

Abstract—Variation in the life history parameters of Dover sole (*Microstomus pacificus*) off the coasts of Washington, Oregon, and northern California was investigated by using research survey data. We compared growth, maturation, and length-weight curves of Dover sole within the International North Pacific Fisheries Commission (INPFC) statistical areas of Monterey, Eureka, Columbia, and Vancouver. We found strong evidence of dimorphism in growth and maturation rates between sexes. In addition, geographic variation in both growth and maturation rates was also suggested. Male and female Dover sole from the Columbia area had lower Brody growth coefficients and larger asymptotic lengths than Dover sole from other areas. Further, there was an apparent latitudinal cline in maturation rates because males and females matured at smaller size and younger ages at higher latitudes. In contrast, no difference between male and female length-weight relationships was detected. In comparison with other pleuronectids, we found that Dover sole matured at relatively larger sizes and younger ages. These differences likely reflect adaptation of Dover sole to the inherent variability of the California Current.

Variation in life history parameters of Dover sole, *Microstomus pacificus*, off the coasts of Washington, Oregon, and northern California

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Dover sole (*Microstomus pacificus*) is a deep-water pleuronectid fish that ranges from Baja, California, to the Bering Sea (Hart, 1973) at depths from 10 m to 1200 m (Percy et al., 1982; Allen and Smith, 1988). Dover sole are demersal and have a complex life history that includes an extended pelagic larval phase of one year or more (Percy et al., 1977; Markle et al., 1992; Toole et al., 1993; Butler et al., 1996) and an ontogenetic migration range from continental shelf to continental slope (Jacobson and Hunter, 1993). Dover sole support an important commercial fishery off the coasts of Washington, Oregon, and California, where annual landings have averaged about 12,000 t during 1956–96 (Brodziak et al., 1997).

Previous research on life history parameters of Dover sole off the west coast of the United States was conducted during the late 1940s and the 1980s. Hagerman (1952) estimated growth, maturation rates, and length-weight curves of Dover sole from commercial fishery samples collected from the ports of Eureka and Fort Bragg, California during 1948–49. Harry (1959) estimated maturation rates of Dover sole from commercial fishery samples collected at the port of Astoria, Oregon, during 1948–49. More recently, Hunter

et al. (1990) have estimated growth and maturation rates of Dover sole from research survey samples collected between Point Conception and Half Moon Bay, California, during 1985–88. Hunter et al. (1992) refined maturation rate estimates of female Dover sole through histological analysis of survey data collected off the coasts of Oregon and California during 1985–89.

In this study, we investigated variation in life history parameters of Dover sole off the coasts of Washington, Oregon, and northern California from samples collected during research surveys during 1984–85 and 1990–93. Dover sole samples were partitioned into geographic regions based on International North Pacific Fisheries Commission statistical areas in order to investigate latitudinal differences among potential management units. We used length-at-age data to estimate growth and to quantify sexual dimorphism and geographic variation in growth. Maturation of male and female Dover sole as a function of length and age was estimated and geographic variation in maturity was quantified. Sexual dimorphism and geographic variation on weight at length were also explored. We discuss apparent differences between life history parameters of Dover sole and other pleuronectids.

Materials and methods

Length-at-age samples

A total of 4780 Dover sole were collected for age determination during 1984–93 from bottom trawl surveys of the upper continental slope (Raymore and Weinberg, 1990; Parks et al., 1993; Lauth et al., 1997). Biological samples were collected from three depth strata (183–549 m, 550–914 m, and 915–1280 m) within the International North Pacific Fisheries Commission (INPFC) statistical areas (Table 1; Fig. 1) of Monterey (38°24'N–40°30'N), Eureka (40°30'N–43°00'N), Columbia (43°00'N–47°30'N), and Vancouver (47°30'N–48°29'33'N). The survey area was length- and depth-stratified to ensure adequate coverage for otolith sampling. For each fish collected, sex was determined, total length (to the nearest cm) was measured, and otoliths were extracted for age determination.

Maturity stage was determined for 4490 Dover sole by visual inspection of gonads. Only samples from surveys conducted by the RV *Miller Freeman* (Table 1) were used for analyzing maturity rates because these samples were collected prior to the spawning season during winter when gross anatomical features provide a reasonably accurate measure for determining whether a fish is mature or not (Hagerman, 1952; Hunter et al., 1992). Total fish weights (to the nearest gram) were also recorded for 3019 samples from surveys conducted by the MV *Half Moon Bay* and the RV *Miller Freeman*; these data were used for length-weight analyses.

Fish ages were determined by the break and burn method, which is the standard for Dover sole (Pikitch and Demory, 1988), although the method has not been validated. In our study, the initial otolith increment was assumed to be an age-1 marker in accordance with the convention for aging adult Dover sole (Chilton and Beamish, 1982). Increments in each otolith were counted two or more times and assigned a single age by one of four readers. In some cases, a mark within the otolith core was counted as the initial increment because it met the identification criteria of an annual increment. A paired comparison of age readings between the most experienced reader and the other readers indicated that there was a mean difference of $\mu=0.22$ years ($\sigma_{\mu}=0.13$) based on a blind sample of 474 Dover sole; this difference was almost significant at the 5% level ($P=0.08$).

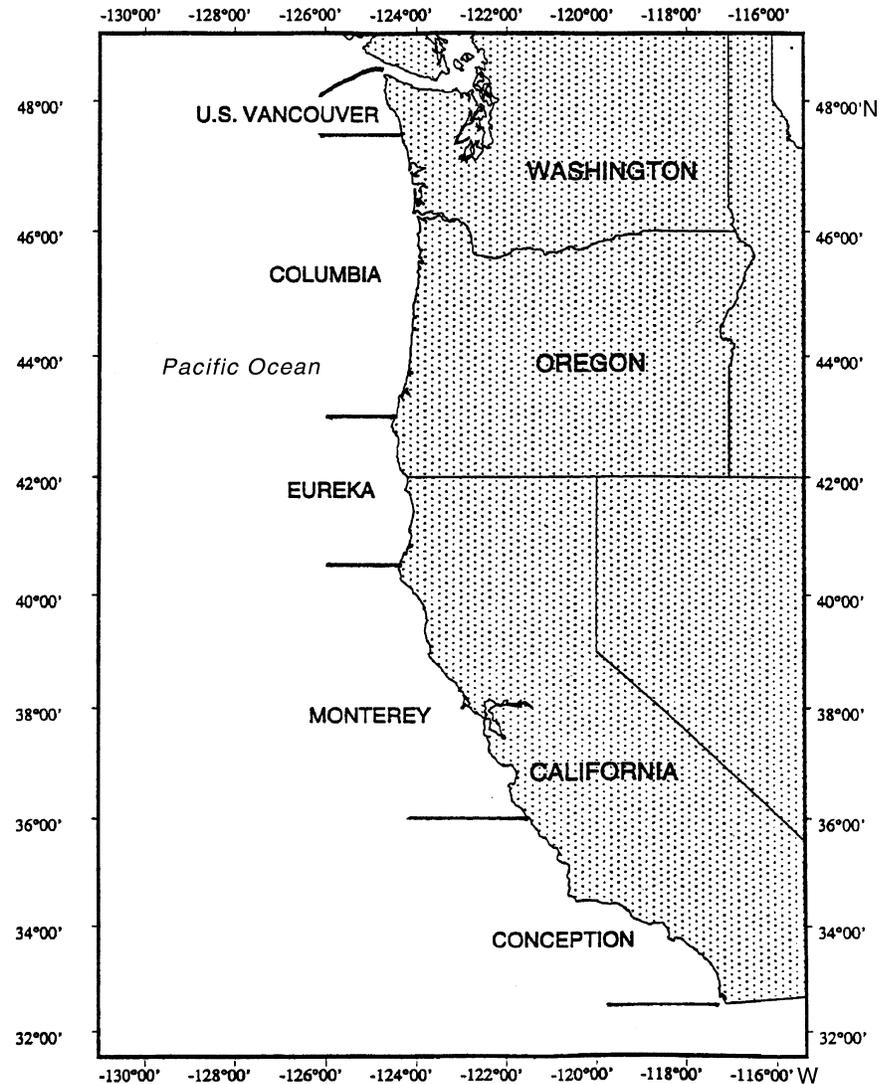


Figure 1

International North Pacific Fisheries Commission statistical areas in the North Pacific Ocean.

Empirical comparisons of mean ages, lengths, and weights by sex within each INPFC area were performed. The GT2 test is appropriate for unplanned comparisons of populations with unequal sample sizes (Sokal and Rohlf, 1981) and it was used to test for differences in mean age, length, and sex among INPFC areas.

Growth curves

Bartlett's test of homogeneity of variance was used to test whether variance in length at age varied by sex for Dover sole from ages 3 to 30 years. Test results were used to select an appropriate error structure for growth curve estimation. Growth curves for male, female, and pooled-sex samples were estimated by maximum likelihood (see Kimura, 1980). We used an alternative parameterization of the von Bertalanffy growth curve (Schnute

Table 1

Dover sole samples used for growth, maturity,¹ and length-weight² analyses by INPFC area, vessel, month and year of collection, and depth range of capture.

INPFC area	Number of males	Number of females	Total	Vessel	Month and year	Depth range (m)
Vancouver	94	97	191	FV <i>Marathon</i>	Apr 1985	221–406
	41	59	100	FV <i>Mys. Babushkina</i>	May 1985	188–280
	77	60	137	RV <i>Miller Freeman</i>	Oct 1992	225–854
	Total	212	216	428		
Columbia	329	54	383	FV <i>Poseydon</i>	Apr 1984	320–450
	596	331	927	MV <i>Half Moon Bay</i>	Sep 1984	110–856
	419	248	667	FV <i>Marathon</i>	Apr 1985	188–448
	230	88	318	FV <i>Mys. Babushkina</i>	May 1985	115–262
	162	236	398	RV <i>Miller Freeman</i>	Oct 1992	210–1211
	182	240	422	RV <i>Miller Freeman</i>	Oct 1993	192–1132
Total	1918	1197	311			
Eureka	226	303	529	RV <i>Miller Freeman</i>	Oct 1990	252–1189
	37	39	76	RV <i>Miller Freeman</i>	Oct 1991	229–1176
	54	75	129	RV <i>Miller Freeman</i>	Oct 1993	243–1163
	Total	317	417	734		
Monterey	209	294	503	RV <i>Miller Freeman</i>	Oct 1991	198–1130

¹ Maturity analyses comprised data from surveys conducted by the RV *Miller Freeman*.

² Length-weight analyses comprised data from surveys conducted by the RV *Miller Freeman* and the MV *Half Moon Bay*.

and Fournier, 1980; Ratkowsky, 1983) because its parameters were simpler to interpret and because it exhibited better statistical properties than other parameterizations of the von Bertalanffy model. This form was

$$L(t_i) = L_{min} + (L_{max} - L_{min}) \frac{(1 - c^{t_i - t_{min}})}{(1 - c^{t_{max} - t_{min}})} + \epsilon_i, \quad (1)$$

where t_i = age of the i^{th} sample;
 L_{min} , L_{max} , and c = parameters;
 t_{min} and t_{max} denote the youngest and oldest ages observed in the length-at-age sample;
 L_{min} and L_{max} denote the predicted lengths at ages t_{min} and t_{max} ; and
 ϵ_i = independent and identically distributed normal error terms with zero mean and constant variance $\epsilon_i \sim N(0, \sigma^2)$.

There is a one-to-one relationship between parameters of the alternative form and the standard von Bertalanffy model (see Ratkowsky, 1983). Residuals from estimated growth models were tested for normality with the Shapiro and Wilk (1965) test. Standard errors of parameter estimates were computed by using the conditional bootstrap with 1000 bootstrap replicates (Efron and Tibshirani, 1993), except for the pooled-sex analysis, where

asymptotic standard error estimates were used owing to the large sample size.

As found in previous research, some sexual dimorphism in growth was expected, but there was no information about geographic variation in growth. A likelihood-ratio test (Kimura, 1980) was applied to determine whether growth curves differed by sex or by INPFC area. This test compared two hypotheses: H_0 , the hypothesis of identical growth parameters between sexes or among areas; and H_1 , the hypothesis of different growth parameters. The test statistic (χ^2) was

$$X^2 = -N \log \left(\frac{\sigma_1^2}{\sigma_0^2} \right), \quad (2)$$

where σ_0^2 and σ_1^2 = sample estimates of residual variance for growth curves estimated under H_0 and H_1 .

The likelihood-ratio test was applied to male and female samples from all INPFC areas and was then separately applied to male and female samples for paired adjacent INPFC areas. When there was no difference between adjacent areas, samples were grouped and the process was repeated. Standard errors of parameter estimates of the final groups were computed by using the conditional bootstrap with 1000 replicates.

Maturation curves

Maturation by length and by age were estimated for female ($n=934$) and male ($n=1232$) Dover sole with logistic regression (McCullagh and Nelder, 1989). Significance of fish length or age as a predictor of fraction mature was tested with the likelihood-ratio chi-square test. Standard errors for model parameters were estimated by using the nonparametric bootstrap method with 1000 replicates.

Geographic differences in maturation rates were also evaluated for male and female samples by using logistic regression. Step-wise model selection was used to determine the best model of length or age and the factors INPFC area and sex, and all possible higher order interactions between these terms. The full model with all possible interactions was

$$\log\left(\frac{\pi}{1-\pi}\right) = (\beta_0 + \beta_A + \beta_S + \beta_{AS}) + (\beta_{1A} + \beta_{1S} + \beta_{1AS})X, \quad (3)$$

where π = the probability of being sexually mature;
 β_A , β_S , and β_{AS} = coefficients of area, sex, and their interaction; and
 β_{1A} , β_{1S} , and β_{1AS} = coefficients of first- and second-order interactions between area, sex, and the variable length (or age), denoted by X .

Akaike's information criterion (AIC) was used to compare competing nested models in a step-wise manner (Hastie and Pregibon, 1993). We also evaluated whether overdispersion due to cluster sampling was present (McCullagh and Nelder, 1989). If the ratio of observed to expected sampling variation (ϕ) for the estimated model was less than 1, we concluded that overdispersion was not present. Nonparametric bootstrapping based on 1000 replicates was used to estimate standard errors for parameter estimates.

Length-weight curves

We estimated length-weight relationships for pooled-sex, male ($n=1549$), and female ($n=1470$) samples based on the allometric equation

$$W_i = AL_i^B \exp(\varepsilon_i), \quad (4)$$

where W_i and L_i = the observed total weight (grams) and total length (centimeters) of the i^{th} fish;
 A and B = parameters; and
 ε_i = independent and identically distributed normal error terms with zero mean and constant variance.

A natural logarithmic transformation was applied to length and weight measurements and linear regression was applied to estimate parameters, denoted as $b_0 = \log A$ and

$b_1 = B$. Because lognormal errors were assumed, the retransformed intercept needs to be adjusted to give an accurate predictive equation for mean weight, and the adjusted intercept was computed as $A = \exp(b_0) \exp((\sigma^2 - \sigma_0^2)/2)$, where σ^2 is the residual variance from the regression and σ_0^2 is the variance of b_0 (Hayes et al., 1995). Nonparametric bootstrapping with 1000 replicates was used to estimate standard errors of parameters and to provide nominal estimates of parameter bias (Efron and Tibshirani, 1993).

Geographic variation and sexual dimorphism in the length-weight relationship for Dover sole were investigated by a step-wise procedure among generalized linear models relating the log-transformed length-weight observations to the factors INPFC area and sex, and all possible higher order interactions between these terms. The full model with all possible interactions was

$$\log W_i = (\log A + \beta_A + \beta_S + \beta_{AS}) + (B + \beta_{AL} + \beta_{SL} + \beta_{ASL}) \log L_i + \varepsilon_i, \quad (5)$$

where β , β_S , and β_{AS} = coefficients of area, sex, and their interaction;
 β_{AL} , β_{SL} , and β_{ASL} = coefficients of first- and second-order interactions between area, sex, and the natural logarithm of length; and
 ε_i = a normally distributed error with zero mean and constant variance.

As in the maturity analyses, the AIC criterion was used to choose among competing models in a step-wise manner (Hastie and Pregibon, 1993). Estimates of standard errors of parameters and nominal estimates of parameter bias were computed with the nonparametric bootstrap with 1000 replicates. Bootstrap estimates of residual variance and $\sigma_0^2 = \text{Var}[b_0] = \text{Var}[\log A + \beta_A + \beta_S + \beta_{AS}]$ were used to compute the adjusted intercept.

Results

Length-at-age samples

Female and male age and total length distributions differed across areas. On average, females were 1 to 2 years older than males (Table 2). Mean ages of males and females were significantly different for all areas combined and within the Vancouver, Columbia, and Eureka areas ($P < 0.05$). Mean ages were lowest in the Vancouver area and highest in the Eureka area. The youngest males were 2 years old and had lengths of 19, 22, and 25 cm, whereas the oldest male was 42 years old and 41 cm long. The youngest female was 2 years old and 21 cm long, whereas the oldest female was 48 years old and 51 cm long. Maximum observed ages of females were greater than those of males in all areas except the Vancouver area where the fewest samples were collected. Females were 4 to 5 cm longer than males on average (Table 2). Mean female

Table 2

Dover sole mean, minimum (Min), and maximum (Max) ages (yr), total lengths (cm), and total weights (g) by INPFC area and sex. Standard errors (SE) of mean values appear in parentheses.

INPFC area	Sex	Age (yr)			Length (cm)			Weight (g)		
		Min	Mean (SE)	Max	Min	Mean (SE)	Max	Min	Mean (SE)	Max
Vancouver	Male	3	10.2 (0.3)	39	20	33.1 (0.4)	49	97	505 (32)	1195
	Female	4	11.1 (0.3)	29	21	37.4 (0.5)	57	114	704 (55)	1850
Columbia	Male	3	11.9 (0.1)	42	17	33.6 (0.1)	51	40	467 (9)	1325
	Female	3	14.0 (0.2)	48	15	38.8 (0.2)	66	33	660 (14)	2479
Eureka	Male	2	13.0 (0.4)	35	16	35.4 (0.4)	49	48	485 (15)	1182
	Female	3	14.5 (0.4)	40	21	40.6 (0.4)	56	75	789 (23)	2296
Monterey	Male	3	12.7 (0.5)	31	19	35.4 (0.5)	49	55	499 (19)	1240
	Female	2	13.6 (0.4)	42	20	39.4 (0.5)	55	65	741 (27)	2157
All areas	Male	2	12.0 (0.1)	42	16	33.9 (0.1)	51	40	478 (7)	1325
	Female	2	13.7 (0.1)	48	15	39.1 (0.2)	66	33	712 (11)	2479
	Pooled	2	12.7 (0.1)	48	15	36.2 (0.1)	66	33	598 (7)	2479

length was significantly greater than mean male length for all areas combined and within each area ($P < 0.05$). Mean lengths were greatest within the Eureka and Monterey areas and smallest in the Vancouver area. The smallest male (16 cm) was 4 years old, whereas the two largest males (51 cm) were 25 and 37 years old. The smallest female (15 cm) was 2 years old and the largest female (66 cm) was 38 years old.

Weight distributions differed by sex across areas. Mean female weights exceeded male values by 200 to 300 g. Significant differences between male and female weight were detected for all areas combined and within each area ($P < 0.05$). Individual fish weights were more variable for females than for males. Mean weights were greatest within the Eureka and Monterey areas and lowest in the Columbia area. The lightest male weighed 40 g and was 5 years old, whereas the heaviest male was 1325 g and 26 years old. The lightest female weighed 33 g and was 5 years old, whereas the heaviest female was 2479 g and 38 years old.

Growth curves

Variances in length at age of male and female Dover sole were homogeneous. For male samples ($n = 2613$), the coefficient of variation (CV) of length at age ranged from 6 to 14% and averaged 10%, with an average variance of 12.5 cm. Male variance in length was homogeneous across ages ($P = 0.83$, $\chi^2 = 20.97$). For female samples ($n = 2514$), the CV ranged from 6 to 16% and averaged 11%, with an average variance of 17.5 cm. Similar to that for males, female variance in length was homogeneous across ages ($P = 0.59$, $\chi^2 = 25.64$). As a result, we used an additive normal error term for estimating growth curves.

There was sexual dimorphism in growth of Dover sole when samples were pooled across areas. Maximum likelihood estimates and standard errors (SE) for pooled-sex samples were as follows: $L_{max} = 51.3$ cm, SE = 0.5; $L_{min} = 20.9$ cm, SE = 0.3; $c = 0.9337$, SE = 0.0030 with corresponding von Bertalanffy values: $L_{\infty} = 52.6$ cm, $K = 0.069$, and $t_0 = -5.4$. Male and female growth parameters for all areas (Table 3) were significantly different ($P < 0.001$, $\chi^2 = 1079$) and showed that females grow more rapidly than males and attain larger sizes. There was greater variation in female size at age, and residual variance from the female curve was roughly twice that value from the male curve. Both female and male curves for samples pooled across areas did not satisfy the assumption of normally distributed residuals ($P < 0.01$). Thus, neither male nor female growth was adequately described by a single growth curve representing all areas.

Geographic variation was evident in male growth curves estimated for each area (Table 3). The hypothesis of identical growth parameters for all areas was rejected ($P < 0.001$, $\chi^2 = 96.25$). Male samples from adjacent INPFC areas were grouped and growth curves were estimated. Homogeneous growth was rejected for Vancouver and Columbia samples ($P < 0.001$, $\chi^2 = 25.88$) and for Columbia and Eureka samples ($P < 0.001$, $\chi^2 = 42.31$) but was accepted for the Eureka and Monterey samples ($P = 0.28$, $\chi^2 = 3.85$). Homogeneous growth was rejected for combined samples from Eureka, Monterey, and Columbia ($P < 0.001$, $\chi^2 = 80.98$) but was accepted for combined male samples from Eureka, Monterey, and Vancouver ($P = 0.35$, $\chi^2 = 6.65$).

We found that growth of male Dover sole differed between the Columbia area and the combined Vancouver, Eureka, and Monterey areas (Table 3) and that male growth curves from the Vancouver, Eureka, and Monterey

areas were not statistically distinguishable. Males from the Columbia area grew more slowly and reached larger sizes, on average, than males from the Vancouver, Eureka, and Monterey areas (Fig. 2A). Estimates of L_{∞} and K for the Columbia area differed from estimates for the combined Vancouver, Eureka, and Monterey areas by 3% and -26%, respectively. Parameters of the alternative growth curve were more precisely determined with CVs of 1–3% for the Columbia and combined areas in comparison to the standard von Bertalanffy model where CVs were 2–14%. Residual variance for the Columbia area was lower than that for the three areas combined. However, residuals from the Columbia area curve did not satisfy the normality assumption ($P=0.01$), whereas residuals from the combined areas did ($P=0.83$). Overall, there was no latitudinal cline in growth parameters.

Similarly, we found geographic variation in growth of female Dover sole by area (Table 3). The hypothesis of identical female growth parameters across areas was rejected ($P<0.001$, $\chi^2=91.70$). Female samples from adjacent INPFC areas were grouped and growth curves were estimated. Homogeneous growth was rejected for Vancouver and Columbia samples ($P=0.002$, $\chi^2=14.92$) and for Columbia and Eureka samples ($P<0.001$, $c=56.90$) but was accepted for Eureka and Monterey samples ($P=0.09$, $\chi^2=6.45$). Homogeneous growth was rejected for combined samples from Eureka, Monterey, and Columbia ($P<0.001$, $\chi^2=89.15$) and weakly supported for combined samples from Eureka, Monterey, and Vancouver ($P=0.025$, $\chi^2=14.47$).

Growth of female Dover sole exhibited geographic variation (Fig. 2B). In particular, females from the Columbia

Table 3

Estimated growth curves for length (cm) at age (yr) of male and female Dover sole by INPFC area. Parameters L_{max} , L_{min} , and c are from the empirical von Bertalanffy curve. Corresponding values for the standard von Bertalanffy curve (L_{∞} , t_0 , and K) are also listed. Bootstrap estimates of standard errors appear immediately below each estimate in parentheses. Other table entries are the residual variance from the nonlinear regression (σ^2) and the probability that residuals were normally distributed ($P(\text{normal})$) based on the Shapiro and Wilk (1965) test.

Growth curves by INPFC area	L_{max}	L_{min}	c	σ^2	$P(\text{normal})$	L_{∞}	t_0	K
Male growth curves								
All areas ¹	46.6 (0.5)	21.2 (0.4)	0.9315 (0.0042)	11.45	<0.01	48.2 (0.8)	-6.2 (0.5)	0.071 (0.005)
Vancouver	45.9 (1.6)	21.8 (1.0)	0.9102 (0.0157)	13.03	0.51	47.8 (2.3)	-3.7 (1.3)	0.094 (0.017)
Columbia	46.4 (0.6)	23.0 (0.4)	0.9347 (0.0053)	10.92	0.01	48.2 (1.1)	-6.6 (0.7)	0.068 (0.006)
Eureka	45.7 (0.9)	20.8 (0.8)	0.9182 (0.0102)	11.37	0.71	47.3 (1.5)	-4.8 (0.9)	0.085 (0.011)
Monterey	43.7 (0.8)	22.6 (0.8)	0.8910 (0.0146)	10.21	0.95	44.6 (1.2)	-3.1 (0.9)	0.115 (0.016)
Vancouver, Eureka, and Monterey	45.7 (0.7)	20.4 (0.6)	0.9121 (0.0072)	11.53	0.83	46.6 (0.9)	-4.3 (0.6)	0.092 (0.008)
Female growth curves								
All areas	51.7 (0.5)	19.7 (0.6)	0.9131 (0.0042)	20.06	<0.01	52.2 (0.6)	-3.2 (0.4)	0.091 (0.005)
Vancouver	51.0 (1.9)	24.5 (1.5)	0.9135 (0.0219)	24.18	0.87	54.1 (5.1)	-2.7 (1.7)	0.091 (0.024)
Columbia	51.8 (0.7)	22.5 (0.7)	0.9206 (0.0057)	19.93	0.63	52.5 (0.9)	-3.8 (0.6)	0.083 (0.006)
Eureka	50.8 (0.7)	20.8 (1.0)	0.8879 (0.0091)	17.94	0.24	51.1 (0.8)	-1.4 (0.6)	0.119 (0.010)
Monterey	49.7 (0.8)	19.1 (1.1)	0.8849 (0.0103)	15.03	0.99	49.9 (0.9)	-1.9 (0.6)	0.122 (0.012)
Vancouver, Eureka, and Monterey	51.0 (0.8)	18.5 (0.8)	0.8965 (0.0060)	18.64	0.58	51.4 (0.7)	-2.1 (0.4)	0.109 (0.007)

¹ INPFC areas sampled in the study: Vancouver, Columbia, Eureka, and Monterey.

area appeared to grow more slowly and achieve greater sizes than females from the other areas. Estimates of female L_{∞} and K from the Columbia area were 2% and -24% different from estimates for the combined Vancouver, Eureka, and Monterey areas (Table 3). As with the results for males, female growth parameters were more precisely estimated for the alternative growth curve with CVs of 1–6% in comparison with CVs of 2–65% for the standard von Bertalanffy curve. In contrast to males, residuals of female growth curves were normally distributed and there was an apparent increase in L_{∞} with latitude. Overall, geographic variation of male and female growth was similar, with the exception that asymptotic female size appeared to increase with latitude.

Maturation curves

We found that male Dover sole matured at smaller sizes than did females when samples were combined across areas (Table 4). Predicted female median length at maturity (L_{50}) exceeded male L_{50} by 6 cm (23%), and the ratio of median length at maturity to asymptotic size (L_{50}/L_{∞}) of females exceeded that of males by 14%. The estimate of male L_{50} (CV=2%) was more variable than the female L_{50} (CV=1%).

Maturity-at-age curves for all areas (Table 5) indicated that males matured at younger ages than females. Predicted female median age at maturity (A_{50}) exceeded male A_{50} by three years (57%), whereas the ratio of female median age at maturity to maximum observed age (A_{50}/A_{max}) exceeded that of males by about 42%. The estimate of male A_{50} (CV=10%) was less precise than the female estimate (CV=3%).

Geographic variation was evident in maturity at length by INPFC area (Fig. 3). The best logistic model for maturity at length included terms¹ for length, sex, area, length \times sex, and length \times area and had a dispersion parameter of $\phi = 1.28$ (Table 4). This factor indicated a moderate degree of overdispersion in the maturity-at-length data. Male maturity curves by INPFC area showed a geographic cline in L_{50} , and median size at maturity decreased with latitude. Male L_{50} values ranged from 22 to 29 cm with CVs of 2% to 9%. Similarly, the ratio L_{50}/L_{∞} decreased from 0.66 in Monterey to 0.47 in Vancouver. Female L_{50} 's showed a similar geographic cline, although female L_{50} 's were more precisely estimated than male L_{50} 's. Female L_{50} values ranged from 35 cm in Monterey to 28 cm in Vancouver. Female values of L_{50}/L_{∞} also decreased as latitude increased. Overall, median length at maturity of both male and female Dover sole decreased with increasing latitude.

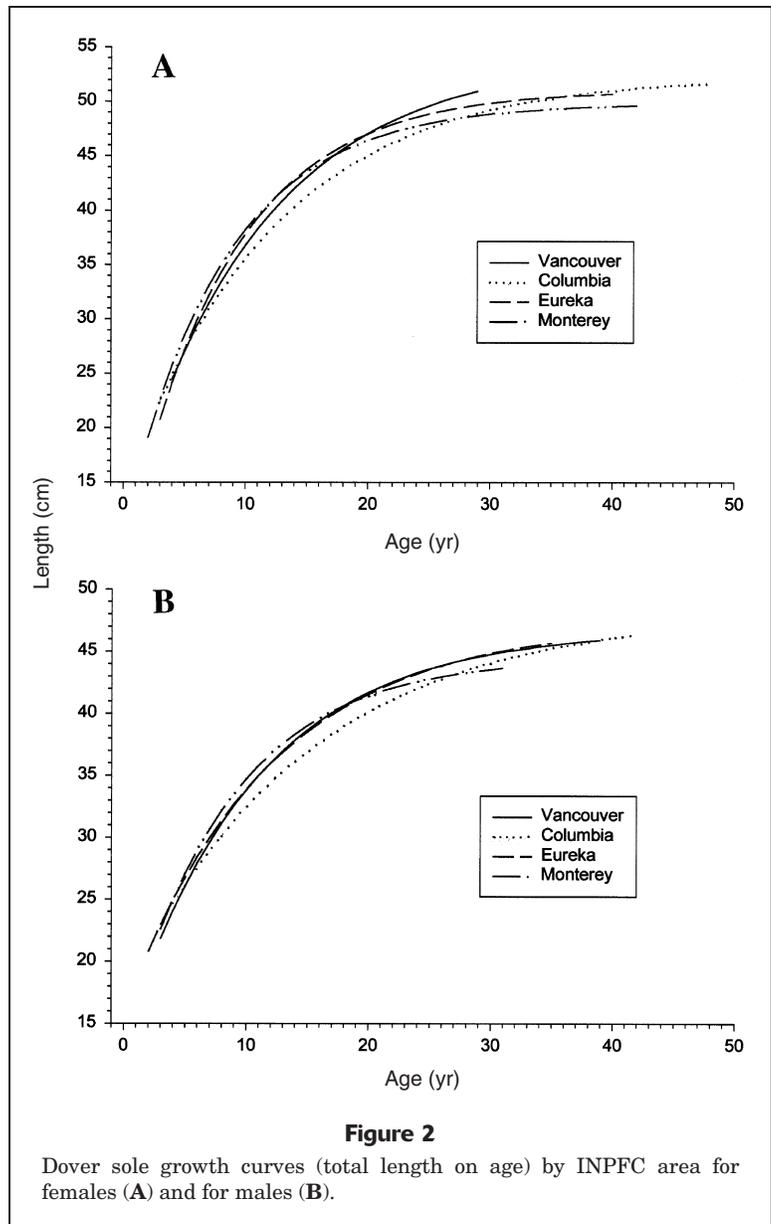


Figure 2
Dover sole growth curves (total length on age) by INPFC area for females (A) and for males (B).

Maturity at age also varied by INPFC area (Fig. 4). The best logistic model included terms for age, sex, area, age \times sex, and age \times area (Table 5). Dover sole maturity-at-age data were highly overdispersed and the ratio of observed-to-expected sampling variance for the selected model was $\phi = 4.86$. Male maturity ogives by INPFC area suggested a latitudinal cline in A_{50} . Male A_{50} values ranged from 3 to 7 years and decreased with increasing latitude, except for the Columbia area. CVs of male A_{50} values were high and ranged from 8% to 70%. The ratio A_{50}/A_{max} showed a clear latitudinal trend and decreased from 0.22 in Monterey to 0.09 in Vancouver. Female A_{50} values decreased as latitude increased and ranged from 9 years in Monterey to 6 years in Vancouver. Estimates of female A_{50} by INPFC area were more precise than those for males (with CVs of 5–20%). Female ratios of A_{50}/A_{max}

¹ XY denotes an interaction between X and Y.

had no obvious latitudinal pattern and were relatively similar (0.16 to 0.21) across areas. Overall, median age at maturity of both male and female Dover sole appeared to decrease with increasing latitude.

Length-weight curves

Length-weight curves for all areas combined were highly significant ($P < 0.001$) for pooled-sex, male, and female samples (Table 6). Males had a larger length exponent than females but there was little apparent difference between male and female curves. For pooled-sex samples, the length exponent exceeded 3 and showed that Dover sole weight in autumn was more than proportional to the cube of length. CVs of intercept parameters ranged from 3% to 5% for

pooled-sexes, males, and females, whereas CVs of length exponents were all less than 1%. Bootstrap estimates of parameter bias were low compared with standard errors and were less than 0.3% of point estimate in all cases. For the intercept parameter, ratios of bias to standard error were -1%, 5%, and 6% in pooled-sex, male, and female samples. Corresponding ratios for the length exponent were 2%, -2%, and -4%.

Geographic variation in length-weight relationships of Dover sole was suggested by the generalized linear model analyses. The best model contained the terms for $\log(\text{length})$, area , and $\log(\text{length}) \times \text{area}$. Although length-weight curves by INPFC area exhibited some geographic variation (Fig. 5), there was no detectable difference between male and female weight at length. Predicted weight at length was smallest for the Vancouver area and greatest for the Monterey area, whereas length-weight curves from the Columbia and Eureka areas were very similar. Length exponents exceeded 3 for all areas except Vancouver, where few length-weight data were available. As above, the length exponent (with CVs less 2%) was more precisely estimated than the intercept (with CVs of 5–19%). Estimates of parameter bias were less than 1.6% of the parameter estimate in all cases. For each area, the ratio of estimated bias to standard error for the intercept parameter was also low: Vancouver (9%), Columbia (0%), Eureka (0%), and Monterey (5%). Corresponding ratios for the length exponent were also low: 1%, 2%, 7%, and -2%. Thus, parameter bias for the length-weight curves was inconsequential.

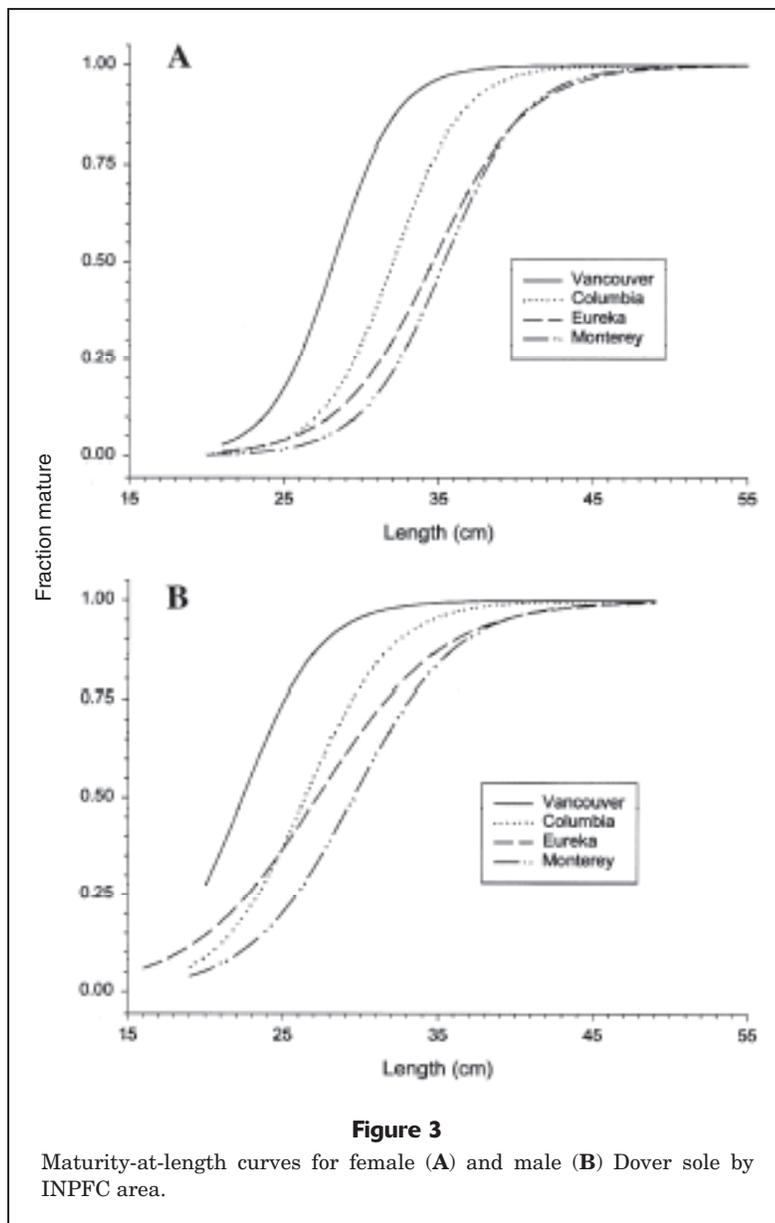


Figure 3

Maturity-at-length curves for female (A) and male (B) Dover sole by INPFC area.

Discussion

We found that the use of the alternative form of the von Bertalanffy growth curve gave satisfactory parameter estimates that had greater precision than those of the standard form. Bootstrap estimates of standard errors and corresponding coefficients of variation were lower with the alternative form. Ratkowsky (1983) recommended the alternative form used in our study because its parameters were more readily interpreted, it had close-to-linear behavior that facilitated comparisons among data sets, and it was insensitive to the choice of initial parameter values. Our results provide further support for its use.

Variance in size at age of females was 40% greater than that of males. This may result from differences in seasonal patterns of movement between females and males. In particular, Hagerman (1952) noted that commercial Dover sole catches were often segregated by sex and that Dover sole appeared to undertake an inshore feeding migration

Table 4

Maturity-at-length (cm) curves for male and female Dover sole by INPFC area. Standard errors appear immediately below estimates in parentheses. The ratio L_{50}/L_{∞} is reported for comparison with other Pleuronectiformes.

curves by INPFC area	Maturity-at-length				n
	L_{50}	β_0	β_1	L_{50}/L_{∞}	
Male maturity-at-length curves					
All areas ¹	27.1 (0.5)	-6.256 (0.533)	0.2305 (0.0173)	0.56	934
Vancouver	22.4 (2.1)	-9.122 (3.854)	0.4078 (0.1371)	0.47	77
Columbia	26.4 (0.6)	-9.627 (0.995)	0.3649 (0.0333)	0.55	331
Eureka	27.2 (0.9)	-6.717 (0.915)	0.2473 (0.0291)	0.57	317
Monterey	29.5 (0.7)	-8.926 (1.051)	0.3029 (0.0315)	0.66	209
Female maturity-at-length curves					
All areas	33.4 (0.3)	-9.969 (0.598)	0.2988 (0.0169)	0.64	1232
Vancouver	28.2 (1.0)	-13.811 (3.880)	0.4904 (0.1376)	0.52	60
Columbia	32.0 (0.4)	-14.315 (1.224)	0.4475 (0.0367)	0.61	464
Eureka	34.6 (0.5)	-11.405 (0.878)	0.3299 (0.0232)	0.68	415
Monterey	35.3 (0.5)	-13.614 (1.220)	0.3855 (0.0350)	0.71	293

¹ INPFC areas sampled in this study: Vancouver, Columbia, Eureka, and Monterey.

during spring and an offshore spawning migration in late autumn. Westrheim et al. (1992) inferred from tag recoveries that two major concentrations of Dover sole were present during summer: an inshore group composed of females and small males and an offshore group primarily composed of large males. Jacobson and Hunter (1993) also found that Dover sole segregated by sex in their analysis of bathymetric patterns in population structure. Overall, if large male Dover sole undertake seasonal movements less frequently than females, their growth rates may be expected to be less heterogeneous than those of females that move from the continental slope to the more productive waters of the continental shelf during spring. Seasonal sampling of Dover sole population structure at depth would improve understanding of the relative movements of male and female Dover sole.

As others have suggested (Hagerman, 1952; Hunter et al., 1990; Turnock et al., 1994), we found that Dover sole exhibit sexual dimorphism in growth. In particular, there was a significant difference between male and female

Table 5

Maturity-at-age (yr) curves for male and female Dover sole by INPFC area. Standard errors appear immediately below estimates in parentheses. The ratio A_{50}/A_{max} is reported for comparison with other Pleuronectiformes where A_{max} is maximum observed age in our study.

INPFC area	A_{50}	β_0	β_1	A_{50}/A_{Max}
Male maturity-at-age curves				
All areas ¹	5.1 (0.5)	-1.254 (0.240)	0.2438 (0.0271)	0.12
Vancouver	3.3 (2.3)	-1.620 (1.336)	0.4838 (0.1820)	0.09
Columbia	5.4 (0.5)	-2.314 (0.456)	0.4273 (0.0555)	0.13
Eureka	5.2 (0.7)	-1.323 (0.397)	0.2563 (0.0467)	0.15
Monterey	6.7 (0.5)	-2.361 (0.425)	0.3510 (0.0470)	0.22
Female maturity-at-age curves				
All areas	8.0 (0.2)	-2.733 (0.256)	0.3423 (0.0276)	0.17
Vancouver	5.6 (1.1)	-3.353 (1.343)	0.5985 (0.1809)	0.19
Columbia	7.5 (0.3)	-4.046 (0.515)	0.5419 (0.0588)	0.16
Eureka	8.2 (0.4)	-3.055 (0.354)	0.3710 (0.0362)	0.21
Monterey	8.8 (0.4)	-4.094 (0.496)	0.4657 (0.0587)	0.21

¹ INPFC areas sampled in this study: Vancouver, Columbia, Eureka, and Monterey.

growth curves because females attain larger sizes. Mean length of females increased more rapidly than that of males at roughly 5 years of age. The result that females attain greater lengths than males is consistent with Hunter et al. (1990) who also found that values of L_{∞} were greater for females. Although our results were not directly comparable to those of Hunter et al. (1990) because of differences in otolith aging technique and sampling design, asymptotic lengths of females were estimated to be 8% greater than those for male samples in both studies. Some of the growth differences between sexes may result from behavioral differences in feeding and habitat use. Although Dover sole feed more intensively and less selectively on the continental shelf during summer (Pearcy and Hancock, 1978), some older fish may remain in deeper water year round (Hunter et al., 1990). Sexually mature Dover sole are commonly found in the oxygen minimum zone at depths of 600–1000 m (Hunter et al., 1990; Jacobson and Hunter, 1993), where low food and oxygen levels depress metabolism and growth potential (Vetter et al., 1994). Differences between male and female patterns of

growth may result from a differential use of deep-water habitat, where adult males spend more time, on average, in the oxygen minimum zone, or may result from the effects of egg production and spawning on growth and deposition of rings in the annuli of females. In summary, Dover sole exhibit a moderate degree of sexual dimorphism, and differences between sexes become apparent, on average, at about 5 years of age.

In addition to differences between sexes, moderate levels of geographic variation in growth of Dover sole off the west coast were apparent. Growth curves for the Columbia area and for the combined Vancouver, Eureka, and Monterey areas differed for both male and female Dover sole. Asymptotic lengths of males and females from the Columbia area were 3% and 2% greater than those for the combined Vancouver, Eureka, and Monterey areas. Male and

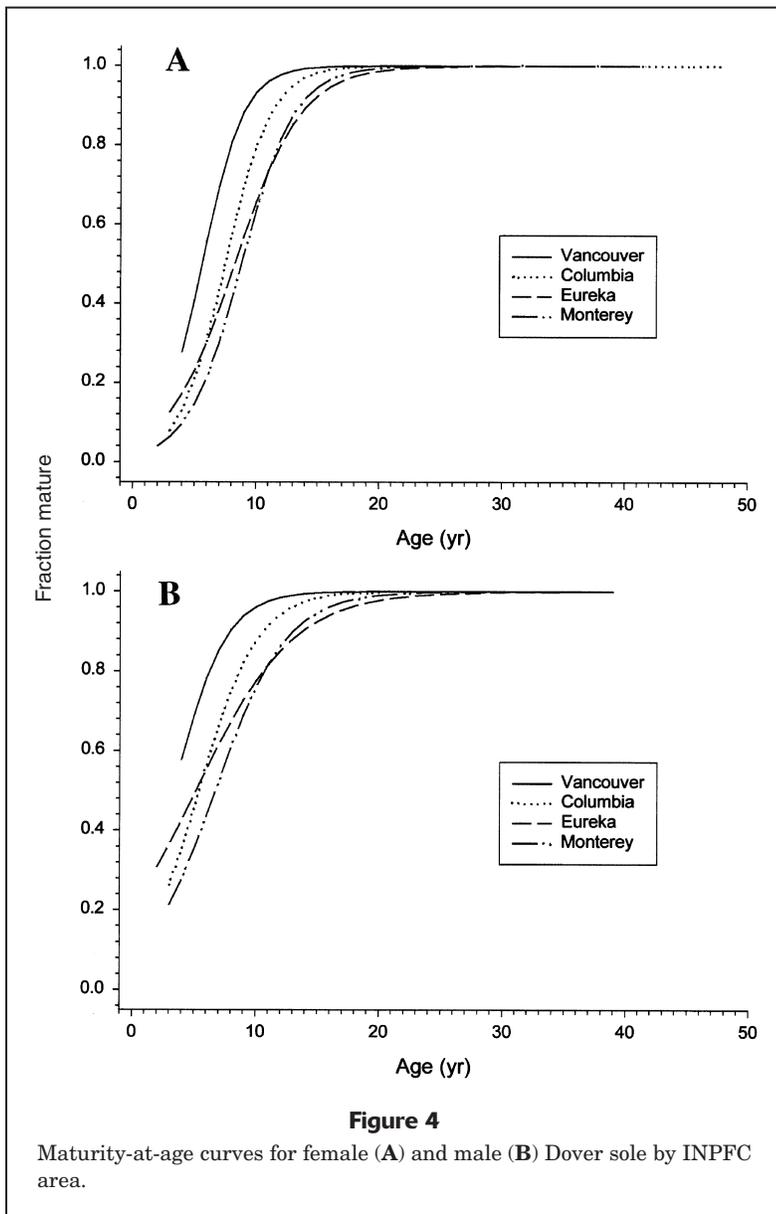
female Dover sole from the Columbia area also had lower Brody growth coefficients and larger asymptotic lengths than other areas. These differences, however, were relatively minor and would not be expected to have a substantial impact on target harvest rates if the Dover sole fishery were managed by INPFC areas rather than as a coast-wide unit.

The reason for geographic variation in growth is unknown but probably stems from regional differences in productivity within the California Current. In particular, oceanographic properties of the California Current differ north and south of Cape Blanco (U.S. GLOBEC, 1994), the southern boundary of the Columbia area, and physical differences in the strength and duration of upwelling may affect the growth potential of Dover sole inhabiting these regions. The fact that adult Dover sole are benthic

feeders (Pearcy and Hancock, 1978) and are relatively sedentary, having negligible north-south movements (Westrheim et al., 1992), indicates that geographic variation in physical habitat and benthic community structure are probably important determinants of Dover sole growth. Indeed, Jacobson and Hunter (1993) showed that there is relatively more Dover sole habitat off Oregon than off central California and that depth preferences of Dover sole appear to differ between these regions.

Alternatively, the cumulative effects of long-term harvest may have also affected the geographic pattern of Dover sole growth because commercial harvests by INPFC area have differed through time. Landings of Dover sole in the Eureka area peaked in the early 1970s, whereas landings in the Columbia, Monterey, and U.S. Vancouver areas peaked in the 1980s (Brodziak, et al. 1997). Although historic size at age of Dover sole has not been documented, some otolith aging data collected off California in the 1940s have provided evidence that mean size at age of males and females may have changed through time (Hagerman, 1952). In particular, Hagerman reported mean sizes at age-5 and age-9 of male Dover sole were 32.3 and 35.5 cm, whereas mean sizes of age-5 and age-9 females were 33.6 and 41.5 cm. In comparison with our estimates, these data suggest that growth may have declined since the 1940s and are consistent with reductions in mean size at age due to fishery-size selection (see Ricker, 1968). Thus, geographic patterns in Dover sole growth may also have been affected by differences in harvest pressure among regions.

Temporal variability of the California Current (Ware, 1995) may have also influenced observed growth, as well as maturation patterns. Research survey samples collected during the 1980s had a higher percentage of



Dover sole that had been spawned prior to a regime shift in the late 1970s (see McGowan et al., 1998) than samples collected during the 1990s. Although temporal changes in growth due to ocean regime may have occurred, such changes would be difficult to detect given the unbalanced temporal and spatial coverage of the available research survey data. Regardless of the mechanism, continued sampling of Dover sole for data on size at age and maturity will be needed to understand whether the observed geographic variation is stable through time.

We found that maturation rates differed between sexes. On average, males matured at a smaller size and at a younger age than did females. This difference might be expected given the sexual dimorphism in Dover sole growth and is consistent with conclusions drawn by Beverton (1992, Fig. 2), who reported that males generally have smaller size at 50% maturity than females within the Pleuronectiformes.

In addition to differences between sexes, we found geographic variation in maturity rates and an apparent latitudinal cline in the median length at maturity of male and female Dover sole. Results were similar for maturity-at-age curves, with the exception of results for Columbia area males. In his review of latitudinal patterns in flatfish reproductive life history, Castillo (1995) found no evidence of a latitudinal trend in age or length at first maturity of Dover sole off Oregon and California. In our study, results suggested that Dover sole mature at smaller size and younger ages at higher latitudes. This finding contrasts with expectations that Dover sole would mature at larger size and older age at higher latitudes (e.g. Castillo, 1995). The apparent trend in Dover sole maturation rates may reflect local adaptation to latitudinal differences in oceanographic properties of the California Current (U.S. GLOBEC, 1994). Nonetheless, sample sizes from some areas (e.g. Vancouver) may have been insufficient to accurately characterize the pattern of maturation in length or age. Also, effects of potential latitudinal differences in the timing of spawning were not accounted for in our study. Thus, although we found some evidence of geographic variation, we recommend further sampling to verify our observed geographic patterns in maturation.

Maturity-at-length estimates from our study were consistent with those from other studies of Dover sole maturation. Although maturation criteria and sampling design differed between our study and those of Hunter et al. (1992), estimated median lengths for female maturity were remarkably consistent. In particular, Hunter et al. (1992)

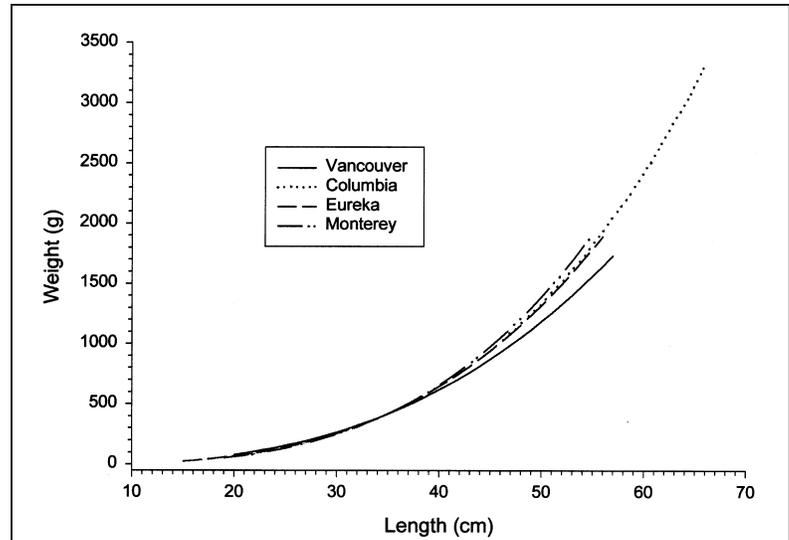


Figure 5
Pooled-sex total length-total weight curves of Dover sole by INPFC area.

Table 6
Estimated parameters and residual variance¹ of Dover sole total length (cm)-total weight (g) curves by INPFC area. Estimated standard errors appear immediately below each estimate in parentheses.

INPFC area	A	B	σ^2	n
All areas	4.0659×10^{-3} (0.1366×10^{-3})	3.2479 (0.0093)	1.295×10^{-2} (0.044×10^{-2})	3019
Male—all areas	3.7064×10^{-3} (0.1992×10^{-3})	3.2736 (0.0151)	1.322×10^{-2} (0.056×10^{-2})	1470
Females—all areas	4.4149×10^{-3} (0.2073×10^{-3})	3.2254 (0.0128)	1.266×10^{-2} (0.063×10^{-2})	1549
Vancouver ¹	13.5571×10^{-3} (2.5797×10^{-3})	2.9093 (0.0521)	1.252×10^{-2} (0.040×10^{-2})	137
Columbia	3.7610×10^{-3} (0.1958×10^{-3})	3.2676 (0.0144)		1645
Eureka	4.9630×10^{-3} (0.4313×10^{-3})	3.1934 (0.0235)		734
Monterey	2.8550×10^{-3} (0.2146×10^{-3})	3.3484 (0.0208)		503

¹ Residual variance estimates from the generalized linear model are identical for each INPFC area.

estimated female L_{50} to be 33.2 cm, whereas in our study, female L_{50} was estimated to be 33.4 cm. These female L_{50} estimates contrast with earlier estimates that were based on commercial fishery samples in which fish were 36 cm (Hagerman [1952] reported within Hunter et al. [1990]) and 38 cm (Harry [1959]). Although it is unknown whether the earlier estimates are directly comparable to

those of our study because of differences in sampling and maturation criteria, they suggest, however, the possibility that female size at maturity may have declined since the 1950s.

We found no difference between male and female length-weight curves. Male and female length-weight curves were virtually identical for fish less than 50 cm in length. Comparisons between large mature females (>50 cm) and males were not possible because maximum observed size of male Dover sole is about 51 cm. In addition, some geographic variation in length-weight relationships was detected. Estimated length exponents from the allometric equation exceeded 3 for all INPFC areas, with the exception of the Vancouver area, where relatively few samples were collected. Overall, it appeared that Dover sole weight during late autumn, when samples were collected, was not proportional to the cube of fish length. In contrast, Hagerman (1952) found that Dover sole weight was roughly proportional to the cube of length in commercial fishery samples collected throughout the year. Hagerman's estimates may not be comparable to ours owing to differences in sampling and analysis. We recommend year-round collection of Dover sole samples for length-weight analysis to determine whether seasonal and geographic variation are important in predicting mean weight at length in the population.

In comparison with other pleuronectids, we found that Dover sole matured at relatively larger sizes and younger ages. Beverton (1992) reported average ratios of L_{50}/L_{∞} of 0.47 and 0.52 for male and female pleuronectids, whereas comparable values in our study were 0.56 and 0.64. Similarly, male and female ratios of A_{50}/A_{max} of 0.28 and 0.39 from Beverton (1992) were higher than corresponding values of 0.12 and 0.17 in our study. Observed differences with other pleuronectids likely result from the complex life history pattern of Dover sole in the California Current. Dover sole are a relatively late-maturing flatfish. The age at first reproduction (α) that maximizes expected lifetime fecundity for this species is roughly $\alpha=15$ years, where $\alpha=\log(1+(3K/M))/K$ (see Roff, 1991) using $K=0.091$ for females from our study and a natural mortality rate of $M=0.09/\text{yr}$ (Brodziak et al., 1997). In contrast, observed ages at first reproduction for Dover sole range from 4 to 6 years (Castillo, 1995), or roughly 1/3 of the optimal age that would maximize fitness. However, these equilibrium calculations do not account for environmental forcing, and differences between the optimal and observed values probably reflect the importance of environmental variation (Roff, 1982) on the reproductive success of Dover sole. It may be necessary for Dover sole to reproduce as soon as possible to hedge their bets against natural cycling in the survival of pelagic larvae in the California Current (Parrish et al., 1981). In comparison to the pleuronectids reviewed in Beverton (1992), the lower A_{50}/A_{max} ratio of Dover sole may reflect the lack of growth experienced by adults that inhabit the oxygen minimum zone. Similarly, Dover sole may have a higher L_{50}/L_{∞} ratio than other pleuronectids because they achieve most of their potential growth as juveniles while resident on the continental shelf. Overall, maturation rates of Dover sole appear to

differ from other pleuronectids and we believe that these differences reflect adaptation of Dover sole to the inherent variability of the California Current.

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