

BATHYMETRIC PATTERNS IN SIZE, AGE, SEXUAL MATURITY, WATER CONTENT, AND CALORIC DENSITY OF DOVER SOLE, *MICROSTOMUS PACIFICUS*

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ABSTRACT

Ninety-eight percent of the spawning biomass of Dover sole, *Microstomus pacificus*, in central California waters live in a region of the continental slope between 640 and 1006 m (350-550 fath.) characterized by low oxygen concentrations (0.27-0.36 ml/l) and cold temperatures (5.9°C-3.2°C). Juvenile Dover sole settle on the continental shelf and gradually move down the slope over their lifetime, reaching the oxygen minimum zone as they become sexually mature. Fifty percent of Dover sole in central California reach sexual maturity when about 31 cm long and about seven years of age. The ontogenetic movement down the slope continues after sexual maturity and is accompanied by a marked increase in water content of the body and a consequent decrease in caloric density per gram wet weight. For example, caloric density decreases from about 0.86 kcal per gram wet weight¹ (83% water) for 275-mm fish living at 200-400 m, to 0.60 kcal per gram wet weight (90% water) for a fish 440 mm long living at about 900 m. Female Dover sole may live as long as 53 years, and males 58 years. Water content appears to be a function of age as well as length and depth.

RESUMEN

El 98% de la biomasa del desove del lenguado de las aguas de California central, *Microstomus pacificus*, vive en un área del talud continental entre los 640 y los 1006 m caracterizada por bajas concentraciones de oxígeno (0.27-0.36 mL/L) y bajas temperaturas (5.9°C-3.2°C). Los juveniles se establecen en la plataforma continental y gradualmente, durante su desarrollo, se van moviendo hacia el talud y a lo largo de él, llegando a la zona de mínimo oxígeno cuando alcanzan la madurez sexual. El 50% del lenguado alcanza la madurez sexual cuando mide aproximadamente 31 cm de longitud, a los 7 años de edad. El movimiento descendiente a lo largo del talud durante la ontogénesis continúa pasada la madurez sexual, y es acompañado por un incre-

¹Calories per gram wet weight have been corrected from original publication by a factor of 10⁻².

mento marcado en el contenido de agua del cuerpo y consecuentemente, por un decrecimiento en la densidad calórica por gramo de peso húmedo. Por ejemplo, la densidad calórica de un pez que mide 275 mm y vive a 200-400 m de profundidad decrece de 86 kcal por gramo de peso húmedo (83% de agua) a 60.3 kcal (90% de agua) para un pez que mide 440 mm de longitud y vive a 900 m de profundidad. Las hembras pueden vivir hasta proxímadamente los 53 años de edad y los machos hasta los 58. El contenido de agua parece estar relacionado con la edad y el largo del individuo y con la profundidad a la cual vive.

INTRODUCTION

Dover sole, *Microstomus pacificus*, are found from the Aleutian Islands in the Bering Sea to Baja California (Eschmeyer et al. 1983). The U.S. fishery for Dover sole occurs from Point Conception, California, to the Canadian border. Dover sole inhabit depths ranging from about 55 to 1300 m. Older and larger fish usually occur in the deeper portion of the depth range, and younger and smaller fish in the shallower depths. A seasonal inshore migration has been described: fish move into deep water in the fall before the spawning season and into shallow water in the summer (Hagerman 1952; Alverson 1960; Percy et al. 1977). Most individuals apparently remain in the same general locality throughout their lives. Although longshore movements of up to 360 mi (579 km) in seven years have been recorded, 97% of tagged individuals were recaptured within 50 km of where they were tagged (Westrheim and Morgan 1963).

Large Dover sole from deep water are often "jellied" (have flesh with an unusually high water content). This "jellied" consistency limits the market value of fillets from large Dover sole because their desirability is reduced (Hendricksen et al. 1986). Owing to the ontogenetic migration into greater depths, and the extensive depth range, the demographic and physiological characteristics of Dover sole change strikingly with depth, age, and length. Thus neither the dynamics nor the ecology of Dover

sole populations can be properly analyzed or understood without a careful evaluation of the relation between depth and key physiological and population variables.

The objective of this paper is to describe the relationships between depth, length, age, sexual maturity, water content, caloric density, and biomass of Dover sole. We also provide data on the temperature and oxygen content of the habitat in which fish of different length and age are found. Our analysis does not include data for the summer months, when fish may have a shallower distribution (Alverson 1960).

METHODS

Sea Collections

Research trawl collections were taken at depths between 69 and 1394 m (38–762 fath.) off the central California coast between Point Conception and Half Moon Bay, California, during 1985–88 by NOAA-Southwest Fisheries Center (SWFC) personnel (table 1). Trawl collections were opportunistic before 1987. In 1987, samples were taken at 183-m (100-fath.) intervals along transect lines; in 1988 a random sampling design stratified by depth was used (figure 1).

In all years fish were sexed and measured for total length. Before January 1987, fish were randomly sampled from each collection until 25 females had been identified and their ovaries preserved for later assessment of maturity; the females and some males were frozen for subsequent extraction of otoliths and determination of water content as described below. During January–February 1987, either all of the Dover sole in the trawl collection or 100 fish were

randomly sampled, and 25 females were assessed for gonad maturation. Four to six fish of each sex were weighed and frozen for later removal of otoliths and tissue for analysis of water content. The bottom temperature (reversing thermometer on Nansen bottle) and oxygen content (Winkler titration) were measured for 17 Nansen cast stations ranging from 183 to 1,280 m (100–700 fath.; figure 1, left, triangles). The total trawl catch of Dover sole was weighed during 1987 and 1988. In 1988, up to 100 Dover sole were randomly sampled and weighed by sex; the maturation state of all ovaries was determined.

Age Determination

Ages were determined from otoliths removed from 341 females and 64 males captured during 1985–86 and from 154 females and 97 males captured in 1987. Left otoliths were embedded in epoxy resin and cut with a diamond wafering blade in a thin cross section through the nucleus from dorsal to ventral (Chilton and Beamish 1982). Thin sections were mounted on microscope slides with Eukitt mounting medium, polished, and read with a compound microscope. A typical otolith section is shown in figure 2. Counting procedures followed those of Chilton and Beamish (1982). Each otolith was read independently by three observers without knowledge of the length of the fish. Otoliths whose readings differed by more than 10% among the readers were reread using the same protocol until the readings agreed to within 10%. Estimated age was the average of the individual readings. Parameters of the von Bertalanffy equation relating length and age were estimated by the simplex method (O'Neill 1971).

TABLE 1
 Sources and Numbers of Dover Sole Used for Analyses

Dates	Sampling type*	Number of positive trawl collections			Number of Dover sole used in various analyses					
		N	Depth		Percent water	Calories	Age	Size at depth	Sexual maturity	Oxygen and temperature
Min	Max									
12/3–12/12/85	OP	11	94	704	108	7	37	195	104	—
1/14–2/24/86	PS	2	330	600	115	—	180	—	—	—
3/5–3/7/86	OP	8	52	500	165	18	14	210	—	—
5/2–5/4/86	OP	3	175	537	60	2	62	74	—	—
1/11–2/15/87	LT	49	99	705	265	—	255	3225	—	17 ^b
2/23–4/9/88	SR	51	38	602	—	—	—	2800	—	—
		Total specimens			713	27	548	6504	104	—

*OP = opportunistic trawl samples; PS = port samples; LT = line-transect trawl samples; SR = stratified random trawl samples.
^bNumber of Nansen cast stations.

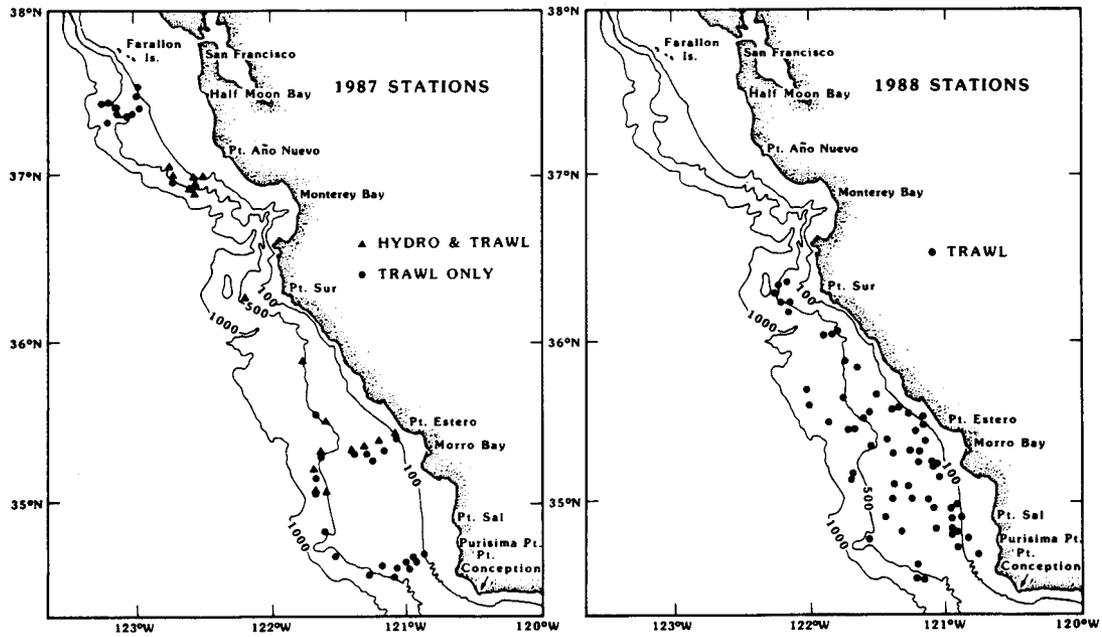


Figure 1. Left, trawl stations occupied on the January–February 1987 groundfish cruise of the R/V *David Starr Jordan*. Right, trawl stations occupied on the February–March 1988 groundfish cruise of the R/V *David Starr Jordan*.

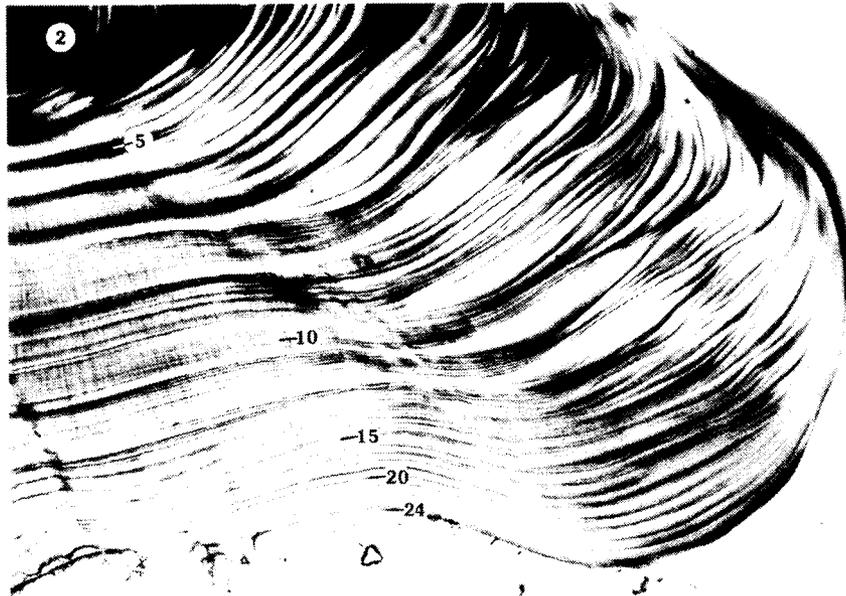


Figure 2. Thin section of the left otolith of a 24-year-old Dover sole. Numbers indicate years.

Biomass

We used the mean biomass in the area swept by trawls, and total area within three depth strata to estimate Dover sole biomass. The survey area extended from 34°30'N, 120°30'W to 36°30'N, 122°30'W (Burler et al. 1989).

Sexual Maturity

The size at first maturity of females taken in December 1985 was estimated by logistic regression analysis (Draper and Smith 1981; Engelman 1988). Data from the other surveys (table 1) were not appropriate for estimating sexual maturity because the spawning season began before the first survey. The possibility of mistaking immature ovaries for post-spawning ovaries was minimized because December appears to be early in the spawning season (Hunter, unpublished data). Ovaries with yolked oocytes were considered to be mature, and those without yolked oocytes to be immature.

Water Content

We measured water content by determining the wet weight of a tissue sample (about 3.5 g) and then drying it to constant weight at 60°C. The white muscle samples were taken from the right side of the fish between the lateral line and the dorsal fin at the insertion of dorsal rays 30 to 36, and the red muscle samples were taken from the right side above the lateral line and behind the eye.

To determine whether a single tissue sample represented water content of the whole fish, we measured the entire water content of 20 females, 6 males, and one fish of indeterminate sex by grinding and drying the entire fish after removing red and white muscle tissue samples from the locations described above. We then regressed water content (in percent of wet weight) of the entire fish (*H*) on tissue sample water content (figure 3):

$$H = -5.08 + 1.05 h_1, \quad (1)$$

where *h*₁ is water content of white muscle (*r*² = 0.906, *n* = 27; *p* < 0.01). The slope of this equation did not significantly differ from 1.0, nor did the intercept differ from 0. On the basis of these results we assumed that the percentage of water in the white muscle tissue samples was the same as that of the whole fish. Whole fish water content was estimated (equation 1) from white muscle tissue samples collected at sea for 106 fish collected in 1985, 335 fish collected in 1986 (90% females), and 265 fish (males and females) collected in 1987.

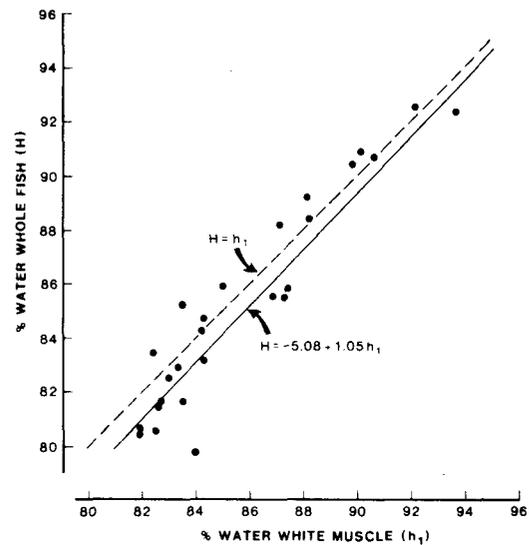


Figure 3. Relation of water content of whole Dover sole to water content of white muscle. Solid line is regression line fit to data; dashed line is one-to-one relationship.

Water content of the red muscle tissue sample was also linearly related to water content of the entire fish, although the relationship was poorer than that for white muscle:

$$H = -51.1 + 1.62 h_2, \quad (2)$$

where *h*₂ is water content of red muscle (*r*² = 0.837, *n* = 27; *p* < 0.01).

Caloric Density and Fat Content

To determine caloric density (kcal/gm) of entire fish for 26 Dover sole, we used a Parr bomb calorimeter and standard techniques (Parr Instrument Co. 1960; Paine 1971). The values reported here are the means of three determinations. Fish were selected by size to obtain caloric measurements over a wide range of water content (the fish sampled ranged from 80% to 94% water).

To determine fat content we used a Soxhlet extraction with 2:1 chloroform-methanol. This technique did not provide an accurate estimate of total fat content because the extraction period (48–72 hrs) was too short for fish with a high fat content, such as Dover sole. Notwithstanding this bias and other problems associated with chloroform-methanol ex-

tractions (Dobush et al. 1985), we believe that the data provided useful information about fat concentration.

RESULTS

Length and Depth

The mean length of Dover sole increases rapidly with depth over the first 300 fath. (549 m) and thereafter more slowly. The relationship between depth and size of Dover sole varied little among years (figure 4, top and middle). The combined data for all surveys clearly indicate that males taken at a given depth are smaller than females (figure 4, bottom).

Age and Growth

Male and female Dover sole differ in size at age (figure 5). Estimates from counts of annuli in thin sections of otoliths indicate that the fish live long lives. The maximum estimated age was 56 years for a 460-mm male and 51 years for a 492-mm female.

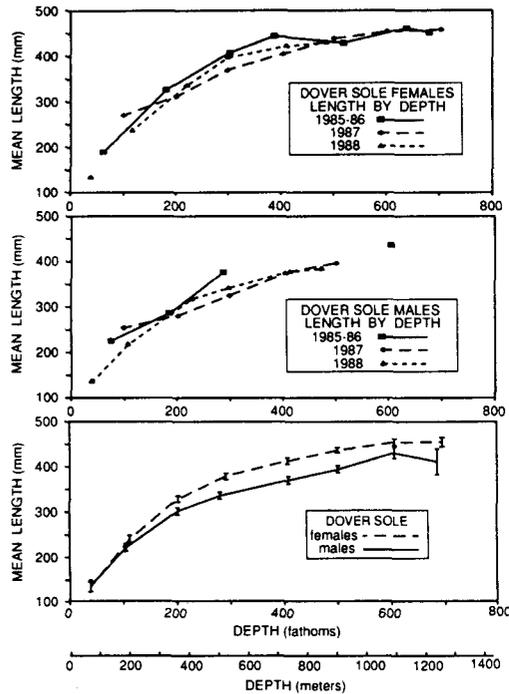


Figure 4. Mean length of Dover sole collected at different depths. Top, females; middle, males; bottom, all years combined with ± 2 SE.

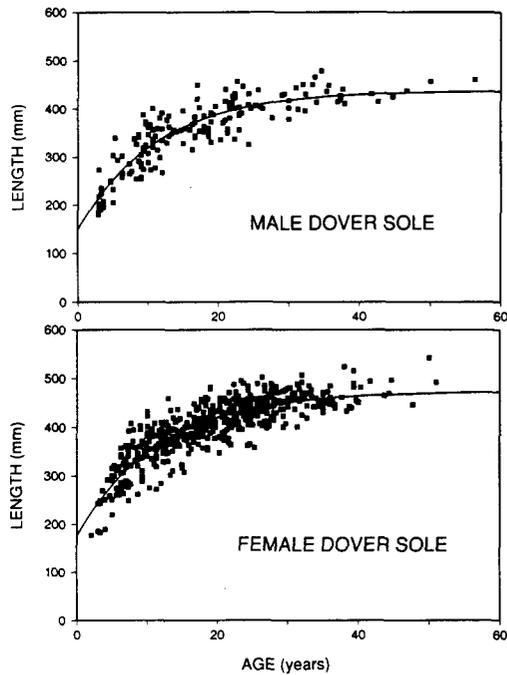


Figure 5. Top, length and age (calculated from otolith section) of male Dover sole. Solid line is von Bertalanffy curve with $L_{\infty} = 437$ mm, growth parameter $K = 0.089$, and $t_0 = -4.7$ yr. Bottom, length and age (calculated from otolith section) of female Dover sole. Solid line is von Bertalanffy curve with $L_{\infty} = 474$ mm, growth parameter $K = 0.085$, and $t_0 = -5.5$ yr. See text for equation 3.

Parameters of the von Bertalanffy growth model,

$$L_t = L_{\infty} (1 - e^{-K(t - t_0)}), \quad (3)$$

were $L_{\infty} = 437$ mm, $K = 0.089$, and $t_0 = -4.7$ years ($n = 161$, $p < 0.01$) for male Dover sole. Estimates of parameters for females were $L_{\infty} = 474$ mm, $K = 0.085$, and $t_0 = -5.5$ years ($n = 495$, $p < 0.01$). Male and female Dover sole longer than 40.0 cm may be any age from 8 years to 40 or 50 years. Neither our methodology nor any other has been validated for Dover sole. Nevertheless, we believe our age estimates approximate the true age, because the otolith section method has been validated for another species in the same habitat (*Anoplopoma fimbria*; Chilton and Beamish 1982).

Our age estimates are much greater than those obtained from scales (Demory 1972; Mearns and Harris 1975). However, tag-and-recapture studies

(Pikitch and Demory 1988) have shown that scales underestimate the age of Dover sole. The maximum age observed in this study (56 years) is in agreement with the longevity that Pikitch and Demory (1988) predicted from tag-and-recapture studies and errors in scale readings. A significant fraction (40%) of females in our samples were older than 20 years. Our results suggest that estimates of the productivity of Dover sole stocks based on ages estimated from scales may be seriously flawed.

Water Content

Data for females taken from December 1985 through May 1986 indicate that the mean water content of white muscle remains constant at about 82% in 15–30-cm females but increases with length in larger Dover sole to about 90% in 50-cm females (figure 6). The concentration of water in the red muscle followed a similar trend, but the increase in water content with length was much less. Average water content of red muscle in 50-cm females was only 85%. These data indicate that red muscle is conserved. The red muscle in the anterior upper trunk region of the eyed side of the body is the largest concentration of red muscle in the body and is probably used to control head movements during feeding. The color of the red muscle changed with fish length. Larger fish had darker red muscle, indicating that the myoglobin content of the muscle may be higher in larger fish.

The mean water content of males taken in January–February 1987 did not differ from that of females from that sample within the same 5-cm length class (ANOVA for five 5-cm length classes, 254–324 to 475–524 mm, per sex where $p = 0.90$;

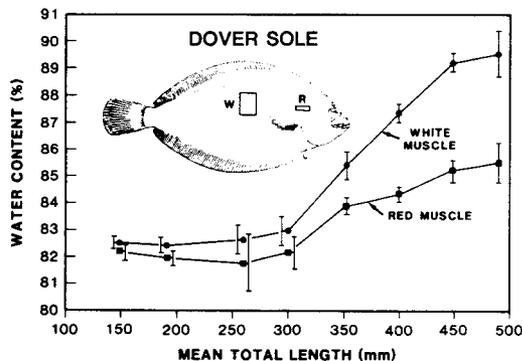


Figure 6. Water content in white and red muscle versus total length of female Dover sole. Insert shows locations of tissue samples—W for white muscle and R for red muscle.

figure 7). The water content of Dover sole (both male and female) as a function of length showed little variation between years; the data for December 1985–May 1986 were essentially the same as those for January–February 1987 (figure 7). Combining data for all years and sexes indicates that the average water content for fish less than 275 mm was constant at 82.9% ($n = 90$, $SD = 1.00$), and for fish greater than 275 mm it increased with length (L) according to the equation

$$H = 72.7 + 0.036 L \quad (4)$$

($r^2 = 0.58$, $n = 506$; $p < 0.01$).

Water Content, Age, Length, and Depth

In the previous sections we showed that water content increases with fish length and that length increases with depth and age. In this section we describe the relationships between water content, length, depth, and age of Dover sole females. A

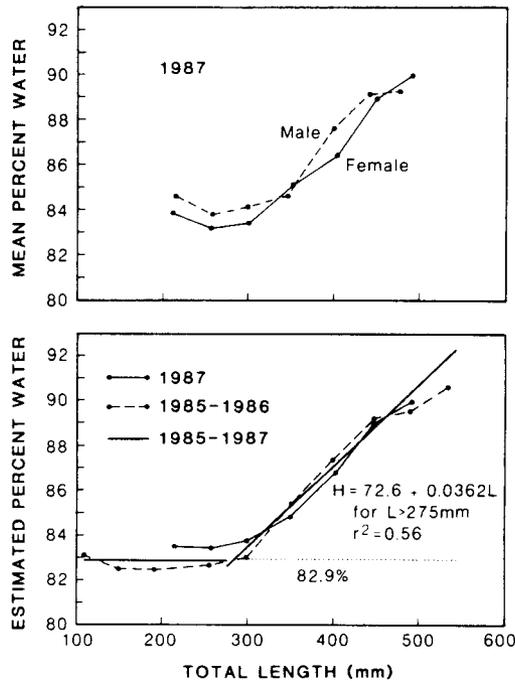


Figure 7. Top, water content of white muscle versus total length of female ($N = 163$) and male ($N = 98$) collected in 1987. Bottom, water content in white muscle of both sexes for 1985–86 (dashed line), 1987 (thin line), and 1985–87 (thick line).

stepwise multiple regression analysis indicated that all three independent variables (age, length, and depth) accounted for significant variation in the dependent variable, water content: the coefficient for age was the first selected (table 2). The final equation was

$$H = 78.7 + 0.1226 T + 0.0123 L + 0.0026 D \quad (5)$$

where *H* is water content (percent of wet weight), *T* is age (years), *L* is length (mm), and *D* is depth (fath.) ($R^2 = 0.69$, $n = 519$; $p < 0.01$). Biological interpretation of the significance of the individual regression coefficients in this equation could be misleading (Sokal and Rohlf 1981) because, as is indicated in the correlation matrix (table 2), all the variables are correlated with each other; length is correlated with age and depth as well as water content.

Caloric Density

Caloric density (kcal per g ash-free dry weight) was correlated with fat concentration (*F*, in percent of dry weight). This relationship was less precise ($r^2 = 0.57$, $n = 26$; $p < 0.01$) than one would expect

on physiological grounds because of our failure to extract all the lipids in some of the fish. Nevertheless, figure 8 clearly indicates that caloric density and fat concentration are linked, as would be expected.

No significant relationship existed between caloric density and water content. There was no apparent relationship between fat concentration and water content ($r^2 = 0.02$) when length was not included as a variable. When length (*L*) was included as an additional third dependent variable in a stepwise multiple regression analysis (table 3), a definite relationship existed between caloric density (*C_d*) and

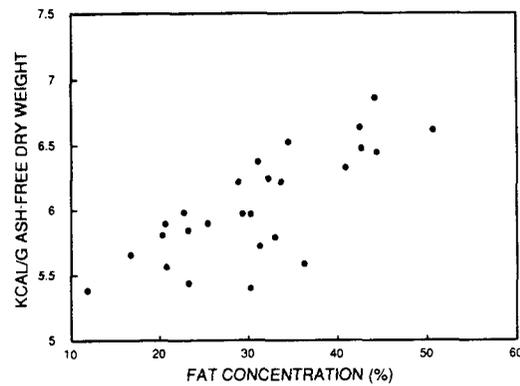


Figure 8. Caloric density versus fat concentration in Dover sole.

TABLE 2
Analysis of the Relation Between Water Content (*H*) of Dover Sole and Their Age (*T*), Length (*L*), and Depth (*D*)

Step	Stepwise regression		
	1	2	3
Constant	82.63	78.31	78.71
Age (<i>T</i>)	0.2213	0.1272	0.1226
<i>t</i> -ratio*	28.28	10.94	10.69
Length (<i>L</i>)		0.0157	0.0123
<i>t</i> -ratio		10.25	7.30
Depth (<i>D</i>)			0.00260
<i>t</i> -ratio			4.61
<i>S</i>	1.82	1.66	1.63
<i>R</i> ²	60.73	67.37	68.62

Source	DF	Analysis of variance			<i>p</i>
		SS	MS	<i>F</i>	
Regression	3	2,981.00	993.67	375.31	<0.0005
Error	515	1,363.52	2.65		
Total	518	4,344.52			

Source	DF	Seq SS
Age (<i>T</i>)	1	2,638.47
Length (<i>L</i>)	1	288.64
Depth (<i>D</i>)	1	53.89

	Matrix of correlation coefficients		
	Water (<i>H</i>)	Age (<i>T</i>)	Length (<i>L</i>)
Age	0.779		
Length	0.773	0.789	
Depth	0.626	0.578	0.682

*For $p = 0.05$, the *t*-ratio is 1.96.

TABLE 3
Analysis of Variance Stepwise Regression of the Caloric Density of Dover Sole (*C_d*, kcal/g ash-free dry weight) on Their Total Length (*L*, in mm) and Water Content (*H*, in Percent)

Step	Summary	
	1	2
Constant	8.755	13.540
Water (<i>H</i>)	-0.032	-0.104
<i>t</i> -ratio*	-1.65	-5.86
Length (<i>L</i>)		0.0042
<i>t</i> -ratio		5.76
<i>S</i>	402	263
<i>R</i> ²	10.21	63.22

Source	DF	Analysis of variance			<i>p</i>
		SS	MS	<i>F</i>	
Regression	2	2.725	1.363	19.76	<0.0005
Error	23	1.586	0.069		
Total	25	4.311			

Source	DF	Seq SS
<i>L</i>	1	0.358
<i>H</i>	1	2.367

*For $p = 0.05$, the *t*-ratio is 2.07.

water content of white muscle (H , in percent wet weight) yielding the equation

$$C_w = 13.540 + 0.0042 L - 0.1044 H \quad (6)$$

with $R^2 = 0.60$, $n = 26$; $p < 0.01$ (figure 9). To further evaluate these data we analyzed covariance by arranging the data into three length classes (114–296 mm, 303–396 mm, and 408–506 mm) and regressed water content on calories within length class. This analysis indicated that the relationship between calories and water content differed significantly among the three length classes (233, 350, and 453 mm mean total length; $p < 0.01$). For the overall mean water content (85.6%), the adjusted mean kcal per g ash-free dry weight are 5.634 at 233 mm, 6.078 at 350 mm, and 6.424 at 453 mm. The relationship between caloric density and length was not significant ($r^2 = 0.037$, $n = 27$; $p = 0.169$). Thus, the relationship between caloric density and water content changes with length.

The relationship between length, water content, and caloric density in terms of wet weight (C_w) was also evaluated. The multiple regression equation was

$$C_w = 651 + 0.0742 L - 7.06 H \quad (7)$$

where C_w = kcal per 100 g wet weight, L = length, and H = water content of white muscle ($R^2 = 0.98$, $n = 26$; $p < 0.001$). R^2 is high because the water content of the fish largely determines the caloric density when it is expressed on the basis of wet weight.

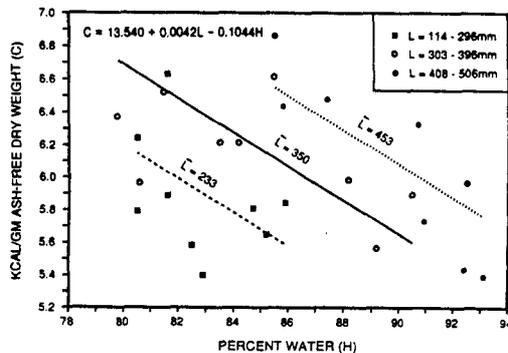


Figure 9. Caloric density and water content of Dover sole in three size classes. (See equation 6 in text for multiple regression relation of caloric density with length and water content.)

We also wished to examine how caloric content varied with depth. We used the multiple regression equation 6 to compute the caloric density (C , in kcal per g ash-free dry weight) of female Dover sole as a function of length and water content. We grouped the estimated caloric densities into seven 100-fath. (183-m) depth classes and calculated a mean and standard deviation (SD) for each class; the SD includes the variance associated with equation 6 (Draper and Smith 1981; figure 10, top).

A significant difference existed between the mean caloric density of females in the 100-fath. depth class and those in all other depth classes combined ($t = -7.34$, d.f. = 37.7, $p < 0.001$; d.f. was computed from the formula given by Zar [1984]). The mean caloric density for females taken in the 100-fath. depth class was 5.761 kcal per g ash-free dry weight ($n = 34$, SD = 292) and that of females taken at

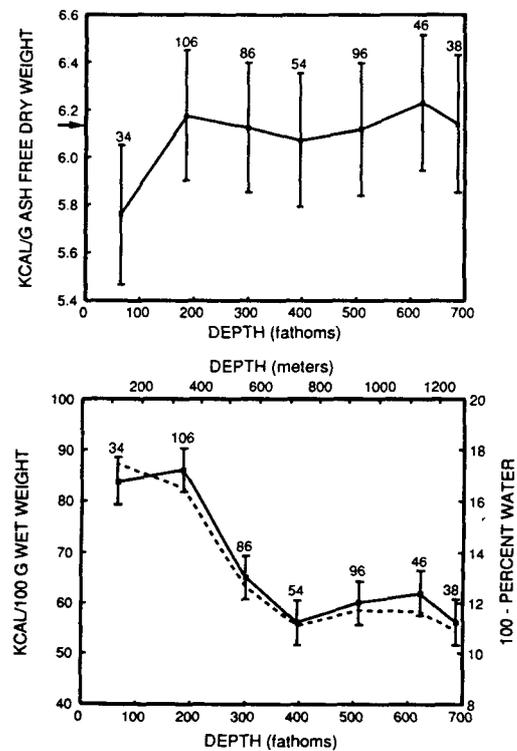


Figure 10. Top, kcal per g ash-free dry weight, SD and N within 100-fath. depth classes. Arrow is mean caloric density for depths >150 fath. Bottom, kcal per 100 g wet weight (left axis) and the complement of water content (right axis) within 100-fath. depth classes.

depths greater than 150 fath. was 6.141 kcal ($n = 426$, $SD = 272$). Thus, the Dover sole living in shallow water (50–150 fath.; 91–274 m) have a lower caloric density per unit dry weight than Dover sole living at greater depths.

A different pattern in the change in caloric density with depth occurs if caloric density is expressed in terms of wet weight rather than dry. Using the same data and equation 7, we recalculated the average caloric density of females on a wet-weight basis per depth class. On a wet-weight basis, the caloric density (kcal per g wet weight) declines with depth because of the increase in water content (figure 10, bottom). As would be expected, the decrease with depth in caloric density of Dover sole wet weight mimics the decline in the complement of the water content (100 – percent water; figure 10).

These measurements were made during the period in which Dover sole mature sexually and begin to spawn (December–February). Other patterns may exist at other times of the year.

Sexual Maturity

The sexual maturity of Dover sole females was estimated by calculating the fraction mature (M) for each of seven 50-mm length classes (255–526 mm). These data were fit by maximum likelihood estimates of the parameters to a logistic model

$$M = \frac{e^{a+bx}}{1 + e^{a+bx}} \quad (8)$$

where $a = -9.947$, standard error (SE) of $a = 0.00688$, and $t = 4.657$ (d.f. = 102, $p < 0.01$); $b = 0.0320$, SE of $b = 2.159$, and $t = -4.608$ (d.f. = 102, $p < 0.01$); and $n = 104$. This equation predicts that 50% of Dover sole females of 311-mm length are mature (figure 11). The smallest Dover sole with advanced yolked oocytes in our collections was 290 mm long. Judging from our age-length relation for female Dover sole (equation 3), a length of 311 mm corresponds to an age of about 7 years, and a length of 290 mm corresponds to about 6 years.

The mean lengths per depth class were used to calculate how sexual maturity varied with depth. Mean female lengths were computed for each of eight 100-fath. (183-m) depth classes (all trawl data, 1985–88; $n = 4,412$; table 1; figure 4), and the maturity was calculated using equation 8. This analysis indicated that sexual maturity increased with depth from about 60% at 200 fath. to 90% or more at depths of 300 fath. (549 m) or greater.

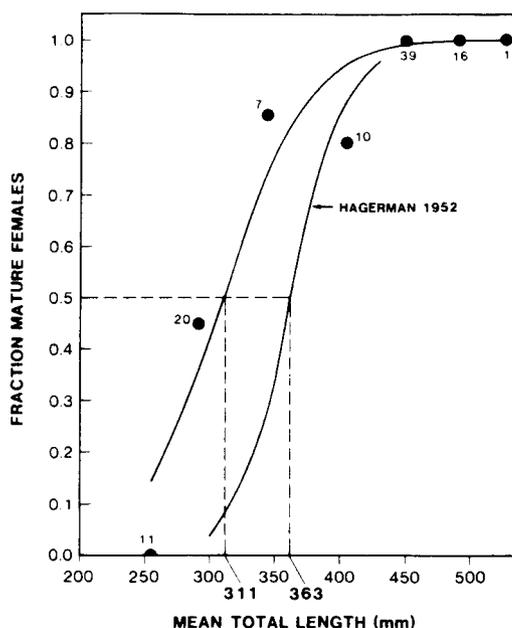


Figure 11. Circles, observed fraction of Dover sole that are mature in December within 50-mm length classes with N indicated; solid line, calculated fraction mature from logistic regression equation (equation 8); Hagerman line calculated similarly; dashed line, length at 50% maturity.

Oxygen Minimum Zone

Perhaps the most striking features of the environment occupied by Dover sole are the oxygen minimum and dysaerobic zones. In the 1987 survey the oxygen minimum zone ($O_2 < 0.5$ ml/l) occurred between 640 m (350 fath.) and 1010 m (550 fath.), which is similar to the depth range (280–550 fath.) during 1981–82 reported by Mullins et al. (1985) off Point Sur, California. The dysaerobic zone ($O_2 < 1$ ml/l) began at 457 m (250 fath.). Most sexually mature females were observed in the dysaerobic zone. We estimated that 86% of the spawning biomass existed in the oxygen minimum zone (table 4; figure 12) on the basis of the middle depth stratum (250–549 fath.) used in the 1987 and 1988 surveys (Butler et al. 1989). We also estimated that nearly all (93%) of Dover sole living above the dysaerobic zone were juvenile.

The oxygen minimum zone is also characterized by low temperatures (figure 12). The water in the dysaerobic zone ranged from 5.9°C at 530 m (290 fath.) to 3.2°C at 1262 m (690 fath.), and that in the

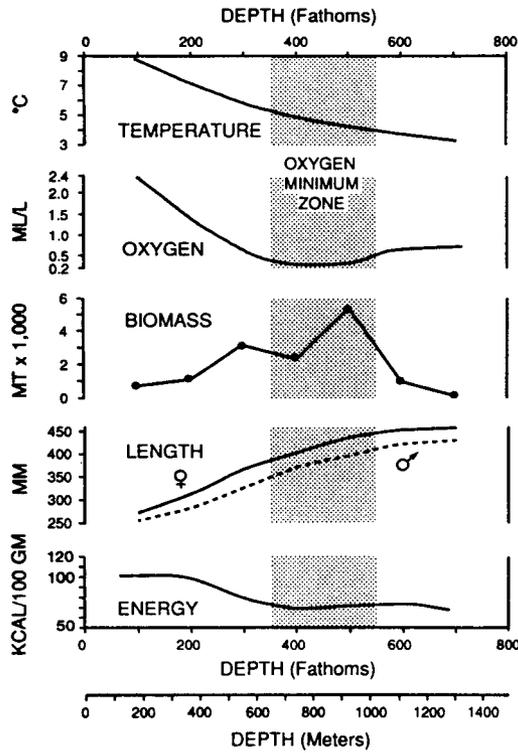


Figure 12. Bottom temperature, dissolved oxygen, biomass (MT) in study area, length (mm), and energy content (kcal/100 g wet weight) of Dover sole as a function of depth for 1987.

oxygen minimum zone from 4.9°C (700 m; 383 fath.) to 4.3°C (902 m; 493 fath.). Reduced metabolism due to temperature may help Dover sole cope with the low oxygen concentrations in the region.

DISCUSSION

Maturity

Our estimate of the length at first maturity differs from that estimated by Hagerman (1952). We fit equation 8 to Hagerman's data (250–630 mm, $n = 846$) and estimated the length at 50% maturity of female Dover sole landed in Eureka, California, during 1948–49 to be 363 mm ($a = -17.85$, SE of $a = 1.975$, $t = -9.042$, d.f. = 842, $p < 0.01$; $b = 0.0492$, SE of $b = 0.0050$, $t = 9.829$, d.f. = 842, $p < 0.01$; and $n = 844$). We compared the coefficients of the logistic regressions for our data to those collected by Hagerman using the Z-test (Zar 1984;

TABLE 4
 Computation of the Proportion of Spawning Biomass of Female Dover Sole (O) in the Oxygen Minimum Zone (OMZ)^a

Variables	1987			1988			1987 + 1988			
	Above	In	Below	Above	In	Below	Above	In	Below	
B	2,677	13,154	824	3,216	14,054	26	17,297	13,604	425	16,975
	907	2,899	499	1,024	2,891	18	2,013			
R	0.77	0.81	0.92	0.77	0.81	0.92	—	0.77	0.81	0.92
Q	2,061	10,655	758	13,474	2,476	24	13,884	2,268	11,019	391
H	275	814	1,122	—	294	976	—	278	819	1,118
S	0.420	0.736	0.816	—	0.420	0.816	—	0.420	0.743	0.816
O	866	7,842	618	1,040	8,777	20	9,836	953	8,187	319
	9	84	7	11	89	<0.1	100	10	86	3

^aOxygen minimum zone O₂ < 0.5 ml/l; depth 250–549 fath. Above OMZ, depth < 250 fath.; below OMZ, depth ≥ 550 fath.
^bFrom Butler et al. 1989. The biomass numbers for 1987 + 1988 are an arithmetic mean of the separate years estimates.
^cEstimated for 1985, 1987, and 1988 trawl survey data combined (no estimate made for individual years; from C. H. Lo, unpublished data, SWFC).
^dF = 0.286, stratum 1; F = 0.152, stratum 2; and F = 0.786, stratum 3, where T = -15 and W = average female weight. The same equations were used for 1987 and 1988 estimates because they were computed by combining survey data from 1985–88 (from C. H. Lo, unpublished data, SWFC).

TABLE 5
 Comparison of the Coefficients for Logistic Length and Maturity Equations for Female Dover Sole

	<i>a</i>	Variance	<i>Z</i>	<i>b</i>	Variance	<i>Z</i>
Present study	-9.947	4.661	2.702	0.03202	0.000047	-2.025
Hagerman (1952)	-17.854	3.901		0.04921	0.000025	

table 5). Because both sample sizes were large, we used the normal deviate *Z* with critical value of $> |2|$. The regression coefficients are significantly different at the .05 level, assuming that these distributions are normal. Thus it appears that Dover sole females from central California matured in 1985 at a smaller size than did those from Eureka, California, in the 1940s. For example, 50% of female Dover sole from central California mature when they reach 311 mm, whereas 50% maturity occurred at 363 mm in females from Eureka (1948-49). This 52-mm difference may be equivalent to an average difference in the age of first maturity of four to five years (assuming fish from central California in the 1980s grew at about the same rate as fish from Eureka in the late 1940s).

Similarly, Yoklavich and Pikitch (1989) compared their 1985 maturity estimate for Dover sole from Oregon to one made for the same area 35 years earlier. They found all females greater than 320 mm were mature in 1985, whereas 35 years earlier (Harry 1959) only 50% of Oregon females of 380 mm were mature and only 15% of the Dover sole less than 380 mm were mature. Yoklavich and Pikitch concluded that Dover sole from Oregon presently mature at smaller size and probably younger age than they did 35 years ago.

Because of possible sampling biases, we hesitate to attribute the differences between recent and older estimates to real biological differences. Bias could result from failure to obtain a representative sample over the full bathymetric range of Dover sole. In addition, the two older estimates (Hagerman 1952 and Harry 1959) may be biased because samples were taken from the fishery during spawning season. This process could lead to an overestimate of the average size of fish at first maturity, because females in postspawning condition could have been wrongly classified as immature. On the other hand, the methods employed by ourselves and Yoklavich and Pikitch (1989) were similar; in both studies the samples were taken in December 1985, which is early enough in the spawning season that biases from misclassification of postspawning fish seem unlikely. If our samples and those of Yoklavich and Pikitch (1989) accurately represent their respective regional populations, then females in Oregon ma-

tured at a smaller size than those in central California. For example, all Oregon females longer than 320 mm were mature, whereas in central California, only 57% (SD = 8%) of 320-mm females were mature. Yoklavich and Pikitch (1989) suggest that the long-term effects of the size-selective trawl fishery off Oregon was a compensatory decrease in the size of first maturity of Dover sole. This hypothesis may also explain the difference between our estimates for central California and theirs for Oregon, since the central California fishery (Morro Bay) for Dover sole is a new fishery with only minor landings until the last four or five years, whereas the Dover sole fishery in Oregon has been active for over forty years.

High Water Content

High water content (jellied flesh) has been reported for four marine flatfishes: Dover sole (Fisher et al. 1987; Puckett 1989); winter flounder, *Pseudopleuronectes americanus* (Pearcy 1961); yellowfin sole, *Limanda aspera* (Kizevetter et al. 1965); and American plaice, *Hippoglossoides platessoides* (Templeman and Andrews 1956). Roff (1982, 1983) attributed high water content in flatfishes to degradation of muscle tissue during periods of gonad development and maintenance during winter fasting (Roff 1982, 1983). On the other hand, Puckett (1989) concluded after examining the water content of Dover sole that depth, annual reproductive cycles, size, age, and the onset of sexual maturity were all involved, but depth was the most important factor. Most significantly, Puckett's analysis indicated that reproductive condition of mature females living at 650-1020 m was not correlated with their water content. He found that the average water content of males and females from deep water remained high throughout the year; for example, quarterly means for females ranged from 89.6% in the winter to 91.6% in the spring. He concluded that the effect of the reproductive season on water content was minimal, and that movement into a deepwater habitat was the key variable.

Dover sole differ from other flatfishes with high water content in two ways: the adult population lives at considerable depths (800-1500 m) and in the

oxygen minimum zone. In deep-sea fishes, the caloric density per g wet weight typically decreases with depth (Somero et al. 1983). The change in caloric density of Dover sole with depth follows a similar pattern (figure 12). The water content of deep-living Dover sole is at the high end of the range for the deep-sea fishes examined by Childress and Nygaard (1973), where 90.5% was the highest value recorded. This indicates that the ontogenetic change in water content in Dover sole may be simply an adaptation to deepwater existence, and the explanations proposed for low caloric density of deep-sea fishes may apply equally well to Dover sole. These include the scarcity of food and development of feeding strategies that permit a great reduction in propulsive systems demanding a high metabolic rate (Somero et al. 1983).

Another plausible explanation for high water content is one linked to life in the oxygen minimum zone. The oxygen and energy required to maintain white muscle in the oxygen minimum zone could be significant. Reduction of white muscle content would reduce basal oxygen demand and increase the scope for activity in an oxygen-limited environment.

In contrast to white muscle, red muscle tissue is conserved in Dover sole. This red muscle is located behind the head and at the base of the pectoral fin. This location may indicate a role in feeding. Feeding behavior has been described for the congeneric lemon sole, *Microstomus kitt*, by Steven (1930). This species feeds on polychaetes and also inhabits muddy bottoms. When feeding, a lemon sole raises its head and tail and sits perched on its side, scanning the substrate. When a polychaete is found, the fish pounces with a forward leap, bringing its head down on the prey and strongly arching the anterior body (Steven 1930). Dover sole also feed on polychaetes (Percy and Hancock 1978; Gabriel and Percy 1981; and Wakefield 1984), and we have observed similar feeding behavior in captive Dover sole in our laboratory. Dover sole perched on the substrate have also been observed by Allen (1982) and Wakefield (pers. comm., October 1988). Conserving red muscle while sacrificing white muscle as the fish becomes more watery may be a mechanism to preserve levels of feeding performance while reducing basal oxygen demand.

Ontogenetic and Seasonal Movements

Tagging studies (Westrheim and Morgan 1963; Quirollo and Kalvass 1987) and fishery data (Alverson 1960) indicate that Dover sole move inshore in the summer. This raises some interesting questions

concerning the ontogenetic movements we have described. Do the fish precisely re-sort themselves by depth each fall as they leave their shallow summer habitat? How do they gradually (over decades) increase the depth of their winter habitat? Does high water content affect the extent of seasonal movements?

No data exist to fully answer these interesting questions, but some inferences can be made on the basis of a tagging study conducted by Quirollo and Kalvass (1987). Their data indicate that all Dover sole may not participate in the summer inshore movement. Mature fish tagged and released in shallow water were usually recovered from deep water in the winter and fall and from shallow water in the spring and summer, indicating annual inshore movement. In contrast, most of the mature fish tagged and released in deep water were recovered in deep water regardless of season. Thus the tagging data indicate that two substocks may exist, one that migrates and one that does not. We suggest that the fish composing the migratory substock may be younger and have a lower water content than those composing the nonmigratory substock.

CONCLUSIONS

The deep, cold, and poorly oxygenated region of the continental slope known as the oxygen minimum zone is the habitat for the mature Dover sole in central California. Ninety-eight percent of the spawning biomass of Dover sole occurs in this region. Dover sole spawn at these depths, and their eggs rise to the surface layers.

Juveniles settle on the continental shelf and, with sexual maturity, gradually move down the continental slope. The onset of sexual maturity and the ontogenetic movement into the cold oxygen minimum zone (350–550 fath.; 640–1010 m) is usually associated with an increase in water content, myoglobin content of red muscle, and fat stores. The movement down the slope corresponds with a consistent pattern of increasing size, age, and water content.

The ontogenetic movement down the shelf is gradual and occurs over decades. The average female Dover sole in central California reaches maturity when about 7 years old and 311 mm long. At this time she lives at a depth of about 329 m (180 fath.), and her water content is about 83.8%. We speculate that over the next nine years the annual inshore and offshore movement gradually ceases. Over the same period the water content of the average female gradually increases as she descends to

greater depths and enters the oxygen minimum zone (640 m; 350 fath.). By then she is 16 years old, is almost 400 mm long, and has a water content of 87%. By this time she, like 93% of her cohort, is sexually mature, and growth has slowed from 14 mm per year when she was 7 years old to 6 mm per year. Eleven years later the average female has descended to 1006 m (550 fath.), is 27 years old, has grown 44 mm (about 4 mm per year), and has a water content of 88.7%. Water content continues to increase slowly over the next decades, and the fish continue to spawn and move deeper. The oldest female we aged was 51 years. The highest water content was 94.1%. The greatest depth at which we collected Dover sole was 1269 m.

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