Bathymetric Demography and Management of Dover Sole

LARRY D. JACOBSON AND JOHN R. HUNTER

National Marine Fisheries Service, Southwest Fisheries Science Center
La Jolla, California 92038, USA

Abstract. — Bathymetry is a key element in the demography of Dover sole *Microstomus pacificus.* Juvenile Dover soles begin life in relatively shallow water on the continental shelf but move gradually down the continental slope into deeper water as they grow and reach sexual maturity. Large and old individuals may eventually reach depths greater than 1,500 m. The ontogenetic migration of Dover soles into deeper water gives rise to a general pattern of increasing fish size with water depth, but there are differences between sexes and locations. To describe these patterns in greater detail, we computed probability distributions for depth, length, and sex using research trawl data for Dover sole taken off central California and Oregon. Our results indicate that females live at greater depths than do males and that abundance of large Dover soles may be lower at depths where lowest oxygen concentrations occur. In addition, major differences in bathymetric demography exist between study sites due, we suggest, to differences in bottom topography. We used one group of probability distributions and logbook data for Oregon and central California in a simple model to demonstrate how depth of fishing and bathymetric demography complicate interpretation of length composition and other data from a commercial fishery. Results from the model indicate that depth-stratified assessment models may be required to interpret fisheries data for Dover sole and other species, like shortspine thornyhead *Sebastolobus alascanus* and sablefish *Anoplopoma fimbria,* that undergo ontogenetic migration from shallow into deep water.

Dover sole *Microstomus pacificus* is a pleuronectid flatfish believed to be long lived (up to 58 years) and found at depths of about 55 m to more than 1,500 m off the west coast of North America (Hunter et al. 1990). Biological characteristics of Dover sole (age, size, sexual maturity, water content, caloric density, and biomass) and key characteristics of their habitat, such as temperature and oxygen concentration, vary with depth (Hunter et al. 1990). Depth-specific properties of Dover sole are becoming increasingly important to fishery managers as bottom-trawl fisheries on the continental shelf expand into deeper water over the continental slope.

Dover sole, like other commercially important species harvested on the continental slope off North America (e.g., shortspine thornyhead *Sebastolobus alascanus* and sablefish *Anoplopoma fimbria*), settle onto the continental shelf as juveniles and then move into deeper water as they age and grow. Some Dover soles eventually move down into the "oxygen minimum zone" where concentrations of dissolved oxygen may be less than 0.5 mL/L (Hunter et al. 1990; also see below). Superimposed on the ontogenetic movement of Dover sole into deep water is a seasonal inshore and offshore movement pattern that has been described in general terms but not precisely quantified (Alverson 1960; Quirollo and Kalvass 1987).

Dover soles undergo profound physiological changes as they grow and move into deeper water. Water content of Dover soles off central Califor-

nia, for example, increases with size, age, and depth from about 82 to 90%, causing a decline in energy content per gram wet weight. Large Dover soles taken from deep water often have "jellied" flesh with water content so high that marketability is affected (Hendrickson et al. 1986).

Ontogenetic movements of Dover sole (and other species harvested on the continental slope) are important in a practical as well as biological sense. Dover sole supports a valuable fishery on the western coast of the United States with annual landings and ex-vessel value during 1982 to 1989 averaging about 19,000 tonnes and US$3 million (1989 dollars). In recent years, the fishery for Dover sole has extended into deeper waters of the continental slope, resulting in increased harvest of older and larger fish (Turnock and Methot 1991). Changes in the depth of commercial fishing have complicated management of Dover sole stocks because effects on age- and size-composition data due to fishing mortality are confounded with effects due to changes in recruitment, mortality, and depth of fishing. It would be difficult, for example, to determine if a reduction in the number of small Dover soles in catches was due to reduced recruitment or a shift in the fishery to deeper water. Stock assessment models that partition fishing mortality rates into year- and age-specific components (e.g., Doubleday 1976; Deriso et al. 1985; Gavaris 1988; Turnock and Methot 1991) assume that age-specific vulnerability to the fishery is constant over time; this assumption may not be valid if the oldest fish are found in the deepest water and the depth at which most fishing takes place has changed. As shown below, an understanding of ontogenetic movements could be used by fishery managers to better manage species like Dover sole.

In this paper we describe biological relationships between size and depth for Dover sole and discuss how this information might be used by fishery managers. First, we develop a simple method for estimating joint, conditional, and marginal probability distributions that are used to describe relationships between depth and length of Dover sole at sites off Oregon and central California. We then show how preferred depth range changes with size at both localities. Next, we use probability distributions for Dover sole and information from commercial fishery logbooks in a simple model to demonstrate effects on fishery length-composition data due to changes in the depth of fishing. We use probability distributions throughout the paper because they naturally describe relationships between size of Dover sole and depth, are mathe-

matically convenient, can be presented graphically, and could be incorporated directly into stock assessment models used by fishery managers. The paper concludes with a discussion of how our results apply to interpretation of other types of fishery data, such as catch rates and age-composition information, and to other species that undergo ontogenetic migrations into deeper water.

Model

Our approach was based on an estimate of the probability distribution

$$p_t(l, d) = p_t(l \mid d)p_t(d). \qquad (1)$$

where $p_t(.)$ is the probability at time t of the event in parentheses. d is the event that a Dover sole is at depth d, and l is the event that a Dover sole is length l. In the language of probability, $p_t(l, d)$ is the joint probability distribution for depth and length of Dover sole at time t or, in plain terms, the odds that a fish randomly chosen at time t would be length l and at depth d. The probability distribution $p_t(d)$ gives the odds that a randomly chosen Dover sole would be at depth d and is called the marginal distribution for depth because it can be obtained by summing elements in the joint distribution across length categories. The probability distribution $p_t(l \mid d)$ gives the odds that a randomly chosen Dover sole would be length l given that it was already at depth d and is called the conditional distribution for length given depth. Expression of a joint probability as the product of marginal and conditional probabilities is a well-known result described in many textbooks (Stuart and Ord 1987: Section 7.7). Length-composition data (aggregated by depth strata) from trawl surveys were used as estimates of the conditional probability distribution for length given depth, $p_t(l \mid d)$, in equation (1).

Catch rates from trawl surveys and bathymetric data were used to estimate the marginal probability distribution for depth of Dover sole, $p_t(d)$, in equation (1):

$$p_t(d) = \frac{f_{t,d} \cdot A_d}{\displaystyle\sum_{d=1}^{d_{max}} f_{t,d} \cdot A_d}, \qquad (2)$$

where $f_{t,d}$ is the catch rate (number of fish/km^2) at depth d and time t (during the survey), and A_d is the surface area of the ocean (km^2) above depth stratum d. Catch rates were computed as the sum of the number of Dover sole caught during positive

tows in a stratum divided by total area swept (distance trawled multiplied by width of the trawl).

The joint probability distribution for depth and length, $p_t(l, d)$, was useful because it concisely summarized bathymetric and survey data and could be used, as shown below, to make informative graphs. Hunter et al. (1990) plotted mean lengths against depth for male and female Dover soles taken off central California using the same data that were used in this study, but their approach obscured some details about relationships between depth and length.

Most conditional and marginal distributions associated with the joint distribution, $p_t(l, d)$, are familiar to fishery scientists and managers. The marginal distribution for depth, $p_t(d)$, is, for example, also known as relative abundance at depth d, and the conditional distribution for length given depth, $p_t(l \mid d)$, is also known as the population length composition for depth interval d. The marginal distribution for length, $p_t(l)$, which is obtained from equation (1) by summing over depth intervals (see below), is often calculated and used as an estimate of the population length composition.

The major benefit in estimating the joint probability for depth and length of Dover sole, $p_t(l, d)$, was that conditional probability distributions for depth given length could be calculated from the joint distribution using Bayes' theorem (Stuart and Ord 1987):

$$p(d \mid l) = \frac{p_t(l, d)}{p_t(l)},\qquad(3)$$

where $p(d \mid l)$ is the conditional probability at time t for depth given length or, in plain terms, the odds that a Dover sole of length l would be at depth d. These conditional distributions were of particular interest because they reflect preferred depth distributions for Dover sole of different sizes and can be used to show how depth distribution changes as fish grow.

We hypothesize that conditional distributions for depth given length, $p(d \mid l)$, for Dover sole in a particular area are relatively constant over time. This hypotheses is important because, if true, our estimates of conditional distributions for depth given length measure preferred depth distributions as an intrinsic characteristic of Dover sole in a particular area. Estimates of preferred depth distribution might, for example, be incorporated into stock assessment models to enhance management. As shown below, distributions for depth given length differ among localities with different bathy-

metric characteristics, so habitat probably affects the ontogenetic movement of Dover sole into deep water. Density-dependent effects due to recruitment, mortality, and growth may also affect preferred depth distributions, but it is possible that density-dependent effects are modest relative to ontogenetic and habitat effects. We omit the subscript for time in the expression $p(d \mid l)$ to emphasize this important hypothesis—the temporal consistency of depth given length—although we were unable to prove or disprove it.

The probability distribution for length, $p_t(l)$, in the denominator of equation (3) is a marginal distribution described above. It can be obtained by summing the joint distribution for depth and length, $p_t(l, d)$, over depths:

$$p(l) = \sum_{d=1}^{d_{\max}} p_t(l, d).\qquad(4)$$

An important assumption in the mathematical development of our methods was that all Dover soles, regardless of size, were equally catchable by trawls used for research surveys. Cod ends in trawls used for research surveys were lined with small mesh to retain as many small fish as possible, and we omitted data for small and large length-groups with fewer than 20 observations (see below). No net is equally effective for fish of widely different sizes, however, so the assumption of constant catchability was not completely met. Thus, probability distributions estimated from trawl survey data differ from the true population probability distributions for Dover sole, particularly for small fish. Fortunately, modest failures of the assumption of constant catchability would not affect our general conclusions, which were qualitative in nature and based on obvious patterns in the data.

We estimated joint, conditional, and marginal probability distributions separately for males and females as well as for males and females together. Separate analyses were used to characterize differences between the sexes, and the combined analyses were used to examine distributions for all of the Dover soles in one area.

Data

We used data from bottom-trawl research surveys conducted by the National Marine Fisheries Service (NMFS) in two areas. Data were collected during two bottom-trawl surveys conducted by the RV *David Starr Jordan* off central California (34°30'–37°30'N) at depths of 69–1,295 m during January–February 1987 and February–April 1988

TABLE 1.—Minimum and maximum total lengths (l) for Dover sole in joint probability distributions before and after exclusion of length-groups with fewer than 20 observations. Also given are the percentages of the original joint probability distribution (percent probability) eliminated by excluding length-groups with fewer than 20 observations.

Length criteria and analytical loss	Central California	Oregon
Before sample exclusion		
Minimum length (l, cm)	8	19
Maximum length (l, cm)	55	61
After sample exclusion		
Minimum length (l_{LO}, cm)	12	25
Maximum length (l_{HI}, cm)	50	52
Percent probability	1.6%	1.4%

(Jacobson and Hunter 1992: Appendix Table 1). Data from the two surveys were combined to increase sample size. Although there were some differences between data from the two surveys, general patterns in the distribution of Dover sole by length, depth, and sex were consistent. Surveys were conducted during the spring of two successive years so seasonal and interannual effects on the data should be minimal. A standard NMFS 400-mesh Eastern otter trawl was used for all tows off central california that were included in our analysis (data for unsuccessful tows or tows made with other gear were not used). Detailed descriptions of cruise activities, nets, and sampling procedures are available from Butler et al. (1989), Hunter et al. (1992), and NMFS (Southwest Fisheries Science Center, Post Office Box 271, La Jolla, California 92038). Length-composition, sex, and catch rate (number of Dover soles per kilometer trawled) data were aggregated into seven 200-m depth strata (70–200 m, 200–400 m, 400–600 m, 600–800 m, 800–1,000 m, 1,000–1,200 m, and 1,200–1,400 m). Cruises off central California were conducted during the spawning season for Dover sole, which extends from January to May (Hunter et al. 1992).

We also used data collected during two bottom-trawl surveys conducted by the RV *Miller Freemen* during November–December 1988 and by the FV *Golden Fleece* during September–October 1989 (Jacobson and Hunter 1992: Appendix Table 2). Data from two cruises were combined in order to increase sample size. Although there were some differences between data from the two surveys, general patterns in the distribution of Dover sole by length, depth, and sex were consistent. The surveys were conducted off Oregon (44°–45°30′N) at depths of 194–1,231 m. Length-composition,

sex, and catch rate data were aggregated into seven 200-m depth strata (100–200 m, 200–400 m, 400–600 m, 600–800 m, 800–1,000 m, 1,000–1,200 m, and 1,200–1,400 m). Data for two tows at depths of 194–200 m were extrapolated to the entire 100–200-m stratum so that results for Oregon would be as comparable as possible to results for central California. A standard NMFS poly Nor'eastern otter trawl was used for all tows in both Oregon surveys. Detailed descriptions of cruise activities, nets, and sampling procedures are available from Hunter et al. (1992) and NMFS (Alaska Fisheries Science Center, 7600 Sand Point Way NE, BIN C15700, Seattle, Washington 98115). Cruises off Oregon were conducted just prior to the January–May spawning season for Dover sole.

The smallest and largest length-classes at each area were undersampled (contained fewer than 20 Dover soles; Jacobson and Hunter 1992: Appendix Tables 1, 2). Undersampling of small fish may have been due to reduced catchability of small fish or lack of trawling in very shallow water (less than 69 m off central California and less than 194 m off Oregon), where small fish are most abundant. Undersampling of large fish was probably due to their low abundance and too few tows in deep water. We avoided irregularities in probability distributions due to small sample sizes by excluding length-classes with fewer than 20 fish from the joint probability distributions of equation (1) and normalizing:

$$p_t'(l, d) = \frac{p_t(l, d)}{\sum\limits_{d=1}^{d_{max}} \sum\limits_{l=l_{LO}}^{l_{HI}} p_t(l, d)} ; \qquad (5)$$

where $p_t'(l, d)$ was the normalized joint probability, l_{LO} and l_{HI} were the first and last length-groups with at least 20 observations included in the normalized distribution, and length-groups (l) were restricted to the interval (l_{LO}, l_{HI}). Little information was lost by normalizing because less than 2% of the original joint probability distributions were excluded (Table 1).

Bathymetric data for Dover sole habitat at the two study sites were obtained by digitizing contours on standard bathymetric charts. For both study sites, we calculated the area (km^2) within each depth interval (boundaries of study sites and depth intervals defined above).

There were pronounced differences in bathymetry between the two study areas (Figure 1; Jacobson and Hunter 1992: Appendix Tables 1, 2). Dover sole habitat (approximately 50–1,500 m in
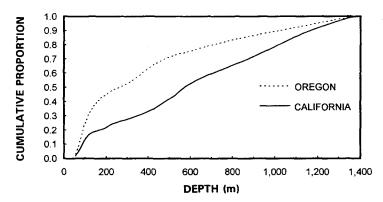
FIGURE 1.—Cumulative probability plots for area and depth of Dover sole habitat in the central California and Oregon study areas. The plots show the cumulative proportion of the total habitat area at or shallower than a given depth. For example, about 64% and 83% of total study areas in central California and Oregon were shallower than 800 m.

depth) was narrow off central California and wider off Oregon. For example, 70% of total area in the central California site is deeper than 400 m compared with only 40% of the total area in the Oregon site. These differences allowed us to make a preliminary assessment of the effects of habitat bathymetry on depth and length of Dover sole. The assessment was preliminary because the two areas were sampled at different times of the year, and effects of seasons and bathymetry may be confounded in our data.

Results and Discussion

Joint probability distributions for both areas (Hunter et al. 1990; Jacobson and Hunter 1992: Appendix Tables 3, 4) show that female Dover soles grow to larger size than males. In both areas female Dover soles longer than 45 cm in total length (TL) were frequently seen but males longer than 45 cm TL were seldom encountered (Figures 2, 3).

Relationships between Sex, Depth, and Area

Percent female Dover soles increased with depth at both sites such that individuals at 1,200–1,400 m were 96% female (Figure 4; Table 2). We used logistic regression implemented as a generalized linear model, or GLIM (McCullagh and Nelder 1983; Chambers and Hastie 1992), to test the statistical significance of this pattern at both sites as well as to test for differences between cruises at the same site and statistical interactions. An advantage of the GLIM approach is that overdispersion in the data can be estimated with quasi-likelihood techniques (McCullagh and Nelder

1983). Quasi-likelihood estimates for logistic regression parameters were the same as normal maximum-likelihood estimates except that an estimate of the ratio of observed and expected sampling variances (ϕ, the dispersion parameter) was obtained. In our analysis, for example, the sample variance for the fraction female in each tow was assumed to be $\phi f(1 - f)/N$ (where f is fraction female and N is the number of fish sampled) instead of $f(1 - f)/N$, which would be expected for a binomial random variable like the fraction of female Dover soles. Logistic regression models for each site treated depth as a covariate (continuous variable) and cruises as factors (categorical variables); F-tests (McCullagh and Nelder 1983) were used to judge the statistical importance of interactions, factors, and covariates because the data were found to be overdispersed ($\phi > 1$).

Interaction terms and cruises were insignificant for Dover sole at both sites (two-tailed $P < 0.14$), so final models for each site included depth effects only (Figure 4). Depth was statistically significant ($P < 0.001$) in the models for both sites, indicating that the proportion of female Dover soles at both sites increased with depth.

Variation in sex ratios for Dover soles taken in different tows at the same depth and site was larger than expected. The ratio of actual to expected sampling variance (as measured by the dispersion parameter ϕ in GLIM) was 5.5 for the Oregon site and 7.0 at the central California site. This indicates that Dover soles at a particular depth in a particular area were not randomly distributed by sex. Instead, groups of Dover soles that were predominantly male or female tended to occur in patches
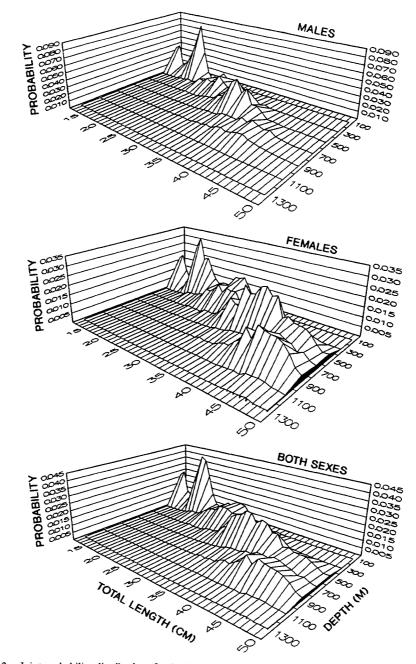
FIGURE 2.—Joint probability distributions for depth and length of Dover soles ($p_t'[l, d]$, exclusive of length-classes with fewer than 20 observations) in the central California study area based on bathymetric data and research trawl surveys conducted during January–February 1987 and February–April 1988. Distributions for males, females, and combined sexes are shown.
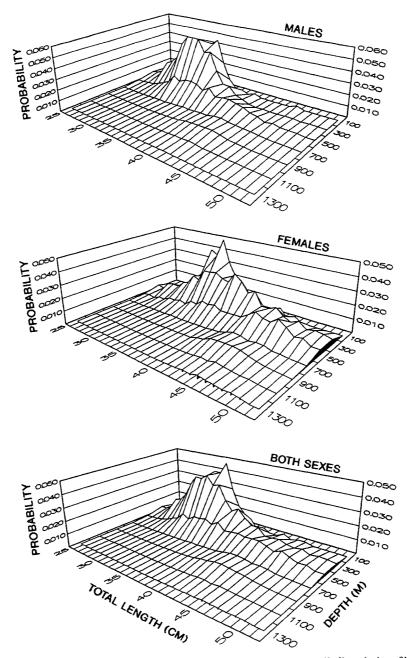
FIGURE 3.—Joint probability distributions for depth and length of Dover soles ($p_i'[l, d]$, exclusive of length-classes with fewer than 20 observations) in the Oregon study area based on bathymetric data and research trawl surveys conducted during November–December 1988 and September–October 1989. Distributions for males, females, and combined sexes are shown.
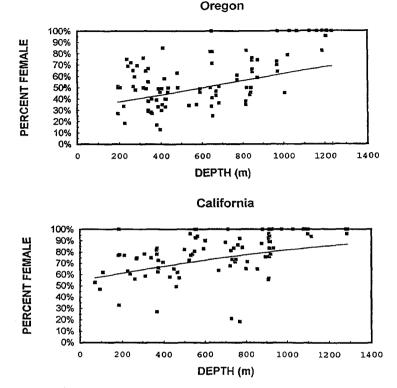
Oregon

California

FIGURE 4.—Sex ratios for Dover soles taken during Oregon and central California surveys. Shown are data for individual tows and lines fitted by logistic regression analyses.

sampled by different tows. Dover soles were taken off central California during their spawning season and off Oregon just prior to their spawning season. It seems likely that excess variability in sex ratios was due to spawning behavior, particularly because there was more excess variability in sex ratios of Dover soles taken off central California during the peak spawning season. Unbalanced sex ratios are associated with spawning behavior of other fish species (Hunter and Goldberg 1980). Among northern anchovies Engraulis mordax, for example, most spawning females are found in male-dominated schools.

A larger proportion of female Dover soles live in deep water. The proportion of females living at depths greater than 600 m, for example, was 11% at the Oregon site and 27% at the central California site, whereas the proportion of males at depths greater than 600 m was 7% at the Oregon site and 19% at the central California site (Table 3).

There were marked differences in overall sex ratios between sites. Females were 67% of the total

population at the central California site but only 43% of the total population at the Oregon site. The differences in sex ratio did not appear to be a sampling artifact or other error because the pattern was consistent for both cruises at each site and across depth intervals (Table 3).

Ontogenetic Movements

General patterns in the ontogenetic movement of immature Dover soles from shallow into deep water were similar for males and females in both areas (Figures 5, 6). Conditional distributions for depth given length $p_l(d \mid l)$, indicated that young Dover soles off central California remain in water less than 200 m deep until they are about 23 cm TL; then an abrupt shift into deeper water (300–400 m) occurs (Figure 5). No information about Dover soles less than 25 cm TL was available for the Oregon site. After the first transition at 23 cm TL, depth preferences of Dover soles off central California did not change until a second, more

TABLE 2.—Percentages of female Dover soles by depth interval and cruise. Values for depth intervals are means for individual tows in each interval weighted by sample size (number of fish sexed). Totals are means for depth strata weighted by catch rate and depth stratum size. Sample sizes are given in parentheses.

Depth (m)	Percent female Dover sole (N)		
	First cruise	Second cruise	Both cruises
Oregon (Nov–Dec 1988; Sep–Oct 1989)			
100–200	50% (6)	39% (200)	39% (206)
200–400	47% (915)	39% (1,162)	42% (2,077)
400–600	43% (648)	45% (531)	44% (1,179)
600–800	49% (261)	51% (382)	50% (643)
800–1,000	60% (641)	55% (653)	58% (1,294)
1,000–1,200	79% (112)	49% (104)	65% (216)
1,200–1,400	96% (53)	100% (2)	96% (55)
Total	48% (2,636)	41% (3,304)	43% (5,670)
Central California (Jan–Feb 1987; Feb–Apr 1988)			
70–200	72% (47)	55% (64)	62% (111)
200–400	64% (96)	58% (291)	60% (387)
400–600	84% (77)	67% (270)	71% (347)
600–800	70% (143)	64% (174)	67% (317)
800–1,000	73% (203)	79% (71)	74% (274)
1,000–1,200	93% (42)	100% (6)	94% (48)
1,200–1,400	96% (23)	(0)	96% (23)
Total	74% (631)	61% (876)	67% (1,507)

TABLE 3.—Probabilities and cumulative probabilities (in parentheses) of Dover sole occurrence by sex and depth interval in the central California and Oregon areas. The probabilities in the table are the same as $p_t(d)$ in equation (1). For example, 41% of male Dover soles in the Oregon area were between 200 and 400 m and 31% + 41% = 72% were in water less than 400 m deep.

Depth (m)	Probability of occurrence		
	Male	Female	Both sexes
Oregon			
100–200	0.31	0.27	0.29
200–400	0.41 (0.72)	0.42 (0.69)	0.43 (0.72)
400–600	0.21 (0.93)	0.20 (0.89)	0.20 (0.92)
600–800	0.03 (0.96)	0.04 (0.93)	0.03 (0.95)
800–1,000	0.03 (0.99)	0.05 (0.98)	0.03 (0.98)
1,000–1,200	0.01 (1.00)	0.02 (1.00)	0.01 (0.99)
1,200–1,400	0.00 (1.00)	0.00 (1.00)	0.01 (1.00)
Central California			
70–200	0.39	0.30	0.33
200–400	0.17 (0.56)	0.15 (0.45)	0.15 (0.48)
400–600	0.25 (0.81)	0.28 (0.73)	0.28 (0.76)
600–800	0.10 (0.91)	0.10 (0.83)	0.10 (0.86)
800–1,000	0.08 (0.99)	0.15 (0.98)	0.13 (0.99)
1,000–1,200	0.00 (1.00)	0.01 (0.99)	0.01 (1.00)
1,200–1,400	0.00 (1.00)	0.01 (1.00)	0.00 (1.00)

gradual, transition into deeper water (800–1,000 m) occurred at about 30–33 cm TL (Figure 5). Off Oregon, the first transition to deeper water occurred at about 37 cm TL (Figure 6). The transitions at 30–37 cm TL may be related to sexual maturity, because the length at which 50% of female Dover soles at both study sites reach sexual maturity is about 33 cm TL (Hunter et al. 1992).

Movements of sexually mature Dover soles into deeper water were similar in both areas although differences existed between the sites in the extent to which fish moved to depths beyond 800 m (Figures 5, 6). In both areas Dover soles gradually moved into deeper water as fish grew beyond the length of initial sexual maturity, and a considerable number of fish were found at depths of 800–1,000 m by the time Dover soles in both areas reached 40 cm TL. Conditional depth distributions, $p(d \mid l)$, for male and female Dover soles larger than 40 cm TL in both areas show a depression at approximately the depth range (600–800 m), where oxygen concentrations are lowest (Figures 5–7). This pattern was especially pronounced off central California, where more Dover soles are found in deep water and the zone of minimum oxygen is narrower (Figure 7), but was evident in the conditional probability distribu-

tions for both areas (Figures 5, 6). Lower probabilities indicate that Dover soles migrate through but may not remain for long at depths where oxygen concentrations are lowest.

Most Dover soles larger than 40 cm TL in the central California area were found below the oxygen minimum at depths greater than 800 m, whereas most fish larger than 40 cm TL in the Oregon area were found above the oxygen minimum at depths less than 600 m (Figure 7). This difference may have been due to differences in topography; less shallow-water habitat is available off central California than off Oregon (Figure 1), although other explanations, such as seasonal migration and intraspecific competition (density of Dover soles and food availability), are also plausible.

Effect of Fishing Depth on Fishery Data

We used the joint probability densities, $p(d, l)$, for depth and length of male and female Dover soles in the central California and Oregon areas along with logbook data in a simple model to investigate effects of changes in the depth of fishing on fishery length-composition data. In the model, we assumed that the population length composition was the same as estimated from the trawl surveys; that is, that the population length com-
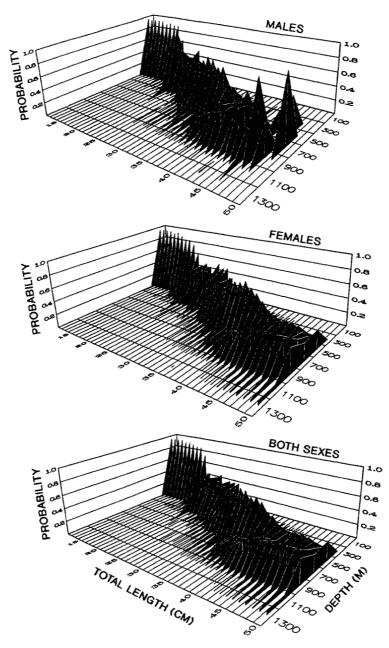
FIGURE 5.—Conditional probability distributions for depth of Dover soles given length ($p[d \mid l]$, exclusive of length-classes with fewer than 20 observations) in the central California study area. Distributions for males, females, and sexes combined are shown. Conditional distributions are given for each 1-cm length-group.
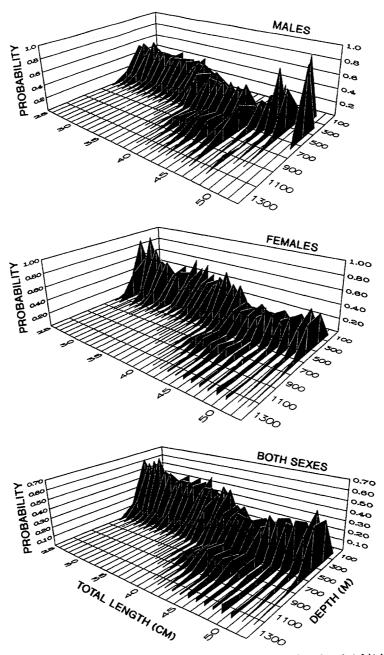
FIGURE 6.—Conditional probability distributions for depth of Dover soles given length ($p[d \mid l]$, exclusive of length-classes with fewer than 20 observations) in the Oregon study area. Distributions for males, females, and sexes combined are shown. Conditional distributions are given for each 1-cm length-group.
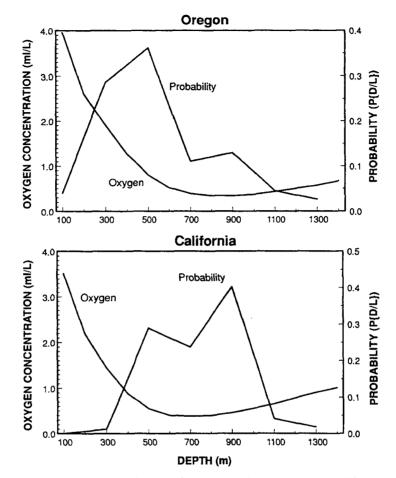
Oregon

California

DEPTH (m)

FIGURE 7.—Oxygen concentration as a function of depth in the Oregon and central California study areas and marginal probabilities for depth of Dover soles larger than 40 cm total length ($p[d \mid l > 40$ cm$]$). Oxygen data were obtained from an atlas and are means for observations recorded during January–December 1920–1970 (Churgin and Halminski 1974). Oxygen data for Oregon are from the area 44–46°N and 123–127°W. Oxygen data for central California are from the area 34–36°N and 118–125°W and the area 36–38°N and 121–126°W.

position was $p_t(l)$ from equation (1). We also assumed that the probability of capture (catchability) for a Dover sole lying in the path of a commercial trawl was independent of the size of the fish. The final assumption was that probability of capture in a depth stratum was proportional to the product of fishing effort (adjusted as described below) and abundance of Dover sole in the stratum:

$$p_t(c, d, l) = p_t(d, l)p_t(c \mid d, l)$$

$$= p_t(d, l)qE_{d,t}, \tag{6}$$

where c denotes capture, $E_{d,t}$ is the amount of fishing effort at depth d and time t, and q is the catchability coefficient. The assumption of constant catchability for all sizes of Dover soles does not hold for bottom trawls used by the commercial fishery, but this issue was not important in our analysis because the model was meant to show general patterns only.

The assumptions described above led to a convenient formula for calculating the length composition of the catch (conditional probability distribution for length given capture, $p_t[l \mid c]$) in our model:

$$p_t(l \mid c) = \frac{p_t(l, c)}{p_t(c)} \tag{7}$$

$$= \frac{\sum\limits_{d=1}^{d_{max}} p_t(c, d, l)}{\sum\limits_{l=1}^{l_{max}} \sum\limits_{d=1}^{d_{max}} p_t(c, d, l)}.$$

Nominal fishing effort data (hours fished) from logbooks for bottom-trawl fishing during 1978 and 1987 in the Columbia management area off Oregon (43°–47°30'N) and the Monterey management area off central California (36°–40°30'N) were used. The fishing effort data were for areas that encompassed the area of the Oregon and central California trawl surveys and showed the shift of the bottom-trawl fishery in the two areas from shallow to deeper water (Table 4). Total hours fished in each depth stratum were calculated by summing effort for all trips in which any Dover soles were taken. Total hours in each stratum was then divided by the area (km²) of the stratum in order to express fishing effort in each stratum on a per area basis (h/km). This was necessary because the probability of capturing a Dover sole during 1 h of trawling in a small area is greater than the probability of capture during 1 h of trawling in a large area. The adjusted measure of effort in each stratum was then converted to a percentage of total adjusted effort because only the relative amount of fishing effort in each stratum was important (Table 4).

Results from the model (Figure 8) indicate that fishery length-composition data for species like Dover sole can differ from the underlying population length composition. This result makes sense because a fishery in shallow water will tend to take small fish and a fishery in deep water will tend to take large fish irrespective of the population length composition. Differences between fishery and population length compositions may be modest, as in our model of the Oregon fishery, or substantial, as in our model of the central California fishery. These differences can be expected even, as in our demonstration, when catchability is the same for all size-classes unless the amount of nominal fishing effort in each stratum is inversely proportional to stratum size, so that fish at all depths experience the same fishing mortality.

Relationships between population and fishery length compositions are sensitive to changes in the distribution of fishing effort with depth (Figure 8) and could confound stock assessment and management efforts. This result makes sense because

TABLE 4.—Percent nominal fishing effort (h) and adjusted fishing effort (h/km) by depth stratum in the central California and Oregon areas by commercial bottom-trawl fisheries, 1978 and 1987.

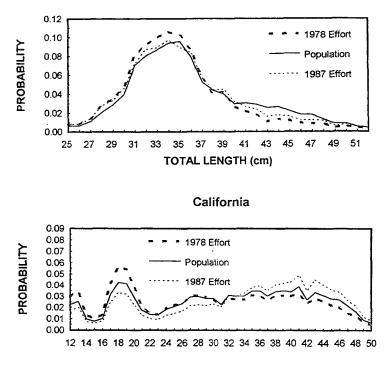| Depth (m)	Area (km²)	Percent fishing effort			
		1978		1987	
		Nominal	Adjusted	Nominal	Adjusted
Oregon					
100–200	2,491	40	32	21	15
200–400	1,820	54	60	56	57
400–600	1,639	5	6	20	22
600–800	919	1	1	3	6
800–1,400	1,988	0	0	0	0
Central California					
100–200	3,436	31	27	16	14
200–400	2,005	10	15	8	11
400–600	3,858	21	16	24	18
600–800	2,729	28	31	31	34
800–1,000	2,621	9	10	19	21
1,000–1,200	2,726	1	1	2	2
1,200–1,400	1,882	0	0	0	0

movement of the fishery to deeper water would result in more large fish caught and movement of the fishery into shallow water would result in more small fish caught, irrespective of the population length composition. Our results indicate that increased fishing effort in deeper water by the bottom-trawl fishery off Oregon and, particularly, central California between 1978 and 1987 would have resulted in changes in fishery length-composition data even if the underlying length composition of the population did not change. Length-composition data from the central California fishery for 1978 and 1987 from our model would indicate, if used in a stock-assessment analysis without information about the distribution of fishing effort with depth, reduced recruitment in later years, increased mortality of young fish, or an increase in the survival of larger fish. The consequences of this error in perception might well be erroneous recommendations to managers.

Conclusion

Our analysis shows that Dover soles were not randomly distributed by length, sex, or depth at two study sites. Dover soles at greatest depths in both areas tended to be female, larger (and presumably older), and more often sexually mature than were Dover soles living at shallower depths. Consistency of these patterns among cruises, sampling dates, and sites indicates that our results were not artifacts of sampling, choice of study sites, or

Oregon

California

FIGURE 8.—Predicted length compositions from a model of the commercial bottom-trawl fishery in the Oregon and central California study areas during 1978 and 1987.

seasons. Superimposed on the general pattern of increasing size, sexual maturity, and percentage female with depth were local patterns due to topography and oxygen concentration, as well as a great deal of variance in sex ratios of Dover soles taken at different locations in the same depth interval.

Problems in interpreting commercial fishery data caused by relationships between depth and size are not confined to Dover sole. Data for shortspine thornyhead, for example, show relationships between length, depth, sexual maturity, and the oxygen minimum zone similar to those of Dover sole (Figure 9).

Our analysis dealt primarily with effects on fishery length-composition data due to the distribution of fishing effort with depth, but our results can be applied to other types of fishing data as well. For species like Dover sole, fishing effort concentrated in shallow water will tend to oversample young (small) individuals, whereas fishing effort

concentrated in deep water will tend to oversample old (large) individuals. A change in the distribution of fishing effort from shallow to deep water will result in age-composition data that indicate reduced recruitment, increased mortality of young (small) fish, or increased survival of old (large) fish even when no change in the underlying population age composition has occurred. Analogously, catch rates from fishing in shallow water will tend to measure the abundance of small young fish, catch rates from fishing in deep water will tend to measure the abundance of large old fish, and a temporal shift in the depth of fishing will complicate interpretation of catch rate data.

It appears difficult to interpret fishery data for species like Dover sole, shortspine thornyheads, and sablefish unless information about the distribution of fishing effort and suitable depth-stratified (and perhaps sex-stratified) models are used. The conditional distributions for depth given length, $p(d \mid l)$, that we obtained for Dover sole
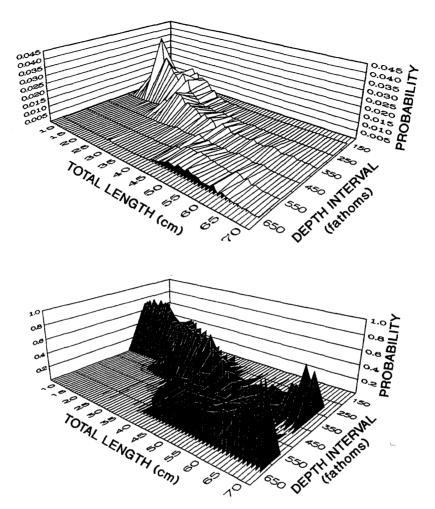
FIGURE 9.—Probability distributions for shortspine thornyhead (both sexes) off the coast of central California during February–April 1988. The top panel shows the joint distribution for depth and length ($p_t'[l, d]$, exclusive of length-classes with fewer than 20 observations). The bottom panel shows conditional distributions for depth given length ($p[d \mid l]$, for length-classes with 20 or more observations).

in the central California and Oregon areas may be useful in the development of suitable models, but information about temporal variation in conditional distributions for depth given length, bathymetry of fishing grounds, depth of fishing, and data from research trawl surveys will also be required.

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