FECUNDITY AND OTHER ASPECTS OF THE REPRODUCTION OF SABLEFISH, *ANOPLOPOMA FIMBRIA*, IN CENTRAL CALIFORNIA WATERS

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ABSTRACT

Along the central California coast from Point Conception to Monterey Bay, sablefish specimens were taken in research trawls, in traps, and from the fishery. Sablefish in spawning condition occurred in October through early February. Fifty percent of the females 60 cm long were sexually mature. Most of the females with active ovaries were taken in the oxygen minimum zone; 96% of the reproductively active females occurred at depths of 800 m or deeper. The mean length of males and females taken in trawls increased with depth.

Five lines of evidence indicated that the standing stock of advanced yolked oocytes was equivalent to the total potential annual fecundity; in other words, fecundity is determinate in sablefish. The potential annual fecundity of a 2.5-kg sablefish was 107 oocytes per gram female weight; the batch fecundity averaged 24 hydrated oocytes per gram female weight for the last spawn, and 41 for earlier spawnings. Thus sablefish would have to spawn about three times to fully use their potential annual fecundity.

RESUMEN

Varios especímenes de pez sable fueron capturados en arrastres de investigación, con trampas y por la pesquería a lo largo de la costa de California, desde Punta Concepción hasta la bahía de Monterey. Desde el mes de octubre hasta los comienzos de febrero se observaron especímenes en condiciones de desove. El 50% de las hembras de 60 cm de longitud se encontraban sexualmente maduras. La mayoría de las hembras con ovarios activos provinieron de la zona de mínimo oxígeno; el 96% de las hembras reproductoras ocurrió a profundidades iguales o mayores a los 800 metros. La longitud promedio de los machos y las hembras recolectados en los arrastres aumentó proporcionalmente con la profundidad de captura.

La evidencia demostró que el stock de ovocitos vitelinos en estadíos avanzados fue equivalente a la fecundidad total potencial anual; en otras palabras, la fecundidad en el pez sable está determinada. La fecundidad potencial anual de un pez de 2.5 kg de peso fue de 107 ovocitos por gramo de hembra. La fecundidad parcial promedió 24 ovocitos hidratados por gramo de hembra para el último desove y 41 ovocitos para los desoves anteriores. De esta manera, el pez sable debiera desovar 3 veces por año para hacer uso completo de su fecundidad potencial.

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INTRODUCTION

The objective of this study was to estimate fecundity, length at first maturity, bathymetric distribution, and frequency of spawning for sablefish, *Anoplopoma fimbria*, from central California, and to identify the spawning period. Sablefish occur along the northern rim of the Pacific Ocean from the southern tip of Baja California to the north-central Bering Sea and from there to central Honshu, Japan. Most of the U.S. catch is taken between southeastern Alaska and central California (MBC 1987).

We use our analysis of sablefish fecundity to evaluate the assumption of determinate fecundity. In fishes with determinate fecundity, the standing stock of advanced oocytes before spawning is equivalent to the total potential fecundity for the year. In many fishes (anchovy, sardine, mackerel, and others) fecundity is indeterminate (Hunter and Macewicz 1985a; Hunter et al. 1985); the standing stock of advanced oocytes is not equivalent to the total potential fecundity because unyolked oocytes are continuously matured and spawned during the reproductive season. Validation of the assumption of determinate fecundity is important because if determinate fecundity is wrongly assumed, total fecundity estimates are meaningless.

Some reports on sablefish reproduction exist: Mason et al. (1983) thoroughly studied fecundity (standing stock of advanced oocytes), identified the peak spawning period, and determined age and size at maturity of Canadian sablefish; Phillips and Imamura (1954) give some incidental values of standing stock of advanced oocytes for a few fish from California; Cailliet et al. (1988) estimated seasonality of reproduction, and report on the relation between bathymetry, size, and sexual maturity for

fish from Monterey Bay, California; Fujiwara and Hankin (1988) report similar information for northern California; and Norris et al. (1987) estimated the seasonality of reproduction for fish from the Oregon and Washington coasts. No sablefish study has considered the frequency of spawning or evaluated the assumption of determinate fecundity.

METHODS

Collections and Shipboard Measurements

Sablefish were collected along the central California coast (Point Conception to San Francisco Bay) during two research trawl surveys (January–February 1987; February–April 1988), during a trap survey conducted by the NWAFC (October 1986), and from the fishery by the California Department of Fish and Game (October 1986–February 1987). Research trawls were about one hour long in 1987, and were taken at fixed and repeated stations at seven depths (100–700 fath., 183–1280 m) in 1987. In 1988, random trawl samples were taken within three depth strata (30–249 fath., 55–455 m; 250–549 fath., 457–1004 m; 550–699 fath., 1006–1278 m) with tow durations of 0.5 hr in the first stratum and 1.0 hr in the middle and the deep strata. The trawl used was a 400-mesh Eastern with a mouth width of about 15 m, and height about 1.5 m (Wathne 1977).

In the 1986 trap survey, the females collected for fecundity were weighed and measured (FL, fork length) at the time of capture. In both trawl surveys (1987 and 1988) the total catch of sablefish was weighed; each fish was sexed and measured (FL); and a wet weight of most of the females was taken. The data were used to describe the bathymetric distribution of sablefish. We used the trawl catch of sablefish (kg/hr) to relate abundance to depth, but because the trawl extended only 1.5 m from the bottom, biomass is probably greatly underestimated by the catch; the average catch altitude for sablefish caught on setlines by Sullivan (1982) was 12 m off the bottom. In the 1987 survey, bottom temperatures and oxygen concentration were measured over the depth range of the survey (100–700 fath., 183–1280 m).

Reproductive measurements were made only during the 1986 and 1987 surveys. Data from the 1988 survey were used only to define the bathymetric distribution of sablefish. In 1988, ovaries were classed on shipboard into three types: hydrated (ovaries containing translucent hydrated yolked oocytes); active (ovaries containing yolked oocytes); and inactive (ovaries containing neither hydrated nor other yolked oocytes). The inactive class includes stages designated in other classification schemes as "spent," "immature," and various "developing" stages. In 1986–87 a five-class table was used, but we believe no useful purpose was served by attempting to make such distinctions, which in some cases are highly subjective. Although "spent" ovaries can be identified with reasonable accuracy immediately after a spawning, we did not use this stage because it is an ephemeral stage of unknown duration. An ovary classified as "spent" transforms into an inactive or active state depending on whether the female has completed all spawnings or will spawn again. Ovaries from females used in fecundity estimates were frozen or preserved in 10% neutral buffered Formalin and then weighed in the laboratory.

The length at first maturity was estimated by calculating the fraction of the ovaries that were active per length class for fish taken early in the spawning season (October 1986).

The fraction of females with hydrated ovaries taken in research trawls (1987 and 1988) was used to estimate the time of day that sablefish spawn.

Total Fecundity

We measured the total fecundity of 45 females captured in sablefish traps (October 20–27, 1986), and of 41 females taken in research trawls (January 17–February 14, 1987). Total fecundity (F_T) is defined as the total number of advanced yolked oocytes in the ovary, including all hydrated oocytes.

We estimated total fecundity gravimetrically. Using this method, fecundity (F_T) is the product of the gonad weight (G) and oocyte density (C). Oocyte density is the number of oocytes, within a specified diameter range, per gram of ovarian tissue, and is determined by counting the number of advanced oocytes in a weighed sample of ovarian tissue. We looked for differences in oocyte density between the right and left ovary and found none. We then removed two tissue samples from the right ovary, and counted all the advanced yolked oocytes in both samples. In one of the samples we also measured the diameters of 30 randomly selected advanced yolked oocytes. Advanced oocytes were identified, counted, and measured using a digitizer linked by a video camera system to a dissection microscope.

Measuring the diameter of the advanced oocytes served several functions. It provided a criterion for selecting ovaries that had matured enough to accurately estimate the density of advanced oocytes (see next section). Diameter was also used to determine seasonal changes in maturity of the advanced group

of oocytes. Finally, diameter provided an alternate method for estimating oocyte density. Oocyte density (C) can be roughly estimated from the mean diameter (D) of oocytes, because the weight of the advanced oocytes is proportional to their volume (assuming a spherical form and a specific gravity of 1). Hence,

$$C = K \frac{1}{\frac{1}{6}\pi D^3}$$

where $\frac{1}{6}\pi D^3$ is the volume of a sphere, and D is mm/10.

The coefficient of proportionality K was estimated for the October and January–February collections to determine if the density of advanced oocytes in the ovarian tissue changed over the spawning season. We did not measure the diameter of hydrated oocytes, nor did we use data from hydrated ovaries to estimate K.

Identification of the Advanced Stock of Oocytes

As a sablefish ovary matures, the standing stock of advanced yolked oocytes, believed to constitute the total fecundity for the season, gradually separates from the stock of smaller immature oocytes. When sufficiently mature, the standing stock is easily identified because it is separated from the immature oocytes by a gap in the oocyte size-frequency distribution where no or few oocytes occur (figures 1C and 1D; and illustrations of Mason 1984). Estimates of the standing stock can be biased in ovaries in which complete separation has not occurred (figures 1A and 1B). Thus for our fecundity estimates we wished to select ovaries in which the advanced oocytes were well separated from the less-advanced oocytes.

The apparent density of yolk within oocytes viewed on the video screen was used to discriminate between developmental stages of yolked oocytes. Four developmental stages were defined: stage 0, no yolk granules present (primary oocytes), oocyte diameter greater than about 0.1 mm; stage 1, initial layer of yolk along the periphery of the oocyte, appearing as a narrow band not extending over 20% of the distance between the nucleus and the zona pellucida; stage 2, layer of yolk extending from periphery to the nucleus, but nucleus is clearly visible; stage 3, yolk sufficiently dense that the nucleus is indistinct or occluded (advanced oocytes).

Examination of six ovaries indicated that when the mean size of the oocytes in stage 3 (advanced yolked oocytes) was greater than 0.7 mm, the separation of the advanced mode of oocytes from those

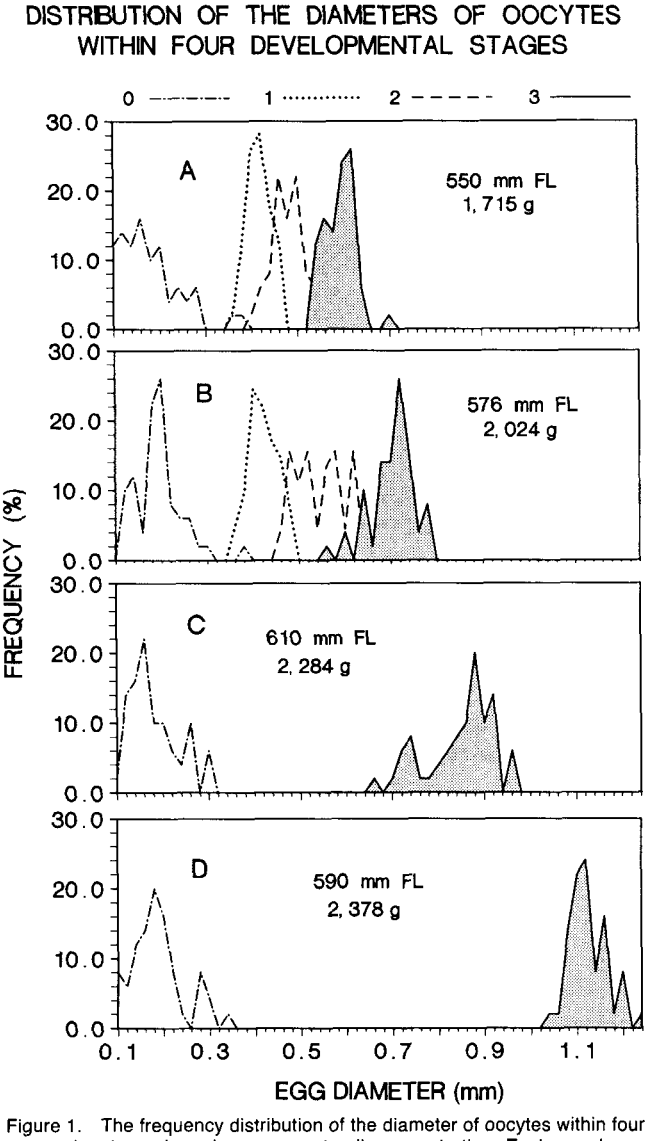

Figure 1. The frequency distribution of the diameter of oocytes within four maturity stages based on apparent yolk concentration. Each panel presents data for one female. Stages range from 0 (no yolk) to stage 3, the most advanced stage (used to estimate fecundity). *A* and *B*, sablefish ovaries in which separation of advanced standing stock (stage 3) is incomplete; *C* and *D*, ovaries where advanced oocytes are completely separated from other yolked oocytes.

in stages 1 and 2 was nearly complete. Thus, in our routine fecundity measurements we counted and measured only advanced yolked oocytes as defined above. If the mean of such oocytes was greater than 0.7 mm we included the data, but if the mean diameter ≤ 0.7 mm, the ovary was rejected because it was not sufficiently mature for an accurate estimate of the standing stock of advanced yolked oocytes.

Batch Fecundity

The number of hydrated oocytes in an ovary is equivalent to the batch fecundity (F_B) — the number of oocytes released during one spawning. Owing to

their large diameter (about 2 mm) and translucent appearance, hydrated oocytes are easily identified. Batch fecundity was estimated for 17 females taken in the 1987 research trawl survey by counting the number of hydrated oocytes in two tissue samples per ovary. We also estimated the number of non-hydrated advanced oocytes present in the same ovary using the procedure described for estimating total fecundity. A sample of 17 ovaries was too small to determine the relation between fish weight (W, always calculated as ovary-free female weight) and batch fecundity; thus batch fecundity was expressed as relative batch fecundity (F_B/W) [batch fecundity/ovary free female weight]. Total fecundity (F_T) for females with hydrated ovaries was the sum of the hydrated and advanced yolked oocytes.

Histological Analysis

Fresh ovaries from the 1987 research trawl survey were preserved in 10% neutral buffered Formalin and embedded in Paraplast. Histological sections were cut at 5–6 μm and stained with Harris hematoxylin followed by eosin counterstain (H&E). We did not histologically examine ovaries from the October 1986 survey because most of the fish had been frozen before being preserved in Formalin. Consequently, they were unsuitable for detailed histological analysis. Ovaries of sablefish taken in 1988 were not preserved.

Each ovary was classified histologically in the manner developed for northern anchovy (*Engraulis mordax*) by Hunter and Goldberg (1980), and Hunter and Macewicz (1980, 1985a,b), with a few modifications appropriate for sablefish ovarian structure. In the ovary we identified the presence or absence of oocytes in the first vitellogenic stages; advanced yolked oocytes; migratory nucleus stage oocytes (precursor to hydration); hydrated oocytes; postovulatory follicles; and three stages of atretic oocytes. The rate at which postovulatory follicles are resorbed in sablefish is unknown. Thus no ages were assigned to postovulatory follicles. Spent ovaries usually contained two groups of postovulatory follicles of differing deterioration, indicating two past spawnings. The oldest group of postovulatory follicles had to be at least 48 hr old; we suspect they were older because of their small size and extent of resorption.

RESULTS

Seasonal and Daily Timing of Spawning

The percentage of all females with reproductively active ovaries declined between October and February (figure 2). Similarly, ovary weight of Monterey sablefish declined markedly between November–December and January–February (Cailliet et al. 1988). These data indicate that the peak spawning period for sablefish in central California probably occurs sometime between October and February.

On a daily basis, peak spawning may occur between 1300 and 1600 hours. The proportion of females with hydrated ovaries was highest (24%) between 0900 and 1200 hrs and was low (2%) during the rest of the day, indicating that most females may have spawned by 1300 (table 1). No females with hydrated oocytes were taken at night (1700–0400), indicating that the hydrated oocyte stage may be shorter than 24 hours and that, collectively,

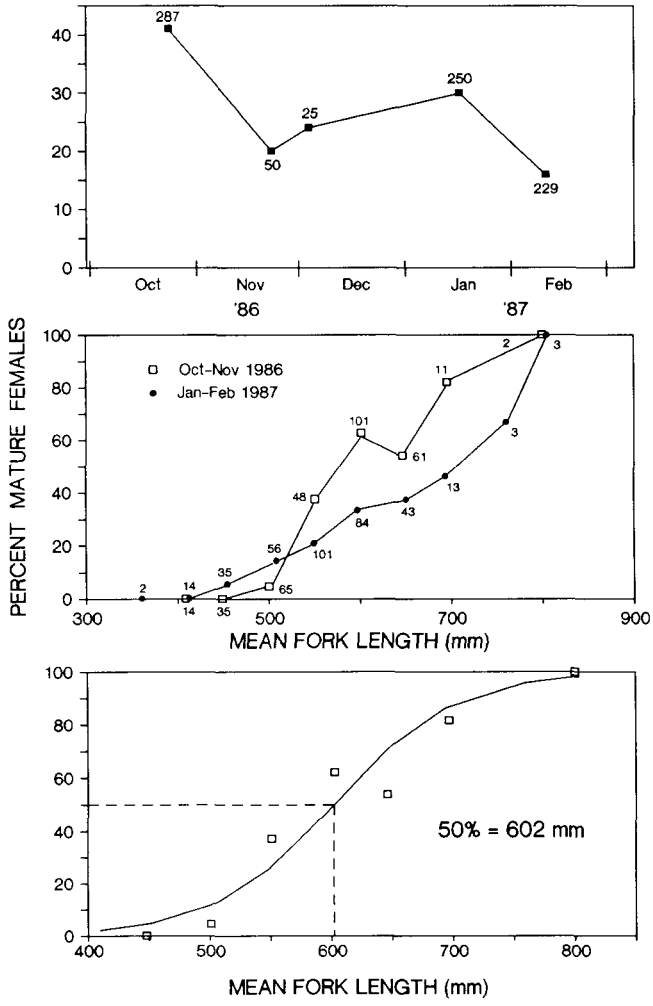

Figure 2. Fraction of sablefish ovaries that were active (yolked oocytes present) during 1986–87 spawning season as a function of collection date (*upper panel*) and fork length (*middle panel*), where squares are sablefish taken in October–November 1986 trap survey, and circles are January–February 1987 trawl survey; fraction active was calculated by 50-mm length classes; numbers are the number of fish per length class. *Lower panel*, fraction of females mature within each 50-mm length class; estimated length at 50% maturity = 602 mm.

TABLE 1
Percentage of Female Sablefish with Ovaries Containing Hydrated Oocytes

Time of capture	Total *N*	Percent hydrated
0030–0429	20	0
0430–0829	50	2.0
0830–1229	67	23.9
1230–1629	111	1.8
1630–2029	30	0
2030–0029	75	0
Entire day	353	5.4

Data from January–February 1987 survey.

the processes of hydration, ovulation, and spawning may require less than 24 hours to complete.

Length, Maturity, and Bathymetry

The percent maturity of sablefish females (P) as a function of fork length was estimated using the logistic regression

$$P = \frac{e^{a+bx}}{1 + e^{a+bx}}$$

where x = forklength in mm; $a = -11.978$, SE(a) = 1.439, $t(a) = -8.322$; $b = 0.020$, SE(b) = 0.00244, $t(b) = 8.177$; and DF = 335. In October the percentage of females with active ovaries increased with length; about 50% of females were reproductively active at 60 cm FL (figure 2). Misclassification of mature females as immature was unlikely because October was early in the spawning season. Our estimate of female length at first maturity (60 cm FL) was similar to that for females from British Columbia, where values ranged from 58 to 62 cm FL (Mason et al. 1983), and to that for females from northern California (56 cm; Fujiwara and Hankin 1988).

The mean length of males and females taken in trawls increased with depth, and the rate of change of length with depth was about the same in the two surveys (figure 3). At most depths, the average female and male sablefish taken in traps were longer than those taken in trawls. The mean length of fish taken in traps increased more slowly with depth than it did for those taken in the trawl. The lengths of fish taken by the two gears were about the same at depths of 500 fath. (914 m) or more, presumably because small sablefish do not occur at such depths.

Of the 87 female sablefish with active ovaries taken in January–February 1987, 96% were taken at depths of 450 fath. (823 m) or greater; most of the active females (75%) were taken between 550 and

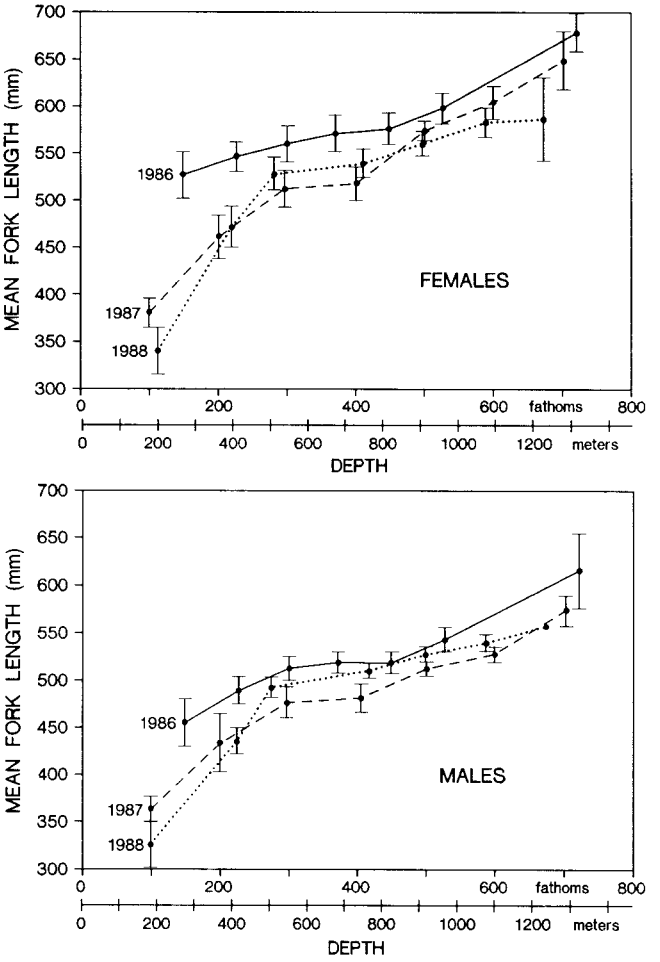

Figure 3. *Upper panel*, mean fork length (± 2 × standard error of mean) of female sablefish for 100-fath. (183-m) depth classes: *solid line*, 1986 October–November trap survey; *dashed line*, 1987 January–February trawl survey; *dotted line*, 1988 February–April trawl survey. *Lower panel*, mean fork length of males for the same surveys.

650 fath. (1006 and 1189 m). Thus in central California, the principal spawning habitat of sablefish seems to be the continental slope at depths of 450 fath. (823 m) or greater. How far down the slope reproductively active sablefish occur is unknown. The mean length of sablefish increased with trawling depth up to the maximum depth of our trawl collections (700 fath., 1280 m), and nearly all of the females taken at 700 fath. (1280 m) were reproductively active. Although reproductively active sablefish probably occur at depths greater than 700 fath. (1280 m), their abundance may be low. The catch rates of sablefish in 1987 and 1988 reached a maximum at 500 fath. (914 m) and declined at greater depths (figure 4). The spawning habitat of sablefish in central California is characterized by low oxygen concentrations as well as low temperature (figure 5).

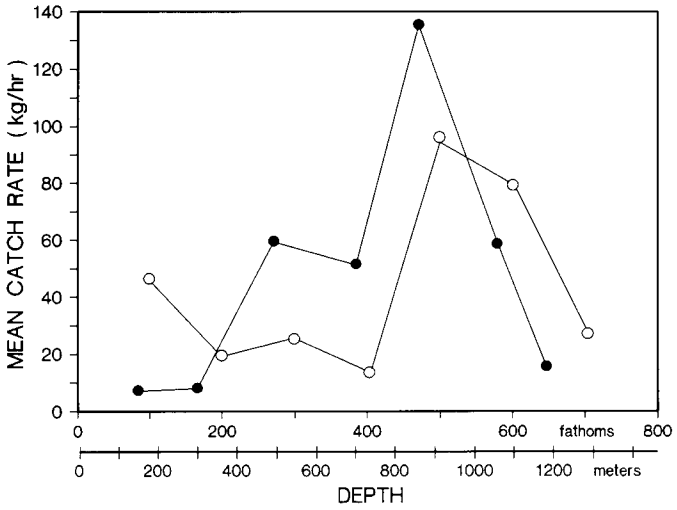

Figure 4. Catch rate of sablefish taken in 400-mesh Eastern trawl at 100-fath. (183-m) depth classes: *open circles*, 1987 survey; *solid circles*, 1988 survey.

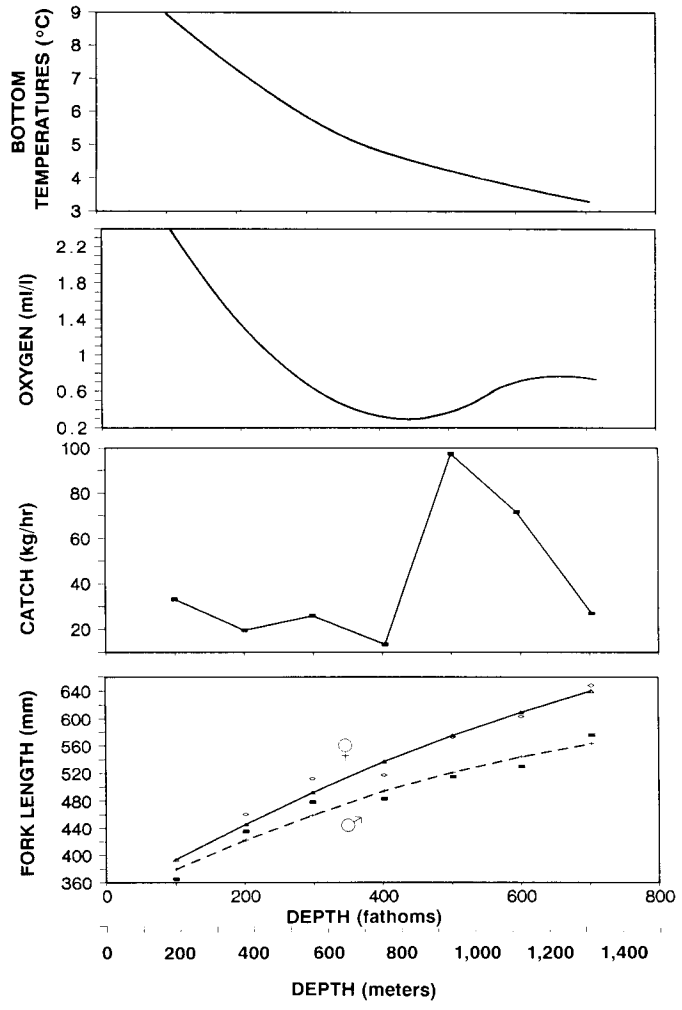

Figure 5. Relation between depth and bottom temperature, bottom oxygen concentration, sablefish catch, and fork length for 1987 survey.

Total Fecundity

The total number of advanced oocytes in the ovaries (F_T) of sablefish captured in October 1986 increased linearly with female weight (W in grams),

$$F_T = -45{,}223 + 125.1\,W,$$

where $r^2 = 0.50$; figure 6, upper, and table 2. According to this equation the total potential relative fecundity (F_T/W) of the sablefish taken in October ranged from 100 oocytes/g female weight for a 1.8-kg female, to 107 for a 2.5-kg fish. The relation between female fork length (L) and fecundity (F_T) was

$$F_T = 2.145 \times 10^{-5} L^{3.616}$$

where $r^2 = 0.40$.

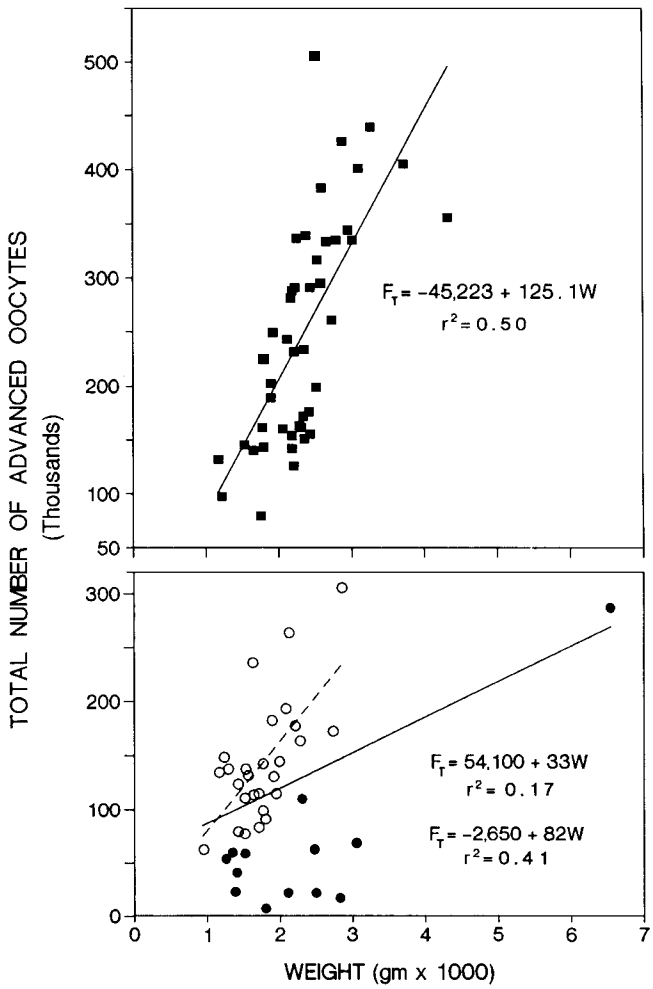

Figure 6. *Upper panel*, number of advanced oocytes in sablefish ovaries in October 1986 as a function of ovary-free female weight ($N = 45$). *Lower panel*, standing stock of advanced oocytes in January–February 1987 as a function of ovary-free female weight: *open circles*, no postovulatory follicles present in ovary; *solid circles*, postovulatory follicles present in ovary. *Solid line*, regression for all data ($N = 41$); *dashed line*, regression where ovaries with postovulatory follicles are omitted ($N = 28$).

TABLE 2

Standing Stock of Oocytes in Sablefish Ovaries in Order of Female Weight (Ovary-Free) Within a Survey Period

October 20 to 28, 1986

Female			Standing stock of advanced oocytes (thousands)
Wet weight (g)	Fork length (mm)	Ovary weight (g)	
1165	500	110	132
1218	510	49	97
1535	560	125	146
1654	540	72	140
1686	550	29	51
1752	560	93	80
1766	560	80	161
1797	550	63	143
1797	580	184	224
1891	570	122	189
1922	570	128	249
1988	630	202	505
2062	570	99	160
2118	590	122	243
2164	590	141	281
2182	590	112	154
2183	620	97	141
2184	610	100	288
2206	590	123	126
2207	600	178	232
2221	610	129	291
2241	580	149	336
2290	610	126	163
2312	620	159	161
2330	600	126	171
2345	590	145	232
2351	590	164	151
2362	600	65	270
2375	600	111	339
2414	620	171	176
2434	630	156	155
2440	610	121	291
2465	620	58	234
2472	610	65	388
2519	650	96	199
2534	620	107	316
2579	630	91	295
2595	610	251	382
2660	620	106	333
2728	620	242	261
2793	640	264	335
2878	640	124	426
2888	560	132	201
2953	640	127	344
3015	670	224	334
3096	670	189	401
3275	650	145	439
3394	680	136	556
3730	690	370	405
4328	720	409	356

January 16 to February 13, 1987

Female			Thousands of advanced oocytes			Post-ovulatory follicles + = present − = absent
Wet weight (g)	Fork length (mm)	Ovary weight (g)	Non-hydrated	Hydrated	Total	
944	474	86	62	0	62	−
1173	528	133	136	0	136	−
1228	500	172	149	0	149	−
1262	515	235	0	54	54	+
1300	520	136	139	0	139	−
1355	502	281	1	59	60	+
1394	538	130	0	23	23	+
1418	552	194	0	41	41	+
1434	522	148	124	0	124	−
1441	530	104	80	0	80	−
1515	540	109	78	0	78	−
1525	557	125	112	0	112	−
1529	548	237	6	53	59	+
1543	550	169	138	0	138	−
1568	540	194	132	0	132	−
1645	632	791	103	134	237	−
1656	540	169	114	0	114	−
1698	547	171	126	0	126	−
1722	572	147	21	63	84	−
1729	545	355	64	51	115	−
1760	524	245	143	0	143	−
1779	545	291	14	86	100	−
1799	577	109	91	0	91	−
1807	595	77	6	0	6	+
1892	550	238	182	0	182	−
1920	560	215	131	0	131	−
1958	595	134	116	0	116	−
2003	605	423	74	71	145	−
2094	590	268	194	0	194	−
2107	610	153	0	22	22	+
2143	597	351	264	0	264	−
2215	590	163	178	0	178	−
2291	594	239	164	0	164	−
2309	620	391	28	82	110	+
2470	630	315	2	62	63	+
2501	636	44	22	0	22	+
2744	582	296	173	0	173	−
2838	625	122	0	17	17	+
2866	660	564	207	99	306	−
3058	665	326	0	69	69	+
6543	818	938	31	255	286	+

By January–February 1987, the standing stock of advanced oocytes had declined to about 60% of oocyte stock observed in October 1986, and was only weakly correlated with female weight:

$$F_T = 54077 + 32.8\,W,$$

$r^2 = 0.17$, (figure 6, lower). Statistical documentation for this seasonal decline in oocyte standing stock is provided by multiple regression of fecundity on elapsed time and female weight:

$$F_T = 95{,}202 - 1150\,T + 5.71\,W,$$

where T is elapsed time from October 20, and R^2 = 0.50. Relative fecundity (F_T/W) declined from 105 oocytes/g (SD = 36.0, N = 45) in October to 64 oocytes/g (SD = 33.9, N = 41) in January–February. A t test showed that the means were significantly different ($p < 0.05$, t = 5.41, DF = 83). This seasonal decline in the standing stock of advanced oocytes indicates that some of the females had spawned part of their advanced stock of oocytes, and these oocytes were not replaced. Therefore determinate fecundity is indicated.

The weak relation between fecundity and fish weight in January–February (r^2 = 0.17) was probably caused by variation in the number of spawnings completed by each female. That females with postovulatory follicles (solid circles, figure 6, lower) had the lowest fecundity for a given weight supports this conclusion. The relative fecundity of females without postovulatory follicles was 81 oocytes/g (SD = 24, N = 28), whereas that for fish with postovulatory follicles was only 26 oocytes/g (SD = 15, N = 13). Thus, spawning has reduced the standing stock of advanced oocytes and consequently supports the assumption of determinate fecundity. The relation between fecundity and female weight for January–February is much stronger if females with postovulatory follicles are excluded:

$$F_T = 82.5\,W - 2652,$$

r^2 = 0.41 (figure 6, dashed line). This indicates that the high variability in the January–February 1987 data was caused by spawning. The slope of the regression of fecundity on weight for January–February 1987 is lower than the one for October 1986 even when fish with postovulatory follicles are excluded. Thus spawning probably occurred in females in which no postovulatory follicles were detected. Presumably, enough time had elapsed before capture for the postovulatory follicles to be resorbed in these fish.

Batch Fecundity and Spawning Frequency

The mean relative batch fecundity (based on counts of hydrated oocytes) was higher when many advanced yolked oocytes occurred with the hydrated batch than when few or none occurred. Thus the size of the last spawning batch was lower than that of earlier batches, and the number of oocytes in the last spawn averaged 24 oocytes/g, whereas the other spawnings averaged 41 oocytes/g (table 3). A t test showed significant difference in the means ($p < 0.05$, t = 2.348, DF = 15).

The mean weight of the 17 females with hydrated oocytes was 2237 g, (SD = 1245). According to our fecundity equation for fish taken early in the season (October), a fish of this weight would have a standing stock of 234,836 advanced oocytes or about 105 oocytes/g female weight. This female would have to spawn three times to use this standing stock of oocytes, assuming that the number of advanced oocytes in the last batch is 24 and the other spawnings are 41 oocytes/g female weight. In other words, division of our estimates of relative batch size into what we believe to be the initial standing stock of oocytes indicates that the average female sablefish spawns about three times per season. We assumed that if the remaining advanced oocytes were fewer than one oocyte/g, the oocytes would not be spawned and would be resorbed. The smallest hydrated batch we observed was 6 oocytes/g.

TABLE 3
Relative Fecundity (Number of Advanced Yolked Oocytes per Gram Ovary-Free Female Weight) of 17 Sablefish Females with Hydrated Oocytes

Potential spawnings ≥ 2			Potential spawnings = 1		
Not hydrated[a]	Hydrated	Total	Not hydrated[b]	Hydrated	Total
72	34	106	0.64	44	45
62	81	143	0.64	25	26
37	35	72	0.09	9.8	10
37	29	66	0.07	43	43
12	36	48	0	29	29
12	36	48	0	22	22
7.6	48	56	0	16	16
4.8	39	44	0	6.0	6
3.9	34	38			
Mean batch fecundity[c]	41.3			24.3	
SD	15.7			14.0	

[a]Mean diameter = 1.44, SD = 0.059, and range 1.31–1.52.
[b]Mean diameter = 1.46, SD = 0.015, and range 1.45–1.48.
[c]Calculated from the number of hydrated oocytes

Females separated into two classes: those likely to spawn two or more batches because, in addition to the hydrated batch, substantial numbers of advanced oocytes exist in the ovary; and those in which the hydrated oocytes may be the last spawning batch because, other than the hydrated batch, few or no advanced oocytes exist in the ovary.

Oocyte Diameter

The mean diameter of the advanced oocytes (excluding hydrated oocytes) increased from 1.0 mm (SD = 0.17, N = 50) in October 1986 to 1.34 mm (SD = 0.15, N = 37) in January–February. A t test showed that the means differed significantly ($p < 0.05$, t = −10.04, DF = 81). This observation supports the assumption of determinate fecundity, because an increase in average diameter of the advanced oocytes would not be likely if new, smaller oocytes were recruited into the advanced

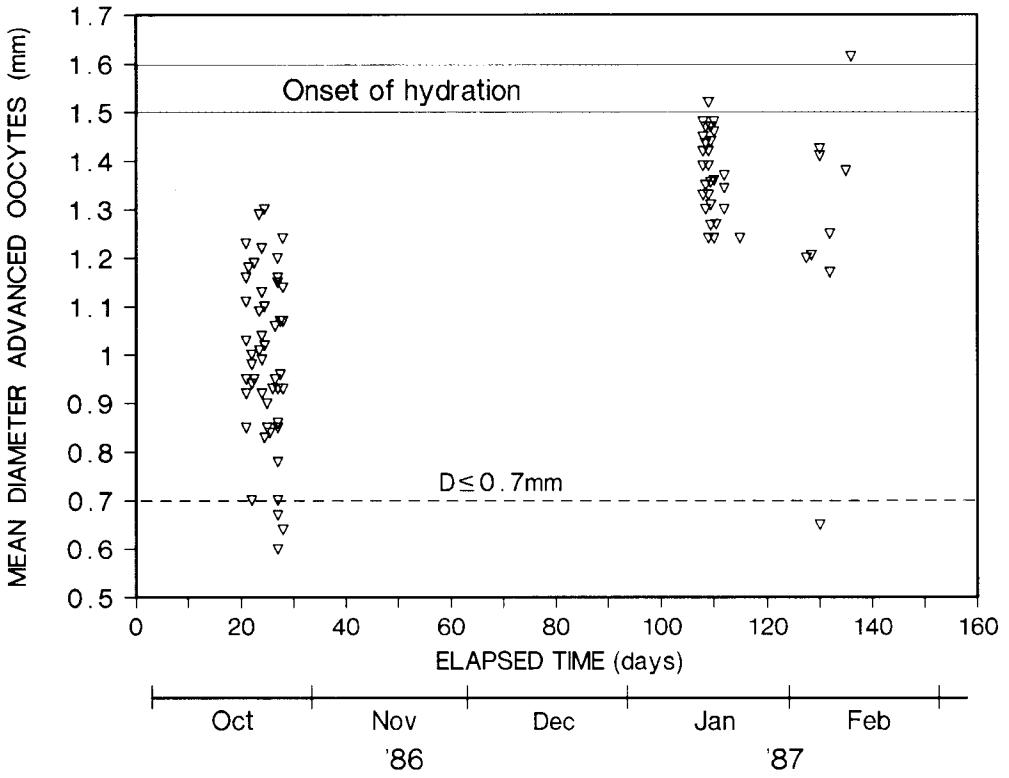

Figure 7. Mean diameter (D) of advanced oocytes in sablefish ovaries as a function of elapsed time (T) in days from October 6, 1986, to February 13, 1987. *Shaded area* indicates oocyte diameters at which the onset of hydration occurs; total fecundity was not estimated for ovaries in which the mean diameter was ≤0.7 mm (*dashed line*).

standing stock during the spawning season. By the middle of January the mean diameter of the advanced oocytes was 1.34 mm, which is close to the diameter at which hydration begins (1.5–1.6 mm) (figure 7). Thus by January, little maturation would be required to hydrate and spawn most of the advanced oocytes remaining in the ovary.

We compared the mean oocyte density (mean count of advanced oocytes in two tissue samples) to one calculated from the mean diameter by regressing mean oocyte density on the computed density $(\frac{1}{6}\ \pi\ D^3)^{-1}$ for fish taken in October and in January–February. In both sampling periods the intercept was very small and did not differ from zero. Assuming a zero intercept, the slope (K) was 0.94 for October and 0.88 for January–February. We tested the equality of the slopes by analysis of covariance (Zar 1974), and the results indicated that the slopes were not statistically different ($t = 0.253$, DF = 65). We combined the data from the two cruises to obtain a common slope of 0.94 (figure 8). K was less than one because samples of ovarian tissue contain material other than advanced oocytes (tissue fragments, postovulatory follicles, immature oocytes, etc.).

That K was nearly the same for fish taken in January–February as for those taken in October indicates that the fraction by weight of materials other than advanced oocytes in the tissue samples remained constant over the season, even though many of the females taken in January–February had spawned some of their oocytes. This indicates that postovulatory follicles are resorbed relatively rapidly after each spawning, and no major proliferation of vitellogenic oocytes had occurred. The relationship between observed oocyte density and the one computed from oocyte diameter was more variable for fish taken in January–February than in October: $r^2 = 0.55$ for January–February and 0.91 for October. Ovaries containing postovulatory follicles were substantially below the 0.94 line (figure 8, insert), indicating that the higher variability in January–February was probably caused by the occurrence of ovaries in which postovulatory follicles had not been resorbed.

The mean diameter of the advanced stock of oocytes was inversely correlated with total fecundity. A stepwise multiple regression of total fecundity (F_T, all data, October–February) on female weight (W), oocyte diameter (D), and elapsed time (T, during the spawning season) indicated that the diameter explained more of the variation in fecundity over the spawning season than did elapsed time (table 4). The final equation was

$$F_T = 351{,}992 + 71.4\,W - 263{,}462\,D,$$

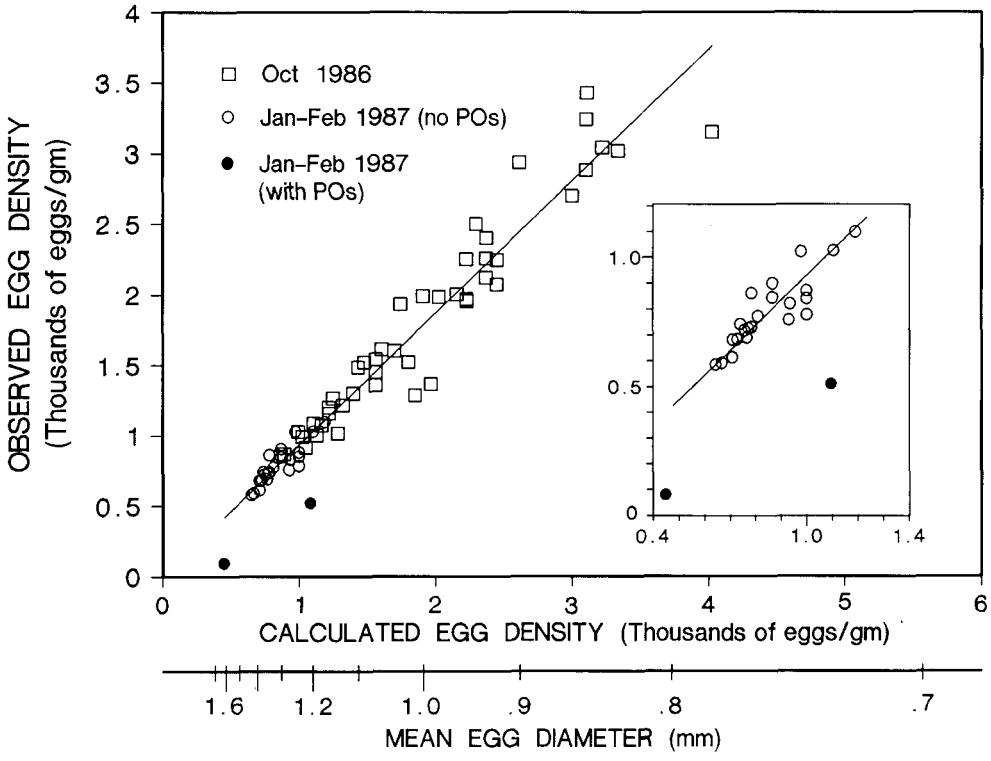

Figure 8. Relation between mean density of advanced oocytes in the ovary (Y axis) and density of oocytes calculated from the average diameter (X axis). The average diameter is calculated using the volume of a sphere and assuming oocyte specific gravity of 1.0:

$$C = K \frac{1}{\frac{1}{6}\pi D^3}$$

For October 1986 data (*squares*), K = 0.91; for February 1987 data (*open circles*), K = 0.89; and K = 0.94 for all data combined (*line*). Inset shows 1987 data in greater detail; *solid circles* represent ovaries with postovulatory follicles.

where $R^2 = 0.61$ (T was deleted as a variable because its contribution to R^2 was negligible when diameter was included in the equation). Thus the mean diameter of the remaining advanced stock of oocytes appeared to be a better index of losses of oocytes due to spawning than was elapsed time. Diameter was also a significant variable in the fecundity equation when only the specimens taken in October were considered. The inclusion of diameter as a variable increased R^2 from 0.49 for female weight alone to 0.66, yielding the equation

$$F_T = 278{,}114 + 127\,W - 317{,}198\,D.$$

We assumed that the ovaries of females taken in October for fecundity estimation were in a prespawning state. That the mean diameter of the advanced oocytes was inversely correlated with fecundity may indicate that some losses due to spawning may have occurred in some of our October specimens.

DISCUSSION

Sablefish Reproduction

Unlike many pelagic fishes such as anchovy, sardine, tunas, and mackerels, the standing stock of advanced yolked oocytes in sablefish is equivalent to the total potential fecundity; in other words, fecundity is determinate. Five lines of evidence support this view. (1) In mature ovaries (mean diameter of advanced oocytes >0.7 mm) a hiatus exists between the advanced stock of mature oocytes and smaller immature oocytes (this hiatus is obvious in our figure 1, and Mason [1984] provides many more illustrations). (2) The standing stock of advanced oocytes declined over the spawning season. (3) The standing stock of advanced oocytes was lower in females having postovulatory follicles. (4) The mean diameter of the oocytes in the standing stock increased over the spawning season. (5) Our estimates of batch fecundity, total fecundity, and numbers of advanced yolked oocytes in hydrated ovaries were consistent with the assumption of determinate fecundity.

Two uncertainties exist. Our analysis does not rule out the possibility that more than one stock of advanced oocytes might be developed and spawned in succession during the year. The extent to which the potential total fecundity is realized is also uncertain. However, the low incidence of atretic oocytes in our specimens indicated that the realized and potential fecundity may have been similar in 1987.

The total potential fecundity of sablefish from central California was about twice that of fish from Canadian waters (Mason 1984; Mason et al. 1983),

TABLE 4
Summary of Stepwise Regression of Total Fecundity on Ovary-Free Female Weight (W), Mean Oocyte Diameter (D), and Elapsed Time (T) and Analysis of Variance Table for Second Step with Independent Variables W and D

Stepwise regression

Step	1	2	3
Constant	13785	351992	340087
W	84.2	71.4	70.7
t-ratio	6.76	7.18	6.90
D		−263462	−248948
t-ratio		−7.08	−4.10
T			−85
t-ratio			−0.30
S	85664	67260	67655
R^2	36.67	61.45	61.50

Analysis of variance

Source	DF	SS	MS	F	P
Regression	2	5.62×10^{11}	2.81×10^{11}	62.18	<0.0005
Error	78	3.53×10^{11}	4.52×10^{9}		
Total	80	9.15×10^{11}			

Source	DF	SEQ SS
W	1	3.36×10^{11}
D	1	2.27×10^{11}

but the length of females at maturity was about the same. This difference in fecundity could be due to differences between the regions. It is also possible that spawning may have been well underway when the Canadian fish were sampled, thus biasing Mason's estimates downward.

Sablefish from central California require about three spawnings to exhaust their standing stock of advanced oocytes; the last spawning batch is smaller than the first two. We are currently preparing a manuscript on reproduction of Dover sole (*Microstomus pacificus*), a species that lives and spawns in the same habitat as sablefish. The fecundity of Dover sole is determinate; relative to their weight, Dover sole have about the same fecundity as sablefish, but they spawn more frequently (9 or more times per year) and have a lower batch fecundity for their body weight. Thus spawning rate is an important life-history variable even in fishes with determinate fecundity.

Perhaps one of the more interesting unanswered questions concerning reproductive biology of sablefish is how a species that lives and spawns far below the penetration of significant sunlight is able to synchronize its spawning with season and possibly time of day. The reproductive energetics of such fishes as sablefish and Dover sole that live and reproduce in the cold and poorly oxygenated water of the oxygen minimum zone also seem of particular interest.

Fecundity Methodology in General

In this section we make a few comments on the analysis of fishes with determinate fecundity. The time of sampling is of key importance in estimating the total potential annual fecundity in sablefish, and probably in most fishes with determinate fecundity. Estimates will be biased if one samples either too early in the spawning season or too late. If one samples too early, the advanced stock may not have matured enough to be completely separate from the smaller immature oocytes, and consequently estimates may be imprecise or biased. We avoided this problem in sablefish by excluding ovaries in which the mean diameter of the advanced oocytes was 0.7 mm or less.

If one samples too late, spawning will have begun, the stock of advanced oocytes will have been reduced, and the total potential fecundity will be underestimated. In sablefish this bias could be large, since a single spawning batch may be a third or more of the standing stock. The possibility that such a bias may exist is usually not mentioned. Some authors may assume that in fishes with determinate fecundity all oocytes are spawned in one batch, or spawning is so frequent that capture of fishes with a partially expended stock of oocytes would be rare. This is not true for sablefish, because females with partially depleted stocks of oocytes were common during the spawning season. In fact, we do not know if our October estimate for sablefish was underestimated because of spawning. One female with hydrated oocytes was taken during the October cruise, indicating that spawning had begun by October. In addition, the inverse correlation of oocyte diameter and fecundity may indicate that some of the October females had spawned.

Accurate measurement of the diameter of advanced oocytes, counts of hydrated oocytes, and occurrence of postovulatory follicles were useful in validating and interpreting sablefish fecundity estimates. Using these measurements to estimate spawning rates for anchovy and other fishes with indeterminate spawning has become routine (Hunter et al. 1985), but their application to determinate spawners is new. Computation of the mean diameter of the oocytes constituting the advanced stock is usually not included in most fecundity studies. This procedure not only provided a quantitative method for selecting fish for fecundity estimates but was also useful in interpreting and validating our fecundity estimates. The mean diameter of the ad-

vanced oocytes increased during the spawning season, was inversely correlated with fecundity, and the reciprocal of the oocyte diameter was proportional to the density of oocytes in the ovary. These relationships helped substantiate the assumption of determinate fecundity. In addition, diameter measurement under certain circumstances may be a rapid method for estimating oocyte density and hence fecundity for determinate spawners.

The mean diameter of the advanced stock of oocytes is also the most accurate measure of ovarian maturity. Our histological analysis of sablefish ovaries indicated that hydration begins when the diameter of the yolked oocyte is 1.5–1.6 mm; investment of yolk ceases at this point, and the remaining increase in oocyte volume is due primarily to water uptake. Thus the ovary can be considered to have a full energy content when all advanced yolked oocytes have a diameter of about 1.5 mm and no oocytes have been spawned. This is a condition we rarely, if ever, encountered. Ovaries in which the mean diameter of the advanced oocytes was close to 1.5 mm were taken late in the season, and some batches may have been spawned. The advanced stock of oocytes in ovaries collected early in the season, when spawning was unlikely, had a smaller average diameter (about 1.0 mm). If one were to use the weight of such early ovaries (dia. = 1.0 mm) as a measure of reproductive effort, it would be necessary to about triple the ovary weight to account for future investment of yolk during the spawning season. Thus even in a determinate spawner such as sablefish, gonad weight is an inaccurate measure of reproductive effort unless values are adjusted for maturity (oocyte diameter) and spawning losses.

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