EARLY LIFE HISTORY OF SABLEFISH, *ANOPLOPOMA FIMBRIA*, OFF WASHINGTON, OREGON, AND CALIFORNIA, WITH APPLICATION TO BIOMASS ESTIMATION

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ABSTRACT

In January–February 1987 we conducted a cruise over the central California continental slope to sample the eggs and larvae of sablefish (*Anoplopoma fimbria*). Sablefish eggs were taken in 35% of the bongo and MOCNESS nets towed through the entire water column. Discrete depth tows showed that eggs were distributed between 200 and 800 m and were most concentrated between 240 and 480 m. On surveys off Oregon in February–April 1989 (slope region) and in January 1990 (slope region and offshore to ca. 170 n. mi.) we employed oblique bongo tows to sample the entire water column to a maximum depth of 1500 m. The inshore limit of eggs was at about 500 m bottom depth, and they were found seaward to about 150 n. mi. Eggs at the most seaward positive stations were four or five days old, suggesting that they were produced by an offshore segment of the sablefish population and did not represent eggs advected from the continental slope. Estimation of sablefish biomass by the egg production method is possible since we now have a quantitative method for sampling the pelagic eggs and simultaneously recording temperature throughout the tow. For the method to be successfully employed in the northeast Pacific, the sampling pattern would have to extend at least 200 n. mi. offshore, and the survey vessel would have to be capable of operating in the heavy seas encountered during the sablefish spawning season (January–March).

RESUMEN

Durante Enero–Febrero de 1987 hicimos un crucero por el talúd continental frente de California central para colectar muestras de huevos y larvas del bacalao negro (*Anoplopoma fimbria*). Encontramos huevos del bacalao negro en 35% de los arrastres hechos por toda la columna de agua con redes "bongo" y "Mocness." Arrastres a profundidades fijas mostraron que los huevos se distribuían entre 200 y 800 m, concentrandose entre 240 y 480 m. Frente a Oregon, hicimos arrastres oblicuos con redes "bongo" por toda la columna de agua hasta una profundidad máxima de 1500 m. En Febrero–Abril de 1989 estos arrastres se hicieron en la zona del talúd, mientras que en Enero de 1990 se hicieron en la zona del talúd y en mar abierto, hasta aprox. 315 km de la costa. El límite de la distribución de los huevos fué de aprox. 280 km hacia mar adentro, mientras que hacia la costa el límite coincidió con la zona de profundidad de aprox. 500 m. Los huevos encontrados en las estaciones en mar abierto tenían 4–5 días de edad, sugiriendo que éstos fueron producidos por un segmento de la población encontrada en mar abierto y nó debidos a la deriva de huevos producidos en el talúd continental. Es posible calcular la biomasa del bacalao negro por el método de producción de huevos, dado a que ahora contamos con un método cuantitativo para obtener muestras de huevos pelágicos y, de manera simultánea, el registro de temperatura durante el arrastre. Las condiciones para que este método tenga éxito en el Pacífico noreste incluyen que los muestreos deben extenderse hasta por lo menos 370 km hacia mar adentro, y que el buque de investigación sea capaz de operar en mares picados, una condición común en la época de desove (Enero–Marzo) del bacalao negro.

INTRODUCTION

The sablefish, *Anoplopoma fimbria*, inhabits continental shelf and slope waters of the north Pacific and Bering Sea from Cedros Island, Baja California, Mexico, to the east coast of central Honshu, Japan (Allen and Smith 1988). Off the United States, sablefish is a member of the commercially important "deepwater complex" that includes Dover sole (*Microstomus pacificus*), shortspine thornyhead (*Sebastolobus alascanus*), and longspine thornyhead (*S. altivelis*). Annual U.S. commercial landings of sablefish for the ten-year period from 1982 to 1991 averaged 12,700 MT, with an ex-vessel value of $14.3 million in 1991 (Pacific Fishery Management Council 1992; Silverthorne 1992). Catch limitations imposed on the fishery (Methot 1992) point to the need for more information on the biology of sablefish; such information could lead to improved methods for assessing biomass.

The early life history of sablefish is unusual. The eggs and yolk-sac larvae are found almost exclusively at depths >200 m; at the end of the yolk-sac period the larvae migrate to the surface and are neustonic for the remaining larval period (Mason et al. 1983; Kendall and Matarese 1987). Early juveniles also inhabit surface waters, where

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they can grow as much as about 2 mm per day (Boehlert and Yoklavich 1985; Shenker and Olla 1986). The neustonic larvae and juveniles are broadly distributed and may be found farther than 200 n. mi. from the coast (Kendall and Matarese 1987). Little is known of the movements of surface-living juveniles and of the means by which they return to shelf waters for settlement.

The study reported herein is an integral part of an overall research program of the Coastal Fisheries Resources Division (CFRD), Southwest Fisheries Science Center (SWFSC), directed to the commercial groundfishes of the continental slope. Dover sole biology, including ichthyoplankton-based biomass estimation, has been a major focus of this work, and the data presented here were collected on cruises designed principally to that end. But because adult sablefish habitat, spawning season, and egg and larval distributions broadly overlap those of Dover sole, data derived from the samples could be used to evaluate ichthyoplankton methods for estimating biomass of sablefish. The objectives of this paper are (1) to provide baseline information needed for evaluating ichthyoplankton methods for estimating sablefish biomass, and (2) to illustrate this application by using existing data to make a preliminary biomass calculation.

Sablefish is a promising candidate for egg production biomass estimation because it is a determinant spawner with a short spawning season (Hunter et al. 1989). Egg production methods require precise information on the areal boundaries of egg distribution and on the vertical distribution of eggs in the water column (Lo et al. 1992). Also required are criteria for staging the eggs, from fertilization to hatching, to determine mortality rates during the egg stage (Lo et al. 1992, 1993). Lastly, a minimum level of spawning activity is required for an ichthyoplankton-based method to be successful. Sablefish are unusual in that the adult spawning habitat spans a huge latitudinal range. The species has been fished commercially from Cedros Island, Baja California, Mexico, to the Bering Sea, but it is unlikely that it spawns successfully throughout this range. Thus knowledge of latitudinal changes in reproductive success is critical for evaluating biomass methods, and also has important implications for fishery management. Abundance of larval stages is the best historic indicator of reproduction because the eggs are too deep to have been taken in routine plankton surveys.

This paper addresses the above topics as follows. First, we compare relative abundance of sablefish larvae in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton time series with data from the Alaska Fisheries Science Center (AFSC) ichthyoplankton time series in the northern California Current region (Kendall and Matarese 1987; Doyle 1992a, b) to determine the change in abundance with decreasing latitude, to define the southern limits of sablefish reproduction, and to provide background information for designing egg production survey cruises. Next, we present the results of CFRD cruises that yielded data on (1) the areal limits of egg distribution, (2) the abundance of eggs over and seaward of the slope, and (3) the vertical distribution of sablefish eggs. Next, we estimate daily egg production of sablefish off Oregon and central California by using abundance-at-age data and egg mortality rates generated from CFRD groundfish cruises. Finally, we estimate spawning female biomass for central California and central Oregon slope regions by using our daily egg production estimates and the daily weight-specific fecundity data listed by Hunter et al. (1989) and Macewicz and Hunter (1994).

MATERIALS AND METHODS

CalCOFI surveys provided information on the distribution and abundance of sablefish larvae in the mid and southern regions of the California Current (table 1). During 1951–84, 9,802 oblique plankton tows were taken in February–April, when sablefish larvae appear in the plankton in this region. Most annual surveys covered a grid of stations that extended from San Francisco, California, to San Juanico Bay, Baja California, and seaward to 160–250 n. mi. Details of CalCOFI sampling methods and laboratory procedures are described in Moser et al. 1993 and in a series of 24 data reports that list the ichthyoplankton and associated station data for each CalCOFI survey conducted from 1951 (Ambrose et al. 1987) to 1984 (Stevens et al. 1990). Information from CalCOFI surveys on the distribution of sablefish larvae in the neuston was obtained from 572 Manta net samples taken in 1980–84 during February–April.

Plankton survey cruises of the AFSC provided comparative information on the distribution of sablefish larvae north of the CalCOFI survey. This time series consists of data from ten cruises off the coasts of Washington, Oregon, and northern California during 1980–87 (Kendall and Clark 1982; Savage 1989; Doyle 1992a, b). Survey lines extended from the shelf to farther than 200 n. mi. offshore, with the number of stations per survey ranging from 91 to 125. Oblique bongo tows to 200 m depth and neuston tows were taken on each station. Neuston tows were made with a "Sameoto" sampler with a mouth opening 0.3 m deep by 0.5 m wide (Sameoto and Jaroszynski 1969). Mesh size for oblique and neuston tows was 505 μm.

Four types of plankton tows were made on the CFRD groundfish cruises: Manta (neuston), CalBOBL (shallow bongo oblique), DBOBL (deep bongo oblique), and MOCNESS (discrete depth strata) (table 1). Mesh size for all nets was 505 μm. The Manta net sampled the upper 15.5 cm of the water column; tow duration was

TABLE 1
Summary of Plankton Collections Made on CalCOFI Surveys and CFRD Groundfish Research Cruises Used in This Study, and Number of Occurrences of Sablefish Eggs (in Parentheses) and Larvae (in Brackets)

				Number of tows			
Cruise	Date	Locality	Plankton stations	Manta (neuston)	Shallow bongo	Deep bongo	MOCNESS-1
CalCOFI surveys	1951–84	Calif. Current region	31,214	1,702 [8]	31,214 [5]	—	—
CFRD groundfish cruises							
8701 JD	1/11–2/15 1987	Central Calif., slope	75	73 [6]	54	42 (15) [2]	20 (9) [2]
8803 JD	2/23–4/9 1988	Central Calif., slope	62	62 [6]	62	44	—
8903 JD	2/21–4/1 1989	Central Oregon, slope	60	54 [15]	59 (5) [2]	46 (32) [18]	—
9001 JD	1/12–1/24 1990	Southern & central Oregon, slope and offshore	33	33	33 (4)	28 (15)	—

15 min at ca. 1 knot. CalBOBL tows were made to a maximum depth of 210 m; DBOBL and MOCNESS tows were made to a maximum of 1500 m or to near-bottom depths over the continental slope. Pay-out (50 m/min) and retrieval (20 m/min) rates and wire angles (45°) were similar for CalBOBL and DBOBL tows. A temperature-depth sensor attached to the DBOBL permitted monitoring and immediate adjustment of the tow trajectory and provided a temperature profile of each tow (Lo et al. 1993). A MOCNESS with a mouth opening of 1 m^2 (Wiebe et al. 1985) was used in 1987 off central California to determine the vertical distribution of the eggs. The MOCNESS tow profiles were similar to those employed during DBOBL tows. The first MOCNESS net sampled the entire water column during pay-out. During retrieval, sequential nets sampled segments of the water column, usually in 80 m depth increments. In most tows the upper 160 m was sampled by a single net, since sablefish eggs were not expected to be found there.

Egg and larval abundance is expressed either as number per 1000 m^3 of water filtered or number per 10 m^2 of surface area. Usually, number per unit volume is used for Manta tows. Abundance of eggs or larvae in oblique unstratified tows is expressed as the number per 10 m^2 of surface area, obtained by multiplying the number of eggs or larvae captured in a tow by a standard haul factor (*SHF*). The equation for *SHF* is:

$$SHF = \frac{10D}{V}$$

where, D = depth (m) of haul and V = total volume (m^3) of water filtered (Smith and Richardson 1977). In MOCNESS tows, egg or larval abundance for individual strata is presented as number per 1000 m^3 or as number per 10 m^2 of surface area. In the latter case, "surface area" refers to the upper limit of the stratum, and abundance is estimated for a discrete section of the water column. In one instance (larval length-frequency analysis), we expressed abundance for Manta tows as the number per 10 m^2 of surface area, computed from the *SHF*.

CFRD groundfish cruises off central California occupied stations over the continental slope and employed bottom trawls and a suite of plankton samplers (figure 1). Cruise 8701 JD (January–February 1987) consisted of a series of transects from Point Sur to just north of Point Conception, California. Cruise 8803 JD (February–April 1988) surveyed the same area using a stratified random station pattern (three bottom-depth strata).

Two CFRD groundfish cruises were conducted off Oregon. Cruise 8903 JD (February–April 1989) was a combined plankton sampling/bottom trawling cruise consisting of nine transects over the central Oregon continental slope (figure 1). Cruise 9001 JD (January 1990) consisted of four evenly spaced transects from Cape Blanco to Newport, Oregon, with stations beginning at the shelf edge and extending seaward to a maximum distance of about 170 n. mi. Station spacing was at 10 n. mi. intervals over the slope and at 20 n. mi. intervals seaward of the slope.

Sablefish eggs were distinguished from those of other species according to characters described by Kendall and Matarese (1987), and by additional features described herein. Larvae were identified by means of the descriptions of Kobayashi (1957), Ahlstrom and Stevens (1976), Kendall and Matarese (1987), and Matarese et al. (1989).

The following staging criteria for the eggs were modified from those used for northern anchovy, *Engraulis mordax* (Moser and Ahlstrom 1985) and for Dover sole (Lo et al. 1993):

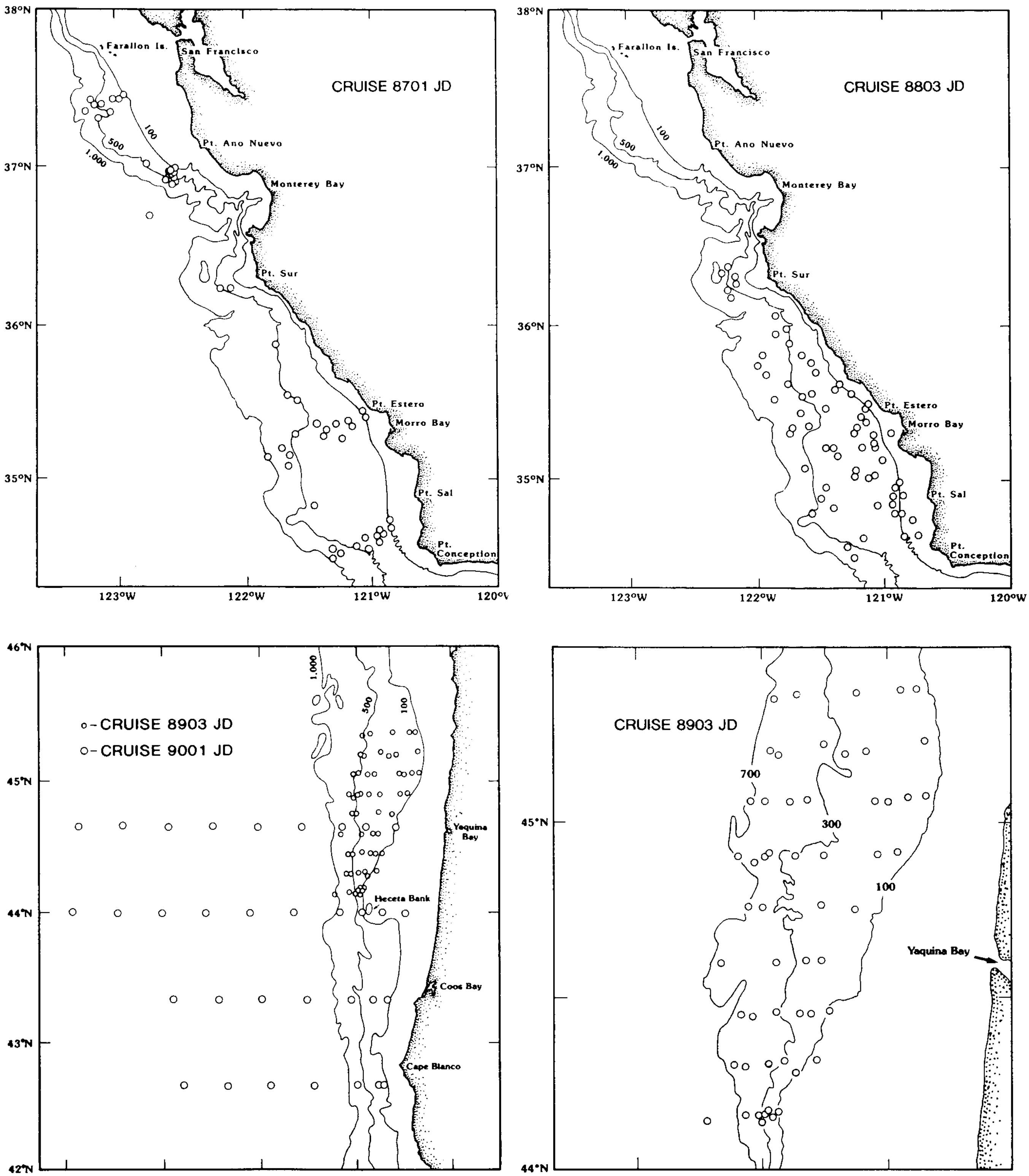

Figure 1. Stations (*circles*) occupied on Coastal Fisheries Resources Division (CFRD) groundfish research cruises. Isobaths are in fathoms.

St. I Prior to the first cell division of embryo.
St. II First cell division and subsequent blastodisc formation.
St. III Blastomeres are minute, and blastodisc has the appearance of tissue.
St. IV Germ ring extends 1/3 of the way around yolk sac (i.e., the blastoderm encloses 1/3 of yolk sac).
St. V Germ ring extends 2/3 of the way around yolk sac (i.e., the embryo encloses 2/3 of the yolk sac).
St. VI Blastopore closed.
St. VII Tail has a rounded tip separated from yolk mass.
St. VIII Free length of tail equals 1/2 head length (head length = distance from tip of snout to posterior edge of cerebellum).
St. IX Free length of tail equals full length of head.
St. X Tip of tail extends to 1/2 yolk-sac diameter.
St. XI Tip of tail extends to 3/4 yolk-sac diameter.

Assignment of age to staged eggs required information on the temperature-dependent development rate for each stage. Data on developmental rates for sablefish eggs were reported by Alderdice et al. (1988a, b), who incubated field-collected sablefish eggs in aquaria. Because Alderdice's staging criteria were different from ours and because his temperature range was lower, we used the temperature-development relationship for Dover sole, a species with similar egg (yolk) size developing at similar temperatures[1]; rate constants in the model were adjusted for the faster development time of sablefish (see Elliot et al. 1987; Pauly and Pullin 1988).

For Dover sole, the time required to reach stage XI, the hatching stage of sablefish, is 29 days at 5°C. Since sablefish reach this stage in 14 days, we assumed that the developmental rate for sablefish eggs at any stage is twice the rate of Dover sole. We checked the accuracy of our assumptions and model by comparing the time to yolk-plug closure, a stage criterion used by Alderdice and by us. At 5°C, sablefish eggs reached this stage in 151 hr in Alderdice's (1988a) experiment and in 144 hr in our model.

Eggs from both DBOBL and MOCNESS tows were used in egg production biomass calculations for central California; only DBOBL tows were available for Oregon. For the MOCNESS samples, the temperature at mid-stratum depth was used in the equation to estimate age of each staged egg. Temperature at depth for each DBOBL tow was obtained from the continuous temperature-depth record. We used the temperature at mid-depth of each tow for aging eggs from these tows.

[1]Moser, H. G., R. L. Charter, P. E. Smith, N. C. H. Lo, D. A. Ambrose, S. R. Charter, C. A. Meyer, E. M. Sandknop, and W. Watson. Distribution and abundance of eggs and larvae of Dover sole, *Microstomus pacificus*, in the California Current region and their application to biomass estimation. In prep.

RESULTS

Egg Identification

Early planktonic eggs of sablefish are large, have a homogeneous, transparent yolk; a narrow perivitelline space; a smooth shell surface; and no oil globule (Mason et al. 1983; Kendall and Matarese 1987; Matarese et al. 1989). Dover sole eggs are similar to those of sablefish, and there was a size overlap in our samples. In a sample of 200 Dover sole eggs from southern California to Oregon, egg diameter ranged from 1.96 to 2.64 mm. Egg diameter in a sample of 152 sablefish eggs from the same region ranged from 1.90 to 2.22 mm, with a mean of 2.09 mm (SD = 0.06 mm). Usually, the perivitelline space is narrower in sablefish eggs than in Dover sole eggs, and the yolk of sablefish eggs is yellow to orange, in contrast to the pale yellow yolk of Dover sole eggs. Moreover, the yolk of sablefish eggs develops small vesicles of varying size, particularly after epiboly is completed, in contrast to the homogeneous yolk of Dover sole. At hatching, sablefish have a large yolk sac and are at a developmental stage similar to that in northern anchovy, even though the two species differ greatly in size.

Distribution

CalCOFI and AFSC time series. Sablefish eggs were not found in oblique plankton tows taken in the upper 200 m on CalCOFI surveys, because the eggs usually occur deeper than 200 m and because much of the CalCOFI survey area is south of the principal reproductive range of sablefish. Also, sablefish larvae are rare in these tows; of 9,802 oblique plankton tows taken off California and Mexico during 1951–84 in February–April, only five contained sablefish larvae (table 1; figure 2). Occurrence in neuston tows was only slightly greater in the same region: of 668 Manta net tows taken during 1980–84 in February–April, occurrence was 5.7% off central California (202 tows, including 96 tows taken during CFRD cruises 8701 JD and 8803 JD); 0.9% off southern California (216 tows); and 0% off Mexico (250 tows).

Decrease in occurrence and abundance of sablefish larvae from north to south in the California Current region is apparent when AFSC neuston tow data are compared with data from CalCOFI surveys and CFRD groundfish cruises (figure 3).[2] Mean abundance decreased by one-half from Washington to northern Oregon and again from northern Oregon to southern Oregon, then decreased by about 80% from southern Oregon to north-

[2]Comparisons of the performance of the "Sameoto" sampler and the Manta net have not yet been done, thus we are not able to evaluate their relative effectiveness in capturing sablefish larvae. Although the quantities in the two samplers are not strictly comparable and the abscissa in figure 3 is not metric, the results for each net show that incidence and abundance decrease equatorward.

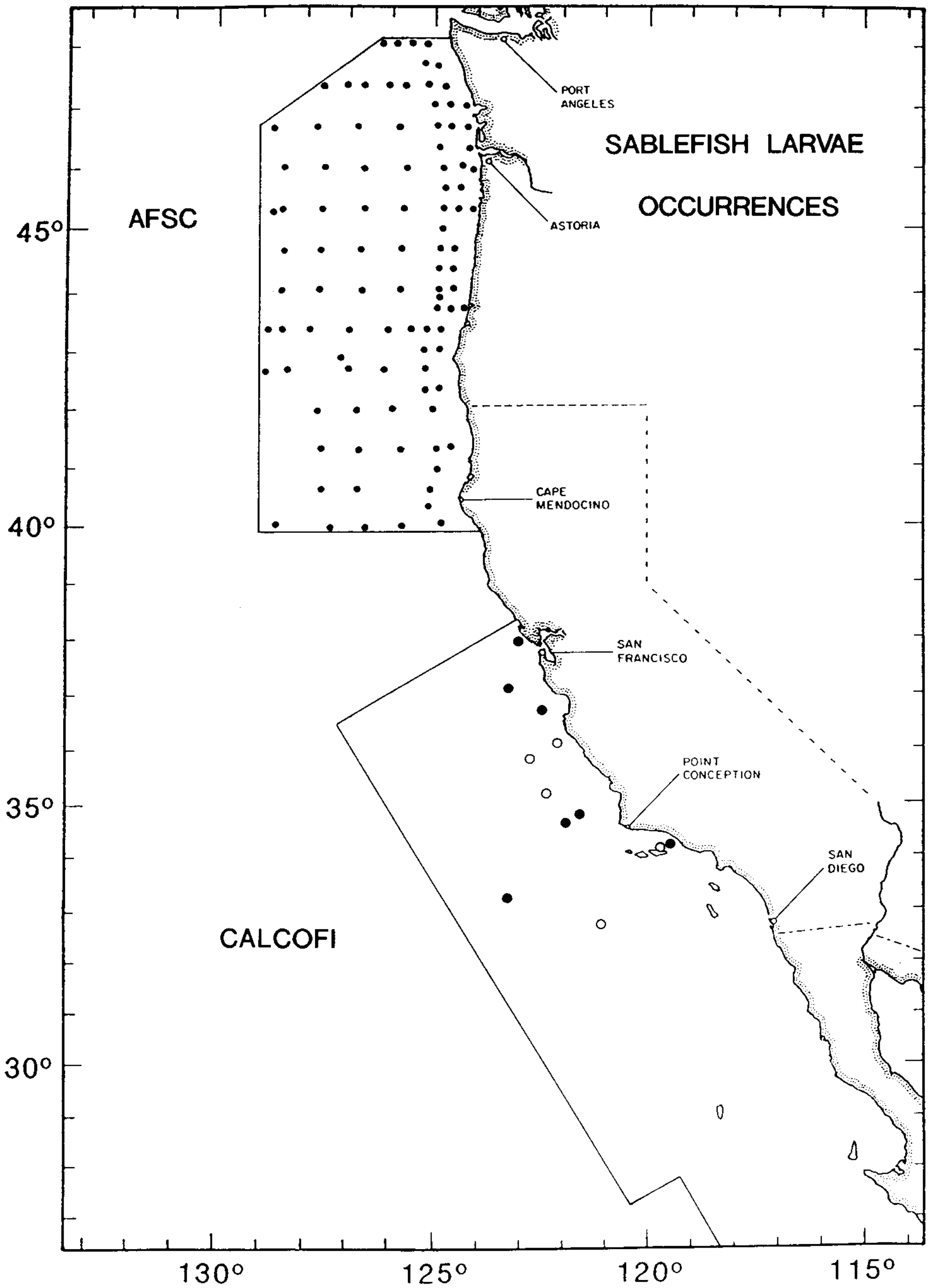

Figure 2. Sablefish larvae taken in plankton surveys of the Alaska Fisheries Science Center (AFSC) and in CalCOFI survey samples. The boundaries of both surveys are outlined. In the AFSC survey region, *solid circles* indicate positive stations for neuston samples. In the CalCOFI survey region, *solid circles* indicate positive stations for neuston (Manta) net samples; *open circles* indicate positive stations for oblique net samples.

ern and central California and by almost 100% from central California to southern California. Larvae have not been captured in neuston tows south of the U.S.-Mexican border. The trend for percentage occurrence shows a similar steep decline from north to south (figure 3).

Latitudinal shifts in peak larval abundance suggest that spawning progresses seasonally from south to north. Mean larval abundance (number per 1000 m^3 for all tows in the region) is highest in February off central California (table 2). Abundance is highest in March off northern California and southern Oregon (probably the peak month, although data are not available for February). Abundance peaks sharply in April off northern Oregon and even more sharply off Washington (table 2). Also, the offshore extent of sablefish larvae diminishes with decreasing latitude (figure 4). In AFSC neuston tows, mean larval abundance was high off Washington and Oregon in successive offshore zones; off northern

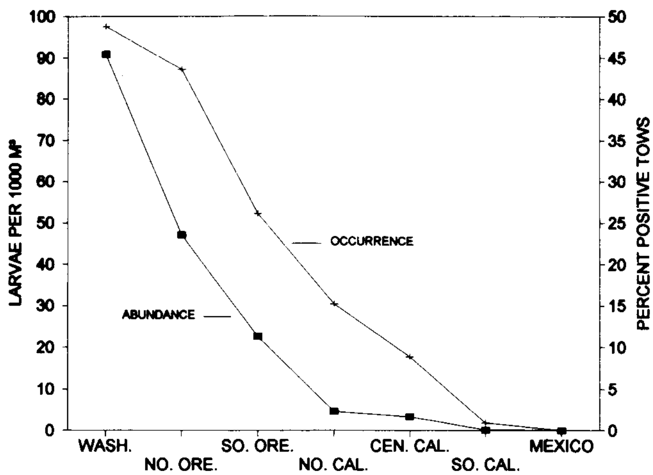

Figure 3. Mean occurrence (percent positive tows) and abundance (number/1000 m^3) of sablefish larvae in neuston samples. Data from Washington to northern California are based on samples taken during March–May on cruises conducted in 1982–87 by the AFSC. Data from central California to Mexico are based on Manta net samples from CalCOFI plankton surveys in 1980–84 during February–April. The central California data include Manta tows taken on CFRD groundfish cruises 8701 JD and 8803 JD. Wash. = Washington; No. Ore. = northern Oregon (north of Newport); So. Ore. = southern Oregon (south of Newport); No. Cal. = northern California (south to Point Delgada); Cen. Cal. = central California (south to Point Conception); So. Cal. = southern California (south to U.S.–Mexico border); Mexico (south to San Juanico Bay, Baja California).

California abundance peaked between 96 and 127 n. mi. from the coast. In our Manta net samples off central California, larvae were found only in water over or adjacent to the slope (figure 4).

CFRD groundfish cruises. On Cruise 8701 JD, abundance of sablefish eggs was low in DBOBL and MOCNESS tows on the four major transects, with nearly all eggs taken at stations between the 500 fath. (915 m) and 1000 fath. (1830 m) isobaths (table 3; figure 5a). The inshore limits of egg distribution were defined, but the offshore limits were not. Few yolk-sac larvae were collected in two DBOBL and two MOCNESS tows along the 500 fath. isobath on three of the four major transects (table 3; figure 5b). Neustonic larvae occurred, also in relatively low abundance, only in the southern region of the survey pattern between the 500 fath. and 100 fath. (183 m) isobaths (table 3; figure 5b). On Cruise 8803 JD, no sablefish eggs or yolk-sac larvae were taken in any of the DBOBL tows; neustonic larvae were taken in six Manta tows in the southern region of the pattern (table 3). Five of the six positive tows were made along the 100 fath. (187 m) bottom contour.

On Cruise 8701 JD, twenty MOCNESS tows taken over the midslope region yielded information on the vertical distribution of sablefish eggs. Of the nine MOCNESS tows positive for sablefish eggs, five sampled equivalent depth strata and could be compared directly (table 4; figure 6). In these tows, eggs were taken between 160 and 800 m; abundance was highest between 240 and 400 m (ca. 2 eggs/1000 m^3). Mean abundance was slightly lower (ca. 1.3 eggs/1000 m^3) in the 400–480 m stratum and fell off sharply below 480 m. Mean temperatures for the three strata of highest abundance ranged from 6.0° to 7.7°C (table 4). A similar pattern is apparent when stratum mid-depth is plotted against mean egg abundance for all nine MOCNESS tows positive for sablefish eggs (figure 7a). A plot of individual egg age against stratum mid-depth for all positive tows shows that eggs were not stratified according to age (figure 7b). Two larvae were captured in these samples—a 4 mm yolk-sac larva in a 280–360 m sample and a 7 mm larva in a 0–160 m sample.

On Cruise 8903 JD, sablefish eggs were taken in DBOBL tows on all transects, with nearly all positive

TABLE 2
Seasonal Abundance (Mean No./1000 m^3 for All Tows in Each Region) of Sablefish Larvae in Surface Tows (Number of Tows in Parentheses) from Washington to Central California

Region	Jan.	Feb.	Mar.	Apr.	May
	Month				
Washington	0	—	37.8	158.1	16.4
	(18)	(0)	(27)	(81)	(54)
Northern	0	—	25.4	87.9	20.9
Oregon	(21)	(0)	(30)	(68)	(81)
Southern	0	—	45.2	22.4	17.8
Oregon	(21)	(0)	(30)	(8)	(142)
Northern	0	—	21.9	11.4	2.1
California	(28)	(0)	(16)	(22)	(173)
Central	0	5.2	1.4	1.1	0
California	(102)	(107)	(59)	(36)	(55)

Data from Washington to northern California are based on neuston net samples taken during 1980–87 by the Alaska Fisheries Science Center (Kendall and Clark 1982; Doyle 1992b).

Data from central California are based on Manta net samples from CalCOFI plankton surveys in 1980–84 and CFRD groundfish cruises 8701 JD and 8803 JD.

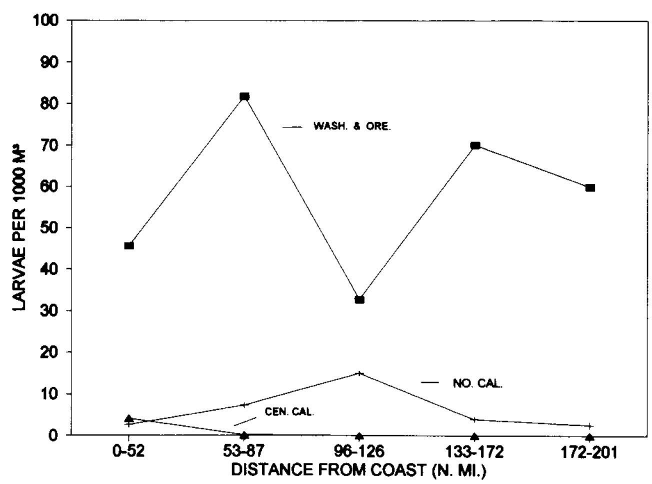

Figure 4. Mean abundance (number/1000 m^3) of sablefish larvae in AFSC and CalCOFI neuston tows for various offshore zones. See figure 3 caption for region boundaries.

TABLE 3
Mean Abundance (All Tows) of Sablefish Eggs and Larvae in Plankton Tows Taken on CFRD Groundfish Cruises off Central California and Oregon

	Eggs		Larvae		
	Shallow bongo (no./10 m^2)	Deep bongo and MOCNESS (no./10 m^2)	Manta (neuston) (no./1000 m^3)	Shallow bongo (no./10 m^2)	Deep bongo and MOCNESS (no./10 m^2)
Central California					
8701 JD	0	2.6	4.3	0	0.2
8803 JD	0	0	3.7	0	0
Oregon					
8903 JD	0.6	30.1	17.6	0.3	4.3
9001 JD	0.7	3.8	0	0	0

Larvae taken in deep bongo and MOCNESS tows were yolk-sac stage; those taken in shallower samples were later-stage.

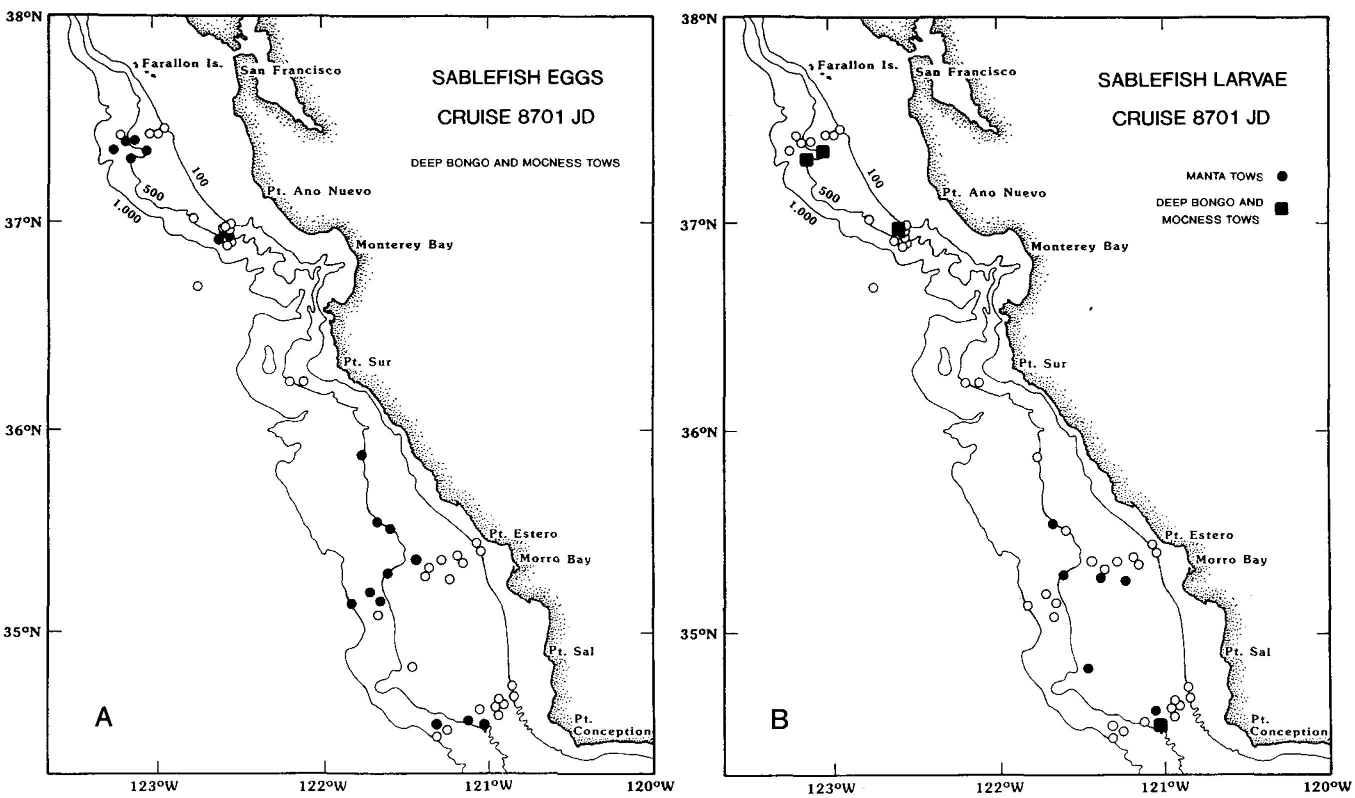

Figure 5. Sablefish eggs and larvae taken on CFRD Cruise 8701 JD. *Open circles* indicate sampling stations. In *A*, *solid circles* indicate stations where deep bongo tows (DBOBL) and MOCNESS tows were positive for eggs. In *B*, *solid circles* indicate stations where Manta tows were positive for larvae; *solid squares* indicate stations where DBOBL tows were positive for larvae. Isobaths are in fathoms.

stations between the 300 fath. (550 m) and 700 fath. (1280 m) isobaths (figure 8a). Mean egg abundance in DBOBL tows was ten times greater than for Cruise 8701 JD off central California (table 3).

Some characteristics of the dispersion of sablefish eggs are apparent when data are stratified according to egg age and bottom depth (table 5). No day "0" or day "1" eggs were captured in this set of samples. Either these eggs were not in the sampled volume at all or were so compact at the time of fertilization that they had not dispersed sufficiently to be encountered in this small sample set. The lower incidence of sablefish eggs of all ages in the shallowest zone (0–456 m) indicates that either there was little drift of eggs into the water over that zone or egg mortality was virtually total for eggs which drifted shoreward into that zone. It is unlikely that any spawning occurred in the shallow zone, since no reproductively active females were captured in trawls from those depths during the cruise (John Hunter, pers. comm.). In zone 2 (457–1004 m) and zone 3 (1005–1280 m), the abrupt rise to a maximum incidence at day 3 may be attributed to dispersal after spawning and fertilization. The gradual decline in occurrence from days 3 to 8 may be attributed to continued dispersion and

TABLE 4
Vertical Distribution of Sablefish Eggs from Five MOCNESS Tows Containing Sablefish Eggs on CFRD Groundfish Cruise 8701 JD, off Central California, January 26–30, 1987

Stratum (m)	Mean no. eggs/1000m^3	Standard deviation	Mean temperature (°C)	Temperature range (°C)	Total volume filtered (m^3)
0–160	0	—	10.9	8.6–13.3	7317
160–240	0.39	0.88	8.5	7.9–9.3	4493
240–320	2.11	1.30	7.7	6.9–8.5	4665
320–400	2.02	2.18	6.7	6.2–7.3	4432
400–480	1.29	1.92	6.0	5.6–6.4	5038
480–560	0.22	0.50	5.5	5.0–6.0	4488
560–640	0	—	5.1	4.7–5.5	3841
640–800	0.11	0.26	4.8	4.3–5.1	7691

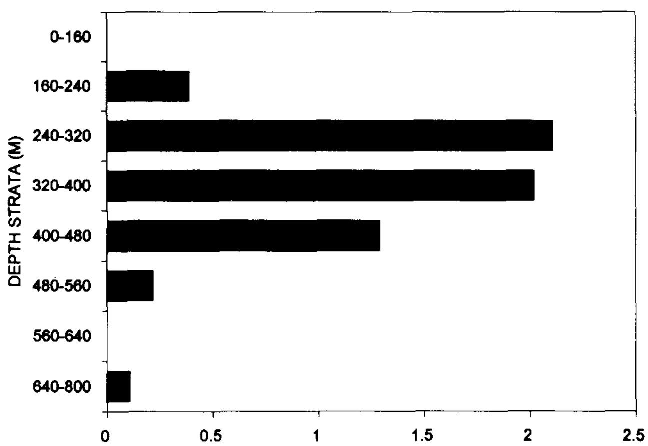

Figure 6. Vertical distribution of sablefish eggs in five MOCNESS tows that sampled equivalent depth strata off central California during CFRD Cruise 8701 JD. Mean egg abundance (number/1000 m^3) is shown for eight strata associated with each tow.

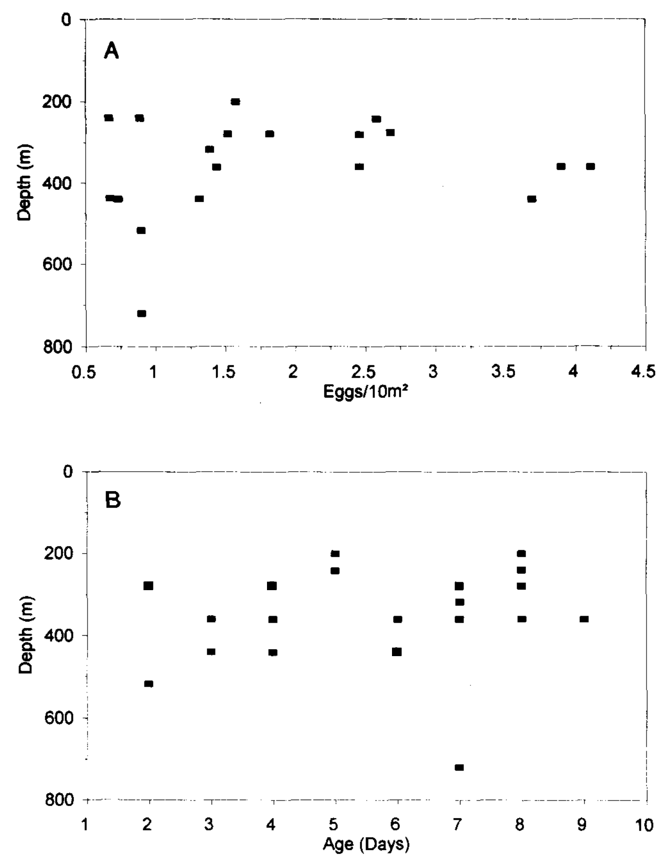

Figure 7. Vertical distribution (*A*) and age/depth distribution (*B*) of sablefish eggs captured on nine positive MOCNESS tows taken off central California during CFRD Cruise 8701 JD. In *A*, egg abundance (number/10 m^2) is plotted against the mid-stratum depth of each positive net; in *B*, ages of eggs are plotted against mid-stratum depth of each positive net. Some points may represent more than one egg.

mortality; the virtual disappearance at 13 days results primarily from mortality and hatching. A better description of spawning time and early stages of dispersal would require more samples.

Eggs were taken in shallow bongo tows at four stations, all in the southern part of the survey area near Hecate Bank, where complex currents might be responsible for their presence in the upper 200 m (figure 8b). Each of these tows captured only single eggs.

The distribution of yolk-sac larvae from DBOBL tows was similar to that of the eggs, and mean abundance was >40 times higher than off central California (table 3; figure 8c). Two shallow bongo tows contained sablefish larvae; these larvae, at the end of the yolk-sac stage (8–9 mm size), were in transit to the surface. Neustonic larvae were found at stations scattered over the entire survey area, and had a mean abundance four times greater than off central California (table 3; figure 8d). Size-frequency distributions of sablefish larvae differ for the three types of sampling gear (figure 9). Larvae captured in deep oblique tows were in the yolk-sac stage and ranged from 5 to 8 mm; larvae from surface nets were 8–18 mm; and the few larvae captured in shallow bongo nets were 8–9 mm—the size overlap for the other two nets (figure 9). All yolk-sac larvae captured were in poor condition; the greatest degree of disintegration appeared in the earliest yolk-sac stages. Disintegration and extrusion of the fragile early yolk-sac larvae are the most likely explanation for their low abundance. Early yolk-sac larvae

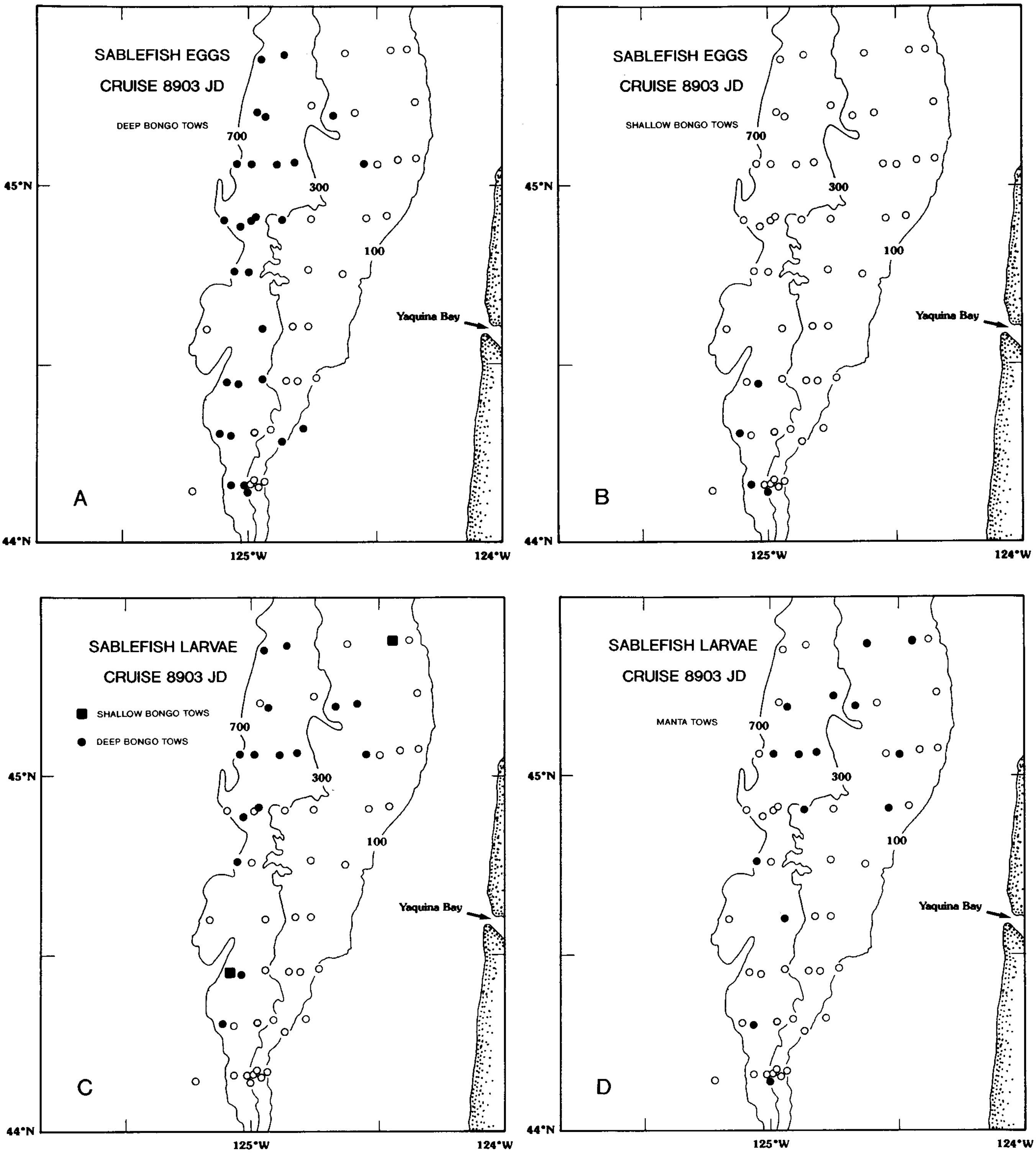

Figure 8. Sablefish eggs and larvae taken on CFRD Cruise 8903 JD. *Open circles* indicate sampling stations. In *A*, *solid circles* indicate stations where deep bongo (DBOBL) tows were positive for eggs. In *B*, *solid circles* indicate stations where shallow bongo (CalBOBL) tows were positive for eggs. In *C*, *solid circles* indicate stations where DBOBL tows were positive for yolk-sac larvae; *solid squares* indicate stations where CalBOBL tows were positive for post-yolk-sac larvae. In *D*, *solid circles* indicate stations where Manta tows were positive for post-yolk-sac larvae. Isobaths are in fathoms.

TABLE 5
Relative Frequency of Occurrence of Sablefish Eggs of Various Ages in Deep Bongo Oblique Plankton Tows on CFRD Groundfish Cruise 8903 JD off Central Oregon, February 22 to March 31, 1989

Age (days)	Zone 1 (0–456 m)	Zone 2 (457–1004 m)	Zone 3 (1005–1280 m)	All zones
0	0	0	0	0
1	0	0	0	0
2	0	0.16	0.05	0.10
3	0.07	0.33	0.36	0.31
4	0.07	0.25	0.11	0.18
5	0.00	0.24	0.20	0.19
6	0.00	0.22	0.18	0.18
7	0.07	0.16	0.11	0.13
8	0.00	0.09	0.07	0.07
9	0.00	0.07	0.05	0.05
10	0.07	0.11	0.00	0.06
11	0.00	0.02	0.05	0.03
12	0.00	0.02	0.05	0.03
13	0.00	0.00	0.02	0.01
Total	0.13	0.67	0.57	0.56

Data are stratified into three zones based on the bottom depth of the tow locality.

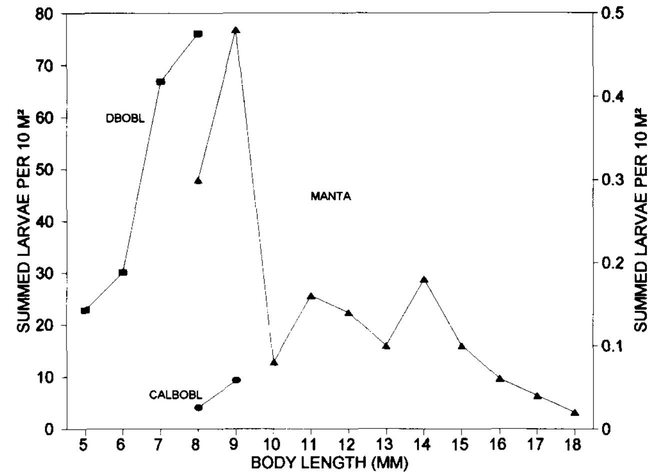

Figure 9. Length frequencies of sablefish larvae captured in Manta (*solid triangles*), deep bongo (*solid squares*), and shallow bongo (*solid ellipses*) nets on CFRD Cruise 8903 JD. Numbers on the left ordinate are summed abundance (larvae/10 m^2) in bongo tows; numbers on the right are summed abundance (larvae/10 m^2) in Manta tows.

should be fully vulnerable to the sampling gear and should be more numerous than more advanced yolk-sac stages.

Cruise 9001 JD examined offshore distribution; sablefish eggs were taken in DBOBL tows at slope stations of all transects and seaward to the next-to-last station (ca. 150 n. mi. offshore) on all but the southernmost transect (figure 10). Mean abundance of eggs over the slope was more than twice that of tows seaward of the slope: ca. 7 eggs/10 m^2 versus ca. 3 eggs/10 m^2. Eggs from samples over the slope ranged in age from 2 to 9 days, with 2- and 3-day-old eggs predominating; eggs seaward of the slope ranged from 3 to 7 days old, with 5- and 6-day-old eggs slightly more abundant. Eggs were taken in shallow bongo tows at five stations scattered over the survey pattern (figure 10). Mean abundance in DBOBL tows was one-eighth that of DBOBL tows made exclusively over the slope the previous year (table 3). No yolk-sac or neustonic larvae were captured in any tows.

Biomass Estimation

Mean abundance at age (eggs/10 m^2/day) was calculated for Cruise 8701 JD off central California and for the two cruises off Oregon (8901 JD and 9001 JD). A mortality curve was fitted to these data to estimate the daily production of newly spawned eggs (P_0/10 m^2/day) for each cruise (figure 11; table 6). The data were fitted to a nonlinear regression equation: $P_t = P_0 \cdot e^{(-Z \cdot t)}$, where P_t = daily egg production at age t; P_0 = daily egg production at age 0; and Z = instantaneous daily egg mortality. P_0 was highest (7.3) for cruise 8903 JD off Oregon and lowest (1.1) for the winter cruise off Oregon (figure 11). P_0 for central California was midway between these (3.5). Instantaneous mortality rates (Z) were similar for the two Oregon cruises: 0.25 for 8903 JD and 0.28 for 9001 JD. The rate was considerably higher (0.47) for central California. Variation was relatively low for Cruise 8903 considering the small sample size.

Egg production data from Cruise 8903 JD can be used for a rough estimation of spawning biomass for this section of the central Oregon coast. According to the calculations above, the daily production rate of newly spawned sablefish eggs is 7.3/10 m^2/day, or 0.73/1 m^2/day. From Macewicz and Hunter (1994), the potential annual fecundity for a 2,500 g female sablefish is 276,346 eggs, or 111 eggs/g/year. The exact length of the spawning season is unknown, as is the seasonal distribution of spawning rate, but available data suggest that the spawning season lasts from 90 to 120 days (John Hunter, pers. comm.). For convenience, in our preliminary biomass calculation we assumed that the spawning season was 111 days and that the fecundity was decreasing linearly at the time of the survey. Given these assumptions, the estimated daily egg production rate by sablefish females is 1 egg/g of female/day. Thus, under each m^2 of sea surface there are 0.73 g of spawning female sablefish, or 0.73 tons/km^2. The survey area was 56 × 170 km, or 9520 km^2. This would give about 6950 tons of female biomass for the central Oregon survey area.

DISCUSSION

Evaluation of Egg Production Methods for Sablefish

Our estimate of about 0.73 tons/km^2 of female sablefish in the central Oregon area surveyed during 1989 may be compared with trawl-based estimates of sable-

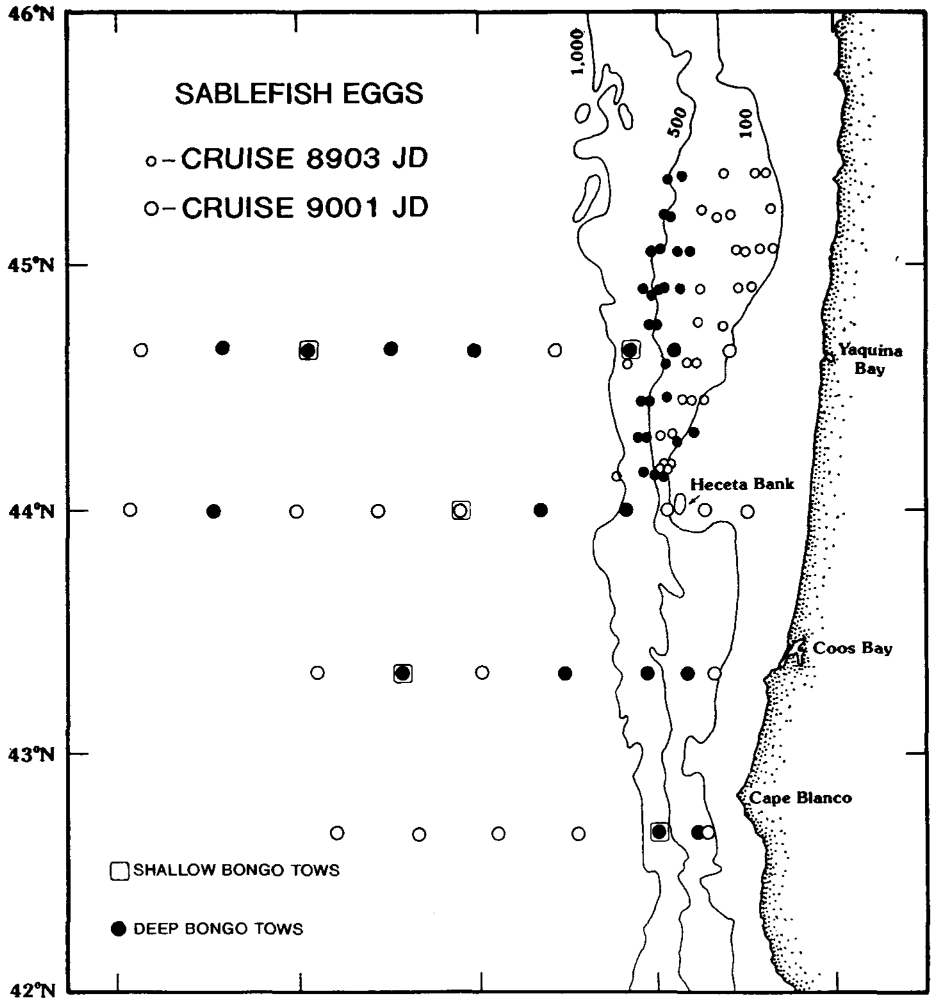

Figure 10. Sablefish eggs taken on CFRD Cruises 8903 JD (*small circles*) and 9001 JD (*large circles*). *Open circles* indicate sampling stations where deep bongo tows were negative. *Solid circles* indicate stations where deep bongo tows were positive; *open squares* enclose stations where shallow bongo tows were positive. Isobaths are in fathoms.

fish biomass densities for regions along the west coast of the United States and Canada. Methot (1992) estimated 3.87 tons/km^2 for the Vancouver-Columbia area (International North Pacific Fisheries Commission statistical area) and 1.41 tons/km^2 for the Eureka area. These estimates represent age 2+ males and females. Butler et al. (1989) gave an estimate of 1.33 tons/km^2 of adult and subadult males and females for the 250–549 fath. (458–1005 m) depth zone off central California. Our biomass density estimate for the central Oregon coast seems reasonable, especially if it were adjusted to account for males and subadults.

The reproductive biology and early life history of the sablefish make it ideally suited for egg production biomass estimation. Simultaneous sampling of planktonic and ovarian eggs is not necessary because potential annual fecundity can be estimated in the fall, before the spawning season (Hunter et al. 1989; Macewicz and Hunter 1994). Planktonic eggs are distinct and readily identifiable. The unique vertical distribution of the eggs below the zone of high primary and secondary production makes it possibile to use discrete depth sampling to reduce sorting time. Despite their relatively low fecundity, sablefish produce eggs that can be sampled effectively with plankton nets. This is a consequence of their dispersion and persistence in the water column and is in sharp contrast with the considerable patchiness of clupeoid eggs (Smith 1973; Smith and Hewitt 1984, 1985; Mangel and Smith 1990).

The fact that the eggs disperse within a confined vertical range may contribute to their availability to plankton tows. Low ambient temperatures in this stratum and a 2-week incubation period certainly contribute to the persistence of the eggs. The high incidence of eggs and

TABLE 6
Daily Egg Production (P_0) and Daily Instantaneous Mortality Rate (Z) for Sablefish Eggs from Three CFRD Groundfish Research Cruises

Parameter	Estimate	Standard error	Coefficient of variation
Cruise 8701 JD Central Calif.			
P_0/10 m^2	3.50	1.19	0.34
IMR (Z)	0.47	0.10	0.22
Cruise 8903 JD Oregon			
P_0/10 m^2	7.34	1.04	0.14
IMR (Z)	0.25	0.04	0.16
Cruise 9001 JD Oregon			
P_0/10 m^2	1.14	0.43	0.38
IMR (Z)	0.28	0.12	0.43

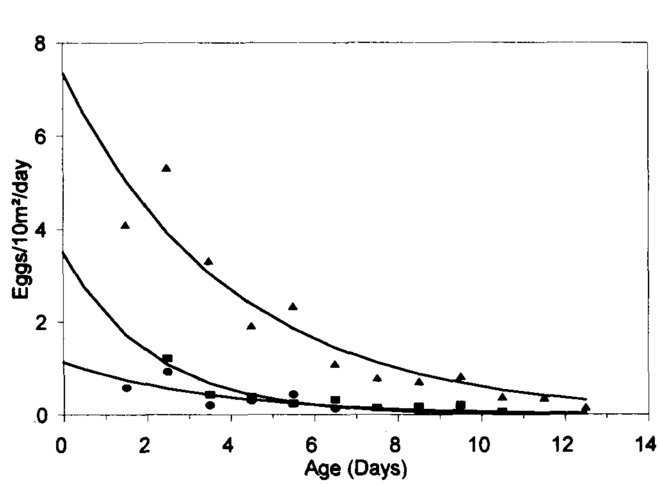

Figure 11. Mortality curve for sablefish eggs captured in deep bongo and MOCNESS tows during CFRD Cruise 8701 JD (*squares*) and in deep bongo tows during Cruise 8903 JD (*triangles*) and Cruise 9001 JD (*ellipses*). Daily egg production (eggs/10 m^2/day) is plotted against egg age (days) for the three cruises. The data were fitted to a nonlinear regression equation, $P_t = P_0 \cdot e^{(-Z \cdot t)}$, where P_t = daily egg production at age t, P_0 = daily egg production at age 0, and Z = instantaneous daily egg mortality.

the relatively low variance for estimates of daily egg production and mortality are remarkable considering the relatively small sample size and low egg abundance.

Most of the information required to plan an egg production biomass estimation survey for sablefish is available. We know that the inshore boundary of egg distribution corresponds approximately to the slope/shelf break. Since the minimum depth for eggs is about 200 m, any eggs over the shelf would be near or on the substrate and probably would not survive. We need to establish the offshore limits of egg distribution and to determine how far from the slope the eggs from slope-living females can be expected to appear. To adequately sample the offshore eggs, we need to establish the proper density for survey stations seaward of the slope.

Plankton sampling for a sablefish egg production survey off Oregon and Washington should be conducted during the peak spawning period (February–March), a time when storms frequently sweep through the region. Off Alaska, the survey would be slightly later in the spring (Kendall and Ferraro 1988). The survey vessel would have to be large and seaworthy to complete the extensive station pattern. Only a limited section of the coast could be surveyed unless more than one vessel was used.

Clearly, our estimate of biomass is heuristic, and some of the methods of calculation are not recommended if one were to embark on a formal estimate of sablefish biomass. For example, the assumption of linear reduction of population fecundity is particularly weak. Despite these reservations, the central conclusion to be drawn from the analysis is that sablefish is an ideal candidate for egg production biomass estimation.

Early Life History Adaptations

The results of this study and of preceding ones (see Mason et al. 1983; Kendall and Matarese 1987; McFarlane and Beamish 1992) reveal the uniqueness of sablefish early life history and invite discussion about the potential adaptive nature of these specializations. The deep, vertically constrained distribution of the eggs is unusual, if not unique, among coastal fishes. Intuitively, one would suspect that this part of the water column would have fewer egg predators and, consequently, that egg mortality rates would be reduced. On the contrary, egg mortality is 2.5 to 5 times higher than in Dover sole, a member of the "deep-water complex" whose similar-sized eggs are found in the upper water column (Lo et al. 1992, 1993; Moser et al.[3]). There appear to be no copepods in the 200–700 m depth stratum that are likely to specialize on fish eggs of this size (M. D. Ohman, Scripps Institution of Oceanography, pers. comm.), but recent findings (Bailey et al. 1993) that gammarid amphipods prey at a high rate on eggs and yolk-sac larvae of walleye pollack (*Theragra chalcogramma*) suggest that invertebrate predators may contribute significantly to sablefish egg and posthatching mortality. Other likely predators are mesopelagic fishes, such as members of the family Myctophidae, that may be able to locate patches of newly spawned eggs as they rise in the water column, and feed on the eggs as they disperse.

Some questions remain to be answered about the duration of the yolk-sac larval period and the vertical distribution of the yolk-sac larvae. McFarlane and Beamish (1992) have hypothesized from laboratory experiments that newly hatched yolk-sac larvae sink to a depth of 1000 m and begin to ascend gradually within about a week after hatching. They estimate that 50% of the yolk is used at about 2 weeks after hatching and that the yolk is fully used at about 40 days after hatching, when the

[3]See footnote 1 on page 148.

larvae have ascended to about 200 m. This scenario has yet to be confirmed by discrete-depth sampling. We know that larvae ascend rapidly through the upper 200 m, since they are extremely rare in time series of oblique plankton tows from this depth zone. The deep distribution of yolk-sac larvae hypothesized by McFarlane and Beamish (1992) may be adaptive from the standpoint of reduced predation, as would rapid passage through the upper mixed layer to the neustonic habitat.

Potential adaptive advantages of inhabiting the neuston have been discussed thoroughly (e.g., Zaitsev 1970; Hempel and Weikert 1972; Moser 1981; Doyle 1992a). Certainly, the high growth rates reported for sablefish larvae and early juveniles (Boehlert and Yoklavich 1985) support the notion that the neuston is a favorable trophic environment. The mesoscale patchiness of sablefish larvae apparent from our observations, from the AFSC time series (Kendall and Matarese 1987), and from the research of McFarlane and Saunders (in press) suggests that sablefish may be aggregating in response to prey concentrations associated with frontal features such as convergence zones and slicks (see Doyle 1992a). Indeed, the possibility of such adaptive contagious distribution prompted the CFRD to develop a research plan to study the fine-scale distribution of sablefish larvae in relation to the Columbia River plume.[4] The hypothesized association of sablefish larvae with this plume might also provide a mechanism for shoreward movement of larvae in concert with the seasonal shoreward progression of the plume.

Sablefish occupy a variety of habitats along the continental slope of the north Pacific; if both latitude and bathymetry are considered, sablefish are the most widely distributed commercial groundfish in the north Pacific. Virtually every habitat in this region is occupied by some ontogenetic stage of the species. Certainly the evolution of a highly vagile neustonic larva has contributed to the widespread distribution of the species. In fact, this vagility characterizes later ontogenetic stages. Pelagic juveniles, up to about 30 cm, have been captured in large numbers at considerable distance from the coast (Brodeur and Pearcy 1986), and recoveries of tagged sablefish on isolated seamounts (Alton 1986; Parks and Shaw, in press) suggest that adult sablefish may migrate great distances in mid-water or over the abyss. The tolerance of this species for low oxygen concentrations has permitted it to colonize the oxygen minimum zone along the entire slope region of the north Pacific arc. Emerging information suggests that this is but one facet of the remarkable adaptive repertoire of sablefish.

[4]A coordinated NOAA plan for fishery oceanography and recruitment research on West Coast groundfishes (FORAGE). Coastal Fisheries Resources Division, Southwest Fisheries Science Center, December 1989.

Latitudinal Range and Reproductive Competency

The time series data for surface-living larvae indicate that mortality of eggs and larvae increases markedly south of Oregon and that there is little or no survival of eggs or larvae south of the Southern California Bight. Substantial populations of sablefish occur along the coast of California north of Point Conception (Methot 1992), in the Southern California Bight (Cross 1987), and off the Pacific coast of Baja California, south to Cedros Island (Silva and Garcia 1988). We know that sablefish achieve sexual maturity and develop reproductively active gonads off southern California (Sullivan 1982) and Baja California (Olivia T. Vasquez, Instituto Nacional de la Pesca, Ensenada, Baja California, Mexico, pers. comm.). Tagging studies indicate little or no southward movement of demersal adults or subadults and, instead, show a tendency for movement to the north (McFarlane and Saunders, in press; Parks and Shaw, in press). Sablefish off Mexico appear to have a very long and tenuous connection to the reproductively successful fraction of the population to the north. It is likely that virtually all recruitment to sablefish populations off Mexico is from larger pelagic juveniles that avoid surface-towed plankton nets. Such large pelagic juveniles of northern origin may also contribute a substantial fraction of recruits to southern California.

An interesting management implication is that there may be limited need to regulate sablefish catch south of Point Conception, since the fraction of the population south of there has little or no reproductive potential. Moreover, sablefish fisheries south of Point Conception may be very unstable and subject to boom-or-bust conditions, since recruitment is dependent on larvae or juveniles that are transported great distances. The meager information we have on these fisheries appears to bear this out (Silva and Garcia 1988).

Drift algae provide a mechanism for the survival and transport of sablefish juveniles in the southern region of the range. Juvenile sablefish are known to associate with drifting seaweed off the coasts of southern California and Mexico. Using a miniature purse seine, Hunter and Mitchell (1970) made 50 collections of fishes associated with drifting seaweed (primarily giant kelp, *Macrocystis pyrifera*) from the Southern California Bight to Cedros Island, Baja California. Sablefish juveniles (66–149 mm SL) appeared in 15% of the samples and were the fourth most abundant species sampled. Kelp-associated sablefish juveniles were taken in samples from June and July, well offshore, where they would be subject to entrainment in the Southern California Eddy or in the southerly flow of the California Current. Drift-algae masses are common in the central and southern regions of the California Current and provide (1) an environment conducive to survival of sablefish juveniles and (2) a means of southerly transport for presettlement individuals. Hunter and Mitchell's (1970) suggestion that drift algae reduced predation was supported by the results of their laboratory experiment in which fishes associated with algae were pursued less often, for shorter periods, and were captured less frequently by predators than were free-living fishes.

Little is known about the biology and distribution of late larvae and pelagic juvenile sablefish in their principal geographic range. Extensive sampling with surface nets (Pacific Northwest—Kendall and Matarese 1987; Canada—McFarlane and Beamish 1983; Gulf of Alaska—Kendall and Ferraro 1988) has not revealed the offshore limits of larval distribution, if indeed there are limits. How these broadly dispersed larvae reach the coast for settlement is unknown. Surface collections with neuston trawls (Shenker 1988) and purse seines (Brodeur and Pearcy 1986) indicate that large pelagic juveniles appear in the vicinity of the shelf break in the summer and fall off Oregon and Washington. Neuston net surveys off British Columbia show a similar seasonal onshore movement of larvae (McFarlane and Beamish 1983; McFarlane and Saunders, in press). How the broadly dispersed larvae and pelagic juveniles reach the coast for settlement is unknown. It is likely that this movement is aided by dynamic hydrographic processes, but such transport mechanisms have yet to be demonstrated.

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