Abstract.—Growth and mortality rates of 0+ English sole were estimated from field data collected from estuarine and nearshore nursery areas off Washington during 1985–88. Growth of 0+ English sole was approximately linear over time and was estimated with the length modal progression method. Point estimates of growth rates during May through September were in the range of 0.33 to 0.49 mm/day. Statistical analysis with a general linear model showed significant year and settlement time effects on growth of 0+ English sole but failed to detect any density or temperature effect. Instantaneous mortality rate varied significantly with season, declining from 0.0175 per day in July and August to 0.0075 per day in September. Changes in population density appeared to play a minor role in causing this decline.

Growth and survival of 0+ English sole, *Pleuronectes vetulus*, in estuaries and adjacent nearshore waters off Washington

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Fish growth depends on numerous factors, e.g. supply of suitable prey items, ambient temperatures, and oxygen concentration. Laboratory studies have shown that growth of juvenile plaice *(Pleuronectes platessa)*, sole *(Solea solea)*, and English sole *(Pleuronectes vetulus)* depends strongly on ambient temperature (Williams and Caldwell, 1978; Fonds, 1979; Yoklavich, 1981).

Field observations also show that growth of flatfishes is regulated by ambient temperature. Applying a model based on Fonds's (1979) laboratory experiment and observed temperature data for predicting monthly growth of North Sea plaice, van der Veer et al. (1990) showed a close overall agreement between predicted growth increments and those observed in the field. Simulated growth rates, however, were consistently lower than field-observed growth rates in June, and this tendency was reversed in August (Fig. 7 in van der Veer et al., 1990). This finding suggests that in addition to temperature there are other factors that also affect the growth of plaice.

Laboratory studies of juvenile English sole (Williams and Caldwell, 1978; Yoklavich, 1981) have

shown that food limitation can significantly reduce growth. Edwards and Steele (1968) suggested that food limitation was the controlling factor for the growth of North Sea plaice in Loch Ewe. Bergman et al. (1988) reported that growth reduction of 0-group plaice occurred in specific areas of the Wadden Sea where there was low food abundance, although this phenomenon was restricted to only a small part of the population.

Isolating the effects of fish density, food supply, and ambient temperature on growth is difficult with field data. Within a certain range of population density or food abundance, growth may be regulated primarily by temperature and, within a certain range of temperature, population density may have a dominant influence.

Survival is the key element in determining success of recruitment. Early research was largely focused on the "critical period" theory (Hjort, 1913), i.e. survival of small first-feeding larvae is critical to subsequent year-class strength. More recent studies have shown that low

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larval abundance may indicate poor year-class strength, but high larval abundance will not guarantee a strong year class (Bailey and Spring, 1992; Bradford, 1992). Survival during the juvenile stage is critical to year-class success. On the basis of simulation, Bradford (1992) concluded that correlation between recruitment and abundance at early life stages increases monotonically with age, especially during the first 100 days of life, because variation in survival weakens the relationship between recruitment and abundance of early life stages. Although monthly or annual instantaneous mortality is usually higher during the larval stage than that at the juvenile stage, the cumulative mortality might be higher, and more variable, during the juvenile stage because it usually lasts much longer. Therefore any variation in mortality at this stage would induce much greater variation in recruitment.

English sole spawn in offshore areas. Timing of spawning is variable and duration of the spawning period is protracted (August to May, Shi, 1994). The egg and larval stages last from two to two-and-a-half months, and survival and transport of eggs and larvae are dependent on oceanographic conditions (Boehlert and Mundy, 1987, 1988; Shi, 1994). Once metamorphosis and benthic settlement have occurred, English sole actively seek out estuarine nursery areas, and oceanographic influence becomes less important. Analyses of tagging data, distribution of adults, available spawning habitat, and egg distribution (Shi, 1994) suggest that the Grays Harbor and Willapa Bay estuaries serve as nursery areas for English sole that spawn as far south as central Oregon.

This study summarizes results from a series of trawl surveys of Grays Harbor, Willapa Bay, and the adjacent nearshore, 1985–88. Previous work (Gunderson et al., 1990; Shi et al., 1995) has shown that these estuaries provide critical nursery habitat for juvenile English sole during their first year of life.

The abundance of 0+ English sole in our study area (Fig. 1) was relatively stable during September, showing only a threefold difference during 1985–88, despite great variation in settlement in May (Shi et al., 1995). If survival is density dependent, then density could function to stabilize recruitment. In this paper, growth and survival rates will be estimated by using data from field surveys, and we will investigate statistically the effects of population size and ambient temperature on the growth and survival of juvenile English sole.
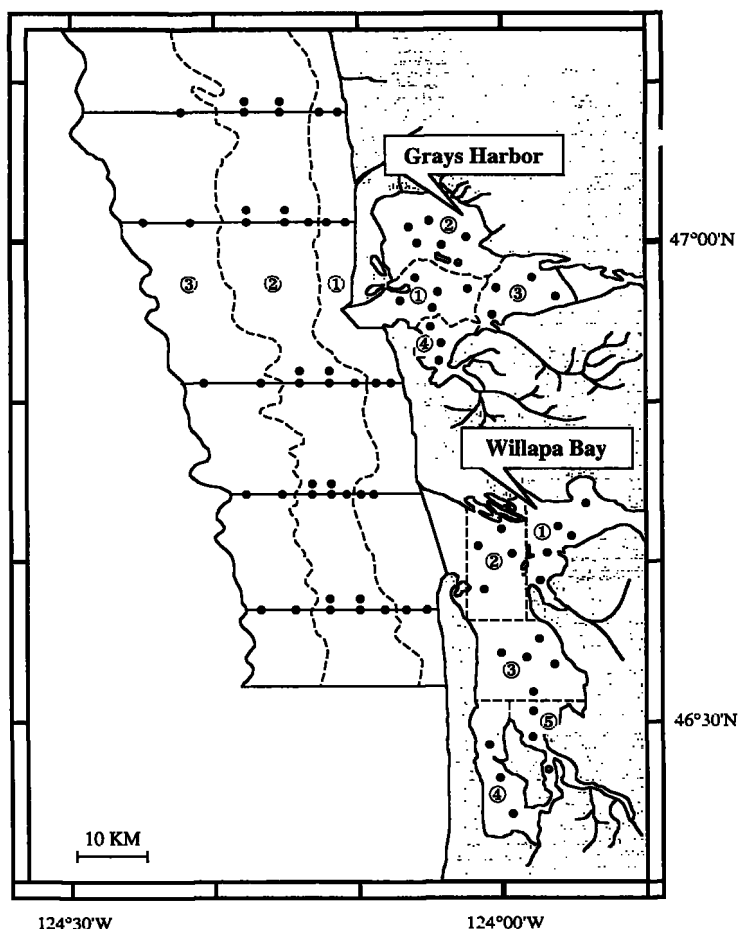

Figure 1

The study area along the southern Washington coast. Shown are subsystem boundaries, nearshore transect lines, trawl stations (filled circles), and stratum numbers (open circles). Dashed lines indicate survey stratum boundaries.

Methods

Study area and field methods

Grays Harbor (8,545 ha) and Willapa Bay (11,200 ha) are two major Washington coastal estuaries characterized by numerous channels, sandflats, and eelgrass beds that provide excellent habitat for 0+ English sole. The nearshore portion of the study area is bounded to the north at 47°15'N, and to the south at about 46°30'N, and extends from the shoreline seaward to 60 m. It encompasses an area of nearly 146,600 ha.

A stratified random trawl survey was performed to estimate population sizes for English sole in both estuaries (Fig. 1) with the area-swept method: $P = A\bar{d}$, where P = population size, A = area of survey stratum (ha), and $\bar{d}$ = mean density (no. of fish caught/

ha) (Shi et al., 1995). Within each stratum, stations were randomly selected from sampling units superimposed on nautical charts, with the constraint that no two stations were immediately adjacent to one another. The effort (number of stations) allocated to each stratum was proportional to the abundance of English sole in that stratum (Shi et al., 1995).

The nearshore area was sampled along fixed transects oriented east–west and trawl stations were located at discrete depths (Fig. 1). Five transects were established, and sampling stations were located at depths of 5, 9, 18, 27, 36, 46, and 55 m. The 55-m station was not sampled on the northernmost transect because of frequent gear damage at this location. Additional effort was allocated to the intermediate stratum; two trawl samples were taken at all 27- and 36-m depths. Sampling stations were stratified according to depth to obtain population estimates. The outer boundary for the nearshore study area was the 59-m (32.5-fm) isobath, and the mean low low water (MLLW) mark was the inner boundary. The boundary separating the inner and middle strata followed the 14-m (7.5-fm) isobath, whereas the boundary between the middle and outer strata was located at 41 m (22.5 fm). The northern and southern limits of the survey area were positioned 5 km beyond the northernmost and southernmost transects.

Each of the three areas was visited once a month. Sampling in estuaries was planned during low spring tides of the month (April or May through September) so that we could navigate among unmarked channels, which otherwise are difficult to see. Stations in close proximity to intertidal areas were sampled preferentially at low tide to minimize bias associated with fish movement onto the tideflats at higher stages of tide. More exposed sites were typically sampled at high water. Trawling operations ceased when tidal currents were judged sufficiently strong that the trawl gear would not tend the ocean bottom properly. Nearshore sampling trips were usually made between the two estuary trips in that month.

Survey samples throughout the study area were collected with a 3-m beam trawl specifically developed for this study (Gunderson and Ellis, 1986). Effective width of the net was 2.3 m, whereas the estimated vertical opening was 0.6 m. The body of the net was composed of 7–9 mm (lumen) knotless nylon, and the codend was lined with 4-mm stretch mesh. A double tickler chain array was attached to a 9.5-kg wingtip weight at each corner of the net. The tickler chain array, together with the turbulent zone it creates, dislodges small animals from the substrate, thus promoting capture by the net.

Nearshore sampling was conducted from the 17-m stern trawler F/V *Karelia*. Tows in the nearshore were taken parallel to isobaths. Scope was routinely 5:1, except at the 5 and 9 m stations where it was 8:1 and 9:1, respectively. Time on the ocean bottom was estimated by using a trigonometric relationship between water depth and wire out, whereas the linear distance towed (mean: 750 m) was determined from LORAN-C readings. Tow duration was routinely 20 minutes at a mean towing speed of 2.6 km/hr (1.4 knots), except at the 5- and 9-m stations, which often yielded excessive quantities of sand dollars (*Dendraster excentricus*) and gravel; tows in these areas were limited to 5 or 10 minutes.

A 6.4-m Boston whaler with a 150-hp outboard engine was used for estuarine trawling. Buoys were deployed at the points where the net first contacted the bottom and subsequently left bottom upon retrieval. The distance towed (mean: 260 m) was estimated with an optical rangefinder. Mean towing speed was 2.8 km/hr (1.5 knots), comparable to that used in the nearshore area.

Data analysis

Length Growth rate estimates were obtained by regressing the mean length of a recruitment influx (indicated by a mode in the length-frequency distribution [Shi et al., 1995]) against the time when samples were taken. There was a linear relationship between modal length and time, as was the case in previous growth studies on juvenile English sole (Ketchen, 1956; Kendall, 1966; Rosenberg, 1982). Because size-dependent migration between nearshore and estuarine systems occurs, with smallest juveniles migrating into estuaries and larger fish moving offshore (Gunderson et al., 1990; Shi et al., 1995), separate estimates of growth rates for nearshore and estuarine fish would be inappropriate. To minimize the effect of interregional migrations, the mean lengths at each mode (defined on the basis of visual inspection of monthly length frequency plots [Shi et al., 1995]) were calculated from the estimated size composition of the overall population. The length statistic used was the mean modal length (MML), which is defined as the mean length within a mode, weighted by the estimated population size for each size group:

$$MML = \frac{\sum_{l=l_{low}}^{l_{up}} l\hat{P}_l}{\sum_{l=l_{low}}^{l_{up}} \hat{P}_l}, \tag{1}$$

where, $\hat{P}_l$ = estimated population (millions) of fish in length group l; l_{up} and l_{low} = length (mm) at upper and lower limits of the mode, which are so defined that l_{up} and l_{low} are the length groups at which abundance has declined to half that at the modal size (Fig. 2). If length is normally distributed, $l\sim N(\bar{l}, s^2)$, the population within the upper and lower limits of the mode so defined would account for about 75% of the total population of that cohort (Shi, 1994).

Date The dates used in growth and mortality estimation were also population-weighted means. The dates when the samples were taken cannot be used directly in growth and mortality estimation without being standardized. Estuarine samples had to be taken during low low tide (LLT) periods, and we were often forced to take estuarine samples at unequal time intervals.
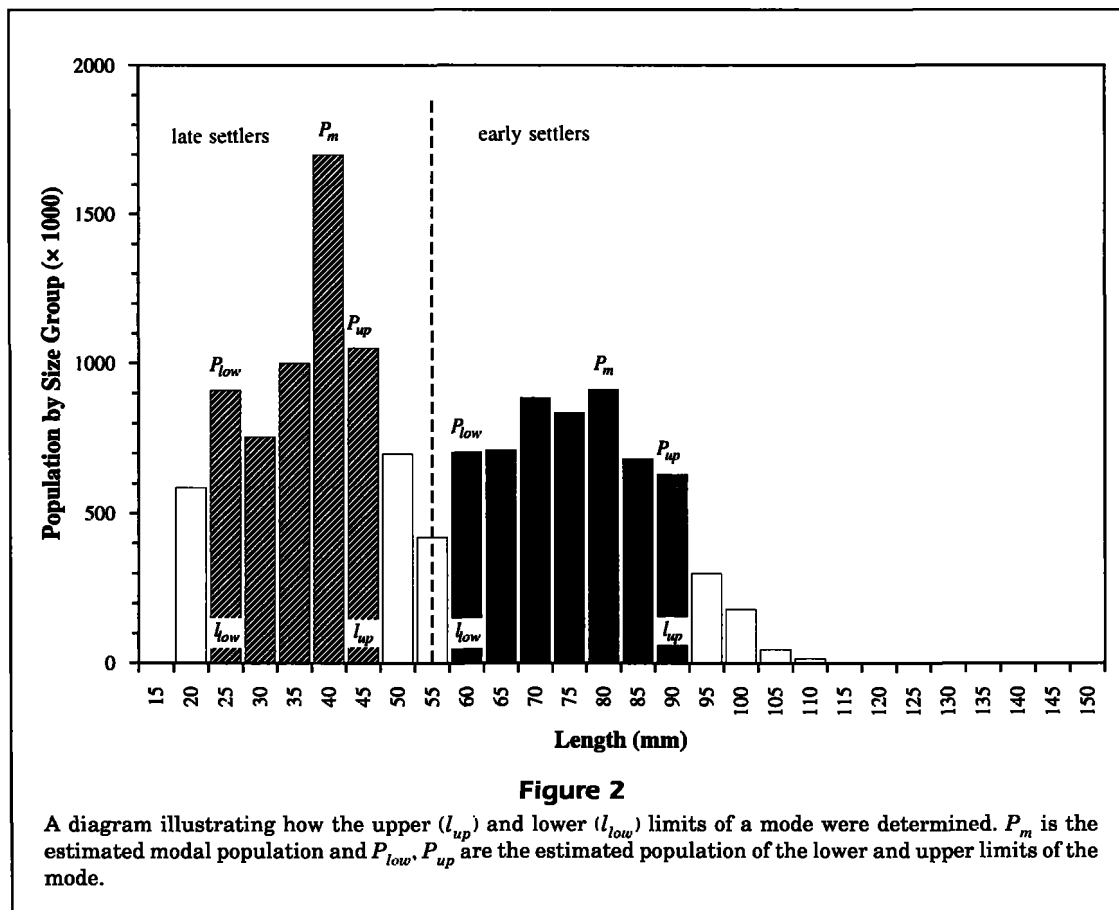
We made every effort to carry out the monthly nearshore surveys during the intervals between the Grays Harbor and Willapa Bay surveys, but they sometimes had to be done either before or after the estuarine trips owing to logistic difficulties. This made the time between the first and last surveys for a given month more than a half-month apart. The population-weighted mean date (PWMD) was chosen to standardize the "date" of monthly surveys and is the best estimate of the average sampling date for the total population in our study area. The PWMD was computed from

$$PWMD_{jm} = \frac{\sum_{i=1}^{3} P_{ijm}\overline{date}_{ij}}{\sum_{i=1}^{3} P_{ijm}}, \qquad (2)$$

where, $PWMD_{jm}$ = population-weighted mean date in month j (May, June, July, August, and September) for mode m (1 or 2); P_{ijm} = population of mode m in system i (GH, WB, NS), month j; $\overline{date}_{ij}$ = mean date of a survey carried out in month j and system i, i.e. number of days from 1 May.

Temperature A population-weighted mean bottom temperature (PWMBT) was developed in this study because of extensive seasonal ontogenetic migrations

Figure 2

A diagram illustrating how the upper (l_{up}) and lower (l_{low}) limits of a mode were determined. P_m is the estimated modal population and P_{low}, P_{up} are the estimated population of the lower and upper limits of the mode.

between estuarine and nearshore areas and because of differences in mean bottom temperatures between estuarine and nearshore systems (2–8°C, Fig. 3).

$$PWMBT_{jm} = \frac{\sum_{i=1}^{3}\sum_{s=1}^{s_i} P_{isjm}\overline{T}_{isj}}{\sum_{i=1}^{3}\sum_{s=1}^{s_i} P_{isjm}}, \qquad (3)$$

where, $PWMBT_{jm}$ = population-weighted mean bottom temperature in month j for mode m; P_{isjm} = population of mode m in system i, stratum s, month j; $\overline{T}_{isj}$ = mean bottom temperature in system i, stratum s, and month j; and s_i = number of strata in system i. $PWMBT_{jm}$ is the best estimate of the average temperature experienced by the population in our study area.

Growth rates A linear model was developed to determine competing factors that had significant effects on the growth of 0⁺ English sole.

$$l_{ji} = \alpha + \alpha_1 c + \alpha_{2j} y_j + \beta t_i + \beta_1 c t_i + \beta_{2j} y_j t_i + \beta_3 d_i t_i + \beta_4 T_i t_i + \varepsilon_{ji}, \qquad (4)$$

where, l_{ji} = mean modal length (MML) at time t_i and year j; y_j and c are dummy variables for year and settlement time; t_i = population weighted mean date (PWMD); d_i = density (no/ha), monthly mean density from May through September; T_i = population weighted mean bottom temperature ($PWMBT$); and ε_{ji} = residual. The d_i and T_i terms were used to examine whether or not there were density or temperature effects (or both) on the growth of 0⁺ English sole in the study areas. The dummy variable y_j (year) was defined as follows:

$$y_1 = \begin{cases} 1 & 1986 \\ 0 & \text{otherwise} \end{cases}, \qquad y_2 = \begin{cases} 1 & 1987 \\ 0 & \text{otherwise} \end{cases},$$

$$y_3 = \begin{cases} 1 & 1988 \\ 0 & \text{otherwise} \end{cases}.$$

Since, settlement time obviously differed between cohorts (Fig. 4), the dummy variable (c) was used to denote early (1) and the late (0) settlement groups:

$$c = \begin{cases} 1 & \text{early settlements (1985, 1986 – 1,1988)} \\ 0 & \text{late settlements (1986 – 2,1987).} \end{cases}$$
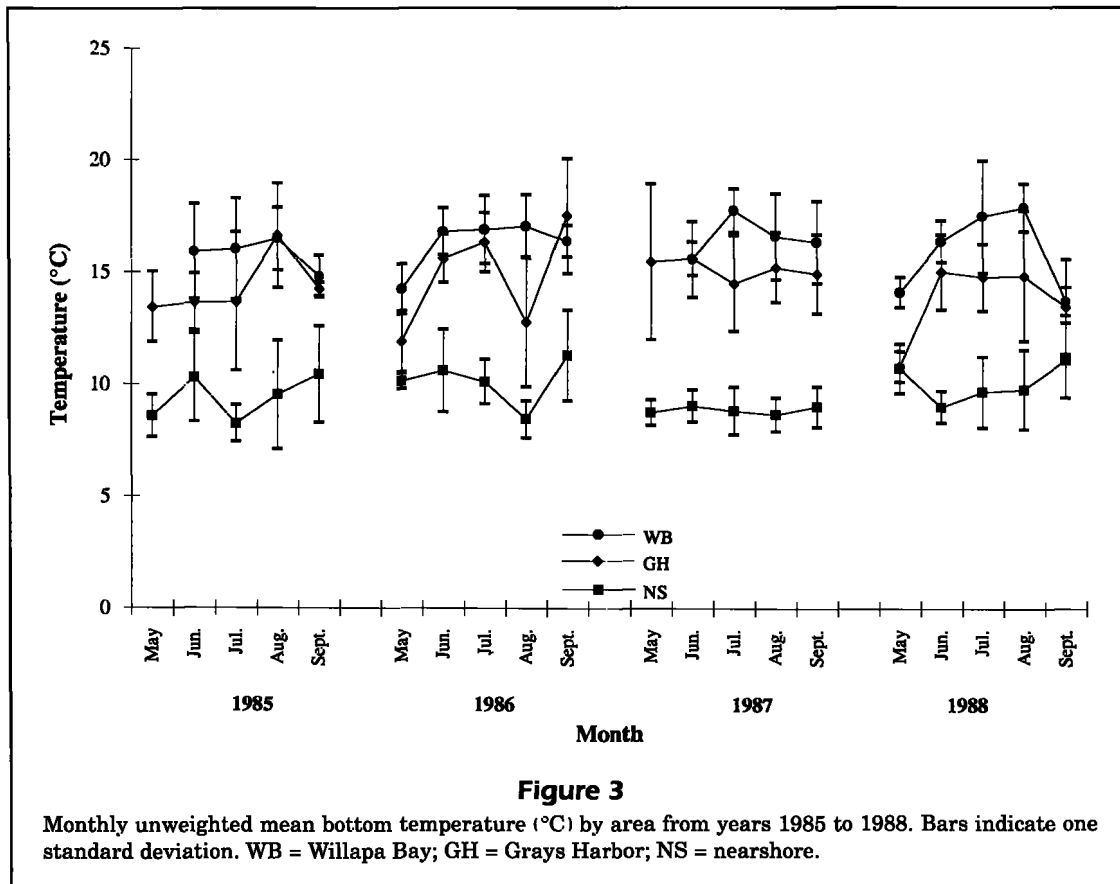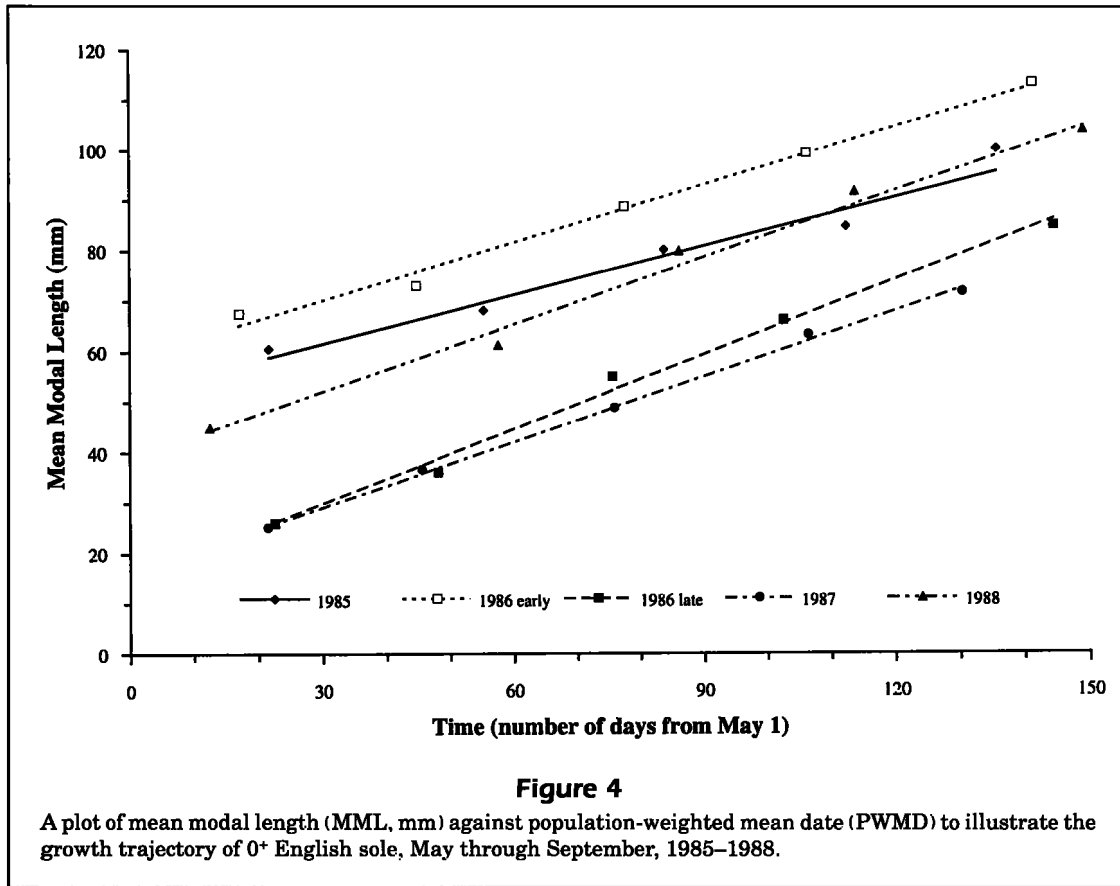

Figure 3

Monthly unweighted mean bottom temperature (°C) by area from years 1985 to 1988. Bars indicate one standard deviation. WB = Willapa Bay; GH = Grays Harbor; NS = nearshore.

Figure 4

A plot of mean modal length (MML, mm) against population-weighted mean date (PWMD) to illustrate the growth trajectory of 0+ English sole, May through September, 1985–1988.

Early and late settlement was defined by visual inspection of length frequency (Shi et al., 1995). A recruitment influx with mean modal length less than 40 mm during the May survey was defined as late settlement, and that with mean modal length greater than 40 mm in May was defined as early settlement. A multiple-partial F-test was used here to test the significance of settlement time $(\beta_1 c)$, year $(\beta_2 y_j)$, density $(\beta_3 d_i)$, and temperature $(\beta_4 T_i)$ effects on growth. The computer program MGLH (SYSTAT [Wilkinson, 1989]) was used to carry out all calculations.

Mortality rates The significance of density and season effects on mortality was examined by using the restated Beverton-Holt equation (Beverton and Iles, 1992):

$$\frac{dP}{Pdt} = -(\mu_1 + \mu_2 \ln P), \qquad (5)$$

where P is the population of juvenile English sole in our study area; μ_1 is the density independent coefficient, as defined in Beverton and Iles (1992), and μ_2 is the density-dependent coefficient.

Population estimates from the surveys were fitted to the following three competing models, by using nonlinear least-squares regression (Wilkinson, 1989):

1) By integrating Equation 5 with $\mu_2 = 0$, the density-independent mortality model is

$$P_{t_i} = P_{oi} e^{-\mu_1 t_i}. \qquad (6)$$

2) Integrating Equation 5 over the time period from $t = 0$ to $t = t_i$ without any constraint on μ_1 or μ_2, the full model is

$$P_{t_i} = e^{\frac{\mu_1}{\mu_2}(e^{-\mu_2 t_i}-1)} P_{oi}^{e^{-\mu_2 t_i}}. \qquad (7)$$

3) Integrating Equation 5 with $\mu_2 = 0$, and allowing μ_1 to vary, the model becomes

$$P_{t_i} = \begin{cases} P_{oi} e^{-\mu' t_i} & t_i = 0 \text{ to } 31 \text{ (July)} \\ P_{oi} e^{-\mu'(32)} e^{-\mu''(t_i -32)} & t_i = 32 \text{ to } 62 \text{ (August)} \\ P_{oi} e^{-\mu'(32)} e^{-\mu''(62-32)} e^{-\mu'''(t_i -62)} & t_i > 62 \text{ (September)} \end{cases} \qquad (8)$$

where t_i = time, number of days elapsed since 1 July for surveys conducted in year i (1985–88); P_{t_i} = the observed total population size (0+ group) for all areas combined at time t_i in year i; and P_{oi} = initial total population size on 1 July in year i. P_{oi} was estimated as a parameter along with the coefficients μ_1 and μ_2. μ', μ'', and μ''' are the density-independent mortality

Table 1

Monthly population-weighted mean date (PWMD), mean modal length (MML), population-weighted mean bottom temperature (PWMBT) and overall mean densities of 0+ English sole, 1985–88.

Year	Settlement time	Month	PWMD (days)	MML (mm)	PWMBT (°C)	Density[1] (No./ha)
1985	Early	May	21.66	60.56	13.07	55.03
		Jun	55.34	68.08	14.66	130.95
		Jul	83.75	79.95	12.94	200.60
		Aug	112.39	84.55	14.34	132.69
		Sep	135.72	99.96	12.24	96.42
1986	Early	May	17.05	67.54	13.61	118.25
		Jun	44.71	72.97	16.24	77.06
		Jul	77.54	88.58	14.66	96.75
		Aug	106.18	99.17	12.07	72.55
		Sep	141.32	112.98	12.49	65.80
1986	Late	May	22.51	25.99	12.33	118.25
		Jun	48.11	36.09	15.31	77.06
		Jul	75.63	55.01	15.43	96.75
		Aug	102.64	66.10	14.63	72.55
		Sep	144.51	84.67	14.81	65.80
1987	Late	May	21.47	25.17	10.48	188.77
		Jun	45.58	36.64	13.70	219.35
		Jul	76.00	48.83	15.28	346.38
		Aug	106.47	63.19	12.48	186.98
		Sep	130.45	71.49	13.65	200.48
1988	Early	May	12.48	45.01	13.21	269.44
		Jun	57.61	61.24	15.20	193.18
		Jul	86.10	79.77	14.91	182.15
		Aug	113.75	91.58	14.78	116.13
		Sep	149.10	103.72	12.26	90.31

[1] The estimated densities are combined densities of early and late recruits.

coefficients during July, August, and September, respectively. Model selection was based on the Bayesian Information Criterion (BIC) proposed by Schwarz (1976).

Results

The mean modal length (MML), population-weighted mean date (PWMD), population-weighted mean bottom temperature (PWMBT), and overall mean densities of 0+ English sole from May through September are shown in Table 1.

Growth

Growth of 0+ English sole was linear over time (Fig. 4). A general linear model pooled all data together and considered the effects of year, time of settlement, density, and temperature on growth. The final, best-fitted ($R^2 = 0.99$, $P < 0.001$) model was

$$l_{ji} = 8.44 + 43.48c + 6.76y_1 + 7.79y_2 - 13.06y_3$$
$$+ 0.43t_i - 0.11ct_i + 0.06y_1t_i + 0.12y_3t_i + \varepsilon_{ji}.$$

The results of partial t-tests (used in all comparisons unless specified otherwise), indicated there was a significant settlement time effect on growth ($P<0.01$), late-settling cohorts growing the fastest. The year effect was also significant (multiple partial F-test $P<0.05$, Table 2). Multiple-partial F-tests indicated that there were no density ($P=0.80$) or temperature ($P=0.37$) effects on the growth of 0+ English sole.

The date of settlement was estimated by fitting separate regression equations to each cohort in Figure 4, then by backcalculating to a length of 20 mm TL (Table 3), or by inverse prediction (Neter et al., 1985). We estimated that settlement of the 1985 and 1986 group-1 cohorts peaked in January, with 95% prediction intervals ranging from 27 November to 22 March. Settlement of the 1986 group-2 and 1987 cohorts peaked in May (with 95% prediction intervals ranging from 21 April to 29 May), and that of the 1988 cohort peaked in March (ranging from 17 February to 16 April).

Mortality The following equations were obtained from nonlinear least-square regression:

Table 2

A summary of effects of year and settlement time on the growth of 0+ English sole.

	Variable	Parameter	Coefficient	Partial-t	P (2-tail)
Intercept	Constant	α	8.44	3.19	< 0.01
	Settlement Time (c)	α_1	43.48	17.03	< 0.01
	Year (y_1, y_2, y_3)	—	—	—	< 0.01[1]
	y_1	α_{21}	6.76	2.61	< 0.05
	y_2	α_{22}	7.79	3.58	< 0.01
	y_3	α_{23}	−13.06	−4.19	< 0.01
Slope (Growth)	PWMD (t_i)	β	0.43	18.45	< 0.01
	Settlement time (c)	β_1	−0.11	−4.04	< 0.01
	Year (y_1, y_2, y_3)	—	—	—	< 0.05[2]
	y_1	β_{21}	0.06	2.13	< 0.05
	y_3	β_{23}	0.12	3.66	< 0.01

[1] Based on the result of an F-test, $F_{3,15} = 4.35$.
[2] Based on the result of an F-test. $F_{3,15} = 13.25$.

$$\text{Model 1}: \mu_2 = 0, \quad P_{t_i} = P_{oi}e^{-0.0123t_i}; \qquad P_{oi} = \begin{cases} 42.82 & 1985 \\ 21.02 & 1986 \\ 66.63 & 1987 \\ 40.40 & 1988 \end{cases}$$

$$\text{Model 2}: P_{t_i} = e^{\frac{-0.0056}{0.0056}\left(e^{-0.0056t_i}-1\right)}P_{oi}e^{-0.0056t_i}; P_{oi} = \begin{cases} 43.80 & 1985 \\ 18.62 & 1986 \\ 73.33 & 1987 \\ 40.46 & 1988 \end{cases}$$

$$\text{Model 3}: P_{t_i} = \begin{cases} P_{oi}e^{-0.0175t_i} \\ P_{oi}e^{-0.0175\times62}e^{-0.0075(t_i-62)}. \end{cases}$$

$t_i = 0$ to 62 (July and August)

$t_i > 62$ (September)

$$P_{oi} = \begin{cases} 49.60 & 1985 \\ 23.23 & 1986 \\ 74.33 & 1987 \\ 47.28 & 1988 \end{cases}$$

The estimated instantaneous mortality rates of 0+ English sole in July and August were equal, therefore model 3 was reduced from a three-step to a two-step model. The data fitted model 3 best (Fig. 5) with instantaneous mortality rates of 0.0175 per day in July and August and 0.0075 per day in September. The value of the Bayesian information criterion was 3.68 for model 1, 4.04 for model 2, and 2.65 for model 3. As a result, we concluded that model 3 was the best for estimating mortality.
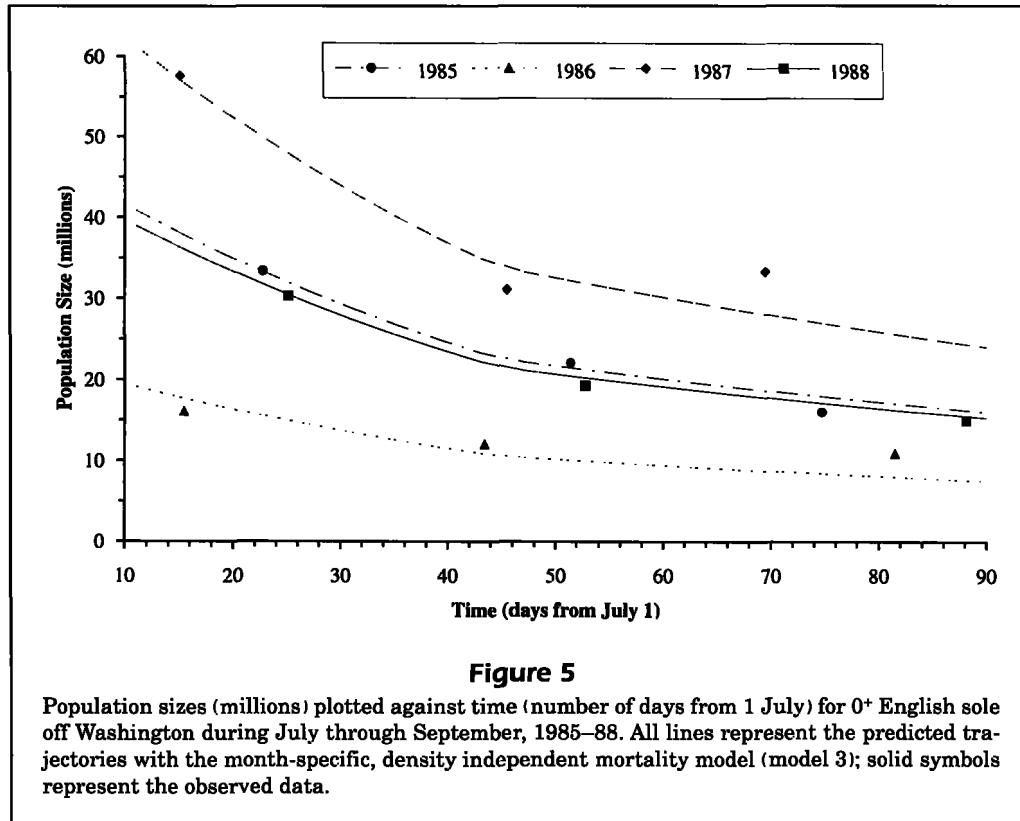
Table 3

Back-calculated settlement dates with their ranges, assuming average length at settling, $l_{settling} = 20$ mm TL.

Year	Settlement cohort	Date of settlement	95% prediction interval
1985	1	24 Jan	27 Nov–22 Mar
1986	1	16 Jan	17 Dec–16 Feb
	2	10 May	21 Apr–29 May
1987	2	8 May	30 Apr–16 May
1988	1	18 Mar	17 Feb–16 Apr

Discussion

Gear efficiency

Our estimates of growth and mortality might be biased if gear selectivity varied with size. Edwards and Steele (1968) suggested that beam trawl efficiency depends on a number of factors, such as towing speed, bottom type, and fish size. At a speed of 35 m/min, the efficiency of their 2-meter beam trawl was 25–35%, depending on fish size. They point out that their results apply only to their particular gear and the special conditions in Loch Ewe. Kuipers (1975) found that the efficiency of a 2-m beam trawl in the Dutch Wadden Sea declined from 100% at lengths below 70 mm to 15–30% for plaice larger than 150 mm. Our gear was a 3-m beam trawl with effective fishing width of 2.3 m, wider than the gear used by either Kuipers or Edwards and Steele, and was towed faster (41–47 m/min vs. 30–35 m/min). Also the ratio of fish-

Figure 5

Population sizes (millions) plotted against time (number of days from 1 July) for 0⁺ English sole off Washington during July through September, 1985–88. All lines represent the predicted trajectories with the month-specific, density independent mortality model (model 3); solid symbols represent the observed data.

ing line out to bottom depth used in our survey (10–15 in shallow waters) was greater than that in Kuipers' experiment (4–8), resulting in better bottom contact and reduced vessel avoidance.

During a series of 15 pairs of day–night comparative tows, for which gear and operating procedures were the same as those described in this paper, Gunderson and Ellis (1986) failed to detect any significant net avoidance by either butter sole (*Pleuronectes isolepis*) over the length range from 40 to 280 mm, or Pacific tomcod (*Microgadus proximus*) over the length range from 60 to 220 mm. In the present study, the data for English sole did not show any decline in estimated growth with size (Fig. 4). We conclude that the efficiency of the gear used in this study does not decrease with fish size over the length range from 20 to 150 mm and has little influence on estimates of growth or mortality.

Growth

It has been shown that English sole juvenile migration in and out of estuaries is size dependent (Gunderson et al., 1990; Shi et al., 1995), and our approach to the length modal progression method (LMP), namely pooling length data from coastal and estuarine areas to estimate growth, accounts for the effect of such migrations. Our nearshore survey area covered the outer limit of 0⁺ English sole bathymetric distribution; less than 1% of the total population was found in the deepest nearshore stratum (Shi et al., 1995). To minimize the effects of inter-area migration, we pooled data from all three areas surveyed (Fig. 1), which cover a major portion of waters available to English sole juveniles along the Washington coast. The resulting estimates fall between faster growth rates estimated from previous LMP analyses (Westrheim, 1955; Smith and Nitsos, 1969; Krygier and Pearcy, 1986) and slower growth rates estimated from fortnightly ring counts by Rosenberg (1982) (Table 4). Gunderson et al. (1990) and Shi et al. (1995) suggested that the population of English sole juveniles in this study may not be closed, however, and that some migrations, especially during May and June each year, involve areas outside the study area shown in Figure 1. Continuous recruitment of young juveniles from outside the study area would result in an underestimation of growth rates, as could emigration of larger juveniles. Our data do not show any decline in growth at either the beginning or end of the survey season (Fig. 4); thus the influence of continuous recruitment of small fish or emigration of larger fish on growth estimation appeared to be minimal.

Table 4

A summary of daily growth rate estimates from field studies.

Location	Size at age 1-yr (mm TL)	Daily growth rate (mm/day)	Data source
Willapa Bay, Grays Harbor, and adjacent neashore, WA	≤150	0.33–0.49 (May–Sep)	This study, 1985–88
Yaquina Bay, OR	130–160	0.49 (May–Oct)	Westrheim, 1955
Monterey Bay, CA	130–150	0.55 (May–Oct)	Smith and Nitsos, 1969
Yaquina Bay, OR	100–140	0.33	Rosenberg, 1982[1,2]
Moolach Beach, OR	100	0.34	
Yaquina Bay, OR	≤150	0.46–0.49 (Mar–Oct) 0.26–0.32 (Dec–Apr)	Krygier and Pearcy, 1986[2]
Moolach Beach, OR	≤150	0.28–0.42 (Apr–Oct)	

[1] The original daily growth rates were estimated from fortnightly ring counts.

[2] Length at age 1 and daily growth rates were converted from standard length (SL) to total length (TL) by using the relationship: $SL = -0.205 + 0.848\ TL$ (senior author, unpubl. data).

Several previous studies with the LMP technique have attempted to estimate growth rates for English sole juveniles from estuaries and open coast but failed to consider the effect of interarea migration on the growth estimates. As a consequence, their results often show significant differences between coastal and estuarine populations (Westrheim, 1955; Smith and Nitsos, 1969; Krygier and Pearcy, 1986). In contrast, growth estimated from fortnightly ring counts showed no differences between coastal and estuarine populations (Rosenberg, 1982).

Previous laboratory studies where ration was held constant (Williams and Caldwell, 1978) showed that ambient temperature had no statistically significant effect on English sole growth rate between 9.5 and 15.0°C but significantly reduced growth between 15.0 and 18.0°C. The artificial food pellets used in that study may have been nutritionally inadequate, however, making it difficult to extrapolate the results to field conditions. Laboratory studies by Yoklavich (1981), where live polychaetes were used as food, showed a significant decline in the mean growth rate of 0⁺ English sole (from 1.87% to 1.17% of body weight per day) between 13.0 and 17.5°C. Our results do not indicate any statistically significant interannual effect of temperature on the growth of English sole juveniles over the range of population-weighted mean temperatures (10.5–16.2°C) observed under field conditions. Higher temperatures presumably result in increased benthic productivity (Johnson and Brinkhurst, 1971) and in more food available to juveniles. On the other hand, metabolic requirements increase at high temperatures. Whether the juveniles grow faster or slower under field conditions probably depends on the bioenergetic balance at higher temperatures.

Peterman and Bradford (1987) found that density had a significantly negative effect on the growth of 1⁺ English sole off the Oregon and Washington coasts (P=0.024, one-tailed t-test); therefore it would be reasonable to expect that growth of 0⁺ English sole is also density dependent. Nevertheless growth rate and mean population size varied over relatively narrow ranges in this study, and we were unable to detect any statistically significant density effect.

The spawning season for English sole can extend from September to April (Kruse and Tyler, 1983), and recruitment processes are also protracted. Multiple peak recruitments are common (Kendall, 1966; Boehlert and Mundy, 1987; Gunderson et al., 1990; Shi et al., 1995), and peak recruitment occurs at different times each year, depending on ocean temperature and transport mechanisms (Ketchen, 1956; Boehlert and Mundy, 1987). Kendall (1966) reported that for Puget Sound English sole juveniles that were recruited earlier, growth was slower than that of later recruits during the same period. Our results led to the same conclusion, that is, timing of settlement influences the growth trajectory (Fig. 4).

Different size groups of English sole have different prey requirements and suffer from different degrees of food limitation (Gunderson et al., 1990). Off the Oregon coast, English sole 17–35 mm standard length (SL) fed primarily on polychaete palps, juvenile bivalves, and harpacticoid copepods, whereas 35–82 mm fish fed on larger prey such as amphipods and cumaceans (Hogue and Carey, 1982). In the Humboldt Bay estuary, English sole smaller than 50 mm TL fed almost exclusively on harpacticoid copepods whereas the diet of 66–102 mm fish was dominated by polychaetes (Toole, 1980).

Winberg (1956) found that individual metabolic requirements and food consumption increase as a function of $W^{0.8}$ (where W=body weight), and Fonds (1979) showed a similar relation for young sole, *Solea solea*. The larger sizes attained by the early-settlement cohorts of English sole would probably also entail increased food requirements for those fish during May–September. The lower growth rates observed for early-settlement cohorts in comparison with those that settled later probably resulted from a combination of higher metabolic demands and reduced availability of suitable prey. Growth of 0+ English sole does not appear to be strictly linear if a sufficiently long period of time is examined.

Mortality

Estimates of mortality rates were subject to some of the same sources of error and bias that the growth estimates were. Previous work (Gunderson et al., 1990; Shi et al., 1995) has shown that migrations of 0+ English sole are size dependent. Typically, larger fish emigrate from estuaries and perhaps out of our nearshore survey area, whereas smaller fish immigrate into our survey area. Immigration of small fish would cause underestimates of mortality. Previous analysis indicated that most immigration probably occurred near the settling period, i.e., May and June or earlier (Shi et al., 1995). Therefore, it is unlikely that immigration had much effect on the mortality estimates because only population estimates for July through September were used in this analysis.

Emigration of large 0+ fish would cause overestimation of mortality rates. Although we cannot completely ignore the possibility of emigration, previous analysis of length increment patterns in estuarine and nearshore areas has indicated that net emigration of large fish from the study area is minor during July–September (Shi et al., 1995). In addition, had substantial emigration occurred during July through September, estimated mortality rates would be consistently higher during September than during July and August, rather than the opposite (0.0075 per day vs. 0.0175 per day).

Seasonally differentiated daily mortality could be related to differences in temperature, individual size, or population density. Water temperatures, however, remained relatively stable in the study area during July through September (Fig. 3). Size-dependent mortality may have occurred, because 0+ English sole grow rapidly during the summer, with increases in individual size of 0+ English sole ranging from 20 to 30 mm TL from July to September. Kramer (1991) estimated the mortality rates for each 5-mm size group of California halibut, *Paralichthys californicus*,

on the basis of daily production by size group, and found that mortality was size specific for fish less than 70 days old (< 30 mm SL), smaller fish suffering higher mortality than larger ones. For older 0+ California halibut (70–115 days of age or 31–70 mm SL), mortality varied little (0.011–0.014 per day, with mean=0.0124 per day and SD=0.001 per day) and no trend was observed. Beverton and Iles (1992) found a significant density-dependent mortality (μ_2) effect for North Sea plaice ranging from ≤15 mm to 35 mm, although this effect was not significant for fish larger than 35 mm. Both Kramer (1991) and Beverton and Iles (1992) found that mortality of juvenile flatfish is highest during and immediately after settlement, and our results for English sole suggest the same.
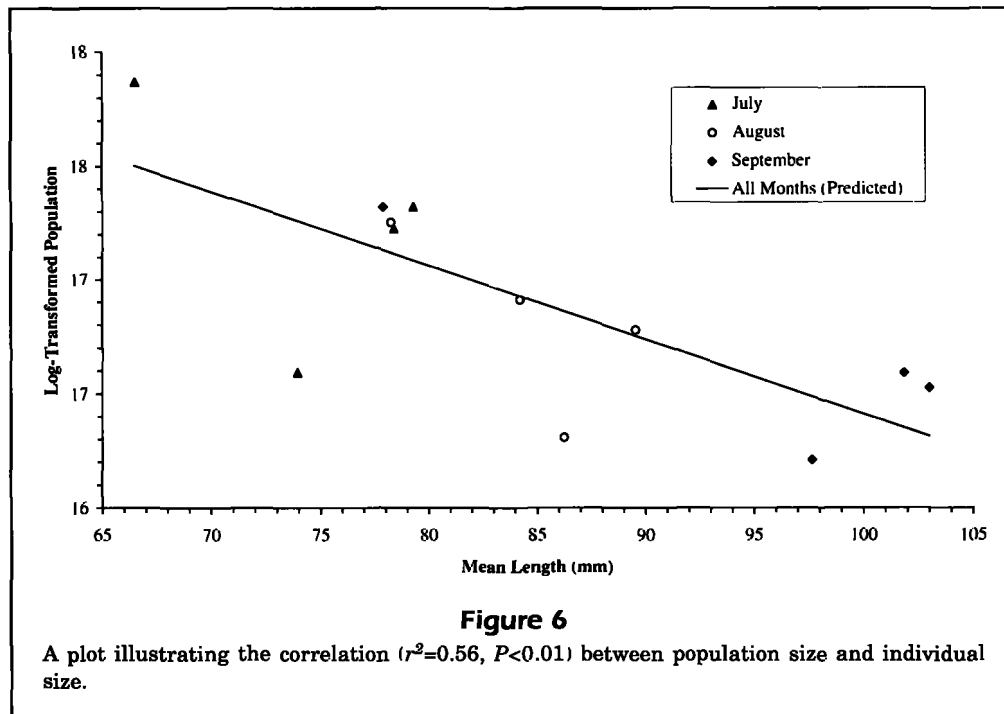
The effects of density and individual size were clearly confounded in our study (Fig. 6). An empirical relation between population size in the survey area (P_t) and mean length (l_t) was fitted as

$$\ln P_t = A + Bl_t,$$

where, P_t = the estimated total population size at time t; l_t = the mean length of all 0+ English sole at time t (July through September); and the correlation between the two confounding factors was highly significant (r^2=0.56, P<0.01). It should always be borne in mind that it is very difficult, if not impossible, to isolate these two confounding factors in field observations; controlled enclosure experiments would probably be required to disentangle them. There is both a theoretical (Peterson and Wroblewski, 1984) and an empirical (McGurk, 1986; Kramer, 1991) basis for assuming that mortality decreases with individual size, and if this is the case, μ_2 (the density-dependent mortality coefficient) would have been overestimated. If mortality of 0+ English sole is density dependent, it appears that this dependence is weak because adding a density-dependent term to the model (model 2) did not improve the fit to the data.

Our surveys showed only a threefold difference in abundance of 0+ English sole during 1985–88, but stock synthesis analysis of commercial fisheries data indicates this was a period of relatively stable recruitment (Sampson[1]). The estimated recruitment of age-2+ females to the commercial fishery varied by no more than a factor of 1.8 for the 1985–88 year classes, whereas it varied by a factor of 6.5 for the

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[1] Sampson, D. B. 1993. An assessment of the English sole stock off Oregon and Washington in 1992. Appendix H *in* Status of the Pacific coast groundfish fishery through 1993 and recommended allowable biological catch for 1994. Pacific Fish. Management Council, 2000 SW 1st Ave., Suite 420, Portland, OR, 43 p.

Figure 6

A plot illustrating the correlation (r^2=0.56, $P<0.01$) between population size and individual size.

1975–90 year classes. Although our results apparently did not encompass periods of poor recruitment, they show that surveys of the nursery areas of 0^+ English sole have the potential to provide estimates of year-class strength several years in advance of the commercial fishery, as well as provide insight into the processes that generate recruitment variability.

Acknowledgments

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