning area. If spawners actually prefer the deeper sites on Hecate or Stonewall Banks (off central Oregon), the actual spawning intensity profile may be skewed further offshore than in Fig. 6a. We explore the effects of this possibility in our sensitivity analysis.

We hypothesized that English sole spawning seasonality could be important to cohort strength because of its large interannual variability. Kruse and Tyler (1983) found much of the variability in spawning seasonality to be accountable by a simulation model, which was driven by monthly values of the shelf temperature index. This model is based on three hypotheses: (1) colder summer bottom temperatures promote gonadal maturation; (2) spawning does not occur below about 8 C; and (3) rapidly increasing temperatures delay spawning. Using the spawning model, we simulated spawning times for the years of interest in our recruitment model. The model predicts periods of no spawning, spawning, or peak spawning. For our recruitment model it is necessary to quantify spawning intensity by month. We chose to divide each month into four subintervals or "weeks". For each spawning season (July to June), we then counted both the total number of weeks of spawning and of peak spawning from

Figure 6. (a) Distribution of available spawning area with distance offshore (from Fig. 4) integrated along the entire Oregon coast, and (b) a similar distribution reflecting possible preference by adults for deep spawning grounds. We used (a) in all modelling and explored (b) in our sensitivity analysis.

Figure 6.



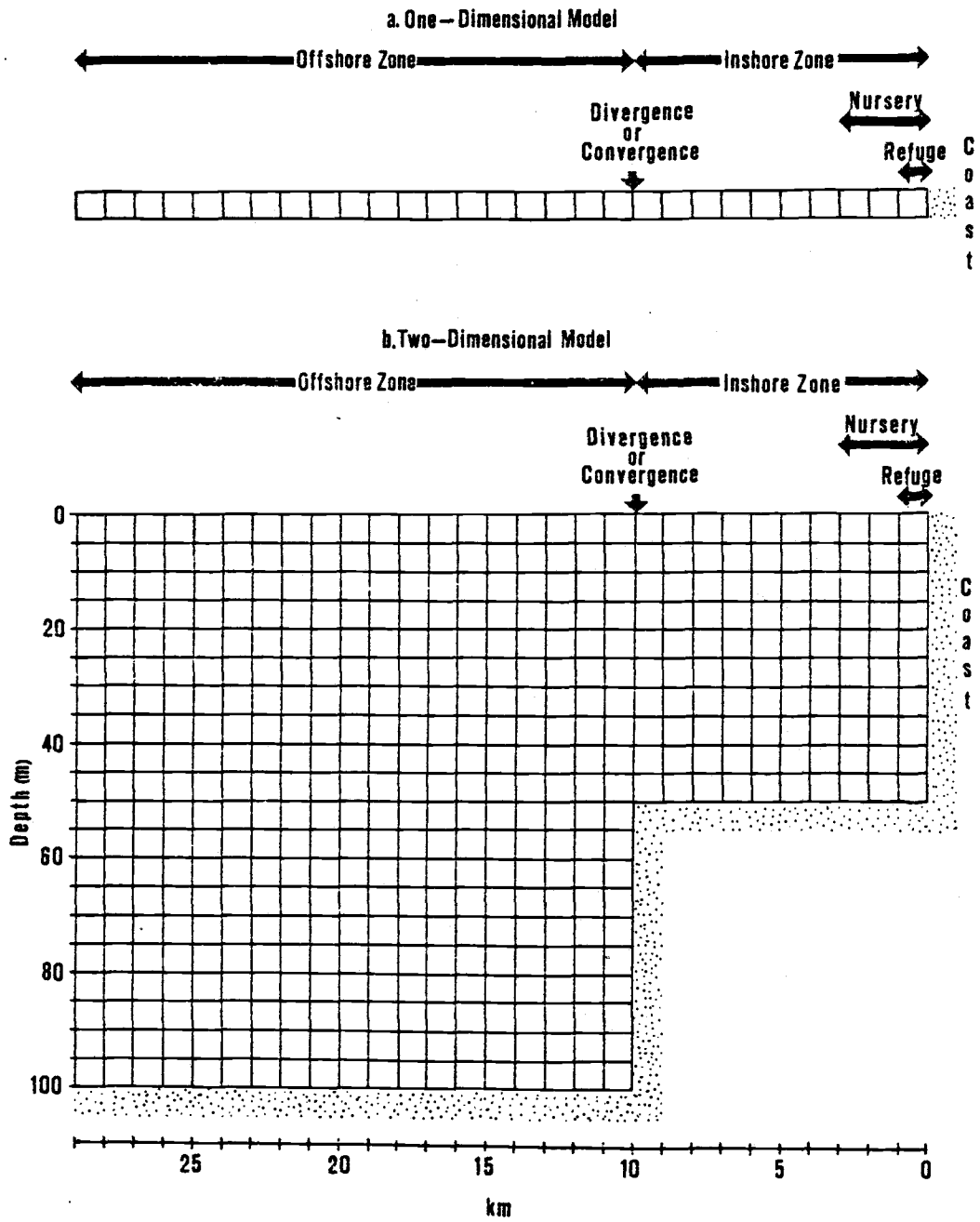
the simulated spawning records. Half of the season's spawning intensity was spread evenly over all weeks of spawning and half was spread evenly over peak weeks. In this way peak spawning included more than 50% of the year's spawning. We then estimated the spawning intensity for each month by summing the spawning intensity for the four weeks of that month. This assignment rule results in predictions which are qualitatively consistent with those made by the spawning model, but there is no assurance that the actual monthly percentages are accurate. This aspect will remain a limiting factor to accurate prediction of year-class strength.

Egg Hatch Success

Physical factors can affect the hatching success of fish eggs. Alderdice and Forrester (1968) examined the effects of temperature and salinity on the hatching efficiency of Parophrys vetulus eggs. Temperature is the most important of the two over the typical range of surface temperatures (8-15 C) and salinities (30-34‰) off Oregon. We constructed a relationship between temperature and percent viable (normal) hatch for salinities near 32‰ using the temperature-salinity-percent viable hatch response surface (Fig. 7 in Alderdice and Forrester 1968). Because the effects of temperatures above 12C were not investigated and because surface temperatures above 12 C do occur along the Oregon coast, we extrapolated (dotted line in Fig. 3d) Alderdice and Forrester's results to warmer temperatures by symmetry. Temperatures of 8-9 C yield the greatest percentage of viable larvae. Warmer or cooler temperatures result in smaller percentages. For each

Figure 7. Physical structure of (a) one-, and (b) two-dimensional egg and larval drift submodels in the recruitment model.

Figure 7.



month of spawning, we can calculate hatch success by driving the relationship in Fig. 3d by empirical surface temperatures (Table 1). The simulated time series of surviving larvae can then be compared with the historical time series of recruitment to determine the ability of the hatch success mechanism to account for variations in year-class strength.

Advection

As discussed earlier, evidence exists in Oregon and British Columbia for the importance of egg and larval drift in the English sole recruitment process. Larvae advected offshore likely experience a high mortality at settling time. Movement from spawning to nursery grounds is critical; in British Columbia favorable transport is northward, while in Oregon it is eastward. To contrast simple onshore-offshore flow indices (such as the upwelling index) with more realistic ones incorporating depth-dependency, we decided to construct two alternative forms of a transport submodel. One form was one-dimensional (cross-shelf), in which all eggs and larvae are assumed to be near the surface. The other form was two-dimensional (cross-shelf and depth), which included vertical profiles of larval density and currents. We first describe transport calculations and then we discuss mortality associated with transport.

Rather than calculating indices of water movement and the drift of eggs and larvae, we would have preferred developing a driving variable from a time series of current meter observations. Because such data are not available on a regular basis, we chose to construct transport

submodels which are driven by wind time series. Winds and currents along the Oregon coast are related (Collins and Pattullo 1970; Huyer and Pattullo 1972; Smith 1974). Ekman theory states that a wind across the sea surface generates surface water movement directed 45° to the right of the wind direction in the northern hemisphere; the surface water speed, \underline{v} , is related to the wind speed (in the same units) 10 m above the sea surface, \underline{w} , by:

$$v = \frac{0.0131}{\sqrt{\sin q}} \cdot w \quad (6)$$

where q is the latitude in degrees (Budinger et al. 1964). The constant, 0.0131, is from Duxbury et al. (1966) rather than 0.0127 from Budinger et al. (1964). This theory compares favorably with observations off Oregon. For example, Halpern (1976) found the current at 3.5 m to be directed almost exactly 45° to the right of the wind stress. In addition, eq. (6) predicts the current speed to be 1.5% of the wind at 45° N; Collins and Pattullo (1970) and others have observed it to be about 2%.

We had access to a time series of wind at 46° N, 124° W (Table 1), which is computed from the large-scale synoptic pressure charts. The agreement between such wind calculations and observed winds is excellent, even on a daily basis (Huyer and Smith 1978). Using this wind series and Ekman theory, we can calculate monthly estimates of surface current flow. We resolved only the onshore-offshore component of this flow, because it seemed more important whether larvae traverse the shelf to coastal nursery areas rather than whether larvae settle in specific areas along the southern or northern coast. This surface

flow calculation forms the basis for our one-dimensional model. In this version, eggs and larvae are assumed to be in the surface waters (0-5 m). We conceptualized the ocean as a series of 1 km squares extending offshore from the coast (Fig. 7a).

We added other components, largely based on the findings of Peterson et al. (1979), to make the model's behavior more consistent with observation. Chlorophyll and zooplankton distributions imply the presence of a surface divergence at 10 km from the coast during upwelling (Peterson et al. 1979). Current meter data show that the surface divergence is associated with a subsurface convergence (Huyer 1976). An offshore region of surface divergence (coupled to rising subsurface waters) or convergence (coupled to sinking subsurface waters) is generated if there is a curl of the wind stress, i.e., if the nearshore and offshore wind velocities are unequal. In addition to coastal upwelling or downwelling, a divergence or convergence zone at 10 km can affect advection of plankton. In recognition of this, we added the option of including an area of divergence or convergence to our model at 10 km (Fig. 7a). We treated the position of this feature as fixed, although it may well move onshore and offshore with fluctuations in cross-shelf circulation. When this option was included in the model, drift of eggs and larvae across the 10 km boundary was impeded when convergence occurred. Monthly values of the offshore divergence index (Table 1) were used to distinguish between convergent and divergent situations. The threshold between the two was made a parameter, although we might guess its value to be zero.

The effect of different parameter values on our results was investigated.

Because upwelled water seems to be transported to 20-40 km offshore (Halpern 1976; Peterson et al. 1979), we allowed the size of the system (i.e., the number of 1 km boxes) to be parameterized up to only 50 km. In addition, because upwelled water apparently can return shoreward during relaxation of upwelling (Halpern 1976; Peterson et al. 1979; and others), we added the option of making the offshore boundary open (larvae can be lost from the system) or closed (larvae are retained in the system).

It is known that waters immediately adjacent to the coast can behave very differently than those offshore (Peterson et al. 1979). It seemed plausible to us that a coastal "refuge area" may exist for larvae. We felt that larvae, transported into this coastal refuge area by favorable winds one month, might be retained in this shallow water zone regardless of the winds the next month. That is, upwelling will not occur very close to the coast. Because such a refuge area is unknown, we made its presence and size optional in our model.

We have now described all of the components involved in calculating the movement of eggs and larvae in our one-dimensional model. For each year, we calculated population egg production (eq. 3), the proportion of individuals spawning each month (from Kruse and Tyler's 1983 model), and the initial offshore distribution of eggs at spawning (Fig. 6a). Using monthly winds and Ekman theory, we calculated monthly surface flow. Eggs and larvae move accordingly except they cannot move past the 10 km boundary when convergence

occurs, and they cannot drift out of the refuge area when one is included in the simulation. Eggs and larvae transported to the offshore edge of the system are retained if the system is closed or lost if the system is open. Finally we applied a mortality rate at settling time (after two months drift) according to the location of larvae relative to nursery areas. This is the mortality applied according to favorable (onshore) or unfavorable (offshore) drift. In Oregon, estuaries (Westrheim 1955; Olson and Pratt 1973; Pearcy and Myers 1974) and sandy beaches along the open coast (Laroche and Holton 1979; Rosenberg 1980; Hogue and Carey 1982) comprise nursery areas for 0-age English soles. Newly-settled young appear to be restricted to waters inshore of 2.5 km of the coast (< 30 m depth). Because Demory (1971) could catch other 0-age flatfish but not English soles in the deeper waters, it is presumed that larvae settling outside nursery areas have a high mortality. In our model we allowed those larvae settling in the nursery area to survive at a maximum rate and those outside the nursery to survive at a rate which decreases exponentially with distance offshore (Fig. 3e). We used the following relation:

$$s = \begin{cases} 1 & \text{if } d \leq n \\ \exp(-(d-n)/a) & \text{if } d > n \end{cases} \quad (7)$$

where \underline{s} is the survival rate, \underline{n} is the size of the nursery area (in km) and \underline{d} is the distance offshore at settling (in km). We added the parameter, \underline{a} (originally set to unity), which could be changed to observe the effect of the rate of exponential decrease on the result.

Our two-dimensional transport submodel includes all of the considerations in the one-dimensional model. However, instead of

squares, we conceptualized the ocean to be constructed of cubes 1 km wide and 5 m deep (Fig. 7b). For simplicity we considered depth to be uniformly 50 m from the coast to 10 km and 100 m thereafter. For the Oregon coast, the actual mean distances of these two isobaths from shore are approximately 10 and 42 km, respectively. We also added depth-dependent larval and current profiles to the model. This was to investigate the ramifications of onshore flow at intermediate depths during upwelling.

Both laboratory and field studies provide limited information about English sole vertical distribution during the pelagic stage. Laboratory experiments (Ketchen 1956) imply that eggs float in the sea, while field studies show few larvae to be in the neuston, the upper 0.18 m of the water column, off Oregon (Laroche and Richardson 1979). Richardson (1973) presented data which suggests a relationship between ichthyoplankton assemblage (inshore versus offshore, see Richardson and Pearcy 1977) and vertical distribution (upper 19-20 m versus deeper than 20 m) of flatfish larvae. Coastal forms (Isopsetta isolepis and Psettichthys melanostictus) are more abundant near the surface than are offshore forms (Glyptocephalus zachirus, Lysopsetta exilis and Microstomus pacificus). We presumed Parophrys vetulus larvae to have a vertical distribution similar to its coastal companions, and used the vertical distribution of I. Isoplepis (Richardson and Pearcy 1977) and the limited knowledge for P. vetulus (Laroche and Richardson 1979) to hypothesize the vertical distributions for English sole larvae (Table 5a, b). Because these profiles are not

Table 5. Hypothesized larval vertical distribution of Parophrys vetulus by depth interval (m) in (a) 50 m and (b) 100 m of water. Frequency is the proportion of larvae found in each depth interval.

Depth Interval	in 50 m		in 100 m	
	Freq.	Cum. Freq.	Freq.	Cum. Freq.
0-5	0.258	0.258	0.258	0.258
5-10	0.291	0.549	0.291	0.549
10-15	0.170	0.719	0.170	0.719
15-20	0.089	0.808	0.075	0.749
20-25	0.054	0.862	0.043	0.837
25-30	0.041	0.903	0.033	0.870
30-35	0.032	0.935	0.026	0.896
35-40	0.026	0.961	0.021	0.917
40-45	0.021	0.982	0.017	0.934
45-50	0.018	1.000	0.014	0.948
50-55			0.011	0.959
55-60			0.009	0.968
60-65			0.007	0.975
65-70			0.006	0.981
70-75			0.005	0.986
75-80			0.004	0.990
80-85			0.004	0.994
85-90			0.003	0.997
90-95			0.002	0.999
95-100			0.001	1.000

well known, we later investigate the sensitivity of our results to them.

Ekman theory cannot be applied to our model of flow at depth off Oregon. Theory predicts the direction of currents to spiral with depth (Pond and Pickard 1978), while observed currents tend to follow local isobaths (Huyer and Smith 1978). The Oregon oceanographic system shows two types of behavior in response to the wind: upwelling and downwelling. The upwelling response differs somewhat inshore and offshore of 10 km (Peterson et al. 1979). Data (Halpern 1976; Kundu and Allen 1976; and others) show that flow is offshore to a depth of 10-15 m and onshore below during upwelling over the 100 m isobath (offshore of 10 km) (Table 6). Data inshore of 10 km (Peterson et al. 1979; Pillsbury et al. 1974a,b; Stevenson et al. 1974) imply a similar profile, but with offshore flow limited to the upper 5 m (Table 6). During downwelling flow is predominantly northward and onshore (Wyatt et al. 1972; Cross and Small 1967), and the mixed layer frequently exceeds 50 m (Huyer and Smith 1978). Using the limited data available (Collins et al. 1966; Huyer et al. 1978), we constructed the onshore velocity profiles for the downwelling season (Table 6). On the recommendation of Adriana Huyer we later altered these downwelling profiles to bring them more in line with mass balance.

Our two-dimensional advection submodel functioned analogously to the one-dimensional submodel. The total annual egg production, fraction of individuals spawning each month (monthly spawning frequencies), offshore distribution of spawners and surface flow calculations were as before. But now using the vertical distribution

Table 6. Cross-shelf current velocity profiles (sources listed in text) relative to the surface by depth interval (m) during the upwelling and downwelling seasons over the 50 and 100 m isobaths off the Oregon coast. Surface currents are typically offshore during the upwelling and onshore during downwelling. Values in parentheses correspond to changes later made to bring profiles more in line with mass balance (A. Huyer, OSU, pers. comm.).

Depth interval	Velocity as a proportion of the surface flow			
	upwelling season		downwelling season	
	in 50 m	in 100 m	in 50 m	in 100 m
0-5	0.333	0.667	0.667	0.667
5-10	-0.267	0.333	0.400	0.400
10-15	-0.593	0.067	0.256	0.256
15-20	-0.500	-0.100	0.167	0.167
20-25	-0.280	-0.300	0.107	0.107
25-30	-0.193	-0.433	0.070 (-0.100)	0.070
30-35	-0.067	-0.400	0.063 (-0.175)	0.063
35-40	0.000	-0.380	0.037 (-0.200)	0.037
40-45	0.067	-0.273	0.017 (-0.225)	0.017
45-50	0.113	-0.267	0.007 (-0.250)	0.007
50-55		-0.247		-0.002 (-0.004)
55-60		-0.200		-0.007 (-0.014)
60-65		-0.153		-0.027 (-0.054)
65-70		-0.133		-0.037 (-0.074)
70-75		-0.127		-0.060 (-0.120)
75-80		-0.107		-0.063 (-0.126)
80-85		-0.087		-0.073 (-0.146)
85-90		-0.053		-0.077 (-0.154)
90-95		-0.020		-0.080 (-0.160)
95-100		0.000		-0.080 (-0.160)

of larvae (Table 5) and relative velocity profiles (Table 6), larvae at each depth were moved according to flows experienced at those depths. The monthly values of the coastal upwelling index at 45° N, 125° W (Table 1) were used to distinguish upwelling from downwelling seasons for the choice of profiles in Table 6. After two months of drift, a mortality rate was applied according to the distance offshore of the nursery at settling (eq. 7 or Fig. 3e).

Both one- and two-dimensional submodels were incorporated into the recruitment model. One or the other was chosen for a particular simulation. Parameter values and some functions were later varied to determine whether our results were dependent on particular sets of specifications.

Storm Mortality

In addition to inducing currents which can carry eggs and larvae away from nursery areas, strong winds can directly cause mortality. Storms may dislodge, beach and kill eggs of freshwater (Clady 1976; Kramer and Smith 1962; Rupp 1962) and saltwater fishes (Pinus 1974 and citations therein).

We hypothesized that storms cause mortality during the English sole pelagic stage. Eggs are likely more vulnerable to storms than larvae, due to their proximity to the surface. We expressed our hypothesis in several forms, because of uncertainties about how storms and survival are functionally related. Using these alternate hypotheses we examined whether substantial recruitment variation may be related to mean monthly wind speed, maximum wind speed in each

month or the number of storms per month (storm frequency). We had access to two driving variables (Table 1): mean monthly winds at 46° N, 124° W calculated from large-scale, atmospheric pressure charts and Columbia River lightship wind observations (up to six per day). We used both, because the latter allowed us to treat storms realistically as events and the former allowed hypothesis investigation over the entire period of interest.

Niiler and Kraus (1977) showed that the rate at which wind adds turbulent kinetic energy to the upper ocean is proportional to the wind speed cubed. On this basis we suggested that English sole mortality is related to the cube of the wind speed (Fig. 3f). We examined the possibility that survival is related in this way to mean monthly wind speed at 46° N, 124° W or maximum wind speed per month at the lightship, indices of average and strongest storms per month, respectively. We also considered that monthly survival \underline{S}_m may be related as in Fig. 3g to monthly storm frequency (number of stormy days per month), \underline{n} , at the lightship by

$$\underline{S}_m = (\underline{S}_s)^n \quad (8)$$

where \underline{S}_s is the survival per storm event. Because of ambiguity in definition, we used three definitions of a storm: an event during which wind exceeded 46, 74 or 102 km/h (25, 40 or 55 kts, respectively).

To investigate storm mortality using our model we calculated annual egg production and monthly spawning frequencies, as with other hypotheses. However, this time we calculated a monthly survival rate during the pelagic stage based on its hypothesized relation to

turbulence (Fig. 3f) or storm frequency (eq. 8 or Fig. 3g). To fully explore these relations, we chose a wide range of values for the slope in the first relation and S_s in the second. We judged the relative importance of storm mortality, based on an observed recruitment and simulated numbers of larvae surviving at settling.

Starvation Mortality

Evidence shows that larval starvation not only occurs in the sea, but could partly determine year-class size for some species (Hunter 1981). No direct evidence of this exists for English soles. However, low winter primary production (Anderson 1964) and zooplankton abundances (Peterson and Miller 1977) leads to the possibility that availability of larval prey could be suboptimal at times. We hypothesized that English sole year-class strength is related to prey abundance during the larval period. Because relationships exist between solar radiation and primary production off Oregon (Small et al. 1972), we chose incident solar radiation near Astoria (Table 1) as the driving variable. Following Hobson and Hartley (1983) and others, we calculated usable (photosynthetically active) radiation as 50% of the monthly values of incident radiation (Fig. 3h). Using relationships (Fig. 3i) between usable radiation and primary production along the Oregon coast for spring (March-May), summer (June-September) and winter (October-February) developed by Small et al. (1972), we then calculated a time series of monthly values of primary production. The relationship (if one exists) between primary production and starvation mortality would be an inverse one; higher productivity

should lead to lower mortality. We chose a linear relationship with a plateau in survival at high levels of production (Fig. 3j). The level of production at which maximum survival is reached was made a parameter. The relation could be made strictly linear over all observed levels of production by choosing large parameter values. We compared observed and simulated recruitment, when larval survival rates were calculated from the relationships in Fig. 3h, i and j and the incident radiation data.

Model Flow Chart

We present a flow chart (Fig. 4) which represents the essential mechanics of our computer model. Boxes denote an operation or set of operations, and diamonds indicate a branch in flow based on contingency. Computer card-shaped symbols signify driving variables (inputs) and the large circle represents output. Numbered letters (e.g. 3a, 3b, etc.) refer to relationships in Fig 3. Roman numerals refer to the following hypotheses: (I) Variations in fecundity are inversely related to bottom temperature (Fig. 3c). This was developed parallel to findings (Kreuz et al. 1982) that variations in growth are inversely related to bottom temperature. The driving variable is the shelf temperature index. (II) Early life survival is related to ocean transport. This follows from a recognition of the distance between spawning and nursery grounds and the variability of the currents between them. Two alternative wind-driven transport submodels are employed. (III) Offshore divergence or convergence affects larval drift. Peterson et al. (1979) developed this idea in their treatment of

copepod distributions during upwelling. Offshore convergence promotes retention of plankton in the coastal zone, while divergence promotes offshore advection. The offshore divergence index is used to distinguish divergence and convergence. (IV) the system's offshore boundary behaves as if it is either open or closed. This option was added to explore the nature of the system. If the ocean off Oregon acts as a closed (rather than open) system in its cross-shelf dimension, the likelihood of larval transport to nursery areas may be enhanced. (V) Egg hatch success is related to temperature by a relationships (Fig. 3d) determined in the laboratory (Alderdice and Forrester 1968). Physiological mechanisms associated with the development apparently have evolved to operate normally only under intermediate temperatures. Surface temperature data were used to drive this relation. (VI) Early life mortality is related to storms. Because storm-generated stress may kill eggs and larvae of other species, it is conceivable that English soles could likewise be adversely affected by high winds during their pelagic life. The next three hypotheses specify the exact relationship. (VII) Storm mortality is related to the cube of mean monthly wind speed at 46° N, 124° W as in Fig. 3f. The fact that turbulence is related to the cube of the wind speed forms the basis for this relation. Mean monthly winds may index average storm conditions for the month. (VIII) Storm mortality is related to the cube of maximum wind speed per month at the Columbia River lightship (Fig. 3f). Perhaps larvae surviving the worst storm of the month can survive lesser storms, but not visa versa. (IX) Storm mortality is related (eq. 8 and Fig. 3g) to

monthly storm frequency at the lightship. This was developed from the rationale that the greater the number of storms per month, the fewer the number of surviving larvae. Lastly, (X) larval starvation mortality off Oregon is related to incident solar radiation near Astoria by relationships of incident to usable radiation (Fig. 3h), usable radiation to primary production (Fig. 3i), and primary production to starvation mortality (Fig. 3j). This pursues a simplified notion of energy flow in the ecosystem, i.e. increased inorganic energy input results in more energy flow at both primary producers and higher trophic levels.

We now trace the flow of logic in Fig. 4 more precisely. The model is started (top step of flow chart) by choosing the years for which it is to be run. This choice is affected by the length of the particular time series used as driving variables and the purpose of the run. The next two steps handle initializations and control of flow through the remainder of the model for each month and year of simulation. The first decision component (diamond) determines whether the present month is August. This month was chosen as a start up because it is the month of little or no overlap between larvae in the water from the previous spawning season and eggs from the new season. If it is August, the model outputs the number of juveniles simulated from the past year (circle at left) and proceeds to the next decision compartment (I) which determines whether the first hypothesis is included in the present simulation. If this hypothesis is being investigated the flow side-steps to the right. The temperature-dependent fecundity relation (Fig. 3c) is switched on, the July bottom

temperature index is read from above, and the variation in fecundity (as a proportion of the mean) is input into the egg production calculation (next step below). This calculation is also based on eq. (3), Fig. 3a, b and numbers at age as a driving variable. If, on the other hand, the first hypothesis (I) is not considered, flow continues down, the relationship of Fig. 3c is not used, and the egg production calculation (step to right) is based only on eq. (3), Fig. 3a, b and numbers at age. Notice that, after this calculation, the flow in all months of the year but August (see uppermost diamond) reunites with our present logic. Total annual egg production need only be calculated once per year.

The next task the model handles is the spawning schedule for the present year. The first step in this process is to determine if spawning occurs in the present month (diamond below egg calculation box). This is resolved by input from Kruse and Tyler's (1983) spawning model (to the right), which is driven by the bottom temperature index. If spawning occurs, flow proceeds to the left and the appropriate numbers of eggs are spawned based on the proportion of individuals spawning that month and the annual egg production. If on the other hand, spawning does not occur and no larvae are in the water (next diamond down), there is no reason to proceed with further calculations. Flow moves left, the month is updated, and logic returns near the top of the model. Only when eggs and larvae occur does flow proceed to the remainder of the model, which deals with early life survival.

Mortalities from each source (temperature, advection, storms, starvation) are calculated separately as each hypothesis is considered. However, they are actually applied simultaneously in a subsequent step (discussed below). Advection is considered first. If the transport hypothesis is included in the model (II), the flow side-steps to allow the choice between one- or two-dimensional transport submodels (diamond to right in Fig. 4; see Fig. 7). Calculations for both alternatives are similar: both calculate surface flow (from eq. 6) using wind velocity as a driving variable. The two-dimensional version also includes larval (Table 5) and current profiles (Table 6) with depth. The upwelling index is an additional driving variable and is used to choose between upwelling and downwelling profiles of Table 6. If divergence and convergence are considered (III) and convergence occurs (diamond to right of III), onshore or offshore advection is stopped at 10 km from the coast. Otherwise free movement is allowed. Convergence or divergence are distinguished using values of the offshore divergence index (read as a driver). A choice of a closed or open system (IV) either prevents drift of larvae offshore of the system boundary (step to right) or allows loss from the system (step to left). Given these specifications, new egg and larval distributions are calculated (box below IV).

After treating advection, the model treats hatching success (V). If temperature-dependent hatch success is included, survival rates are calculated (box to left) from the relationship in Fig. 3e with surface temperature as a driving variable.

Storm mortality (VI) is treated next. If this hypothesis is switched on, a decision (diamond to right) is made on the particular form of the hypothesis (VII, VIII, or IX). Monthly wind speed drives hypothesis VII and daily winds drive VIII and IV.

If the hypothesis about starvation is switched on (X), mortality is calculated using the relationships in Fig. 3h, i, j and incident solar radiation as a driving variable.

All that remains is to apply mortalities from the various sources operating on the eggs and larvae. Hatch, storm and starvation mortalities are applied first (box above two lowermost diamonds in Fig. 4). If transport was included (II) and larvae are two months old (lowermost diamond), a mortality rate on larvae is also applied according to distance offshore at settling (box to left on Fig. 4; see Fig 3e). Finally, the month is updated and flow is returned to the top of the chart.

RESULTS

Evaluation of Hypotheses Individually

Due to the length of the time series of fishery statistics and the methods used to calculate population egg production and recruit numbers, we could compare simulated and observed cohort strength for only the 1960-1970 year classes. Our convention is such that eggs spawned in the winter of 1959-1960 result in the 1960 year class. We first examined the relation between calculated egg production (using eq. 3) and cohort size (age-4 numbers from Table 4) over these eleven years. Scatter plots did not suggest curvilinear relationships. The correlation coefficient (0.26) is similar to that obtained (0.21) when stock size (the sum of numbers at ages 4 and greater) is substituted for population egg production.

The first hypothesis incorporated into the model was that variations in fecundity and bottom temperature are related (Fig. 3c). That is, we still calculated population egg production by eq. (3), but allowed fecundity-at-age to vary according to its hypothesized relation to temperature. The resulting correlation over 1960-1970 is 0.34. The correspondence was particularly improved over 1960-1966. We decided to retain the temperature-dependent fecundity relation in all subsequent runs, based both on our contention that it exists and on the observed improvement in r . Evaluation of further hypotheses was based primarily on their ability to improve on this correlation between egg production and recruitment.

We examined the effects of the relationship between egg hatch success and surface temperature by estimating population egg production (as just described) and calculating egg survival according to the relationship in Fig. 3d driven by coastal surface temperatures during the months of spawning. The spawning schedule came from Kruse and Tyler's (1983) spawning model (Fig. 2 or 4, this report) and temperature data are averages over a 2° latitude by 1° longitude rectangle (Table 1). The correlation coefficient between the simulated numbers of hatched viable larvae and age-4 numbers was 0.66 (Table 7). Because this represents a substantial increase from 0.34, we took this as a favorable indication that the temperature-hatch relation operates in nature and could account for a portion of the observed recruitment fluctuations.

We pursued a notion that perhaps eggs occur just below the surface (due to turbulence) and that temperatures actually experienced might be somewhat colder than at the surface. A series of simulation runs were made in which a constant was subtracted from each temperature datum before using Fig. 3d to calculate survival. We also made simulations using the bottom temperature index or an average between bottom and surface temperature to drive the relationship. The best results were obtained when surface temperatures were used directly (Table 7).

We next considered advective loss as a source of mortality. Egg production calculations and spawning schedules were as before. However, instead of using temperature-dependent hatch success, mortalities due to settling on unfavorable bottoms were applied.

Table 7. Correlation coefficients (r) between observed and simulated recruitment when the latter is obtained using population egg production estimates and survival rates from the hatching success relationship (Fig. 3e) driven with either surface data or the bottom temperature index.

Temperature Data	r
surface	0.66
surface - 0.25 C	0.63
surface - 0.50 C	0.61
surface - 0.75 C	0.59
surface - 1.00 C	0.59
surface - 2.00 C	0.54
(surface + bottom)/2	0.41
bottom	0.24

Pelagic young were moved according to either the one- or two-dimensional advection submodels driven by the monthly wind record at 46° N, 124° W. Mortalities were presumed related to distance from the nursery at settling time (Fig. 3e). Eight sets of simulation experiments were conducted (Table 8). We proceeded by first ordering the four parameters (refuge size, nursery size, system size, divergence/convergence threshold) of the advection submodels according to decreasing sensitivity of the correlation coefficient (between observed and simulated recruitment) to them. We then found a value of the first parameter (refuge size) which resulted in the highest correlation. Fixing its value, we next varied the value of the second (nursery size) and located its maximum. After doing this for all four parameters, we explored other combinations to ensure that we had indeed found the maximum correlation possible. In some instances multiple local maxima were found and in others a range of some parameter values yielded the same correlation. We treat this in more detail in our sensitivity analysis.

Pairwise comparisons from Table 8 reveal that, all else equal, inclusion of the divergence/convergence zone at 10 km from the coastline improved the correspondence between observed and simulated records on four of four occasions. An open system (rather than a closed system) gave higher correlations on three of four times (one was a tie), and the one- or two-dimensional advection models each resulted in greater values on two of four instances. On this basis we chose the one- and two-dimensional models parameterized in columns five and six of Table 8 as the best advection submodels. These versions

Table 8. Correlation coefficients (r) between observed and simulated recruitment when the latter is obtained using population egg production estimates and survival rates calculated from advection submodels. Parameters are: (1) system size, the width of the model ocean, (2) nursery size, the width of the coastal zone of maximum larval survival at settling (width of plateau in Fig. 3e), (3) refuge size, the width of a hypothesized coastal zone in which currents are never offshore, and (4) divergence/convergence threshold, a value of the offshore divergence index which distinguishes divergence from convergence.

	divergence/convergence at 10 km ignored				divergence/convergence at 10 km considered			
	open system		closed system		open system		closed system	
	1-D model	2-D model	1-D model	2-D model	1-D model	2-D model	1-D model	2-D model
System size (km)	45	29	45	50	40	29	45	50
Nursery size (km)	3	5	3	3	1	5	2	3
Refuge size (km)	0	0	0	0	0	0	0	0
Div./Conv. thresh. (mm/d)	-	-	-	-	-100	-115	+150	-150
r	0.65	0.59	0.54	0.57	0.69	0.67	0.63	0.67

performed equally well ($\underline{r} = 0.69$ and 0.67 , respectively) to the version which included the temperature-hatch success relation.

Before considering the next hypothesis, we pursued several aspects of the transport submodels that were of concern. Significant uncertainty exists regarding the (1) larval depth distribution, (2) geographic distribution of spawning adults, (3) relationship between survival and distance offshore at settling time, and (4) current depth profiles during the downwelling season. Because of these uncertainties, the ability of the advection submodels to account for variations in the observed recruitment record (Table 8) could be misleading.

We made changes in the uncertain profiles and examined their effects on the correlation coefficient (Table 9). The purpose was to determine the dependence of the advection modelling results on these profiles and not to produce better correlations nor to "curve-fit". First, we made extreme changes in (1) and (3) above, the larval depth distribution (from those in Table 5 to Table 10) and survival rates (from $a = 1$ to $a = 4$ in eq. 7), respectively. The former moves the majority of larvae from surface waters to depths at which onshore movements will occur during both downwelling and upwelling (compare Table 5 and 10 to Table 6). That is, rather than intense upwelling favoring advective loss, strong upwelling is now favorable for drift to the nursery and survival. The latter change greatly reduces the rate of exponential decrease in survival with distance offshore. This effectively creates a broader nursery area. Next, we changed (2) above, the spawning distribution (Fig. 6b rather than Fig. 6a), to

Table 9. Changes made in some poorly established profiles to examine the sensitivity of the advection submodels to them.

Profile	Model	Change from	Change to	Optimum Parameter Values				
				System size (km)	Nursery size (km)	Refuge size (km)	Div./Conv. threshold (mm/d)	r
Larval depth dist.	2-D	Table 5	Table 10	45	2	0	-110	0.69
Spawning dist.	1-D	Fig. 6a	Fig. 6b	50	0	0	-125	0.70
	2-D	"	"	29	0	1	-120	0.71
Survival rate	1-D	Eq. (7) a = 1	Eq. (7) a = 4	45	0	0	-105	0.68
	2-D	"	"	29	1	0	-115	0.65
Current dist.	2-D	Table 6	Values in parenthesis in Table 6	29	6	0	-115	0.66

Table 10. Larval vertical distribution of Parophrys vetulus by depth interval (m) in (a) 50 m of water and (b) 100 m of water used to investigate the sensitivity of the RECRU model.

Depth Interval	in 50 m		in 100 m	
	Freq.	Cum. Freq.	Freq.	Cum. Freq.
0-5	0.041	0.041	0.033	0.033
5-10	0.054	0.095	0.043	0.076
10-15	0.175	0.270	0.175	0.251
15-20	0.229	0.449	0.222	0.473
20-25	0.229	0.728	0.222	0.695
25-30	0.175	0.903	0.175	0.870
30-35	0.032	0.935	0.026	0.896
35-40	0.026	0.961	0.021	0.917
40-45	0.021	0.982	0.017	0.934
45-50	0.018	1.000	0.014	0.948
50-55			0.011	0.959
55-60			0.009	0.968
60-65			0.007	0.975
65-70			0.006	0.981
70-75			0.005	0.986
75-80			0.004	0.990
80-85			0.004	0.994
85-90			0.003	0.997
90-95			0.002	0.999
95-100			0.001	1.000

allow for the likelihood that adults prefer deeper spawning areas rather than showing no preference for any particular depth strata within the spawning region. We made simulation runs with the new larval depth distribution and then with the new survival rates. These alterations did not result in significant changes in the correlation coefficient obtained as output (compare rows 2 and 4 in Table 9 to column 5 in Table 8, and rows 1, 3 and 5 in Table 9 to column 6 in Table 8). That is, the model is robust to changes in parameters and structures. We interpret this to imply that the most important feature of the transport submodels is the wind velocity, not the chance selection of particular structures or parameters resulting in good correlations. Rather than either incorporating changes which increased the correlation coefficient (such as in rows 2 or 3 in Table 9) or curve-fitting in other ways, we retained our original choices of the first three profiles in Table 9 for two reasons. Firstly, we did not want to abandon our original constructs based only on increased correlation coefficients. Secondly, our purpose was not to artificially obtain high correlation coefficients without empirical justification.

We improved the velocity profiles during downwelling (A. Huyer, OSU, pers. comm.) such that they more closely achieve mass balance (values in parentheses in Table 6). The resulting correlation coefficient was virtually unchanged (last row in Table 9 versus column 6 in Table 8), but we retained this change in our final two-dimensional transport model in the pursuit of realism. Our final one-dimensional transport model was as before (column 5 in Table 8).

Storm mortality was investigated independently by estimating population egg production, as before, but now calculating survival from either of two wind time series (Table 1). We wished to determine if relationships between early life survival and winds could help improve the correlation between observed and simulated recruitment when the later was based on egg production alone ($r = 0.34$). We investigated two relationships between survival and winds, as shown in Fig. 3f and Fig. 3g (eq. 8). Because we do not know the parameter values specifying these relations, we first tried different values to determine the magnitude of the best correlation attainable. We varied both the intercept along the horizontal axis, S_{\max} (the survival at maximum wind speed), in the relation in Fig. 3f and S_g in the relation (eq. 8) in Fig. 3g. In each case the survival when wind speed was zero was fixed at unity, so the first changes the slope in Fig. 3f and the second changes the rate of exponential decay in Fig. 3g. The results are shown in Table 11. For the relation (Fig. 3f) with mean monthly wind speed, the best correlation was achieved when the slope was zero ($S_g = 1.0$). That is, no improvement could be made on the model results obtained with egg production alone. In fact, stronger year classes and increased survival are actually associated with years of stronger monthly winds. When the maximum wind speed at the Columbia River lightship was used as a driving variable in the same relation (Fig. 3f) rather than monthly mean wind speed at 46° N, 124° W, the correlation coefficient was increased only slightly. For the relationship (eq. 8) shown in Fig. 3g, the coefficient was increased

Table 11. Correlation coefficients (r) between observed and simulated recruitment, when the latter is obtained using population egg production estimates and survival rates calculated from relationships (Fig. 3f or g) to winds at 46° N, 124° W or the Columbia River lightship (CRL). Parameters are S_{\max} , the intercept of the relation and the horizontal axis in Fig. 3f, and S_s , the survival rate per storm in eq. (8).

Wind data	Statistic	Relation	Optimum parameter values	r
Mean monthly winds at 46° N, 124° W	monthly mean speed	Fig. 3f	$S_{\max} = 1.0^1$	0.34
hourly winds at CRL	max. speed per mo.	"	$S_{\max} = 0.0$	0.38
"	monthly storm freq. (no. days winds exceed 46 km/h)	Eq. (8) and Fig. 3g	$S_s = 1.0^1$	0.34
"	monthly storm freq. (no. days winds exceed 74 km/h)	"	$S_s = 0.3$	0.40
"	monthly storm freq. (no. days winds exceed 102 km/h)	"	$S_s = 0.6$	0.40

¹ Survival rates are independent of winds at these parameterizations.

above 0.34 only when storms were defined as winds greater than 74 km/h or 102 km/h.

The final hypothesis examined was that starvation mortality is related to primary production. We used relationships in Fig. 3h, i and j in combination with the time series of incident solar radiation. We varied the horizontal location of the plateau in Fig. 3j and obtained the highest correlation coefficient ($r = 0.87$) when it was set to be larger than the highest production ($0.68 \text{ m}^{-2} \text{ d}^{-1}$) over the period considered. This results in a linear relationship over the range of production experienced. Because of the short overlap in the solar radiation and recruitment records, observed and simulated recruitment could be compared only over 1960-1965. The correlation coefficient between population egg production and observed recruitment over the same years is 0.80. We investigated this further with an additional simulation run with the same parameter values, but allowing egg production to be constant in time. We calculated $r = -0.25$ over 1955-1965. The year of greatest simulated survival (highest primary production) matches up with the weakest year class (1958). Both sets of simulations suggest that the solar radiation time series can account for little or no variation in year-class strength.

Evaluation of Hypotheses Operating Together

Based on simulation results when hypothetical mechanisms operated individually, we considered the collective roles of the following hypotheses: (1) fecundity variations are related to bottom temperatures (Fig. 3c), (2) egg survival is related to surface

temperatures (Fig. 3d), and (3) larval survival is related to ocean currents. We chose to use the two-dimensional advection model, because we felt that onshore movement of intermediate water layers during upwelling might be important to larval transport. The changes in the velocity profiles suggested by Adriana Huyer (Table 6) were retained with this model structure.

The correlation between simulated and observed recruitment (Fig. 8) is 0.73 at optimum parameter values (refuge size = 0, nursery size = 5, system size = 29, and the divergence/convergence threshold = -20). We chose this as our final RECRU model version. Storm mortality was deleted from our model because inclusion of it could at best increase the correlation to 0.74.

To examine how model components integrate to yield the simulated recruitment record of Fig. 8, we plotted simulated variations about the mean for female stock size, individual fecundity, hatch success and advection mortality (Fig. 9). Each was expressed in standard deviations to standardize the units. High stock size (Fig. 9a), coupled with rather favorable environmental conditions for gonadal development (Fig. 9b) and early life survival (Fig. 9c, d, and e), led to an outstanding 1961 year class. On the other hand, a large spawning stock and environmental conditions favorable to gonadal development did not result in a large 1967 year class, due to poor conditions for hatch success and larval transport. The 1969 brood was large, not because of stock numbers, but because of pre- and post-spawning environmental conditions. Likewise, if the 1971, 1973,

Figure 8. Observed and modelled (from both Hayman and Tyler 1980 and this paper) English sole year-class strength for PMFC Area 3A over 1955-1977. The simulation from Hayman and Tyler (1980) are predictions from a regression with September and October barometric pressure. Our simulation results are from our final RECRU model using calculations of population eggs production (eq. 1), a fecundity-bottom temperature relationship (Fig. 3d), a hatch success-surface temperature relationship (Fig. 3e) and a wind-driven, two-dimensional advection model coupled to a relationship (Fig. 3g) between survival and distance offshore at settling.

Figure 8.

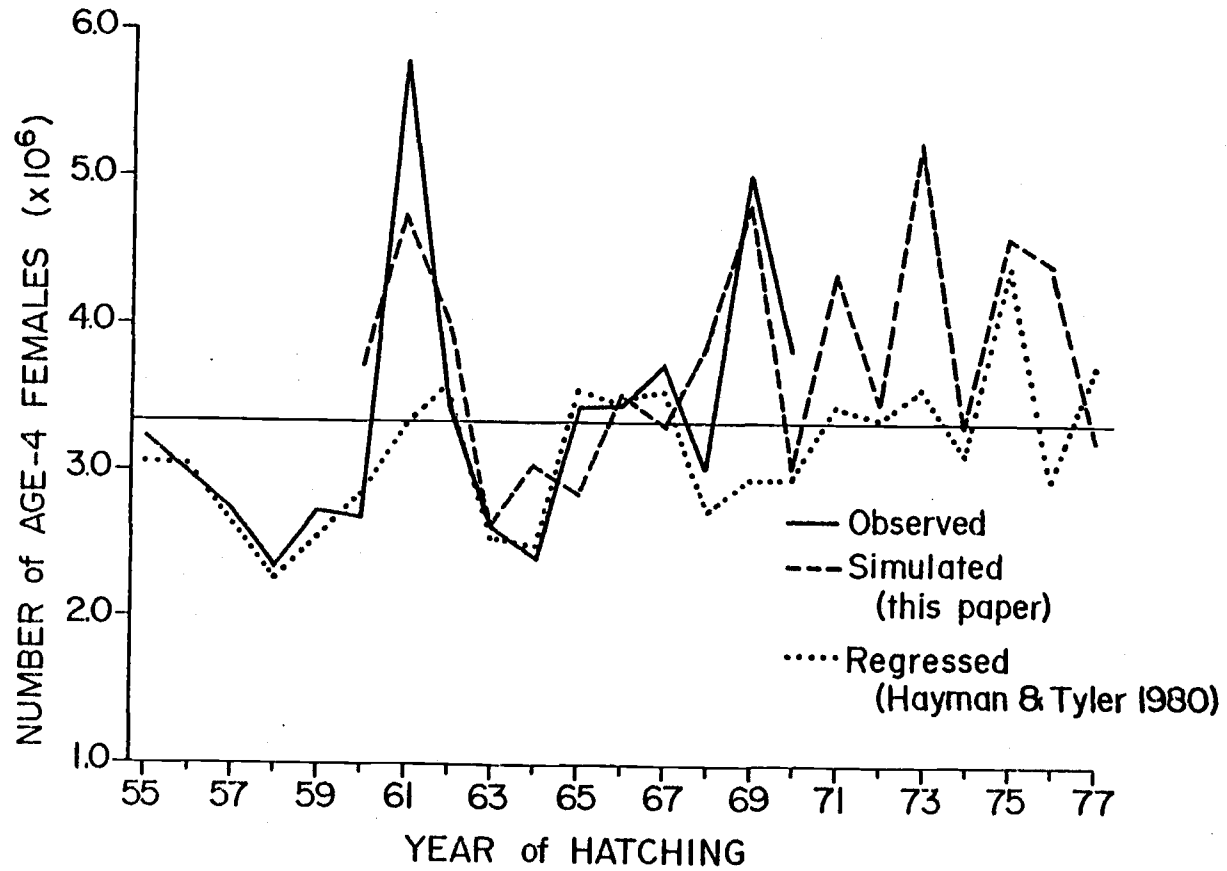
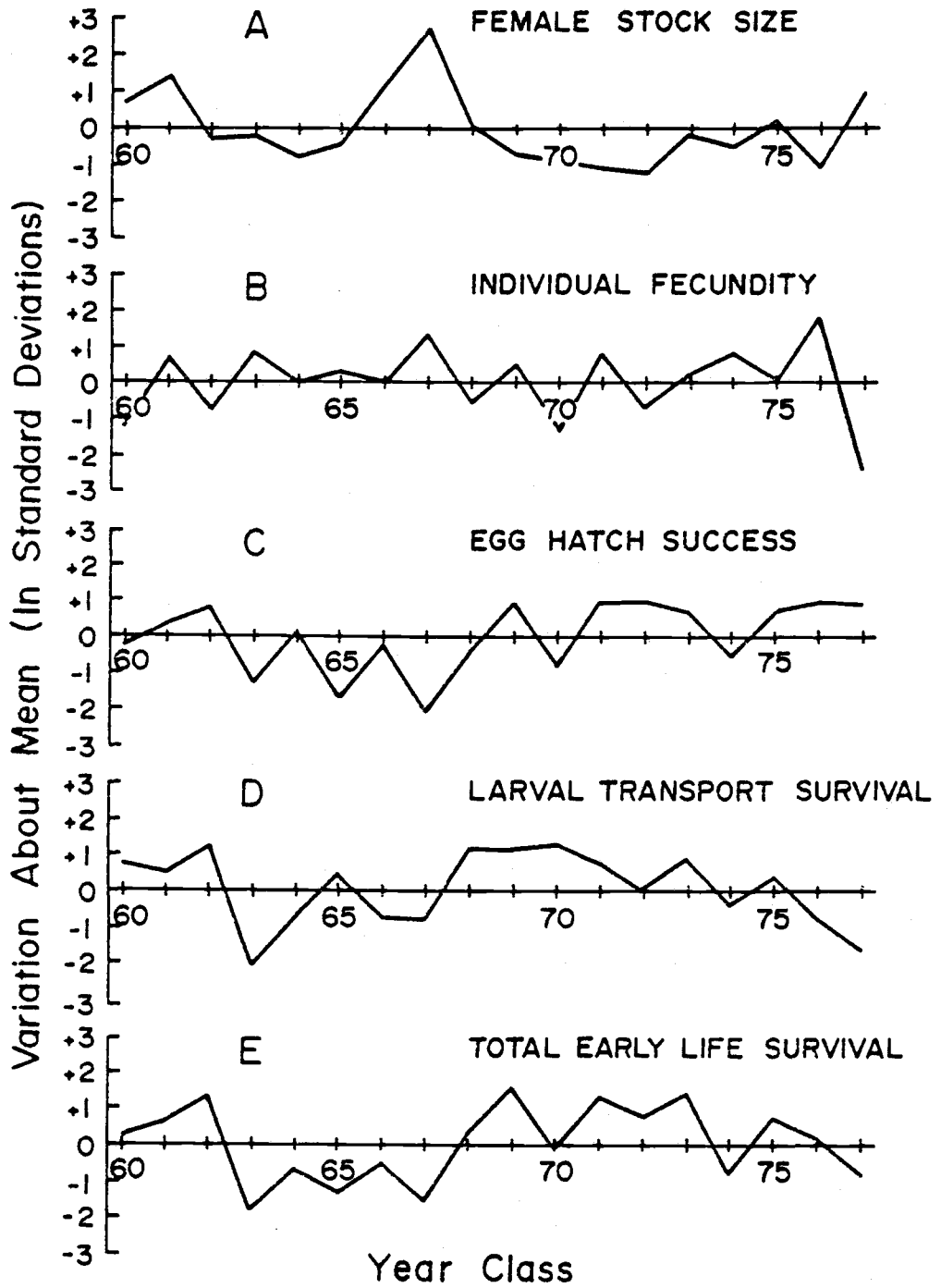


Figure 9. Variations about the long-term 1960-1977 means of (a) female stock size calculated from Area 3A fishery statistics; (b) individual fecundity simulated using a hypothesized relation to bottom temperature (Fig. 3c); (c) egg hatch success simulated using a laboratory-determined relation to surface temperature (Fig. 3d); (d) larval survival simulated using a two-dimensional transport model, wind records and a hypothesized relation between survival and distance offshore at settling time (Fig. 3e); and (e) egg and larval survival simulated from both (c) and (d). All plots are made such that annual figures correspond to year class.

Figure 9.



1975, and 1976 year classes prove to be large, it will be due to environmental conditions, not a large spawning biomass.

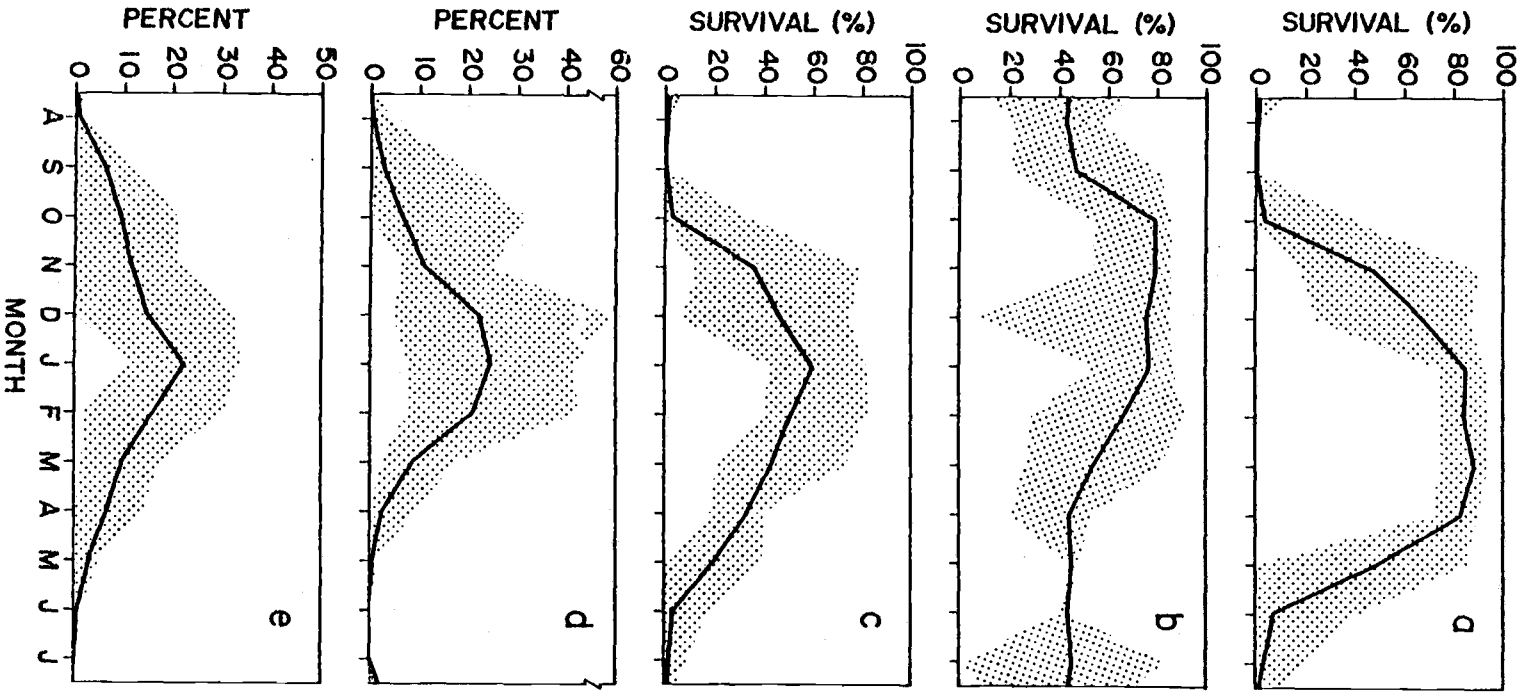
To contrast the roles of temperature-dependent hatch mortality and wind-dependent advection mortalities, we plotted mean, maximum and minimum survival rates over the 1960-1970 period for spawning occurring in different months (Fig. 10). Calculated survival rates should not be interpreted as actual survival rates, but as relative rates. For example, hatch success calculated from monthly mean surface temperatures will not equal the mean hatch success of eggs experienced along the coast during each month. The important characteristic of each plot is the shape of the curve rather than absolute value. In general, the best months to spawn to maximize hatch success are January through March (Fig. 10a). Likewise, for transport to coastal nursery areas, the best spawning months are October through January (Fig. 10b). Both mortality sources taken together results in a profile (Fig. 10c) not unlike the English sole spawning time distribution (Fig. 10d,e). We quantified the spawning time distribution using the rules described in "The Model" section of this paper. Again, the actual fraction spawning each month may not be accurate, but the shape of the profile should be reliable. It appears, then, that English sole might have evolved spawning times to optimize both hatch success and advection to nurseries.

Sensitivity Analysis

Sensitivity analysis is a procedure by which the effect of a change in one part of the model on another is examined (Brylinsky

Figure 10. Mean, maximum and minimum survival rates over 1960-1970 by month of spawning from simulations using the: (a) egg hatch success relation with surface temperature (Fig. 3d); (b) settling survival related to distance offshore (Fig. 3e) from the two-dimensional transport model; and (c) egg hatch success and settling survival taken together. We also estimate (see text) mean, maximum and minimum monthly spawning frequencies (proportion of total annual spawning occurring by month) for (d) observed records over 1947-1951, 1969-1972, and 1977-1979; and (e) simulated records (from Kruse and Tyler 1983) over 1960-1970.

Figure 10.



1972; Patten 1969). For example the sensitivity of the output to particular parameter, variable or function may be examined. Absolute sensitivities are changes in one component per unit change in another. Relative sensitivities are also changes in one component per unit change in another, but taken relative to the original state of these components.

For numerical changes in these components, calculations of absolute and relative sensitivities are straight-forward. However, in addition to these types of changes, we made structural changes for which such calculations are inappropriate. For these cases, we discuss sensitivity in a more qualitative sense. We already examined the sensitivity of the advection submodels to the larval vertical distribution, geographic distribution of spawning adults, current depth profiles and the survival rate of larvae with distance offshore (Table 9).

We next examined the sensitivity of our model to changes in (1) various other aspects of the advection submodel, (2) the fecundity-temperature relationship, and (3) the temporal distribution of spawning adults. We chose not to examine sensitivity to the temperature-hatch success relation, because it is known from a laboratory study (Alderdice and Forrester 1968). We estimated the absolute sensitivity (rate of change in the correlation coefficient between observed and simulated recruitment per unit change in the parameter) for each parameter. We chose values of each parameter both slightly above and below the optimum value and calculated the sensitivity in each of the two directions. We present

the greater of these two estimates as the absolute sensitivity (Table 12).

The model was found to be very sensitive to the slope of the temperature-fecundity relationship (Fig. 3c). For each change of 0.1 units in the slope, the correlation changed 0.1 units. When the slope was changed from -0.412 to -0.312 the correlation dropped from 0.73 to 0.63. When the slope was decreased to -0.512, the correlation increased to 0.81. Recall that we did not parameterize the fecundity-temperature relation to achieve maximum correlation. Instead, we took fecundity to vary with regard to temperature in the same way as growth (from Kreuz et al. 1982).

For each 1 km change in the size of the refuge area, nursery area and system size, the correlation changed by 0.005, 0.002, and 0.00002 units, respectively. Because refuge and nursery areas are likely 0-10 km wide and the system size (as far as English soles are concerned) is 29-50 km wide, it is clear that our model results are rather insensitive to the particular selection of these parameters. Strongest correlations were obtained with no refuge, a 5 km wide nursery and system of 29 km width. Our estimates for refuge and nursery area sizes, given our understanding of the system, are 1 km and 2 km, respectively. The system size corresponds to the greatest distance of spawning adults offshore. This is a boundary condition. That is, we did not allow for a narrower system because of the adult spawning distribution. This does not worry us, because the results are so insensitive to the choice of system size. Values of the

Table 12. Absolute sensitivity (change in correlation coefficient between observed and simulated recruitment per unit change in parameter) corresponding to several parameters in the RECRU model.

Parameter	Units	Absolute sensitivity
Slope in Fig. 3d	none	1
Refuge size	km	0.005
Nursery size	km	0.002
System size	km	0.00002
Div./Conv. Thresh.	mm/d	0.001

divergence index vary by a few hundred mm/d, so the results are also relatively independent of the particular choice of a threshold.

We examined the sensitivity of the final model to a structural feature: an open or closed system boundary. The correlation between observed and simulated recruitment was found to be independent of the selection of an open or closed system boundary (to 3 decimal places).

Lastly, we examined the sensitivity of the RECRU model results to the spawning model results. That is, we wanted to know how critical the variations in spawning timing were to early life survival. Instead of using the spawning schedule from the Kruse and Tyler (1983) model, we used a fixed spawning time schedule each year corresponding to the long-term mean (Fig. 10d). As a result of this change, the correlation coefficient dropped from 0.73 to 0.60. That is, the percent of the accountable recruitment variation dropped from 53% to 36%. That r is as high as 0.60 is probably due in part to (1) the contribution of population egg production to recruitment, (2) the fact that the mean spawning time distribution is a good approximation to the actual spawning schedule in some years, and (3) autocorrelation in the monthly sea surface temperatures and wind records. This autocorrelation or "memory" of the ocean is influential, because it reduces the consequences of inappropriate selection of particular months as critical to early life survival.

DISCUSSION

To comprehend the processes that lead to year-class formation of any fish species, it is necessary to have an adequate knowledge of both its life history and environment. Each of these are largely satisfied for English soles off Oregon. In spite of this wealth of knowledge, there are some critical problems which affront a conceptual or simulation modelling study such as ours. In many ways the most significant results of a model can be the exposure of these problematic areas, which include the absence of time series of appropriate variables, the presence of biased data and simply lack of knowledge. Only after these areas are satisfactorily addressed can we hope to develop models which generate reliable predictions of recruitment.

The reliability of the "observed" numbers of fish (Table 4; Fig. 8) is somewhat suspect due to both possible nonrepresentative samples of the age composition in the catch (mentioned earlier) and difficulties in estimation of species-specific effort in the multispecies fishery (Tyler et al. in press). Additionally, our calculations (unpublished) reveal that the cumulative fishing mortality on English sole cohorts does not always exceed 2.0; this value is one criterion for reliability in the estimates of stock numbers at the young ages (Pope 1972). The lack of knowledge about larval vertical distribution and the locations of spawning and nursery areas have limited our treatment of larval transport.

Oceanographic data are no less problematic, particularly with regard to minimal coverage in the season (winter) most critical to sole eggs and larvae. Cayan (1980) has shown that sampling density can affect the variance of temperature data. We have tried to reduce the variance by averaging temperatures over a fairly wide, but representative, area. However, this may cause another problem. Because of a particular temperature regime and nonlinearities in the relationship between hatch success and temperature, the calculated egg hatch success at monthly mean temperature need not equal the true monthly mean hatch success. We feel that this new problem is not very large, because typical Oregon surface temperatures predominantly lie along the descending (linear) limb of the relation in (Fig. 3d). Errors are incurred because of the use of proxy data such as the indices of bottom temperature (Kruse and Huyer 1983), turbulence (Niiler and Kraus 1977) and primary production (Small et al. 1972). Errors in our calculation of currents exist, partly due to the existence of geostrophic currents (Pond and Pickard 1978), which are not wind-driven. As Peterson et al. (1979) pointed out, there are uncertainties in the upper 20 m and the first 20 km or so from the coast. We can add to this the onshore flow during downwelling at virtually all depths and locations. We strongly advocate measurement of currents (and other variables) at these times and places to strengthen understanding of year-class strength formation.

We constructed a computer simulation model to investigate recruitment mechanisms of English soles off Oregon. Using the terminology of Bakun et al. (1982), ours is a rational, rather than an

empirical, approach. Correlation (Sutcliffe et al. 1977), regression (Hayman and Tyler 1980) and principle component analyses (Hayman 1978) are examples of the latter. Their purpose in fish recruitment studies are usually to generate hypotheses and ideas for further consideration. Although we use the correlation coefficient to measure the association between observed and simulated records, our approach is quite different. We have generated hypotheses based on our understanding of the life history of English sole, its ocean environment, and relevant field and laboratory studies. Our purpose is to "test" or investigate the hypotheses' ability to account for recruitment variations. This procedure reduces the chance of interpreting spurious correlations as meaningful relationships, but likewise reduces the likelihood of discovering mechanisms lacking precedence. Thus our method is preferable for well-known species and environments, while correlation analysis is preferred for species with poorly understood life histories and environments.

Differences in application of our approach and correlation analysis are also noteworthy. We have already mentioned the difficulties which nonlinearities, complex factor interactions and synchrony of events can pose to correlation analysis. Nonlinearities and some complex interactions can be handled by correlation analysis, if appropriate transformations are made prior to calculation of correlations. However, many other complex interactions and processes with interannual variations in timing or time/event contingencies are problematic. These can be handled efficiently with a computer simulation approach. Our spawning model (Kruse and Tyler 1983) is an

example of the manner in which nonlinear and conditional logic can be incorporated into a simulation. In this model spawning occurs if (1) gonadal maturation is completed, (2) temperature is above a critical threshold, and (3) temperatures do not increase rapidly. If any of these contingencies are not met, spawning is delayed. The relationship between maturation rates and temperature is modelled to be curvilinear. Because organisms tend to respond to their environment in conditional and nonlinear ways, we should not generally expect simple linear correlations to explain variations in ecological processes.

Rational (modelling) and empirical (e.g. correlation) approaches have some commonality. They both rely on the assumption that cause and effect relationships are correctly modelled, and they both base conclusions on the similarity between two time series. Spurious correlations can affect both approaches. It should be recognized that time series of many oceanographic variables are interrelated. That is, good correlations between recruitment and one oceanographic factor could be due to the effects of another, related oceanographic factor. A purely rational approach is usually not possible (Bakun et al. 1982). This is true in our recruitment model where some functions are rational but the parameters specifying them are not known from the laboratory and field. In the face of this, we have tried not to curve-fit to get good correlation coefficients. Instead, we have turned this around to investigate the range of parameter values for which the particular functional relationship may explain considerable variance in recruitment. For this reason we do not strongly emphasize

the percentage of accountable variation in the observed record. Rather, we stress that the hypothesized mechanisms yield trends consistent with observed patterns.

The fact that the model is very sensitive to the slope of the fecundity-temperature relation suggests to us that high priority should be given to testing this relationship empirically. It could account for a greater percentage of the variation in recruitment than we suspect. In a sense a "test" of the temperature-fecundity relationship is now in progress. This relation had little effect on our correlation, because stock trends and fecundity calculations parallel over 1960-1968 (see Fig 9a, b). Over 1969-1972 no correspondence exists, but over 1973-1977 variations in both variables are inversely related. If the 1974 and 1976 year classes are actually below average and that of 1977 above average, the importance of a temperature-fecundity relation would be discounted.

Our results suggest that the temperature-hatch success relation has a significant effect on recruitment. There is no doubt of its integrity, at least in laboratory conditions (Alderdice and Forrester 1968). Over the range of temperatures experienced off Oregon, the relation is effectively negative (right-hand limb of Fig. 3d). However, off British Columbia, a positive relation should exist due to lower temperatures (left hand side of Fig. 3d). Yet, a negative correlation was found by Ketchen (1956), and more recently the presence of any simple temperature relationship was questioned (Westrheim 1977). Explanations include: (1) in British Columbia other mechanisms mask the hatch success effect of temperature; (2)

the negative relation of recruitment to surface temperature off Oregon (and off British Columbia?) is really due to some yet-unknown, covariant mechanism; (3) the correlations for British Columbia are meaningless because no allowance was made for spawning time variability; or (4) simple linear correlation between recruitment and surface temperature is an inadequate means to evaluate the temperature-hatch success relation. There may be some truth to each of these. Findings by Alderdice (Pacific Biological Station, pers. comm.) supports (4). He accounted for much variation in English sole recruitment in British Columbia only when using both temperature and sea level (an index of northward currents) in combination as driving variables in curvilinear relationships. That is, factor interactions cannot be ignored and the hump in Fig. 3d is significant, even though most observed temperatures are actually to the left (as in British Columbia) or right (as in Oregon) of it.

We obtained rather good results when the larval transport hypothesis was incorporated into the model. In their correlation studies, Ketchen (1956) found evidence of the importance of transport to recruitment and Hayman and Tyler (1980) found positive correlations between year-class success and onshore transport (downwelling) in January-March. Parrish et al. (1981) have found some patterns of fish reproductive strategies to coincide with drift patterns. Bakun and Parrish (1982) produced evidence that spawning northern anchovy (Engraulis mordax) avoid centers of offshore transport (and turbulence), and Bailey (1980; 1981) presented evidence for the role of transport in Pacific hake (Merluccius productus) recruitment. On

the contrary, Mundy (1983) found many larval fishes at 6-9 km offshore during the early upwelling season, and Richardson et al. (1980) found consistent larval fish assemblages over four years along the Oregon coast. These observations are not readily congruent with the hypothesis that larvae are adversely advected offshore during upwelling. Yet, 87% of the taxa of the coastal assemblage (includes English soles) are fishes which spawn demersal eggs; only six, the flatfishes, have pelagic eggs (Richardson and Pearcy 1977). Of the offshore assemblage, 81% produce planktonic eggs. Such patterns imply that demersal or pelagic eggs have different adaptive significance over the inner and outer continental shelf. Transport is a likely candidate as a selective force; perhaps there are others (Kendall 1981). If transport operates on natural selection, fluctuations in transport and recruitment should be related.

Storms are known to adversely affect eggs of fishes. There could be several mechanisms involved. Shear forces, applied parallel to the surface of eggs or larvae, can kill by causing rotation and deformation (Morgan et al. 1976). Yolk may be dispersed or separated from the developing embryo. Changes in pressure associated with breakers could affect mortality (Pommeranz 1974). Sublethal effects, those experienced at one stage and influencing survival at a later stage, may also result from storm-related stressors (Rosenthal and Alderdice 1976). For example, high water velocities can lead to yolk-sac malformations in Pacific salmon (Emadi 1973) and higher mortalities at later stages. We found little evidence in our simulations that storms impart a significant mortality on egg and

larval soles. Larval transport may be a factor that masks the effects of storms on eggs in our case. Winter storms tend to blow from the southwest, and winds from this direction are favorable for onshore transport. Using the logic of Husby and Nelson (1982), English sole eggs may be insensitive to storms. Unlike northern anchovy, soles spawn during the season of highest turbulent energy production off Oregon (Fig. 5 in Husby and Nelson 1982). However, Laroche and Richardson (1979) and Mundy (1983) found suggestions that English sole larvae are more abundant in winters of few storms, so the possibility of a storm effect cannot be discounted.

We could not relate an index of primary production to English sole year-class success. Because 66-100% of the total number of prey items in the diet of sole larvae consists of appendicularians (Gadomski 1983), a general index of primary production may be unrelated to prey concentrations. Peterson and Miller (1976) found the abundances of tunicates in summer samples to be related to low surface salinity offshore. Thus, it is conceivable that even if offshore advective loss of sole larvae is actually inconsequential because they predominate at depths where currents always move onshore (e.g. Table 10), we could get good transport modelling results. Instead of only modelling onshore advection of larvae, we inadvertently could have also modelled onshore advection of larval prey and reduced starvation.

By incorporating hypotheses into a simulation model, we are able to separate those hypotheses which are consistent with observed recruitment patterns from those which are not. From this treatment we build the following conceptual model of English sole year-class

formation: (1) The size and age structure of the English sole stock partly determines the recruitment strength. (2) Fecundity of mature soles appears to be important, because interannual fluctuations are probably related to bottom temperature dynamics. (3) Processes operating during the pelagic stage also contribute to cohort strength. Optimum surface temperatures of 8-9° C promote maximum hatch success, with lower survival in colder or warmer temperatures. (4) Onshore movement of surface waters and waters at depth promote onshore movements of eggs and larvae from the spawning to the nursery grounds. This movement may also promote onshore movement of tunicates which are the predominant prey of larval soles. (5) Larvae settle approximately 60 days from hatching. Those settling offshore tend to experience poorer survival than those settling near shallow beaches and estuaries. Reduced mortalities in nursery areas may be due to fewer predators or abundance of prey. Certainly other factors operating both during the egg/larval and juvenile stages do act to control recruitment. Such factors may include predator-prey relationships, which are not well understood and for which time-series are lacking.

The relationship of English sole spawning times to the recruitment process should not be underestimated. Because spawning is partly cued by the warming of shelf waters (Kruse and Tyler 1983), egg releases tend to be timed to match periods of onshore transport coincident with increased bottom temperatures. Increased availability of their prey, an Appendicularian, may be another beneficial covarying factor. There may well be others. Frank and Leggett (1982) have analogously found the coincidence of capelin (Mallotus villosus) emergence times to be

coincident with "safe sites", waters with favorable oceanographic, feeding and predator conditions.

We have shown that stock structure, fecundity variations, hatch success and transport can account for more than half of the variance in the English sole recruitment record. Our simulation model predicts a series of strong cohorts for the early to mid-1970's. If these materialize, a period of good English sole fishing along the Oregon coast should be realized. If these patterns are not observed, this should not be cause for complete rejection of our theory of English sole cohort formation, but our conceptual and simulation models should be modified in the appropriate places.

DISCUSSION OF THESIS WITH REGARD TO ENGLISH SOLE BIOLOGY,
ENVIRONMENT AND FISHERY PRODUCTION

Because the first part of this thesis was written as a manuscript to be submitted for publication, it is short in two areas. First it lacks an extensive literature review of the biology and environment of English soles. Second, it lacks a discourse on the originality of this dissertation and a discussion of its significance to the investigation of English sole fishery production. I address both of these areas here.

English sole have been caught from the surf zone to a depth of 550 m (Alverson et al. 1964), but catch records show greatest abundances between 55-130 m (Alverson 1960). Seasonal catch patterns have been used to indicate adult onshore-offshore migrations (Alverson 1960; Hewitt 1980). In early winter adults tend to concentrate in deep water. Over much of the remainder of the year they seem to be shallower and dispersed over a wide range of depths. Tagging studies generally show a southward migration associated with offshore movement and northward migration coupled with onshore movement (Golden et al. 1979; Pattie 1969). Offshore and southward migration appear to prelude spawning activity, which is usually most intense during the winter, although quite protracted and variable (Kruse and Tyler 1983).

Spawning occurs demersally, but laboratory experiments show that eggs float to the surface at seawater densities common over the continental shelf (Ketchen 1956). Eggs hatch in 4-8 days at temperature and salinity conditions typical off Oregon (Alderdice and

Forrester 1968). Larvae remain pelagic for approximately two months (Ketchen 1956; Laroche et al. 1982) and settle at a mean size of about 20 mm standard length (Ahlstrom and Moser 1975). Newly-settled juveniles (about 25 mm) have been found only in estuaries (Olson and Pratt 1973; Westrheim 1955) and off sandy beaches to depths of approximately 25 m (Laroche and Holton 1979; Rosenberg 1980). With age, the young flounders move to progressively deeper waters, eventually joining the adult population (Ketchen 1956).

General features of the North Pacific Ocean have been reviewed by several authors (Fleming 1955; Tully 1965; Tabata 1975, 1976). Only average seasonal features will be discussed here, although considerable variability exists at shorter (Huyer and Smith 1978; Huyer et al. 1978) and longer frequencies (Namias and Huang 1972; Stewart et al. 1958). Winter characteristics include a well-developed low pressure system over the Aleutian Islands and a high pressure system located about 1500 km west of southern California. During the summer the low pressure system disperses and the high pressure system intensifies and shifts 1500 km to the northwest (Tabata 1975). These pressure systems generate winds which correlate to many coastal oceanographic features such as currents and sea level (Huyer and Smith 1978; Huyer et al. 1978; Smith 1974).

Along the Oregon coast, winds generally blow northeastward from late fall to early spring and southward during most of spring and summer (Huyer et al. 1975). Water masses move predominantly in the alongshore direction, but the onshore component may be of most consequence to many resident marine organisms. Over the continental

shelf, winter current flow is primarily northward at all depths, while summer currents tend to be southward at the surface and northward at depth (Huyer et al. 1975). Onshore flow at most depths seems to be coupled with winter northward currents (Huyer et al. 1978), although the sparsity of winter data limit generalizations. Summer is typified by upwelling, a process in which current flow is offshore in the upper layers and onshore below (Halpern 1976). This process is responsible for thick phytoplankton blooms (Small and Menzies 1981) and approximately a five-fold increase in nearshore zooplankton densities over winter levels (Peterson and Miller 1976).

Temperature, salinity, and density are quite variable within the region inhabited by English soles (Huyer 1977). By far the greatest variation in the characteristics occurs during the summer, not only with regard to depth, but also with distance from the coast (Huyer 1977). In summer the bidirectional, alongshore flow stratifies the water column with regard to temperature and salinity. Over the 100 m isobath water is 9-15 C and 30.0-32.5 ‰ at the surface and 7-8 C and 33.5-34.0 ‰ near the bottom. In the onshore-offshore direction the low salinity (often less than 30 ‰), solar heated (as high as 15 C), Columbia River plume lies at the surface in offshore waters (Barnes et al. 1972). It is separated from the coast by a ribbon of cold (as low as 8 C), saline (greater than 32.5 ‰), upwelled water (Holladay and O'Brien 1975). Due to these phenomena, surface temperatures are at an annual minimum in the upwelling zone and an annual maximum offshore. Conversely surface salinities are greatest close to the coast and lowest offshore. Deep temperatures are at an

annual minimum across the shelf, although there is a trend toward colder water with depth and distance from the coast. Deep salinities are greatest in summer, but the annual cycle becomes nearly imperceptible at about 45 km from the shoreline (Huyer 1977).

A prominent autumn feature is a sharp rise in coastal surface temperatures, likely due to the relaxation of upwelling and the resultant onshore movements of warmer, less saline, offshore waters.

During the winter, the unidirectional alongshore flow with depth is reflected in nearly isothermal conditions (Huyer 1977). Over the 100 m isobath surface temperatures are low (9-11 C), but deep temperatures are at their annual maximum (8.5-11 C). Surface salinities are high in winter (33-34 ‰), except in waters adjacent to the coast, where seasonally high runoff from coastal streams is important.

Spring appears to be primarily a transitional period between the extremes of winter and summer. Temperatures begin to increase at the surface and decrease at depth. Deep salinity increases in spring, as does the nearshore surface salinity. Offshore surface salinity declines steadily through midsummer.

This thesis is unique in its approach to the investigation of recruitment variations. It differs from most other recruitment models, which use multiple regression to fit relationships between dependent and independent variables by parameter selection. The model presented is a synthesis of hypothetical logic with components based on the biological and environmental information. An advantage of this type of synthesis is that it facilitates examining the internal

consistency among system components. I chose to concentrate on the compatibility of selected recruitment mechanisms with biological and physical data sets. Mechanisms are not proven or disproven, but instead are regarded as likely or unlikely. The result is the development of theory of the English sole recruitment process, which is consistent with present knowledge and data. In the future our ideas will undoubtedly be modified with the addition of new, and perhaps contradictory, information.

This thesis is the last of a series of studies that I have been involved with at Oregon State University. All have been directed toward investigation of English sole fishery production. It became clear that fishes respond to temperature variations in several ways. Off Oregon time series of the deep temperatures experienced by demersal shelf fishes are sparse. To supplement available data, a shelf temperature index was developed from a relationship to coastal sea level (Kruse and Huyer 1983). This index later proved invaluable to our fish production studies. Firstly, it allowed us to account for interannual variations in growth rates of English soles (Kreuz et al. 1982). As shown in the laboratory, fluctuations in growth are inversely related to bottom temperature. Secondly, the temperature index allowed us to account for much of the variance in spawning timing (Kruse and Tyler 1983). English soles are rather unique in that their spawning times are so variable; peaks may occur in autumn of one year and spring of the next year. Finally, in this present study, we have investigated the ramifications of variable spawning times on early life survival and subsequent recruitment.

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