Age, Growth, Life History, and Fisheries of the Sand Sole, *Psettichthys melanostictus*

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Introduction

Sand sole, *Psettichthys melanostictus*, is a common nearshore pleuronectid flatfish in the northeast Pacific Ocean. Also known as fringe sole, spotted flounder, or sand flounder, this species is often caught recreationally from shore, and it also makes up a small part of commercial trawl catches (Kramer et al., 1995). Commercial landings of sand sole in California, Oregon, and Washington have brought in over $11 million between 1981 and 2004 (PacFIN, 2005). In comparison, Dover sole, *Microstomus*

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ABSTRACT—Sand sole, Psettichthys melanostictus*, is a small but important part of the west coast groundfish fishery. It has never been assessed and there is a limited amount of biological data for the species. We provide the first estimates of age and growth for California populations and compare them with studies from other areas. We found that sand sole is a rapidly growing species which may show a strong latitudinal gradient in growth rate. We also found evidence of a recent, strong cohort-related shift in the sex ratio of the population towards fewer females. In addition we examined data from the Washington, Oregon, and California commercial fishery to make an initial determination of population status. We found that catch per unit of effort in commercial trawls experienced a decline over time but has rebounded in recent years, except central California (the southern part of its commercial range), where the decline has not reversed.*

pacificus, the most abundant commercial flatfish on the west coast of the United States, was valued at $200 million in the same period.

Although the sand sole's overall economic value is low, it consistently commands a high price per pound, with only three other flatfish species commanding a higher price (California halibut, *Paralichthys californicus*; Pacific halibut, *Hippoglossus stenolepis*; and starry flounder, *Platichthys stellatus*). As a comparatively minor commercial and recreational species, and with little data available, sand sole has never been the subject of a formal stock assessment, nor is one likely to be conducted in the near future.

The sand sole ranges from the Bering Sea (Allen and Smith, 1988) to Redondo Beach, southern California (Fitch and Schultz, 1978). It is common on sandy bottoms at depths <70 m (Kramer et al., 1995), but it has been taken as deep as 325 m (Allen and Smith, 1988).

Previous studies have described the growth and life history of sand sole larvae and juveniles (Hickman, 1959; Sommani, 1969), but little has been reported about the adult life history of this species. Virtually all previous sand sole studies have been conducted in Oregon, Washington, and Canada, but little is known about its California populations. Furthermore, no studies have been published on the fisheries for this species.

This study was conducted to determine the age, growth, spawning season, life history, and sex ratio of California sand sole populations and to compare them to published values from other areas. In addition, we describe the fishery to evaluate whether there was any

evidence of a decline in abundance and determine where the fisheries were conducted. We also reviewed the scientific literature on sand sole and compared our results to previous studies. We also present, to the best of our knowledge, the first attempt at age validation.

Materials and Methods

Collection of Samples

Samples of adult sand sole were collected by trawl net off central California in the vicinity of Monterey Bay, during 39 tows conducted between November 2001 and March 2005. Sampling equipment consisted of a commercial bottom trawl net with a 4.6 m vertical opening, 41.2 m footrope, and a 10.2 cm mesh in the codend. A net liner with 1.3 cm mesh was inserted in the codend. The net was towed at a ground speed of about 2.5 knots, typically for 1 h. Tows were made at various depths between 20 and 600 m.

Fish were processed onshore to determine fork length (FL) to the nearest millimeter, weight in grams, sex, and maturity. Sagittal otoliths were removed and stored dry in coin envelopes. Sex was determined by dissection and examination of the gonads. Our previous experience suggested that determining maturity state for flatfish is difficult without careful microscopic examination. To assign a maturity state, we classified females as mature if eggs were clearly visible and could be easily separated, or if there was evidence of recent egg release (i.e. loose oocytes within the ovary). If the ovaries were small and no eggs were apparent, we classified the fish as immature. In cases where no oocytes were readily visible to

the naked eye, but the ovaries were large, we classified the maturity as unknown. Males were classified as mature if either sperm ran freely or the testes were enlarged and well developed. Males were classified as immature if the testes were small and translucent. If the testes were intermediate, the maturity state was classified as unknown.

Age and Growth

To validate yearly annulus formation, we examined the whole sagittal otoliths of 226 fish under 25× magnification using ScionImage processing software.[1] Presumed annuli were measured along the dorso-ventral axis through the nucleus. Sand sole otoliths are asymmetrical with respect to one another: the left otolith has annuli oriented around the center of the otolith, whereas in the right otolith, the core is closer to the posterior end. This asymmetry between left and right otoliths was evident in all sizes of fish that we examined.

We chose to use only the left otolith for validation in this study for three reasons: 1) the annuli were generally more distinct and were easier to read on the left otolith, 2) the central axis of the annuli corresponded more closely with the central axis of the otolith, and 3) the annuli were slightly wider than those of the right otolith, reducing the likelihood of errors in measurement. We measured along the dorso-ventral axis since the annuli were more regularly shaped, than along the somewhat longer anterior-posterior axis.

Only the diameters of the first three presumed annuli (if present) were measured. We chose not to attempt to measure more than three annuli since the annuli became quite close together with age, making it difficult to obtain accurate measurements. Otoliths from male and female fish were measured separately to account for possible differences among the sexes. A marginal increment analysis was attempted, but it proved to be inconclusive due to the difficulty of

determining edge type on many of the fish, particularly older ones.

This study utilized a combination of surface readings and the break-and-burn method (Chilton and Beamish, 1982) to determine the ages. Generally, fish larger than 340 mm FL were aged using the break-and-burn method, while surface readings were used for smaller fish. Surface ageing was performed at 15× magnification, while break-and-burn readings were done at 20–30× magnifications. Lengths at estimated age were fitted to a von Bertalanffy growth curve by least squares. The form of the equation was:

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

where L_t = fish length (mm FL) at age t (years),
L_∞ = average maximum length (mm FL),
K = growth completion rate (per year),
t_0 = theoretical age (in years) when the fish was length zero.

Parameters for the growth curve were computed iteratively using the method described by Schnute (1981). Growth curves were fitted separately for males and females to account for possible sex-specific growth rates.

We estimated a weight-length relationship by applying a nonlinear regression, fitting the equation $W = aL^b$, where W = weight (g), L = Length (cm FL), where a and b are fitted parameters (Ricker, 1958). Body length was converted to centimeters for this equation to more easily compare our estimates with previous studies.

We used three methods to estimate the natural mortality rate of sand sole: the Hoenig (1983) method based on longevity, the Lorenzen (1996) method based on maximum weight, and the Beverton (1992) method based on growth rate. For this analysis, we combined commercial sample data and research samples to increase sample size.

To estimate total mortality rate (Z) we examined the catch-at-age from the research samples using the Heincke

method (Heincke, 1913) as described in Ricker (1975). In this method, the change in catch of the descending catch-at-age plot is used to estimate Z.

Fisheries Data

Annual estimates of commercial landings in California, Oregon, and Washington were obtained from the Pacific Fisheries Information Network (PacFIN, 2005), and summarized by the five International North Pacific Fisheries Commission (INPFC) areas: Conception, Monterey, Eureka, Columbia, and U.S.–Vancouver. The Conception INPFC area is south of lat. 36°N, and the Monterey INPFC area is between lat. 36°N and 40°30′N. The Eureka INPFC area is between 40°30′N and 43°N. The Columbia INPFC area is between 43°N and 47°30′N. The U.S.–Vancouver INPFC area is from lat. 47°30′N to the U.S.–Canada border including the Puget Sound.

We obtained recreational landings estimates for sand sole landings from the Recreational Fisheries Information Network (RecFIN, 2005). The recreational data provided estimates of metric tons of fish caught in California, Oregon, and Washington combined from 1980 through 2004.

Commercial trawl logbook data were obtained from PacFIN (2005) and catch per unit effort (CPUE) was calculated for depths and areas where sand sole were most abundant. To determine the areas and depths of greatest sand sole abundance, we summed reported logbook catches by degree of latitude and by depth interval. By visual inspection of the plots, we determined regions of the coast where sand sole were caught most frequently.

To determine the commercial catch depth distribution, we summed catches by depth and selected the depth range which accounted for 95% of the catch. Since the sand sole is a comparatively minor species, we also wanted to determine how well it was identified in logbooks. To test this, we compared annual landings by state from the logbooks to the reported landings from the PacFIN database which relies on landing receipts.

Very little length data are available from the commercial fishery for sand sole; however, we were able to use some sample data collected by the California Cooperative Groundfish Program, which conducts commercial market sampling of groundfish in California (CALCOM, 2005).

Results

Research Catch

A total of 540 females, 239 males, and 33 unsexed fish were collected in 39 tows (Table 1). Data from the un-sexed fish were used only when male and female data were combined. Most specimens were collected in less than 50 m of water (Table 2). Individuals ranged from 116 mm to 477 mm FL (Fig. 1).

Age Validation

Of the 226 otoliths examined for age validation, 75 were from males and 151 from females. Mean diameters of the second and third presumed annuli were notably different between sexes, with females having larger annuli on average (Fig. 2). For both sexes, the presumed second annulus presented the most variability, overlapping considerably the ranges of the first and third.

The overlap problem was resolved by comparing the range of annuli diameter within cohorts, after production ageing was completed. For instance, the standard deviation for all female second annuli combined was 0.45 ($n = 102$), but only 0.39 ($n = 34$) for females subsequently estimated to be born in 1998. Thus, different cohorts appear to have different annuli sizes, at least for the first 3 years of life, suggesting differences in otolith growth rates among years.

A marginal increment analysis (Hyndes et al., 1992) proved inconclusive due to numerous false marks, but Smith (1936) found that translucent (hyaline) zones were formed between January and March. Thus, we conclude that only one annulus is formed per calendar year.

Age and Growth

The oldest female fish aged in this study were two 8-year-old fish, while the oldest males were three 6-year-old fish (Fig. 3). The majority of females were 2–4 years old, while the males were mainly 1–3 years old.

Our estimated von Bertalanffy growth curve parameter estimates indicated that sand sole grow very rapidly with K values of 0.60 and 0.79 for males and females, respectively (Table 3). Average maximum length (L_∞) was substantially different for males and females, with females reaching a much larger size (376 mm for females as compared to 310 mm for males).

In this study we estimated the weight-length relationship to be W (grams) = 0.0175 $FL^{2.8294}$ for males, and $W = 0.00674$ $FL^{3.1367}$ for females. The

sample size for males was 116, the r^2 was 0.89, and the range in lengths was 130 to 376 mm. The sample size for females was 269, r^2 was 0.97 and the range in lengths used was 126 to 445 mm.

Mortality Rate

The three methods used to estimate the natural mortality rate of sand sole provided estimates of 0.37 to 0.42 yr^{-1} for females and 0.41 to 0.56 yr^{-1} for males (Table 4). For the Hoenig (1983) method, we used a maximum age of 10 years for females and 8 years for males. Since we felt we did not have the true maximum age fish, both ages are greater than the observed maximum ages in our samples (8 years for fe-
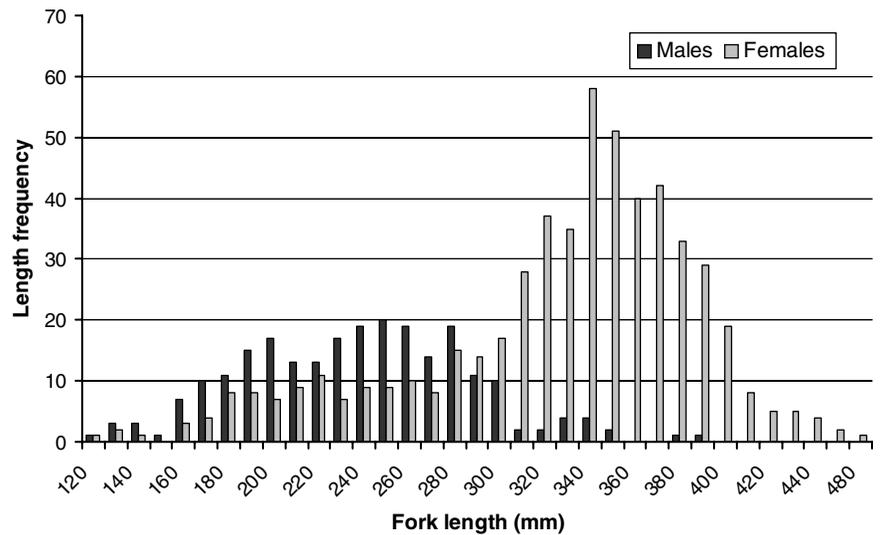

Figure 1.—Length frequency distribution of sand sole collected by research bottom trawls (*n*=540 for females and 239 for males).

Table 1.—Number of trawl tows conducted, number of tows with sand sole, and total number of sand sole collected from the groundfish ecology cruise program from November 2001 to March 2005, classified by mean depth strata (m).

No.	Depth strata (m)							
	0–19	20–49	50–99	100–149	150–199	200–249	250–299	>299
Tows	8	28	14	23	16	8	8	25
Tows with sand sole	4	31	2	1		1		
Sand sole	171	631	6	2		2		

Table 2.—Catch rate of sand sole by depth bin caught in research bottom trawls.

	Depth bin (m)					
	<20	20–50	50–99	100–149	150–199	200–249
Catch/Tow	23.6	22.8	2.0	0	0	2.0

males and 6 years for males). We used weights of 1.9 and 1.4 kg for females and males, respectively, for the Lorenzen (1996) method. For the Beverton (1992) method, we used a growth rate of 0.60 yr^{-1} for males and 0.79 yr^{-1} for females. We therefore suggest that M is between 0.35 and 0.45 for females and 0.40 and 0.60 for males using the most likely maximum ages.

Total mortality values (Z) for each sex were estimated using catch-at-age from the research samples (Fig. 3). We used a modal age of 2 years of age for males and 3 years for females to represent fully vulnerable fish. The total mortality estimate for males was 0.94 and 0.57 for females.

Reproduction

Size and Age at Maturity

We found that males mature at a slightly earlier age and smaller size than females. In our study, 87% of 2-year-old females had reached sexual maturity, while over 92% of 2-year-old males were mature (Table 5). Based on our estimated von Bertalanffy growth curves, a 2-year-old male would be about 250 mm while a 2-year-old female would be about 310 mm.

Reproductive Season

An attempt was made in our study to track relative monthly proportions of immature, mature, and spawning fish, but this proved inconclusive due to difficulty in distinguishing maturity stages. The distinction between late ova maturity and early maturity is difficult to distinguish without the aid of a microscope, and individual researchers had different criteria for visually determining the ova stage. Nonetheless, a large proportion of fish taken in January, February, and March were believed to be ripe or spawning.

Sex Ratio

We found a strongly skewed sex ratio in the population, with females constituting 69.3% of the 779 fish for which sex could be determined. Within the 10–40 m depth range, there was no apparent segregation by sex among tows. However, in depths greater than 40 m, only females were caught: one at 60 m and two at a depth of at least 196 m. When we plotted the sex ratio by cohort we found that there has been a substantial decrease in the proportion of females from the 1997 cohort to the 2003 cohort (Table 6).

Table 3.—Estimated von Bertalanffy growth parameters for sand sole with 95% confidence intervals (*n*=177 for males and *n*=433 for females).

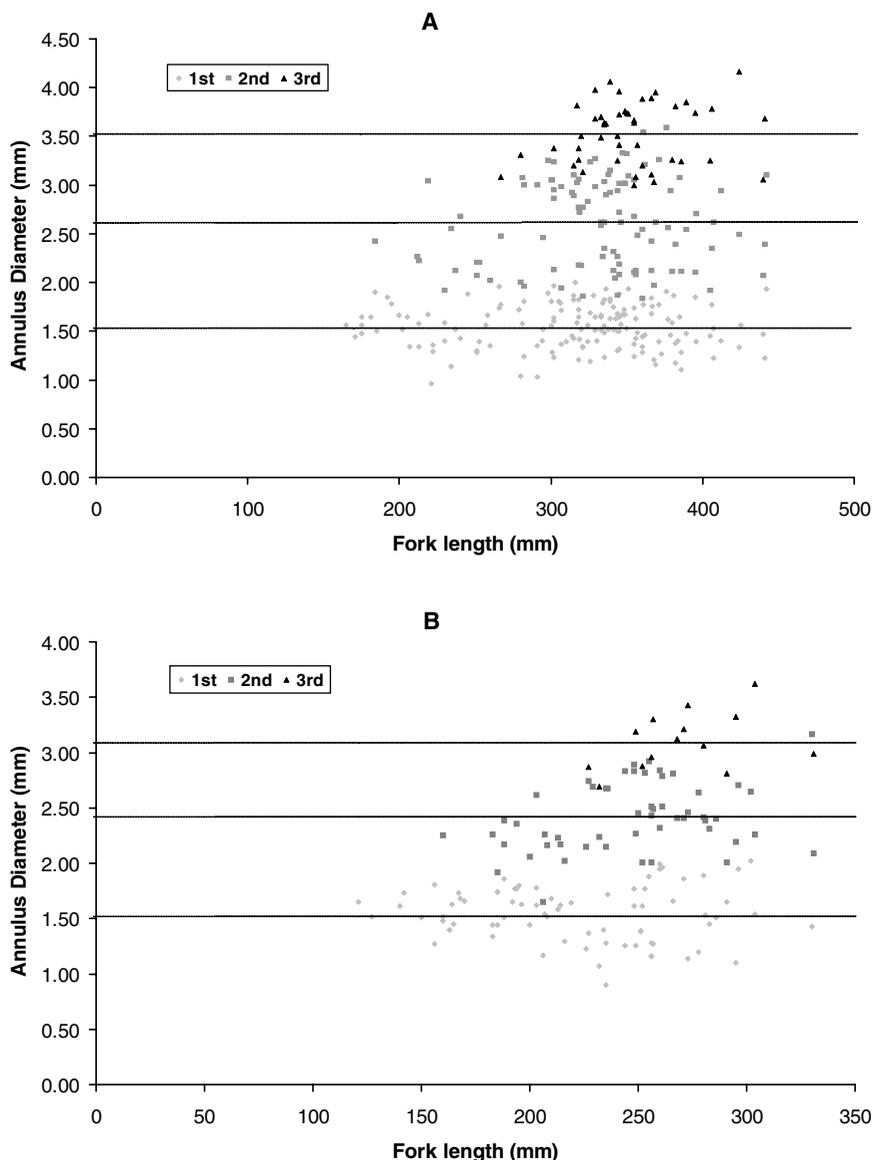| Sex	Parameter	L_∞	K	t_0
Male	Estimate	310.5	0.60	−0.68
	95% C.I. (±)	33.7	0.34	0.74
Female	Estimate	376.1	0.79	−0.16
	95% C.I (±)	10.6	0.17	0.27

Figure 2.—Diameter of the first, second, and third presumed annulus of female (A) and male (B) sand sole. Horizontal lines indicate mean diameters (*n* = 151 for females and 75 for males).

Table 4.—Estimates of natural mortality rate (M) for sand sole using Hoenig (1983), Lorenzen (1996), and Beverton (1992).

Method	Mortality rate	
	Male	Female
Hoenig	0.53	0.42
Lorenzen	0.41	0.37
Beverton	0.56	0.40

Fisheries

Recreational

Recreational landings have declined from a high of 18 t in 1980 to about 2 t in recent years (Table 7) (RecFIN, 2005). Combined annual coast-wide recreational landings have never been greater than 5% of annual coast-wide commercial landings.

Commercial

Commercial landings for California, Oregon, and Washington totaled 4,629 t between 1981 and 2004, with annual landings gradually declining from a high in 1987 (401 t) to an annual average of 97 t during 1999–2004 (Table 7) (PacFIN, 2005). Landings for the Columbia INPFC area were far greater than the other INPFC areas for most of the 1981–2004 time period, comprising a total of 65.5% of all commercially landed sand sole. Landings in areas north and south of the Columbia INPFC area (U.S.–Vancouver and Eureka, respectively) were considerably less, while the Monterey INPFC area had the second highest landings, comprising 17.9% of total landings. Landings from the Conception INPFC area were negligible, comprising just 0.4% of total landings. While the Columbia INPFC area experienced a substantial increase in landings from 1987 to 1994, the other INPFC areas gradually declined.

Trawl logbook data were available for all three states from 1987 through 2005 (PacFIN, 2005). Catch of sand sole was first aggregated by latitude (Table 8), and four regions were selected for further examination based on total catch: lat. 37°N–38°N, lat. 41°N–43°N, lat. 44°N–47°N, and lat. 48°N–49°N. Since these regions were quite similar to the INPFC areas, we used INPFC areas to define our spatial

Table 5.—Percent of sand sole that are sexually mature by age (*n*=126 for males and *n*=276 for females, from research trawls).

	Age (yr)							
	1	2	3	4	5	6	7	8
Males (%)	73	92	96	100	100	100	100	100
Females (%)	41	82	95	98	100	95	100	100

Table 6.—Sex ratio (percent females) in research samples of sand sole by cohort. Standard errors and sample size for each cohort are shown.

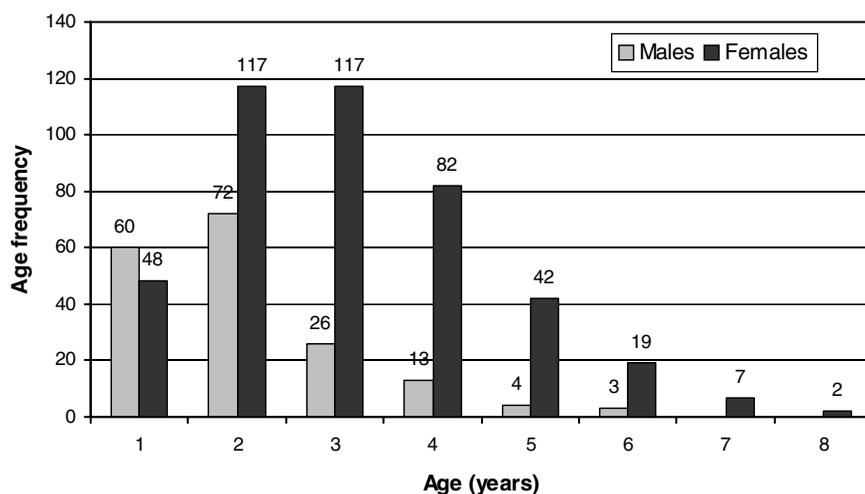|	Cohort						
Item	1997	1998	1999	2000	2001	2002	2003
Percent female	90	84	83	71	62	58	25
S.E.	0.047	0.047	0.040	0.036	0.038	0.058	0.108
No.	40	62	88	157	161	73	16

Figure 3.—Age frequency distribution for sand sole collected by the groundfish ecology cruise program (*n*=178 for males and 434 for females).

strata. Next, total catch was summed by depth, and it was found that 95% of reported catch occurred in depths of 80 m or less (Table 9). We created four depth strata for our subsequent analyses: 1–20 m, 21–40 m, 41–60 m, and 61–80 m. We also defined five time intervals: 1987–1990, 1991–1994, 1995–1998, 1999–2001, and 2002–2005. The total catch for each region-depth-time bin was then divided by total hours fished to determine the CPUE for each stratum. We found that CPUE was highest for the shallowest depths and decreased with depth (Fig. 4). We also found that the CPUE for the Columbia INPFC area was consistently higher than the other areas. With respect to interannual variability,

CPUE decreased somewhat from 1987 through about 1995 and then began to increase, except for the Monterey INPFC area where CPUE remained low.

To confirm that the logbook data accurately represented the fishery, we summed the total pounds reported from the logbook data and compared it to the total reported catch from the landing receipts from 1987 through 2005, for all three states. Results showed that 89% of the landings from landing receipts were reported by the trawl logbooks, suggesting that the logbook data are probably representative of the fishery.

A comparison of the length frequencies from the commercial market samples for northern California (Eureka)

versus central California (Monterey) shows a substantial difference in the length composition, with central California having much smaller fish (Fig. 5). Mean length of fish in central California was 367 mm while it was 407 mm for fish from northern California. Sample sizes were small (169 fish for central California and 121 fish for northern California) and sexes were combined in this comparison. Since the size frequency distributions were so different, we did not attempt to pool them to estimate size and age at recruitment to the fishery. Moreover, since otoliths were not collected from the market samples, it was not possible to examine differences in growth rate.

Discussion

Life History

Adult sand sole are rarely found in estuaries. Smith (1936) noted a high abundance in the northern portions of Puget Sound (i.e. nearer to the ocean), yet they were nearly absent in the lower parts of the Sound (more estuarine). Likewise, Nybakken et al. (1977) found sand sole to be the second most abundant fish at ocean stations located just outside Elkhorn Slough in central California, but no adults were caught in the slough.

Spawning occurs in late winter through mid spring (Smith, 1936; Hickman, 1959). Eggs hatch after about 5 days, although the egg stage may be

less in warm water (Hart, 1973). Larvae average 2.8 mm at hatching, and metamorphosis (migration of the left eye and formation of fin rays) is complete at 22–25 mm (Hickman, 1959).

Sommani (1969) found larval abundance to be greatest in July. He also reported the vertical distribution to be evenly distributed about a mean depth of 10–15 m. Boehlert et al. (1985) found evidence of vertical migration, noting that larvae were much more abundant near the surface at night. Rogers (1985) reported that post-metamorphosis juveniles settle out by 30 mm TL in both estuarine (May to September) and offshore habitats (May to August). Although Rogers (1985) found that settlement rate was higher in offshore areas than in estuarine areas, high mortality reduced offshore abundances of settled juveniles to levels similar to that observed for the estuaries.

The larval stage lasts 60–68 days (Thornburgh, 1978), but it is unknown whether this refers to completion of metamorphosis or to the time of settling. Further confounding the issue, Kendall (1966) suggested juveniles might not become demersal upon metamorphosis, but remain as plankton for an extended, unspecified period.

We speculate that 1-year-old fish were underrepresented in this study because Kendall (1966) collected several small specimens (23–51 mm) during beach seines in Puget Sound, indicating that young sand sole may be most abundant in waters shallower than we were able to sample.

Sand sole are active diurnal predators (Miller, 1965) that feed chiefly on small crustaceans while young, switching to a heavily piscivorous diet at around

Table 7.—Annual landings of sand sole for California, Oregon, and Washington. Recreational landings are combined for all INPFC areas (source: RecFIN, 2005). Commercial landings are shown by INPFC area (Conception=CON, Monterey=MNT, Eureka=ERK, Columbia=COL, U.S.–Vancouver=VAN). Source: PacFIN, 2005.

Year	Recreational	Commercial INPFC Area				
		CON	MNT	ERK	COL	VAN
1980	17	N.d.[1]	N.d.	N.d.	N.d.	N.d.
1981	13	4	143	51	45	19
1982	7	2	94	51	107	49
1983	9	0	73	34	29	7
1984	2	0	53	10	33	11
1985	3	0	66	25	93	8
1986	2	0	65	12	69	19
1987	5	0	25	9	357	10
1988	8	0	24	10	176	12
1989	3	0	13	8	244	42
1990	N.d.	0	13	4	238	15
1991	N.d.	0	1	1	317	22
1992	N.d.	0	1	0	206	20
1993	2	0	5	2	216	11
1994	2	0	27	27	173	20
1995	1	0	26	10	78	19
1996	1	3	35	23	70	4
1997	3	1	31	17	83	3
1998	1	0	19	15	43	4
1999	2	0	22	4	79	0
2000	1	0	20	0	22	0
2001	2	0	15	1	40	4
2002	1	0	9	2	103	10
2003	2	0	10	0	104	2
2004	1	0	21	1	122	4

[1]N.d.=no data available

Table 8.—Total trawl logbook catch (in metric tons) of sand sole from 1987 to 2005 (combined) by latitude. Source: PacFIN, 2005.

Lat.	36°	37°	38°	39°	40°	41°	42°	43°	44°	45°	46°	47°	48°	49°
Catch(t)	2	112	414	1	1	139	77	128	473	288	833	492	142	37

Table 9.—Total trawl logbook catch of sand sole from 1987 to 2005 by 10 m depth bin. Catches in 200 m or deeper waters were pooled. Source: PacFIN, 2005.

Depth (m)	20	40	60	80	100	120	140	160	180	200+
Catch (t)	1,485	904	578	72	29	19	20	7	7	32

150 mm (Nybakken et al., 1977; Barry et al., 1996). About 80% of the diet of small sole consists of mysid shrimps (mysidacea), as well as amphipods (amphipoda), decapods (decapoda), and polychaetes (polychaeta) (Nybakken at al., 1977). Larger fish prey on juvenile fish, including sanddabs, *Citharichthys* spp.; sculpins, Cottidae; herring, *Clupea harengus*; tomcod, *Microgadus proximus*; anchovy, *Engraulis mordax*; young sand sole; and

squid, Teuthida (probably *Loligo*) (Manzer, 1947; Clemens and Wilby, 1961; Miller, 1965; Barry et al., 1996). Sand sole may reduce or cease feeding during periods of spawning (Smith, 1936; Manzer, 1947), although Miller (1965) challenged this idea, noting that spawning fish in his study did not usually have empty stomachs and found cessation of feeding to be more closely correlated with lower water temperature.

Age and Growth

The maximum age of sand sole is unknown. Manzer (1947) found females from the Vancouver area to be "10 years old or more" but noted that the otoliths "were not clearly enough marked for positive age determination"; therefore, it is uncertain if 10 years is a valid estimate. Demory et al. (1976) found that sand sole in Oregon could reach an age of 10 years; however, they did not
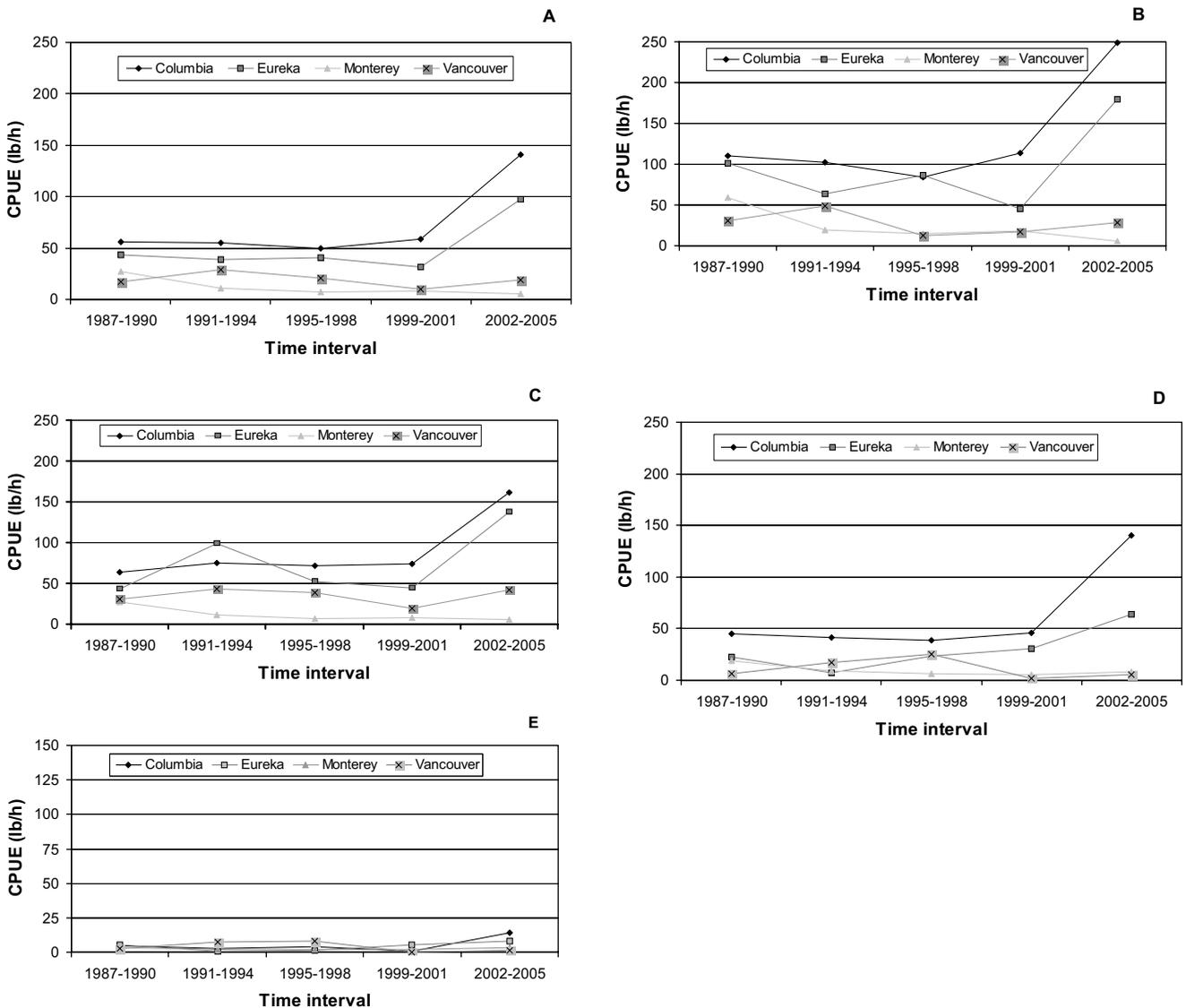
Figure 4.—Catch per unit effort for sand sole from 1987 to 2005 from commercial trawl logbooks. CPUE's were stratified by INPFC area and annual intervals. Panel A = all depths less than 81 m combined, Panel B = 0–20 m, Panel C = 21–40 m, Panel D = 41–60 m, and Panel E = 61–80 m. Source: PacFIN, 2005.

attempt to validate the ages. Since the reported maximum length is 629 mm (Clemens and Wilby, 1961), and since the maximum age fish in this study was 8 years for a 445 mm female fish, we believe that 10 years may be an appropriate estimate of total longevity.

Previous estimates of the von Bertalanffy growth parameters by Demory et al. (1976) have greater K values than our study, showing faster growth in the first 4 years of life (Fig. 6). It should be noted that the trawl used in their study had an 8.9 cm mesh with no codend liner. As a result, smaller fish would not have been retained, tending to select larger, more rapidly growing fish, which could bias their parameter estimates.

Sand sole are said to attain a maximum length of 629 mm and weigh as much as 2,268 grams (Clemens and Wilby, 1961; Kramer et al., 1995), although there is no reference to where fish of this size were observed. Manzer (1947) reports females of 533 mm from Vancouver Island, but does not specify the type of measurement (standard length or fork length). Since the largest fish in our study was 477 mm, and only one study reports fish greater than 533 mm, we suspect that fish greater than 533 mm are very rare in California, Oregon, and Washington.

Demory et al. (1976) estimated weight-length relationships for males and females separately using a linear regression model. Converted to an exponential growth model, their estimate was: $W = 0.0171 \, FL^{2.848}$, and $W = 0.0113 \, FL^{3.129}$ for males and females respectively. Their estimates of a- and b-coefficients for males are similar to ours, as are the b-coefficients for females. However, their a-coefficient for females (0.0113) is 1.68 times greater than ours, suggesting that Oregon females may be heavier than California females of similar length.

Rogers (1985) estimated a relationship of $W = 0.00514 \, F^{3.114}$ (sexes combined) for fish ranging in length from 2.6 to 45.1 cm. As this estimate was taken from a survey of juvenile flatfish, and the mean length of fish in that study was only 11.1 cm, it is possible that this equation is more appropriate for small fish. Although Rogers (1985) did not specify the type of measurement, it probably was total length based on other results presented in the paper.

Reproduction

Smith (1936) found that 100% of 2-year-old males and 3-year-old females (a total of 14 fish) were mature, although he noted that gear selectivity failed to retain fish smaller than 200 mm. These results are similar to our findings.

Sand sole spawn mainly in late winter and spring (Smith, 1936; Hickman 1959). Smith (1936) found females spawning between February and April in Puget Sound, Wash., with peak spawning in March, and noted that males were in spawning condition as early as 1 month prior to females. Hickman (1959) found pelagic eggs locally abundant from January to March in Puget Sound. Sand sole may occasionally spawn later in the year, since Manzer (1947) reported specimens spawning in July around Vancouver Island, Canada.
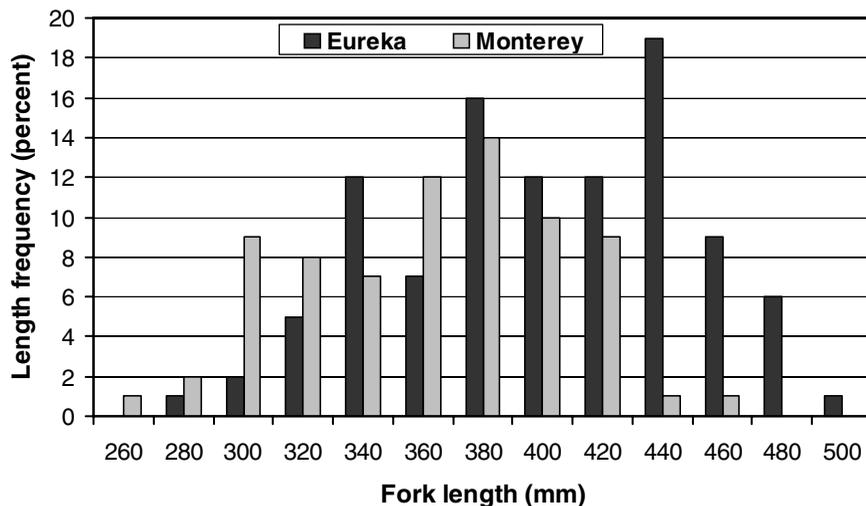

Figure 5.—Length frequency distribution for samples of sand sole from commercial market samples in the Eureka and Monterey INPFC areas. Source: CALCOM, 2005.
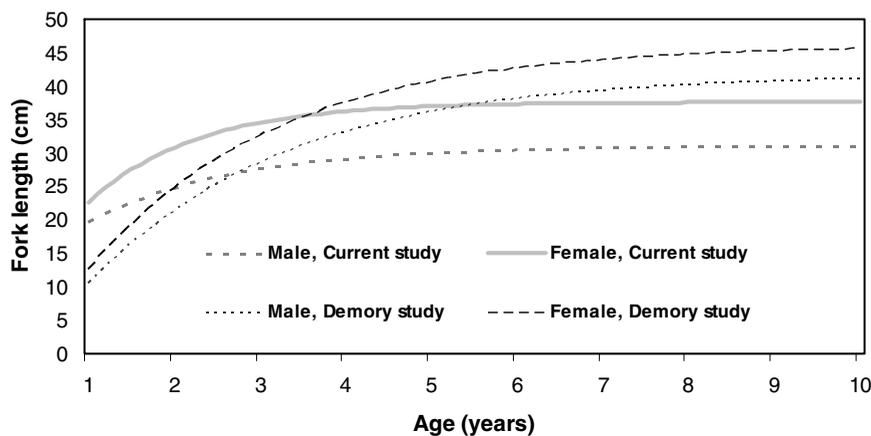

Figure 6.—Predicted von Bertalannfy growth curves from this study compared to those from Demory et al. (1976).

Garrison and Miller[2] (cited in Casillas et al.[3]) stated that a female of 26 cm may produce 900,000 eggs, while a fish of 37 cm may produce 1,400,000 eggs. They did not report, however, what their sample size was for estimating fecundity.

Examination of previous reports supports the existence of a skewed sex ratio: Smith (1936) and Manzer (1947) caught, respectively, 78% females ($n = 97$) and 60% females ($n = 43$), although they did not explicitly report this finding. Although males are generally smaller than females (Fig. 1), the trawl net liner used in our study would have caught them had they been present. It is possible that males reside in shallower water (<10 m) or in unfishable habitats. Commercial fishing mortality would tend to select more females due to mesh size restrictions, thus increasing the proportion of males in the population if fishing mortality was affecting the sex ratio. We therefore propose that the skewed sex ratio is real, and not an artifact of sampling. Yamamoto (1999) found that for Japanese sole, *Paralichthys olivaceus*, genetic females will become phenotypic males if exposed to water warmer than 25°C or colder than 15°C during their larval stage. The normal temperature for larval Japanese sole is about 20°C. Goto et al. (2000) found the same effect for marbled sole, *Pseudopleuronectes yokohamae*, and barfin flounder, *Verasper moseri* (Goto et al., 1999).

Fisheries

Sand sole may be particularly abundant off the central Oregon coast. Boehlert et al. (1985) found sand sole larvae to be the most abundant coastal fish on the Oregon coast (within 28 km of the shore) during six plankton tows in 1982. In addition, the CPUE from the logbook data show that catch rates

are substantially higher for Oregon than anywhere else on the coast.

The low CPUE (Fig. 4) for central California, and the smaller size in the commercial market samples suggests there is a possibility that stocks in central California may have been subjected to more fishing pressure than those in northern California. Alternatively, habitat quality may be inferior further south. Furthermore, growth rate may be slower in central California than farther north as suggested by the higher growth rates for sand sole in Oregon found by Demory et al. (1976) (Fig. 6), and the larger size of fish in the Eureka commercial fishery.

Further Research

Still unexplored, to our knowledge, are genetic characteristics, spawning frequency, age and size at recruitment into the fishery, and age at first maturity. A sample of fish between the ages of zero and one, either laboratory hatched or wild-caught, would provide more refined validation of otolith growth, and the timing of gonadal development may be determined. In addition, fecundity needs to be more clearly established. Tag and recapture studies with oxytetracycline (OTC) would provide better validation of ages in adult fish than was possible in our study. Finally, additional work needs to be done to establish the preferred habitat of young fish.

The data presented in this paper suggests that although landings are currently low for most of the sand sole's commercial range (Monterey through U.S.–Vancouver INPFC areas), the stock may be in good condition based on the increasing CPUE values in the three northern INPFC areas. The CPUE for the Monterey INPFC area declined over time and has not shown a recovery in recent years, suggesting the population may have experienced heavy fishing pressure there or environmental conditions may have deteriorated. Furthermore, the shift to more males in the population in the Monterey INPFC area suggests that the stock may not recover quickly. There is evidence for a latitudinal gradient in growth based on the Oregon age and growth data as well

as the length composition data from the California commercial fishery.

Literature Cited

Allen, M. J., and G. B. Smith. 1988. Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 66, 151 p.

Barry, J., M. Yoklavich, G. Cailliet, D. Ambrose, and B. Antrim. 1996. Trophic ecology of the dominant fishes in Elkhorn Slough, California, 1974–1980. Estuaries 19(1):155–138

Beverton, R. J. H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. J. Fish Biol. 41(Suppl. B):137–160.

Boehlert, G. W., D. M. Gadomski, and B. C. Mundy. 1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull. 83:611–622.

CALCOM. 2005. California Cooperative Survey database. Calif. Dep. Fish Game, Belmont, Calif.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. 60, 102 p.

Clemens, W. A., and G. V. Wilby. 1961. Fishes of the Pacific coast of Canada. 2nd ed. Bull. Fish. Res. Board Can. 68, 443 p.

Demory, R. L., M. J. Hosie, N. T. Eyck, and B. O. Forsberg. 1976. Marine resource surveys on the continental shelf off Oregon, 1971–1974. Oreg. Dep. Fish Wildl. Compl. Rep., 47 p.

Fitch, J. E., and S. A. Schultz. 1978. Some rare and unusual occurrences of fishes off California and Baja California. Calif. Fish Game. 64(2):74–92.

Goto, R., T. Mori, and K. Kawamata. 1999. Effects of temperature on gonadal sex determination in barfin flounder *Verasper moseri*. Fish. Sci. 65:884–887.

_____ , T. Kayaba, S. Adachi, and K. Yamauchi. 2000. Effects of temperature on sex determination in marbled sole, *Limanda yokohamae*. Fish. Sci. 66:400–402.

Hart, J. L. 1973. Pacific fishes of Canada. Bull. Fish. Res. Board Can. 180, 730 p.

Heincke, F. 1913. Investigations on the plaice. General report. 1. Plaice fishery and protective regulations. Part I. Rapp P.-v. Reun. Cons. Perm. Int. Explor. Mer 17A:1–153.

Hickman, C. P., Jr. 1959. The larval development of the sand sole (*Psettichthys melanostictus*). Wash. Dep. Fish., Fish. Res. Pap. 2(2):38–47.

Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rate. Fish. Bull. 81:898–903.

Hyndes, G. A., N. R. Loneragan, and I. C. Potter. 1992. Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead Platycephalus speculator. Fish. Bull. 90:276–284.

Kendall, A. W., Jr. 1966. Sampling juvenile fishes on some sandy beaches of Puget Sound, Washington. M.S. thesis, Univ. Wash., 119 p.

Kramer, D. E., W. H. Barss, B. C. Paust, and B. E. Bracken. 1995. Guide to northeast Pacific flatfishes: families Bothidae, Cynoglossidae, and Pleuronectidae. Alaska Sea Grant Coll. Prog., Fairbanks, Alaska, Mar. Advisory Bull. 47, 104 p.

Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. J. Fish Biol. 49:627–647.

Manzer, J. I. 1947. A July spawning population of sand soles in Sydney Inlet. Fish. Res. Board Can., Pac. Prog. Rep. 73:70–71.

Miller, B. S. 1965. Food and feeding studies on adults of two species of pleuronectids (*Platichthys stellatus* and *Psettichthys melanostictus*) in East Sound, Orcas Island (Washington). M.S. thesis, Univ. Wash., 131 p.

Nybakken, J., G. Cailliet, and W. Broenkow. 1977. Ecologic and hydrographic studies of Elkhorn Slough, Moss Landing Harbor, and nearshore coastal waters July 1974 to June 1976. Moss Landing Mar. Lab., Moss Landing, Calif., 465 p.

PacFIN. 2005. Pacific Fisheries Information Network database. Pacific States Marine Fisheries Commion, Seattle, Wash.

RecFIN 2005. Recreational Fisheries Information Network database. Pacific States Marine Fisheries Commion, Seattle, Wash.

Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 119, 300 p.

_____ . 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

Rogers, C. 1985. Population dynamics of juvenile flatfish in the Grays Harbor estuary and adjacent nearshore area. M.S. thesis, Univ. Wash., 195 p.

Schnute, J. 1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. 38:1128–1140.

Smith, R. T. 1936. Report on the Puget Sound otter trawl investigations. Wash. Dep. Fish. Biol. Rep. 36B, 61 p.

Sommani, P. 1969. Growth and development of sand sole post larvae (*Psettichthys melanostictus*). M.S. thesis, Univ. Wash., 60 p.

Thornburgh, K. R. 1978. Patterns of resource utilization in flatfish communities. M.S. thesis, Univ. Wash., 123 p.

Yamamoto, E. 1999. Studies on sex manipulation and production of cloned population in hirame, *Paralichthys olivaceus*. Aquaculture 173:235–246.