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Reproductive Status of Dover Sole, *Microstomus pacificus*, off Northern Oregon

Dover sole, *Microstomus pacificus*, range latitudinally from northern Baja California to the Bering Sea (Hart 1973) but are commercially abundant only from central California to British Columbia. They inhabit a wide depth range, from shallow, inshore waters (juveniles) to at least 1,000 m. Maximum recorded size is 71 cm total length (Hart 1973). On the basis of biomass, Dover sole is the most abundant species of flatfish landed commercially off Oregon (Demory et al.[1]) and dominates the Columbia Slope Assemblage (located at depths >220 m) described by Gabriel and Tyler (1980). Landing and effort statistics for this species in the International North Pacific Fisheries Commission (INPFC) Columbia Area (lat. 43°00′–47°30′N) were relatively stable for the 20 years prior to 1977, but have since almost tripled (Demory et al[2]).

From data extending back to 1951, Demory et al. (fn. 2) suggested a decline in age-specific length for this species during the last several years (mean length at age 10 years was about

43.5 cm, 42.3 cm, and 38.3 cm in 1951, 1965, and 1982, respectively). Because fecundity is proportional to size, this decline implies that the reproductive capacity of the stock has decreased (Bagenal 1973; Borisov 1979), provided that relative fecundity or size and age at first maturity have not undergone compensatory changes. Data on fecundity and state of maturity of Dover sole off Oregon have not been collected since 1950 (Harry 1959).

In this paper, we describe fecundity of Dover sole from the Columbia area during the 1985–86 spawning season as a function of length, weight, and age, and compare the relationship between length and fecundity with that previously estimated from fish collected between 1948 and 1950 in the same geographical area (Harry 1959). Size and age at maturation are also assessed and compared with the limited information presented by Harry (1959).

Materials and Methods

Samples for estimating fecundity were obtained from commercial trawlers fishing off northern Oregon (about lat. 46°N) during December 1985. Fish total length (TL, nearest mm) was measured and both otoliths were removed and stored in 50% ethanol for age determination. Ovaries were preserved in a 10% phosphate-buffered formaldehyde solution. Maturity stages were assigned using macroscopic inspection of ovaries and oocytes and applying criteria described by Hagerman (1952). Comparable criteria were used by Harry (1956). Because most specimens were filleted prior to sampling, the relationship between total length and ovary-free body weight (nearest 0.1 g) was established from intact fish collected at the same time. Body weight at length for filleted fish was estimated from this relationship. Additional specimens (collected from 44° to 45°N) were sampled in December 1985 and January 1986 from processing plants in Newport, OR and used to describe state of maturity. Total length was measured and otoliths were removed.

Oocyte counts for fecundity estimates were made using the gravimetric subsampling method for MacGregor (1957), as described by Hunter et al. (1985). Both ovaries preserved from each fish were blotted dry and weighed to the nearest 0.1 g. Three subsamples of oocytes were removed from each fish (one each from the anterior, middle, and posterior regions of one ovary, either left or right). Subsamples were weighed

to the nearest 0.1 mg, placed on microscope slides in 33% glycerin, and teased apart to form one layer of oocytes. Minimum and maximum diameters of mature, yolked oocytes were estimated from each subsample. Subsamples weighed between 30 and 80 mg, and contained about 100–300 oocytes.

Ovaries were advanced enough to allow discrimination of large, mature oocytes from smaller partially-yolked oocytes and non-yolked oocytes by the unaided eye. Oocyte size-frequency distributions were determined microscopically from the ovaries of 10 fish (MacGregor 1957). Using a Zeiss Videoplan II[3] image analyzer, and a dissecting microscope with camera lucida attachment, approximately 250 oocytes lying along transect lines etched in the microscope slide were measured to the nearest micron, and size-frequency distributions were evaluated. The modal size group of advanced oocytes was determined by visual inspection of the size-frequency plots. An average minimum size-threshold for oocytes associated with the most advanced and distinct modes in these 10 plots was determined. Ovaries with advanced oocytes that all exceeded this size-threshold were used in estimating fecundity. Individual fecundity was calculated by multiplying total ovarian weight by mean number of advanced oocytes per mg in the three subsamples.

Age was determined for each fish used in estimating fecundity and for a subsample of those fish used for maturity assessment. The left otolith was prepared and sectioned as described by Boehlert and Yoklavich (1984). Annuli were counted on a dissecting microscope at 80× magnification using reflected light and a black background. Age was determined twice for each fish, approximately one month apart, to establish precision of the age estimate. There was no difference between the two age determinations for each of 75 fish (paired t-test, $P > 0.50$). The first estimate was used in further analyses. There has been no age validation for Dover sole, but similar methods have accurately aged other long-lived species (*Sebastes diploproa*, Bennett et al. 1982; *A. fimbria*, Beamish et al. 1983; *S. flavidus*, Leaman and Nagtegaal 1987).

Results

To determine fecundity, 97 ovaries were col-

lected during the first two weeks of December 1985. Eighteen ovaries were spent, while the others were classified as mature ovaries, full of developing oocytes that were distinguishable by the unaided eye. Fifty-seven of the mature ovaries, from fish 345 to 550 mm TL, were used for fecundity assessment; ovaries of the remain-

ing 22 fish were either poorly preserved or not intact. No hydrated or translucent oocytes were evident in the ovaries used for fecundity. Size-frequency distributions of oocytes from 10 mature, prespawning fish were generally bi-modal (Fig. 1). Seven of these ovaries had distinct modes of advanced oocytes; from these
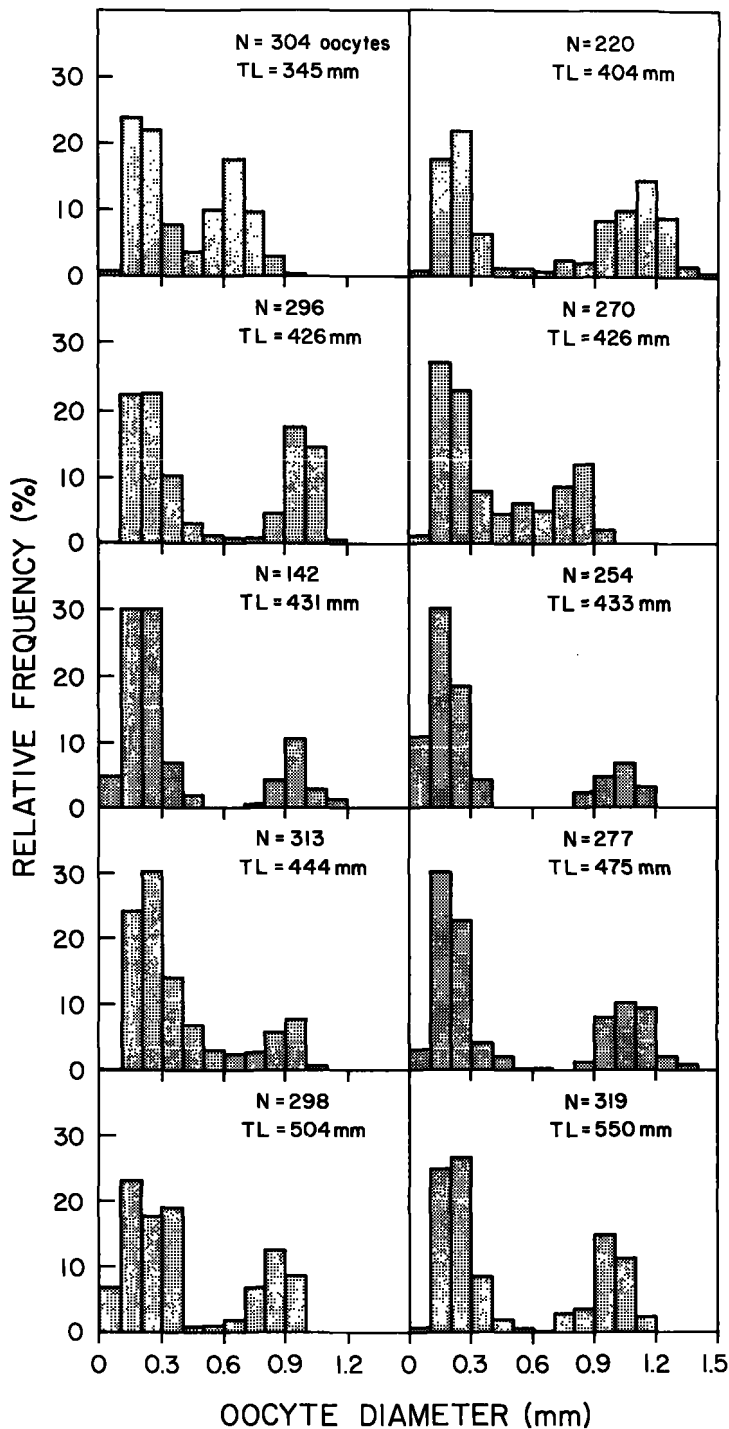

FIGURE 1.—Size-frequency distributions of oocyte diameter from ovaries of 10 Dover sole. Total length of fish and number of measured oocytes are indicated.

distributions, the mean minimum size was 0.65 mm for advanced, yolked oocytes to be used in fecundity estimates. The largest measured oocytes were 1.45 mm in diameter.

The number of advanced, yolked oocytes ($\geq$0.65 mm in diameter) per mg of tissue was calculated for each of three subsamples from 32 of the 57 ovaries. The coefficient of variation ranged from 0.1 to 9.1%, with a mean of 4.0%. This range is comparable to that found when enumerating the eggs of sablefish, *Anoplopoma fimbria*, (Mason et al. 1983) and widow rockfish, *Sebastes entomelas*, (Boehlert et al. 1982).

Fecundity of Dover sole ranged from 39,748 to 167,046 oocytes. As expected, fecundity increased with increasing length of fish (Fig. 2); this relationship was best described by the following power equation, using nonlinear, least squares regression methods:

$$F = (1.637 \times 10^{-6})L^{4.02} \qquad r^2 = 0.82,$$

where F is fecundity (total number of advanced oocytes per fish), L is total length of fish (mm), and r^2 is the coefficient of determination.

We found no statistical difference between the fecundity-length relationship from Dover sole collected by Harry (1959) and those reported here. A linear, least squares regression of our logarithmically transformed length-specific fecundity data was compared with an analogous function we derived from Harry's data, for lengths of fish common to both studies (425–550 mm TL; Fig. 2). Neither slopes (t-test, $P > 0.510$) nor intercepts (t-test, $P > 0.078$) of the regression lines differed significantly. The proportion of the total variation in fecundity that is accounted for by the fitted regression ($r^2 = 0.82$ in the present study and $r^2 = 0.75$ in Harry (1959)) is typical for many species of fish and reflects variable body weight, nutritional condition, age, and possible onset of spawning (Bagenal 1973; Hempel 1979).
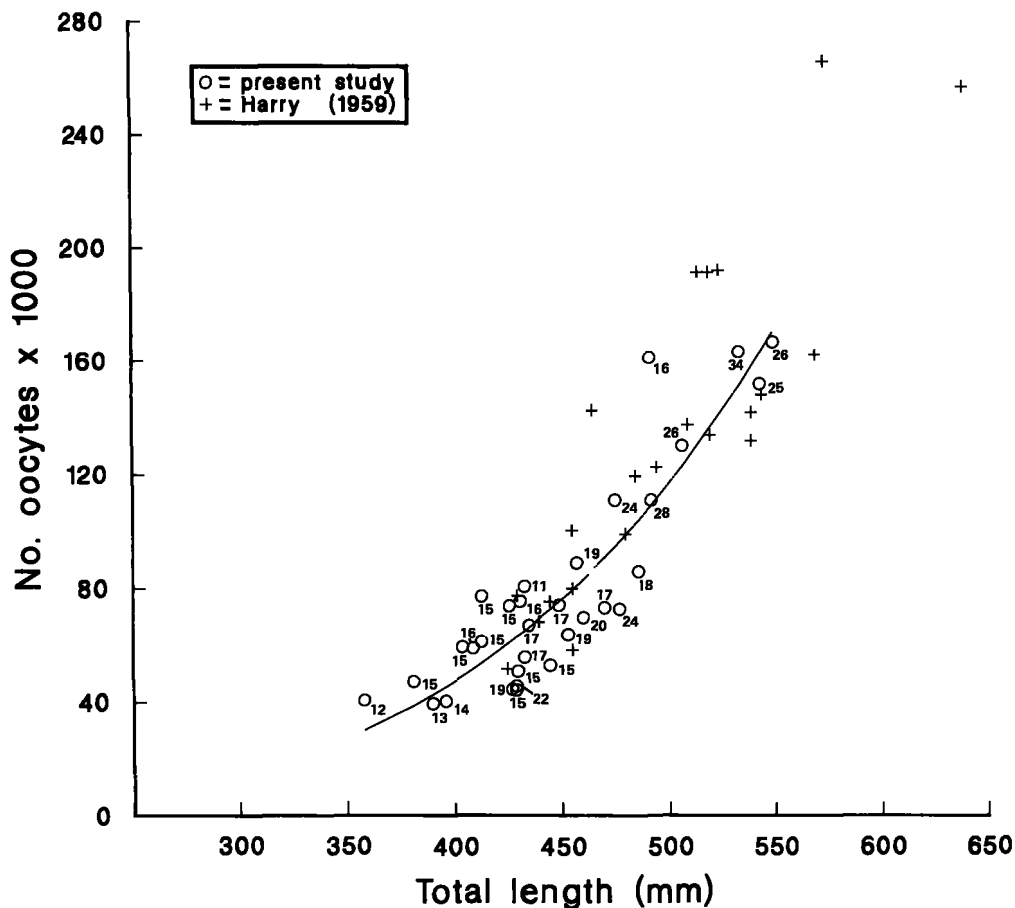

FIGURE 2.—Fecundity of Dover sole relative to total length. Open circles represent fecundity from present study ($N = 32$) and line is the predicted relationship through these points ($F = 1.637 \times 10^{-6} \, L^{4.02}$). Crosses represent fecundity estimated by Harry (1959; $N = 22$). Number adjacent to open circle indicates age of female.

Ovary-free body weight (W; 185–1,490 g) and total body length (L; 287–550 mm) from a sample of 115 female Dover sole were fit with a nonlinear, least squares power function:

$$W = (3.34 \times 10^{-6})L^{3.147} \qquad r^2 = 0.96.$$

Ovary-free body weight was subsequently estimated from total length for those Dover sole that were filleted prior to sampling. Fecundity was expressed as a linear, least squares function of ovary-free body weight, resulting in the fitted equation:

$$F = 133.4W - 21,890.3 \qquad r^2 = 0.81$$
$$N = 32,$$

where N is number of ovaries. Although weight was estimated from total length of fish, this fitted equation is adequate because the variance of errors associated with estimated weight is very small when compared with the variance in the weights themselves (Draper and Smith 1981, p. 124). Weight-specific fecundity averaged 102.4 eggs/g ovary-free body weight (SD = 22.0, N = 32).

The Dover sole used for determining fecundity were 11–34 years of age. Fecundity and age were not as strongly correlated as fecundity and length or weight, yet fecundity generally increased with increasing age (Fig. 2). The relationship between fecundity and age, from the 32

fish evaluated in this study, was best fit by a nonlinear, least squares exponential function:

$$F = 25,080 \, e^{(0.0586A)} \qquad r^2 = 0.65,$$

where A is age of the fish in years.

Stage of maturity was determined for 370 female Dover sole, ranging in size from 235 to 489 mm TL (Fig. 3). Because samples were collected from processing plants, many small fish had been discarded at sea and were poorly represented. Emphasis was placed on obtaining information from fish below fillet size (320 mm TL). Nearly 99% of the fish examined were classified as sexually mature; 67.2% of these were spent, and 32.5% contained ovaries with advanced, yolked oocytes that were clearly discernible upon macroscopic inspection. Only four fish (305–318 mm TL) were immature, and one fish was in a resting stage. Advanced oocytes occurred in fish of all lengths. This relationship suggests that fish were maturing at a much smaller size than that reported by Harry (1959; Fig. 3). State of maturity seems to be dependent on the size of the fish. Frequencies of fish in five 5 cm length groups (24–28; 29–33; 34–38; 39–43; and 44–48 cm) and in two states of maturity (advanced oocytes and spent ovaries) were arranged in a 2 × 5 contingency table; the independence of total length and state of maturity was tested. Significantly more of the small fish were spent (Chi-square = 78.76; $P <$
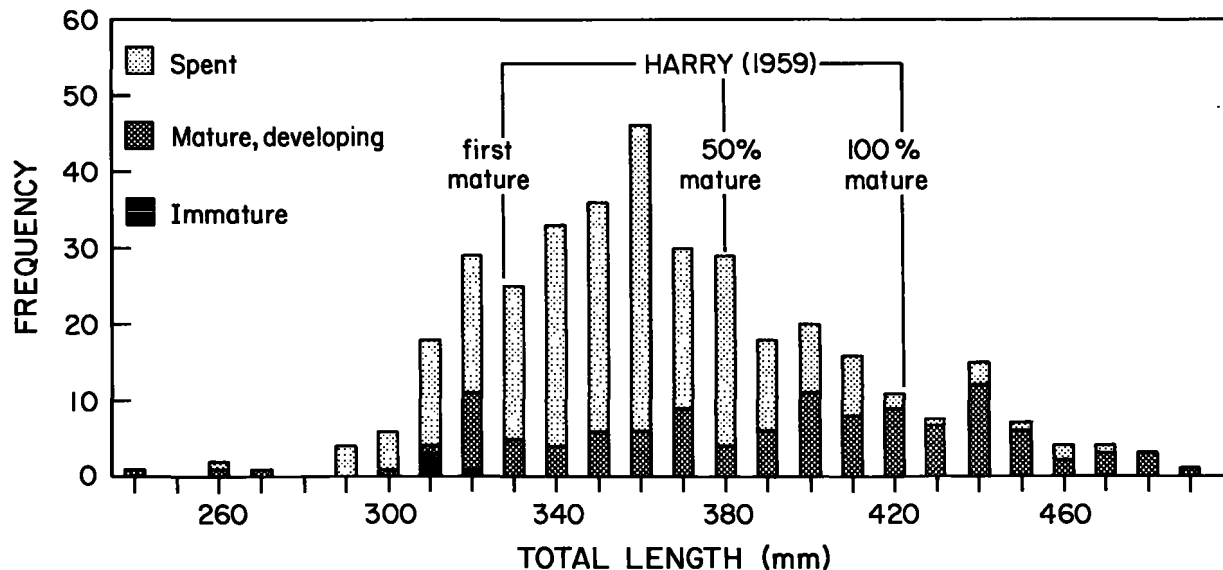

FIGURE 3.—Length frequency of 370 female Dover sole at three stages of maturity. Comparative information from Harry (1959) is indicated.

0.001); smaller fish appear to have an earlier, and possibly shorter, spawning season. Preliminary data on Dover sole collected in California indicated that larger fish still contained eggs in late spring (Hunter[4]), thus supporting our findings.

From those fish assessed for state of maturity, a subsample of 162 was selected for age determination. All were mature; 78% were spent, and 22% contained advanced, yolked oocytes. Fish were 5–24 years old (Fig. 4). As expected from the length at maturity analysis, most (77.1%) of the 35 fish with advanced oocytes were older than 10 years of age; 53.5% of the spent fish were older than 10 years.

Discussion

One cannot conclude unequivocally that the estimated number of advanced oocytes prior to

spawning corresponds to reproductive output of Dover sole, owing to incomplete spawning events or resorption of oocytes (Foucher and Beamish 1980). In addition, considering that 20% of the females collected for fecundity estimates during December were spent, some fish with advanced ovaries may have partially spawned. If so, fecundity would have been underestimated for those fish. We maintain that our data reflect the potential fecundity of Dover sole for the following reasons: 1) oocyte size distributions did not demonstrate a distinct spawning batch (oocyte diameter >1.80 mm), suggesting that these females had not yet spawned; 2) no hydrated oocytes were observed in the ovaries used for fecundity estimates, although hydration could occur rapidly and therefore its absence could be a sampling artifact; and 3) our coefficients of determination for regressions of fecundity on length and on weight are relatively high ($r^2 = 0.82$ and 0.81, respectively); if a significant number of oocytes had been released, variability could have conceivably been much greater. An additional source of underestimation
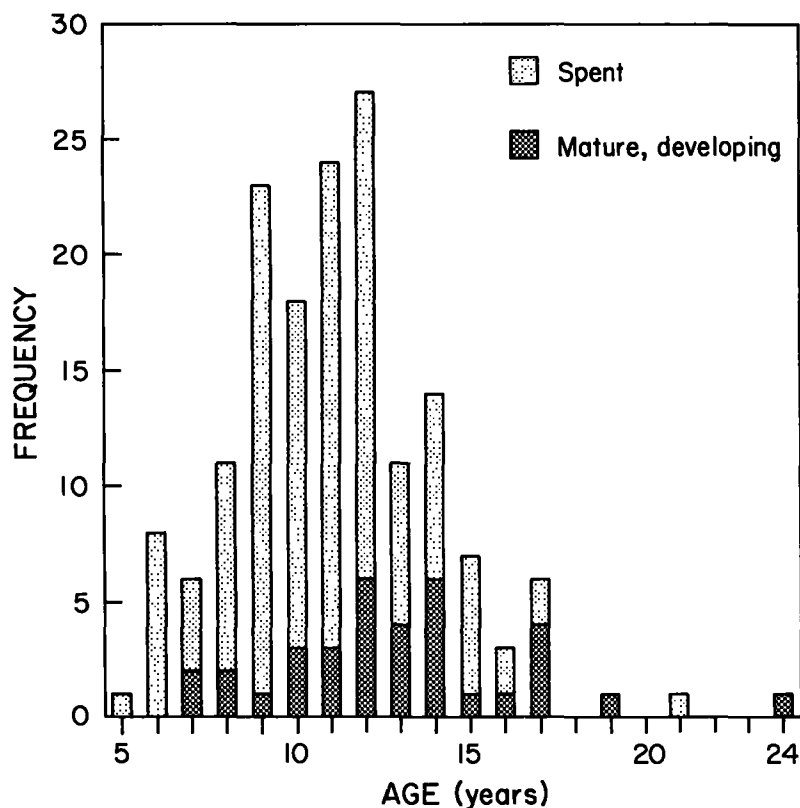

FIGURE 4.—Age-frequency distribution of 162 female Dover sole, classified as either mature with advanced oocytes, or mature and spent.

concerns the small, partially-yolked oocytes (<0.65 mm) that potentially could be recruited to the advanced mode but were excluded from fecundity estimates. Using the average lower limit of advanced oocyte diameters (from only those seven ovaries with clearly separated, advanced modes) as the minimum size of oocytes destined for release, it was assumed that further contribution of smaller oocytes would be unlikely and minimal in the current season.

A compensatory increase in fecundity following a reduction in population density was suggested by Bagenal (1973). We did not detect significant changes in length-specific fecundity for Dover sole despite tripled landings and the suggested decrease in age-specific length since 1977 (Demory et al., fn. 2). However, a decline in reproductive output is unlikely because our data indicate a compensatory shift in size at first maturity. Dover sole now mature at significantly smaller sizes than reported by Harry (1959). We found all fish >320 mm to be mature (the smallest mature fish was 240 mm). Although only 15% (or 245 specimens) of those fish in Harry's study were smaller than 380 mm, they were 330 mm at first maturity, 380 mm when 50% mature, and 420 mm when 100% mature (Fig. 3). Similar sizes at maturity were reported by Hagerman (1952) for Dover sole collected in northern California in 1949. The 45 females (5% of total sample) <330 mm were all immature.

The evident change in size at maturity during the interim 35 years may reflect differences in the criteria used for assessing stage of maturity, and in the time of year and size of the fish used for maturity assessments. Harry collected samples between May and October, which excludes the peak spawning months of December and January. Postspawning, inactive, mature ovaries are difficult to differentiate from immature ones during the early summer months using anatomical or histological criteria (Hunter, fn. 4). Classifying postspawners as immature would lead to a greater size at 50% maturity than that estimated from samples collected within the peak spawning period. Size at first maturity, however, should be relatively independent of season, since it seems unlikely that stage of maturity would be incorrectly identified in all smaller fish. Also, as egg development becomes more evident with the approach of spawning season, the mature ovaries become easier to identify (at least in Harry's August–October samples). Despite these potential problems with data comparisons, a decrease in length at maturity is clear and supported by evidence that Dover sole ≥370 mm collected in the Columbia area during the 1980–81 spawning season were all mature (Demory et al., fn. 2).

We cannot assess possible changes in the age-maturity relationship, because comparable ageing methodology was not used by Harry (1959). It cannot be inferred, however, that Dover sole are maturing at younger ages concurrently with smaller sizes, because length at age has also declined.

Although the decrease in length at maturity implies that individual reproductive potential is improved, lack of historical information on accurate age-specific maturity and fecundity makes it impossible to detect any net change in reproductive output per individual. To identify changes in the reproductive output of the Dover sole off Oregon, a reliable assessment of spawning biomass, size and age structure of the population, and both length and age at maturity is required.

Increased landings and effort may have affected the duration and timing of the spawning season, which could influence year class strength. Size-selective exploitation removes relatively more of the larger and older Dover sole (Best 1961). Larger individuals are not only more fecund, but appear to have a longer and/or later spawning period than small, young fish. The reproductive status and population dynamics of Dover sole, as influenced by factors discussed here, can be further understood with continued, appropriate, long-term research.

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Digestive-Gland Histology in Paralarval Squids (Cephalopoda: Loliginidae).

The transition from hatchling to adult in cephalopods does not involve a radical metamorphosis as is found in many other marine invertebrates (Boletzky 1974), but distinctive changes occur early in development (Vecchione 1979, 1981, 1982), similar to those found in fishes. The highest, and perhaps the most variable, rates of prespawning mortality in cephalopods occur during this paralarval development. A recent review of the early life history of cephalopods (Vecchione 1987) presented evidence that starvation, resulting from failure to feed successfully after absorption of the internal yolk, may be a major cause of paralarval mortality. However, other explanations, such as predation or suboptimal environmental conditions, may also explain high paralarval mortality rates. To test among these alternatives, methods must be developed to determine whether paralarval squids are suffering from starvation.

Similar problems exist in ichthyoplankton