9143

THE SHALLOW-WATER FLATFISHES OF SAN DIEGO COUNTY

SHARON HENDRIX KRAMER[1]
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

Seven species of flatfish live in the shallow marine waters (depth 14 m) of San Diego County: California halibut, *Paralichthys californicus*; fantail sole, *Xystreurys liolepis*; speckled sanddab, *Citharichthys stigmaeus*; spotted turbot, *Pleuronichthys ritteri*; hornyhead turbot, *Pleuronichthys verticalis*; diamond turbot, *Hypsopsetta guttulata*; and California tonguefish, *Symphurus atricauda*. Speckled sanddab was most abundant, representing 79% of the flatfish catch. California halibut had the highest biomass, and represented 46% of the catch.

Only California halibut and diamond turbot used bays as nursery areas; they had distinct ontogenetic distributions, with length increasing with depth. The remaining species settled on the open coast but were not found together during early juvenile stages; they settled at different depths, and at different times of the year. Older juveniles and adults partitioned the habitat by eating different foods and by living at different depths and locations.

Life histories of nearshore flatfishes varied widely: speckled sanddab settled at a large size on the open coast and matured rapidly, whereas California halibut settled at a small size, used bays as nurseries, and delayed maturity.

RESUMEN

Siete especies de lenguados viven en aguas marinas someras (profundidad de 14 m) en el condado de San Diego: *Paralichthys californicus, Xystreurys liolepis, Citharichthys stigmaeus, Pleuronichthys ritteri, P. verticalis, Hypsopsetta guttulata,* y *Symphurus atricauda. Citharichthys stigmaeus* fué la especie mas abundante representando un 79% de la captura de lenguado. *Paralichthys californicus* presentó la mayor biomasa y un 46% del lenguado capturado.

Solamente *Paralichthys californicus* y *Hypsopsetta guttulata* utilizaron bahías como zonas de cría. Estas dos especies presentan distribuciones características durante la ontogénesis, con aumento de longitud del individuo con profundidad. Las otras especies se establecieron en la costa pero no coincidieron durante los períodos juveniles más tempranos: se establecieron a diferentes profundidades, y en tiempos del año diferentes. Los juveniles más viejos y los adultos dividieron el habitat comiendo alimento diferente y viviendo a profundidades y localidades diferentes.

Los ciclos de vida de los lenguados en aguas de poca profundidad variaron ampliamente: *Citharichthys stigmaeus* se estableció después de alcanzar tamaño grande y maduró rapidamente, mientras que *Paralichthys californicus* se estableció con tamaño pequeño, utilizó las bahías como áreas de cria, y demoró la maduración.

INTRODUCTION

Flatfishes (order Pleuronectiformes) have complex life histories of pelagic eggs and larvae and demersal adults. Larvae are symmetrical, but transform into asymmetrical juveniles (both eyes on one side of the head) that settle to the bottom. The duration of the pelagic larval stage and the size at transformation vary among flatfishes, but the general trend is toward longer pelagic larval stage and larger settlement size with increasing depth of adult habitat (Moser 1981).

Interspecific differences in morphology among flatfishes result in interspecific differences in soft-bottom resource use. For example, flatfishes can be divided into two groups: species that have large, symmetrical mouths and feed on fish and large crustaceans living on or above the bottom, and species that have small, asymmetrical mouths and feed on worms and small crustaceans living on or in the substrate (Allen 1982).

Off southern California, Pleuronectiformes are the most abundant soft-bottom fishes caught in otter trawls (Allen 1982). Reports of bottom-trawl surveys off southern California lack information on size-specific abundance of soft-bottom species (Allen 1982; DeMartini and Allen 1984; Love et al. 1986). Most of these surveys sampled depths greater than 12 m.

The objective of this paper is to describe the size-specific distribution and abundance of the seven most abundant flatfish species found along the shallow open coast and bay habitats of southern California. The organization and dynamics of the flatfish assemblage will be discussed in light of these findings.

[1]Present address: Australian Institute of Marine Science, PMB No. 3, Townsville M.C., Queensland 4810, Australia

[Manuscript received February 19, 1991.]

MATERIALS AND METHODS

Monthly collections were taken on the open coast and in bays from September 1986 to September 1988, and followed a stratified random design (for details see Kramer 1990a). Four blocks were sampled that represented 40 n.mi. of the open coast between Mission Bay and San Onofre: San Onofre, offshore of Agua Hedionda Lagoon, Torrey Pines, and Mission Beach (figure 1).

The two bays sampled were Mission Bay and Agua Hedionda Lagoon. Each was divided into blocks of similar habitat (five blocks in Mission Bay, three in Agua Hedionda Lagoon) (Kramer 1990a). Three to four randomly selected isobaths were sampled within three depth strata for each block. On the open coast, the three depth strata were from about 5 m (near the first breaker line) to 8 m, 9 to 11 m, and 12 to 14 m. In bays, strata ranged from "shoreline" (<1 m) to "open water" strata of 1–2-m and 2–4-m depths. San Diego Bay was sampled in June and July 1988, by means of a similar design but with 12 blocks (figure 1). The area of each habitat was computed from navigational charts (Kramer 1990a).

Gear consisted of two beam trawls with mouth openings of 1.6 and 1.0 m, and a 1-by-6-m beach seine. Gear was lined or made of 3-mm mesh netting. A meter wheel was mounted on the trawls to track distance traveled along the bottom, and to allow estimation of the area swept by each trawl (Krygier and Horton 1975).

The 1.6-m beam trawl was fished from a small (15-m) vessel, and the 1.0-m beam trawl was fished from a skiff (5 m) or pulled by hand in shallow water (<1 m). The beach seine and 1.0-m beam trawl were pulled parallel to shore at depths <1 m, for a distance of 20–50 m.

All flatfishes taken in trawls and seines were measured (standard length [SL] in mm), and fish were selected at random and frozen for later analysis in the laboratory (Kramer 1990b). At the laboratory, each fish was thawed, measured (SL in mm), and weighed (wet weight in g). Biomass was estimated by converting standard lengths into wet weight using allometric equations describing the relationship between standard length and wet weight (Kramer 1990b).

Mean density (no./ha) was determined for flatfish species and their length classes by season, location, and depth. Five length classes were used for speckled sanddab: SL ≤40 mm, 41–60 mm, 61–80 mm, 81–100 mm, and >100 mm. Six 50-mm length classes were used for California halibut: SL ≤50 mm, 51–100 mm, 101–150, 151–200, 201–250, and >250 mm. For the remaining species, five 50-mm length classes were used: SL ≤50 mm, 51–100, 101–150, 151–200, and >200 mm. No corrections were made for bias due to gear type.

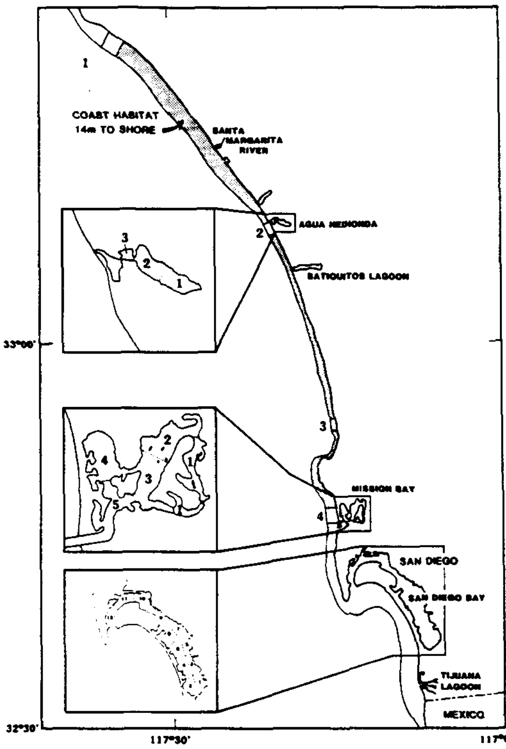

Figure 1. Map of location of sampling blocks. Open-coast blocks are (*1*) San Onofre, (2) adjacent to Agua Hedionda Lagoon, (3) Torrey Pines, and (*4*) Mission Beach. The two bays routinely sampled were Agua Hedionda Lagoon and Mission Bay, with sampling in San Diego Bay in June–July 1988.

Seasonality of settlement was determined by the temporal pattern of settlement. For each species, "newly settled" individuals were classified by length; maximum was 10 mm above the minimum estimated transformation length in published literature (Ahlstrom et al. 1984).

Analysis of variance (ANOVA) was used to describe the variability in density by length class (density in no./ha) with respect to location (four open-coast blocks and two bays), season (fall 1986 through summer 1988), and depth (<5 m, 5–8 m, 9–11 m, 12–14 m). An accepted significance level of $P \leq 0.05$ was used for all analyses except where noted. Abundance was determined by multiplying the mean density for each habitat by the area of each habitat. Abundance estimates were summed for open coast and bay habitats.

RESULTS

Thirteen flatfish species representing three families were captured. Seven species belonged to the family Paralichthyidae (Hensley and Ahlstrom 1984): California halibut, *Paralichthys californicus*; fantail sole, *Xystreurys liolepis*; speckled sanddab, *Citharichthys stigmaeus*; Pacific sanddab, *Citharichthys sordidus*; longfin sanddab, *Citharichthys xanthostigma*; gulf sanddab, *Citharichthys fragilis*; and bigmouth sole, *Hippoglossina stomata*. Five species were of the family Pleuronectidae: spotted turbot, *Pleuronichthys ritteri*; hornyhead turbot, *Pleuronichthys verticalis*; curlfin turbot, *Pleuronichthys decurrens*; English sole, *Parophrys vetulus*; and the diamond turbot, *Hypsopsetta guttulata*. California tonguefish, *Symphurus atricauda*, was the only member of the family Cynoglossidae.

The total number of flatfishes caught was 32,546; seven of the thirteen species accounted for >99% of the catch (California halibut, speckled sanddab, spotted turbot, hornyhead turbot, fantail sole, diamond turbot, and California tonguefish). Paralichthyidae represented 91.9% of the catch, followed by by Pleuronectidae with 7.7%, and Cynoglossidae with 0.4%. Three species of paralichthyid flatfishes accounted for 91.89% of the catch (California halibut, speckled sanddab, and fantail sole), and three species of pleuronectid flatfishes accounted for 6.9% (spotted, hornyhead, and diamond turbots).

Total biomass of the seven most abundant flatfish species was estimated at 662 kg. Paralichthyidae represented 68.3% of the total biomass, followed by Pleuronectidae with 31.3%, and Cynoglossidae with 0.4%.

The sampling design covered only a portion of the depth range of many species, and the beam trawls undersampled California halibut and probably other flatfishes >250 mm SL relative to otter trawls (Kramer 1990a). For example, speckled sanddab is small (maximum length = 144 mm SL) and is probably sampled effectively by the gear; however, the species is abundant at greater bottom depths than those sampled (depths of maximum abundance 5 to 40 m; figure 2). Thus abundance estimates did not fully represent the entire population of any species.

Density, abundance, and distribution of tonguefish were poorly estimated in this study because of their diurnal behavior. Tonguefish is nocturnally active: it remains buried in the sand or mud during the day and feeds at night. Tonguefish is the only flatfish in southern California coastal waters that has diel behavior that affects availability to trawling (DeMartini and Allen 1984).

Size Range (Figure 2)

Speckled sanddab was the smallest flatfish species captured (5–135 mm SL), followed by California tonguefish (21–208 mm). Spotted turbot (7.5–237 mm), diamond turbot (7–266 mm), and hornyhead turbot (10–265 mm) were similar in size: spotted turbot and diamond turbot have a maximum recorded length of 375 mm SL, whereas hornyhead turbot has a maximum recorded length of 290 mm (Miller and Lea 1972).

The largest flatfishes were California halibut and fantail sole. Fantail sole ranged from 7.5 to 340 mm SL, but has a maximum recorded length of 423 mm (Miller and Lea 1972). California halibut was the largest flatfish taken in this survey; standard length ranged from 6.1 to 600 mm, which is considerably less than the maximum recorded length of about 1,300 mm (Miller and Lea 1972).

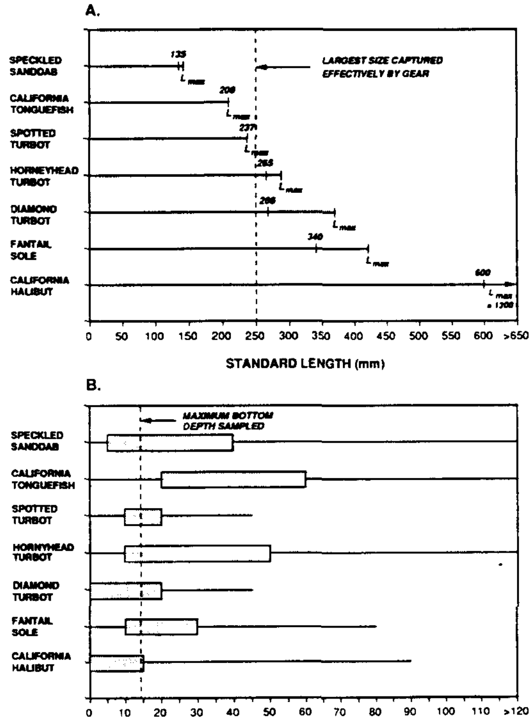

Figure 2. *A*, Maximum standard length and range captured effectively by sampling gear. *B*, Maximum depth, depths of maximum abundance, and outer bound of sampling depth. Lengths and depths obtained from literature (Ford 1965; Miller and Lea 1972; Allen 1982; DeMartini and Allen 1984; Love et al. 1986).

Catch Statistics (Figure 3)

Numbers captured. Speckled sanddab was the most abundant flatfish (25,298 fish), and represented 78.6% of the flatfish catch. Distribution of speckled sanddab varied in both space and time; 45% were caught at Torrey Pines, and 27.1% were caught in spring 1988. Almost all (99.6%) speckled sanddab were found on the open coast, and most were caught deeper than 10 m.

California halibut ranked second in number captured (4,085), and represented 12.6% of the flatfish catch. Most halibut were caught in bays: 60.2% came from Mission Bay and Agua Hedionda Lagoon, and 46.2% from Mission Bay alone. The total number of halibut captured decreased with depth.

Spotted turbot followed California halibut (956), and represented 2.9% of the flatfish catch. Greatest numbers (36.3%) were caught at Mission Beach. Most spotted turbot were caught on the open coast (83.9%); some were taken in the outer areas of Mission Bay.

Diamond turbot was fourth in number taken (848), representing 2.6% of the flatfish catch. Most diamond turbot were caught in bays — 43% in Mission Bay and 40% in Agua Hedionda Lagoon. The number captured decreased with depth.

Hornyhead turbot ranked fifth in number (423), and represented 1.3% of the flatfish catch. Most hornyhead turbot (33.3%) were caught at Torrey Pines. Only four were caught in bays (0.9%), all in the entrance channel to Mission Bay. Hornyhead turbot increased in abundance with depth.

Fantail sole ranked seventh in numerical abundance (228), and represented 0.7% of the flatfish catch. Most (99.1%) fantail sole came from the open coast, and 45% were taken offshore of Agua Hedionda Lagoon.

California tonguefish ranked seventh in numerical abundance (129), and represented 0.4% of the flatfish catch. Mission Bay yielded 48% of the California tonguefish catch.

Biomass. California halibut had the highest biomass at 307.0 kg, or 46.4% of the flatfish biomass. Highest biomass was on the open coast offshore of Agua Hedionda Lagoon (67.3 kg, or 21.9% of the halibut biomass, and 10.2% of the flatfish biomass). Total biomass increased with depth to 11 m, and then declined.

Spotted turbot was second highest, at 117.5 kg, or 17.8% of the flatfish biomass. Highest biomass was at Mission Beach (46 kg, or 39.2%), followed by Carlsbad (29.4 kg, or 25%). Biomass was highest in the 9–11-m depth stratum on the open coast.

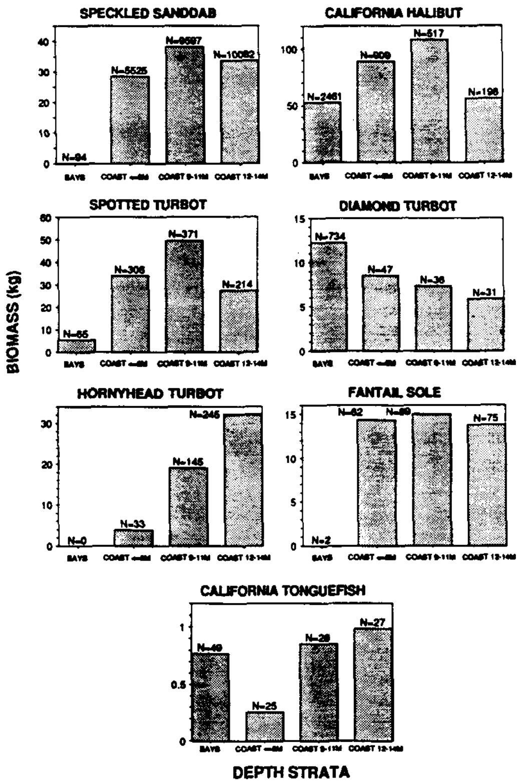

Figure 3. Total biomass and number captured by depth stratum for seven flatfish species.

Biomass of speckled sanddab was 101.0 kg, and ranked third (15.3%) in flatfish biomass, followed by hornyhead turbot with 55.4 kg, or 8.4% of flatfish biomass. Hornyhead turbot biomass increased with increasing bottom depth.

Fantail sole ranked fifth in biomass, with a total of 43.3 kg, or 6.6% of the flatfish biomass. Biomass was relatively constant across all open-coast depth strata, and ranged from 14 to 16 kg.

Diamond turbot had the sixth highest total biomass, at 34.3 kg, or 5.2% of the total biomass. Biomass was highest in bays (12.5 kg, or 36.5%), and decreased with depth.

Biomass of tonguefish was the lowest, at 2.9 kg, or 0.5% of the flatfish biomass. Greatest biomass was in Mission Bay (1.0 kg, or 35%). Biomass on the open coast increased with depth.

Variations in Density[2]

Depth. Density of speckled sanddab and hornyhead turbot varied significantly with depth (F = 387.1, df = 3, 3516, $P < 0.01$; and F = 52.7, df = 3, 3516, $P < 0.01$, respectively), and increased with depth. Speckled sanddab density increased from a mean of 272.5/ha (SE = 17.5) in the shallowest open coast stratum (5–8 m) to 630.8/ha (SE = 50.7) in the deep stratum (12–14 m). Hornyhead turbot increased from 1.24/ha (SE = 0.36) in the shallowest open-coast stratum to 16.2/ha (SE = 1.36) in the deepest stratum.

Density of California halibut also differed significantly with depth (F = 37.6, df = 3, 3516, $P <$ 0.01). The smallest length class (≤50 mm) was most dense in bays (mean = 46.7, SE = 4.5), and decreased with depth on the open coast (shallowest coastal stratum mean = 11.7, SE = 2.7; deepest coastal stratum mean = 1.9, SE = 1.0). Density of the larger classes increased with depth; the largest class (>250 mm) was least dense in the bays (mean = 0.5, SE = 0.1) and most dense in the deepest coastal stratum (mean = 5.7, SE = 0.6). Halibut <150 mm were found primarily in the bays; larger halibut were found on the open coast.

Density of spotted turbot differed significantly with depth (F = 12.9, df = 3, 3516, $P < 0.01$). Spotted turbot was most dense in the shallow and mid-depth strata (5–11 m) on the open coast ($mean_{shallow}$ = 20.7/ha, SE = 1.9; $mean_{middle}$ = 21.5/ha, SE = 1.5), with the lowest open-coast density in the deep stratum ($mean_{deep}$ = 14.5, SE = 1.1). Lowest densities were found in bays, with a mean of 2.1/ha (SE = 0.4). Spotted turbot were found in shallow coastal habitats, but not in bays (figure 4).

Density of tonguefish in the 151–200-m class varied significantly with depth (F = 5.7, df = 3, 3516, $P < 0.01$). However, the smallest (<50 mm) and the largest (151–200 mm) tonguefish were caught in deeper coastal waters (9 m), with intermediate length classes in shallow coastal water (<7 m) and in the bays (figure 4).

Density of fantail sole did not vary significantly with depth for any of the length classes (F = 2.2, df = 3, 3516, $P > 0.05$).

Location. Densities of California halibut and diamond turbot differed significantly with location (F = 33.0, df = 5, 3516, $P < 0.01$; and F = 47.0, df = 5, 3516, P < 0.01, respectively). These fish were most dense in bays, where there were seasonally high concentrations of juveniles. The highest density of diamond turbot occurred during the period of peak settlement of juveniles, with a maximum of 864/ha (SE = 248) in Agua Hedionda Lagoon in winter 1987, and 51.8/ha (SE = 20) in Mission Bay in spring 1987. Halibut was also most dense during settlement of juveniles, with a maximum of 188/ha (SE = 15.7) in Mission Bay in spring 1987, and 797/ha (SE = 410) in Agua Hedionda Lagoon in winter 1987.

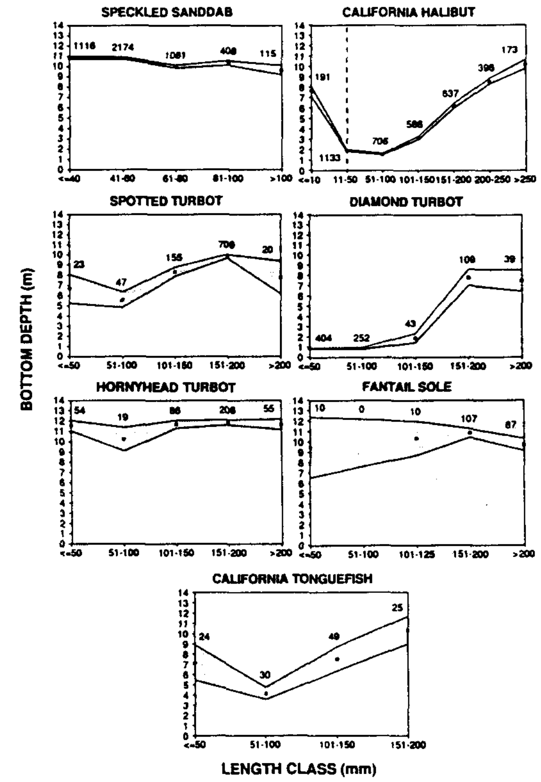

Figure 4. Mean bottom depth of standard length classes for seven flatfish species.

There were more California halibut and diamond turbot at open coast locations adjacent to bays than in areas far from bays. Density in bays ranged from 36.5/ha (SE = 2.9) offshore of Agua Hedionda Lagoon to 12.1/ha (SE = 1.3) at San Onofre. Maximum coastal densities of diamond turbot were at Mission Beach, ranging from 1.3/ha (SE = 0.85) in fall 1986 to 12.7/ha (SE = 3.6) in fall 1987. Density of diamond turbot in the >250-mm class did not vary significantly with location (F = 0.6, df = 5, 3516, P = 0.71).

[2] Tables of density for each species by sample block, quarter, and length class are available in Kramer 1990b.

TABLE 1
Key Life-History Characteristics of Inshore Flatfishes

A. Juveniles

Species	Size at settlement	Settlement location*	Settlement depth Mean	SD	N	Ontogenetic distribution
California halibut	≤17	B, C	5.05	3.67	398	Yes
Diamond turbot	≤14	B	1.25	0.46	51	Yes
Speckled sanddab	≤35	C, B	11.02	2.25	773	No
Fantail sole	≤17	C	6.35	5.91	4	No
Hornyhead turbot	≤17	C	8.84	2.54	5	No
Spotted turbot	≤16	C	9.19	4.35	4	No
California tonguefish	≤29	C, B	11.37	1.20	10	?

B. Adults

	Size at 1st maturity (a)	Maximum SL (mm)	Depth distribution	Major prey	Season of spawning†
California halibut	300+	1274	≤15 (d,e,j,k)	Anchovies (b,e)	W,Sp,Su
Diamond turbot	160	373	≤20 (d,j,k)	Polychaetes (c)	W,F
Speckled sanddab	70	144	5–40 (d,e,j,k)	Mysids (d,e)	Sp,Su,F (g)
Fantail sole	160	423	10–30 (d,e,j,k)	Crabs (e)	Su,F
Hornyhead turbot	140	290	10–50 (d,e,j,k)	Polychaetes (e,f)	W,Sp,Su?,F? (h)'
Spotted turbot	140	237	10–20 (d,j,k)	Anemones (e,f)	Sp,Su,F?,W?
California tonguefish	120	208	20–60 (d,e,j,k)	Amphipods (e)	Su,F? (i)

(a) Miller and Lea 1972; (b) Plummer et al. 1983; (c) Lane 1975; (d) Ford 1965; (e) Allen 1982; (f) Luckinbill 1969; (g) Goldberg 1987; (h) Goldberg 1982a; (i) Goldberg 1981; (j) Love et al. 1986; (k) DeMartini and Allen 1984.
*B = bays; C = coast
†W = winter; Sp = spring; Su = summer; F = fall

Diego Bay. High abundance there suggests that the bay may be an optimal habitat for spotted turbot and tonguefish, or that it is an area of increased susceptibility to capture with the beam trawl. The entrance is dredged to about 15 m and has a sandy bottom similar to the open coast. The channel is protected from large swells, but is influenced by tidal currents. The bottom was populated with sea pens, *Stylatula* sp., and was the only location where dense stands of sea pens were found. *Stylatula* has been found in the stomachs of spotted turbot, and may be an important food (Ford 1965).

Fantail sole, hornyhead turbot, speckled sanddab, and English sole did not depend on shallow-water nursery habitats. Newly settled fantail sole and hornyhead turbot were caught from March to September 1989, whereas speckled sanddab settled throughout both 1989 and 1990 but were caught in greatest numbers from March to September 1989 (figure 5).

Juvenile English sole were found only on the open coast, although they use bays as nursery areas in northern California, Oregon, and Washington (Toole 1980; Krygier and Pearcy 1986; Rogers et al. 1988). The English sole settled on the open coast between April and September, at about the same time as halibut, but in deeper water and at a larger size (figure 5; table 1).

The seasonal spawning pattern is winter and spring for species using bays and the shallow open coast as nursery areas (diamond turbot, California halibut). But species that settle in deeper waters of the open coast spawn throughout the entire year or in other seasons (table 1).

Annual Variation in Settlement

Variability in rates of settlement could be caused by differences in larval survival due to food availability or predation, variability in reproductive effort and abundance of adults, or variability in oceanographic conditions influencing the transport of larvae to the nearshore. Newly settled and small juveniles of all species were more abundant in 1988 than 1987, suggesting that the factors influencing settlement success affect the entire nearshore environment. Ford (1965) also found considerable variability in population estimates for speckled sanddab in 1962 and 1963, which suggests that there is high interannual variability in speckled sanddab abundance.

Spatial patterns in settlement were also evident, with most of the coastal settlement of speckled sanddab and California halibut at Torrey Pines in 1988. It seems unlikely that increased egg production would account for the spatial and temporal settlement patterns for all species; therefore the increased settle-small juvenile diamond turbot use bays as nursery areas.

Size and Season of Settlement (Figure 5)

Diamond turbot larvae are the smallest of the flatfishes at transformation, ranging from 4.4 to 8.8 mm SL (Ahlstrom et al. 1984). Juveniles of ≤14 mm were considered "newly settled"; 51 newly settled juveniles were caught—45 (88%) in winter 1988. All settlement occurred in bays, in the blocks farthest from the entrances.

Length at transformation of California halibut ranges from 7.5 to 9.4 mm SL (Ahlstrom et al. 1984). Juveniles ≤17 mm were considered newly settled. A total of 398 newly settled halibut was caught from February to May 1987 and from January to September 1988. Most newly settled halibut (271) were caught on the open coast in 1988, with over 50% (144) at Torrey Pines, followed by offshore of Agua Hedionda Lagoon (41, or 15%). Fewer newly settled halibut (127) were caught in 1987, and nearly all (124, or 97.6%) were in the bays. Of these, most settled in the blocks between the entrance and the middle of the bays.

Speckled sanddab larvae are the largest of the flatfish group at transformation, ranging in length from 24 to 35.5 mm SL (Ahlstrom et al. 1984). Juveniles of ≤35 mm were considered newly settled, and 7,456 newly settled speckled sanddab were caught in the survey. Although some settlement occurred throughout both years, peak settlement was between May and October in 1987, and from February until the end of the sampling program in September 1988. Speckled sanddab settlement was greatest in 1988, with over 50% at Torrey Pines (n = 2,920), followed by the open coast offshore of Agua Hedionda Lagoon (n = 1,614).

Newly settled juveniles of the remaining species were relatively rare. Spotted turbot, hornyhead turbot, and fantail sole all transform at a small size (Ahlstrom et al. 1984), and were considered newly settled at ≤17 mm SL. Only 4 newly settled spotted turbot were caught, in May and June 1988. Five newly settled hornyhead turbot were captured in August 1988 on the open coast offshore of Agua Hedionda Lagoon and at Torrey Pines. From March through September 1988, 4 newly settled fantail sole were captured: 2 in Mission Bay, and 2 on the open coast at Torrey Pines.

California tonguefish transform at a relatively large size (19–24.2 mm; Ahlstrom et al. 1984), with juveniles of ≤ 29 mm considered newly settled. Ten newly settled tonguefish were caught on the open

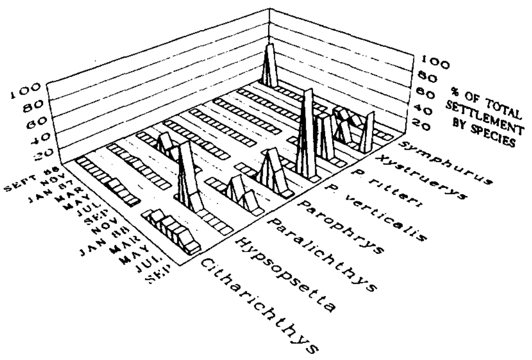

Figure 5. Settlement seasonality (percentage of newly settled fish by species each month) for eight flatfishes: speckled sanddab, *Citharichthys stigmaeus* (n = 7,456); California halibut, *Paralichthys californicus* (n = 398); spotted turbot, *Pleuronichthys ritteri* (n = 4); diamond turbot, *Hypsopsetta guttulata* (n = 51); hornyhead turbot, *Pleuronichthys verticalis* (n = 5); fantail sole, *Xystreurys liolepis* (n = 4); California tonguefish, *Symphurus atricauda* (n = 10); and English sole, *Parophrys vetulus* (n = 159).

coast at depths ≥9 m: 7 in fall 1986, and 3 from December 1987 through March 1988.

Abundance Estimates

Speckled sanddab. Speckled sanddab was most abundant in 1988 (figure 6). Total abundance estimated for both spring and summer 1988 by location was: San Onofre, 1,562,539 (SE = 183,131), Agua Hedionda, 833,415 (SE = 71,099), Torrey Pines, 1,293,550 (SE = 154,833), and Mission Beach, 1,036,291 (SE = 98,419). Estimated abundance for spring and summer 1987 was significantly less than that for 1988. For example, abundance at Torrey Pines for both spring and summer 1987 was 372,317 (SE = 69,400), which is about one quarter of the abundance in 1988.

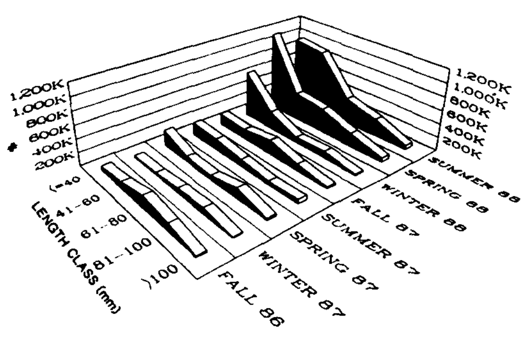

Figure 6. Total abundance of speckled sanddab estimated by season for the open coast.

California halibut. Nearly all halibut in the 51–100-mm length class were found in the bays, whereas most of the halibut in the 201–250-mm class were found on the open coast (figure 7).

In 1987, 50-mm juveniles were more abundant in bays than in 1988; conversely, they were more abundant on the coast in 1988 than in 1987. Abundance of halibut <50-mm summed over all habitats for both years differed significantly, being higher in 1987 than 1988 (n_{1987} = 227,055, SE = 17,623; n_{1988} = 155,407, SE = 16,966). Although settlement occurred on the open coast in 1988, juvenile halibut in the 51–100-mm length class were not found on the open coast.

Spotted turbot. Lack of small spotted turbot on the shallow open coast suggests that they did not use shallow habitats as a nursery area (figure 8). Density of spotted turbot in all except the 150–200-mm class appears to be underestimated or incompletely sampled.

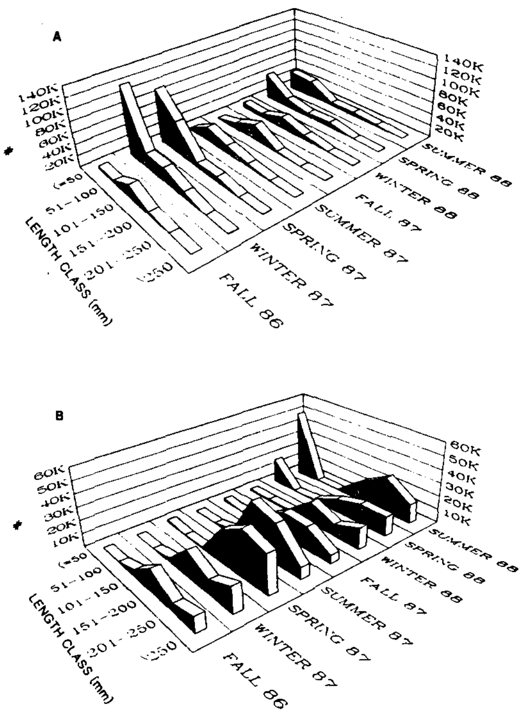

Figure 7. Total abundance of California halibut estimated by season for (*A*) bays and (*B*) open coast.

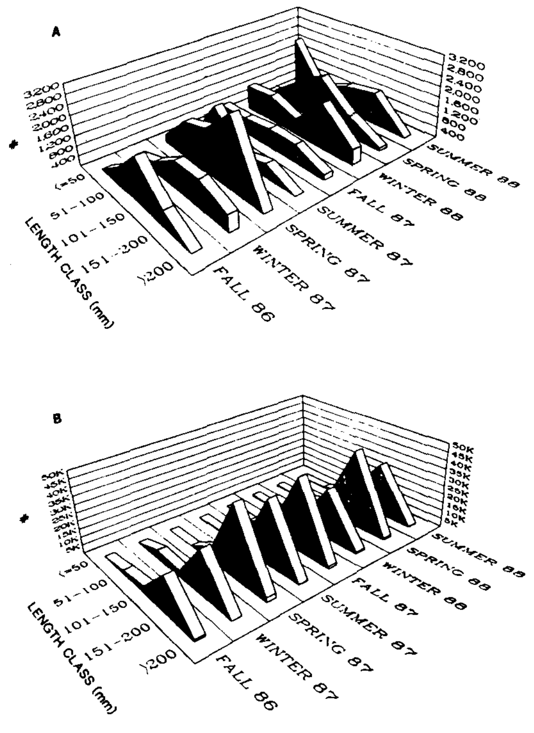

Figure 8. Total abundance of spotted turbot estimated by season for (*A*) Mission Bay and (*B*) open coast.

The most juvenile spotted turbot in the three smallest size classes (≤50, 51–100, and 101–150 mm) were found in the entrance channel to San Diego Bay during the June and July 1988 survey. Density of spotted turbot ≤50 mm ranged from 214 to 739/ha (mean = 473/ha, SE = 88), and was much higher than that at any other location.

Abundance of spotted turbot ≤50 mm at the San Diego Bay entrance (area = 600 ha) was 164,632 (SE = 53,433). Abundances of the 51–100, 101–150, and 151–200-mm length classes at the entrance to the bay were 12,432 (SE = 8,580), 35,640 (SE = 17,670), and 82,320 (SE = 26,452). These accumulations of small spotted turbot suggest that they may prefer the habitat at the entrance to San Diego Bay.

Total abundance of adults in the 151–200-mm class on the open coast ranged from a low of 23,000 (SE = 8,178) during fall 1986 to 45,264 (SE = 10,776) during spring 1988. Abundance was lower in the fall and winter than in the spring and summer (figure 8).

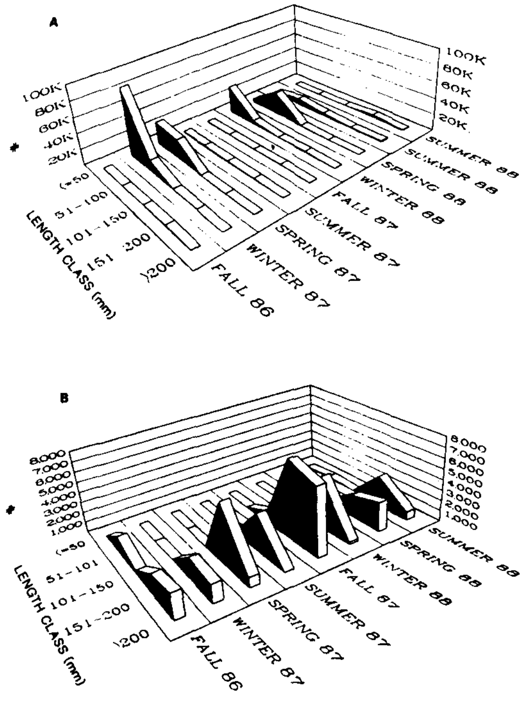

Figure 9. Total abundance of diamond turbot estimated by season for (*A*) bays and (*B*) open coast.

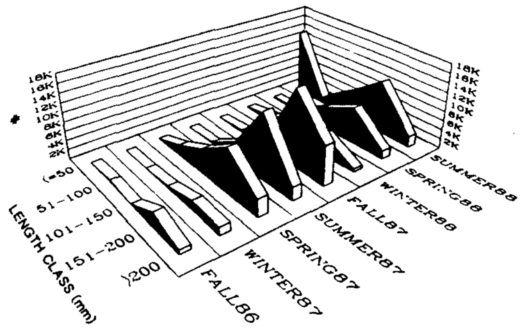

Figure 10. Total abundance of hornyhead turbot estimated by season for the open coast.

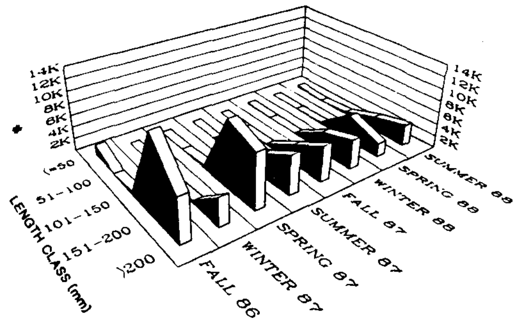

Figure 11. Total abundance of fantail sole estimated by season for the open coast.

Diamond turbot. The number of juvenile diamond turbot in bays appeared sufficient to support the adult population on the open coast (figure 9). Diamond turbot of 51–100 mm SL were most abundant in bays in spring, with 24,164 (SE = 554) in 1987 and 28,108 (SE = 580) in 1988. Maximum abundance of adults (151–200 mm) on the open coast was 7,632 (SE = 573) in fall 1987—considerably lower than the estimated production of juveniles from bays.

Hornyhead turbot. Hornyhead turbot ≤50 mm were most abundant on the open coast in summer 1988, with an estimated abundance of 13,853 (SE = 5,116) (figure 10). No small juveniles were caught on the open coast in 1987. Hornyhead turbot do not appear to use bays as nursery areas.

The 151–200-mm length class was most abundant, with greatest numbers in summer and fall of 1987: there were 14,006 (SE = 5,312) in summer and 16,210 (SE = 7,519) in fall on the open coast. Abundance was lower in winter, with 1,973 (SE = 1,973) in 1987 and 4,567 (SE = 2,151) in 1988. Winter lows and summer-fall peaks in abundance were consistent for both years of the survey, and may represent seasonal movements of adults across the shelf.

Fantail sole. Juvenile fantail sole <100 mm were rare or missing in collections, indicating that they did not use shallow habitats as nursery areas. Their nursery area is probably deeper than 15 m.

Abundance of adults on the open coast was comparable to abundance of diamond turbot and hornyhead turbot. Fantail sole in the 151–200-mm length class were most abundant in 1986 and 1987, with maximum seasonal abundance of 13,191 (SE = 1,161) in fall 1986, followed by 11,084 (SE = 791) in spring 1987 (figure 11). The abundance of >200-mm fantail sole ranged from 2,280 (SE = 360) in spring 1988 to 9,155 (SE = 755) in summer 1987. The fish appeared in the study in low numbers, without any obvious seasonal trends.

California tonguefish. Although density and abundance are underestimated, trends in the data are probably valid. Greatest density of tonguefish on the open coast was off Agua Hedionda Lagoon, with seasonal means ranging from 0 to 5.8/ha (SE = 2.35) for the 101–150-mm class and from 0 to 4.7/ha (SE = 1.79) for the 151–200-mm class (figure 12).

San Diego Bay had the highest density of tonguefish. Like spotted turbot, tonguefish were found primarily at the entrance of the bay (blocks 10–12, figure 1). The 51–100-mm class was most dense in the outermost block (block 12), with density ranging from 474 to 1,089/ha (mean = 705.9/ha, SE = 248.3). Density decreased farther into the bay, and was lower at block 10 (mean = 301.6/ha, SE = 143.5).

Estimated abundance of tonguefish in the 51–100-mm class from San Diego Bay was 368,303 (SE = 71,826). Tonguefish in the 51–100-mm class were caught in both Mission Bay and San Diego Bay, but not on the open coast.

Other Flatfish Species

Six additional flatfish species captured include *Citharichthys sordidus, C. xanthostigma, C. fragilis,* *Hippoglossina stomata, Pleuronichthys decurrens,* and *Parophrys vetulus.* Of the *Citharichthys* sp., *C. sordidus* and *C. fragilis* were rare, with only 6 fish captured along the open coast. Numbers captured and range in standard length were: *C. sordidus* (1; 21.5 mm) and *C. fragilis* (5; 18.3–24 mm). Longfin sanddab, *C. xanthostigma,* was more abundant: 96 were caught on the open coast. They ranged from 19.5 to 233 mm: 5 were <40 mm, and 91 were 129–233 mm. Only 1 *Hippoglossina stomata* (204 mm), and 8 *Pleuronichthys decurrens* (143–180 mm) were caught, all on the open coast.

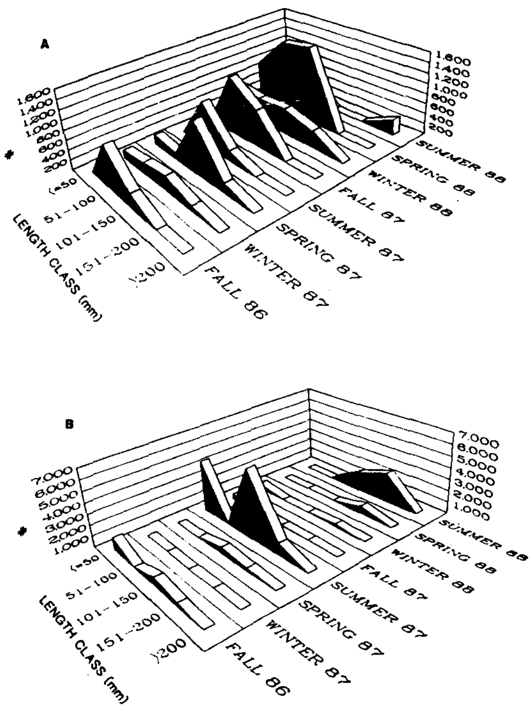

Figure 12. Total abundance of California tonguefish estimated by season for (*A*) Mission Bay and (*B*) open coast.

English sole (*Parophrys vetulus*) was relatively uncommon: 262 were captured, and ranged from 10 to 295 mm. Most (159, or 61%) were newly settled, with standard length ≤30 mm (transformation length ca. 20 mm; Ahlstrom et al. 1984). Settlement occurred between May and September (figure 5). English sole were most abundant in summer 1988, when 134 fish, representing 51% of the English sole catch, were taken. Combined catch in spring and summer 1988 was 247, or 94% of the total catch of English sole.

There was no relationship between standard length and depth of capture; the mean bottom depth was 10.82 m for 50-mm fish (n = 207, SD = 2.48) and 10.81 m for 51–100-mm fish (n = 52, SD = 2.02). Only one English sole was taken from a bay, which suggests that in southern California, the open coast serves as a nursery.

DISCUSSION

Season and Location of Settlement

Only California halibut and diamond turbot used bays as nursery areas, but timing and location of settlement were slightly different. Diamond turbot settled between January and March in back bays, whereas halibut settled primarily between March and September, either on the open coast or closer to the entrance in bays (figure 5). Both species settle at a small size (table 1) and spend little time in the plankton, perhaps as a strategy to decrease dispersal away from the nearshore habitats where adults spawn. Diamond turbot adults probably spawn in or near bays (Lane 1975), and halibut larvae are known to be distributed nearshore (Gruber et al. 1982; Barnett et al. 1984; Lavenberg et al. 1986; Moser and Watson 1990).

Tonguefish settled in the late fall and winter of both years, whereas spotted turbot settlement was observed only in May and June 1989 (figure 5). Spotted turbot and tonguefish both use nearshore nursery areas, probably including the entrance to San

Density of spotted turbot differed significantly with location ($F = 66.0$, df = 5, 3516, $P = 0.01$). There were more spotted turbot on the open coast than in bays, with highest density at Mission Beach (mean = 28.5/ha, SE = 2.0) and lowest at Agua Hedionda Lagoon (mean = 0.30/ha, SE = 0.30). The open coast offshore of Agua Hedionda Lagoon had the second highest density (mean = 17.8/ha, SE = 1.4), with lowest open-coast densities at the two locations farthest from bays ($\text{mean}_{\text{Torrey Pines}} = 9.1$/ha, SE = 1.2; $\text{mean}_{\text{San Onofre}} = 7.2$/ha, SE = 0.9).

Density of speckled sanddab also differed significantly between coastal locations ($F = 138.4$, df = 3, 1004, $P < 0.01$); highest density was at Torrey Pines (overall mean = 948.3/ha, SE = 73.0); the lowest was at San Onofre (mean = 180.9/ha, SE = 13.5). Highest density obtained in a single tow was 8,463/ha, or nearly $1/m^2$, and was taken in the deep stratum at Torrey Pines in summer 1988.

Density of hornyhead turbot, fantail sole, and California tonguefish also varied significantly with location, except for the following rare length classes: hornyhead turbot 51–100 mm; fantail sole juveniles ≤50 mm; and tonguefish 51–100 mm. Like speckled sanddab, hornyhead turbot was most dense on the open coast at Torrey Pines (mean density = 12.7/ha, SE = 1.42), and least at San Onofre (mean = 1.65/ha, SE = 0.38). The highest density of >200-mm fantail sole was also at Torrey Pines, with a mean of 2.58/ha (SE = 0.5). Tonguefish was most dense on the open coast offshore of Agua Hedionda Lagoon (mean = 3.1/ha, SE = 0.62), and least at Torrey Pines (mean = 0.24/ha, SE = 0.17).

Seasonality. Density of speckled sanddab, California halibut, diamond turbot, and hornyhead turbot varied significantly with season. Most of the seasonal variability was due to settlement of juveniles in the smallest length classes. Highest densities of speckled sanddab were obtained in spring and summer of 1988 (overall mean summer = 630.8, SE = 50.7). These high densities were due to large numbers of small juveniles in the ≤40-mm length class ($\text{mean}_{\text{spring}} = 495.2$, SE = 41.9; $\text{mean}_{\text{summer}} = 405.3$, SE = 49.3). Lowest density occurred in winter 1987 (overall mean = 102.5, SE = 11.4).

California halibut ≤50 mm had maximum densities in winter (mean = 63.9/ha, SE = 17.6) and spring of 1987 (mean = 96.9/ha, SE = 13.6), and in spring (mean 43.5/ha, SE = 6.2) and summer 1988 (mean = 34.0/ha, SE = 5.1).

Density differed significantly with season only for diamond turbot ≤50-mm, and did not differ significantly for the larger classes ($P_{\text{SL101–150 mm}} = 0.07$, $P_{\text{SL151–200 mm}} = 0.75$, $P_{\text{SL201–250 mm}} = 0.52$, and $P_{\text{SL>250mm}} = 0.39$). Overall density was greatest in winter and spring, with mean densities ranging between 40.0/ha (SE = 8.75) in spring 1988 to 56.0/ha (SE = 13.4) in spring 1987. These peaks were due to settlement of juveniles.

Density of hornyhead turbot varied significantly with season for the ≤50-mm, 101–150-mm, and 151–200-mm length classes. The 51–100-mm and >200-mm classes did not differ significantly with season ($P_{\text{SL50–100 mm}} = 0.61$, $P_{\text{SL>200 mm}} = 0.14$), and were relatively rare, with maximum seasonal densities of 0.82/ha (SE = 0.55) for the 51–100-mm class and 2.47/ha (SE = 0.77) for the >200-mm class.

Density of large fantail sole (>151 mm) also differed significantly with respect to season. No fantail sole between 51 and 100 mm were caught. The fish were relatively uncommon, with overall densities ranging from 0.82/ha (SE = 0.23) in summer 1988 to 2.96/ha (SE = 0.53) in fall 1986.

There were no seasonal patterns in density of spotted turbot or California tonguefish. Spotted turbot ranged from a low mean density of 5.2/ha (SE = 1.1) in winter 1987 to a high of 11.9/ha (SE = 1.7) in spring 1987. The 151–200-mm class was most dense, regardless of season, and ranged from 2.7/ha (SE = 0.6) in winter 1987 to 7.8/ha (SE = 1.2) in spring 1987.

Relationship between Size and Depth (Figure 4)

There were insignificant or weak linear relationships between length and depth of capture for speckled sanddab, hornyhead turbot, fantail sole, tonguefish, and spotted turbot. California halibut length was positively correlated with depth, which suggests ontogenetic changes in depth distribution (Allen 1982; Plummer et al. 1983). The relationship between standard length (mm) and depth of capture (m) is:

$$SL = 14.87 * DEPTH + 48.19$$

(SE slope = 0.29, $r^2 = 0.40$, $n = 3898$). Transforming stages (SL ≤ 10 mm) were found on the open coast, with small juvenile halibut in bays at depths of 4 m and less, and larger halibut in the deeper coastal strata (>12 m).

Diamond turbot had a similar ontogenetic depth distribution to halibut, with the smallest individuals in the shallowest habitats. The linear regression describing standard length at depth of capture is:

$$SL = 15.12 * DEPTH + 41.27$$

($r^2 = 0.59$, SE slope = 0.43, $n = 848$). Like halibut, ment may be due to differential larval mortality or transport on the coast.

Oceanographic conditions can lead to variability in the transport of larvae and juveniles to their prospective nearshore nursery habitats (Nelson et al. 1977; Mearns 1979; Cohen 1985; Boehlert and Mundy 1988). Currents in the Southern California Bight are characterized by minimal offshore Ekman transport and a gyral geostrophic flow pattern, resulting in minimal seaward dispersion (Owen 1980; Parrish et al. 1981).

Fish larvae can be transported onshore by internal waves, which occur when the water column is thermally stratified in spring, summer, and fall (Winant and Bratkovich 1981; Shanks 1983, 1988). Postflexion diamond turbot and California halibut are neustonic, and are distributed within 2–3 km of shore (Barnett et al. 1984; Moser and Watson 1990). Most of the nearshore coastal flatfishes have relatively short-lived planktonic larvae and settle at a small size, which may decrease the risk of dispersal to unfavorable areas.

Comparison of Life Histories

Size at settlement increases with settlement depth: diamond turbot settle at the smallest size in the shallowest habitats, and speckled sanddab settle at a larger size in deeper water (figure 13; table 1). Smaller size at settlement suggests shorter duration of pelagic stages and less dispersal, which may be advantageous for species using bays as nursery areas.

After settlement, juveniles of some species allocate energy to growth, and others to reproduction. However, there is no apparent relationship between size at maturity and size at settlement (figure 14; table 1). Sizes at maturity and at settlement of 25 flatfish species indicate the range in these life history

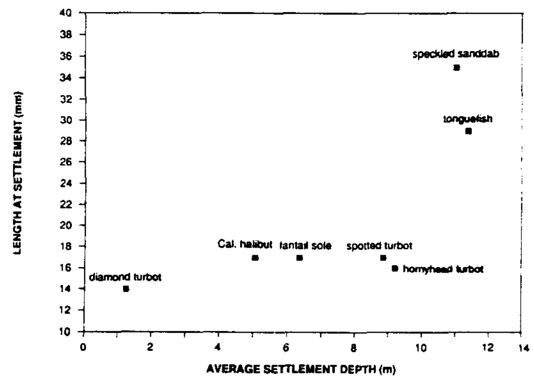

Figure 13. Size at settlement versus settlement depth.

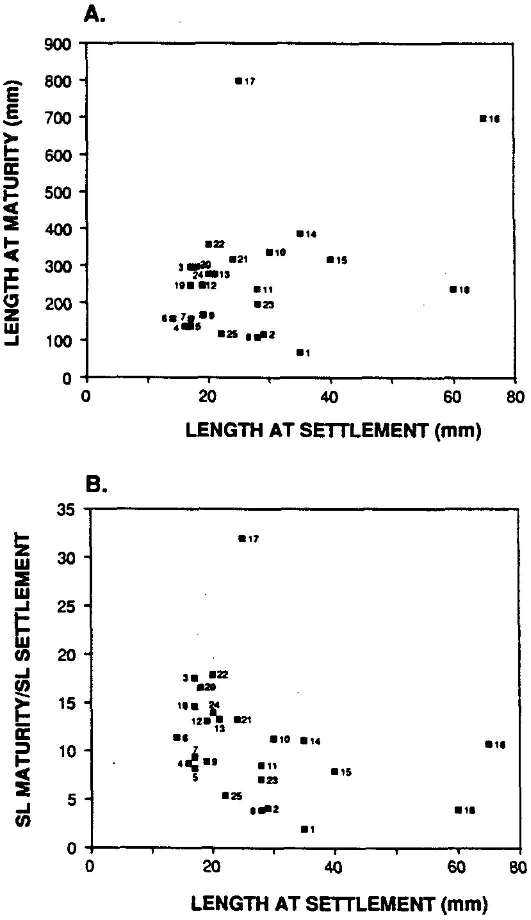

Figure 14. *A*, Length at maturity versus length at settlement for 25 species of flatfishes. *B*, Ratio of size at maturity/size at settlement versus length at settlement for 25 species of flatfishes. Length at settlement determined by adding 10 mm to smallest size at transformation (Ahlstrom et al. 1984). Size at maturity was obtained from Kramer 1990, or referenced below. Numbers in figure refer to fishes listed as follows: 1. *Citharichthys stigmaeus*; 2. *Symphurus atricauda*; 3. *Paralichthys californicus* (Haaker 1975); 4. *Pleuronichthys verticalis*; 5. *Pleuronichthys ritteri*; 6. *Hypsopsetta guttulata*; 7. *Xystreurys liolepis*; 8. *Citharichthys xanthostigma* (Goldberg 1982b); 9. *Hippoglossina stomata* (Goldberg 1982a); 10. *Parophrys vetulus* (Roff 1981); 11. *Microstomus kitt* (Roff 1981); 12. *Platichthys flesus* (Roff 1982); 13. *Pleuronectes platessa* (Roff 1982); 14. *Glyptocephalus cynoglossus* (Roff 1982); 15. *Microstomus pacificus* (Roff 1982); 16. *Reinhardtius hippoglossoides* (Roff 1982); 17. *Hippoglossus stenolepis* (Roff 1982); 18. *Glyptocephalus zachirus* (Hosie and Horton 1977); 19. *Pseudopleuronectes americanus* (Klein-MacPhee 1978); 20. *Platichthys stellatus* (Orcutt 1950); 21. *Limanda ferruginea* (Royce et al. 1959); 22. *Paralichthys dentatus* (Smith and Daiber 1977); 23. *Hippoglossoides platessoides* (Roff 1982); 24. *Limanda aspera* (Roff 1981); 25. *Limanda limanda* (Roff 1982).

characteristics; speckled sanddab mature at the smallest size, and Pacific halibut (*Hippoglossus stenolepis*) at the largest (figure 14).

The ratio of size at maturity to size at settlement indicates the relative amount of energy put into growth or reproduction after settlement. This ratio is lowest for speckled sanddab; they settle and begin to reproduce soon afterwards, investing energy primarily in reproduction, not growth. The ratio is highest for Pacific halibut, which settle and then grow to a large size before reproducing.

Community Structure

Size-structured distribution patterns. Several species have size-structured distribution patterns, including California halibut and diamond turbot (figure 4). Separation of small juveniles from large adults may reduce the risk of cannibalism: large California halibut have been found with smaller halibut in their stomachs (Drawbridge 1990).

Juvenile halibut and diamond turbot both use bays as nursery areas, but there is little overlap in diet. Small diamond turbot eat primarily polychaetes and clam siphons, whereas small halibut eat crustaceans and small fish (Lane 1975; Haaker 1975; Peterson and Quammen 1982; Allen 1988; Drawbridge 1990). Potential juvenile competitors with diamond turbot include English sole, spotted turbot, and hornyhead turbot, but these three species do not use bays as nursery areas.

Speckled sanddab of all sizes are found together on the open coast. Risk of cannibalism is low, because sanddab settle at a size larger than the largest prey consumed by adults (most adult prey are 20 mm or shorter; Ford 1965). Species that do not segregate by size (including hornyhead turbot) may not have the risk of mortality due to cannibalism.

Habitat partitioning. Seven flatfish species inhabit shallow inshore habitats, but do not occur at the same size in the same habitats and do not eat the same prey (table 1). For example, halibut and speckled sanddab do not occur together over the same size range (20–130 mm SL); the halibut live in bays, speckled sanddab on the open coast (figure 4). Halibut's change in distribution suggests that movement from the bays to the open coast occurs when the fish are between 100 and 200 mm (Kramer 1990a). Larger halibut (>250 mm) are primarily piscivorous, and have been found with speckled sanddab in their stomachs (Ford 1965; Allen 1982; Plummer et al. 1983; Hobson and Chess 1986; Drawbridge 1990). Ford (1965) estimated that predation by California halibut could account for 78% of the total monthly mortality of speckled sanddab. Speckled sanddab may also prey upon newly settled halibut, which settle at a size small enough to be within the range (<20 mm) eaten by sanddab (Ford 1965).

Speckled sanddab and juvenile English sole both inhabit the open coast, and settle at about the same size (≤35 mm). They both eat copepods and mysids as small juveniles (<50 mm), but speckled sanddab continue to feed on mysids while English sole switch to a predominately polychaete diet by the time they reach 70 mm (Ford 1965; Toole 1980). Juvenile English sole and speckled sanddab have been found in Humboldt Bay, but not in the same habitats; English sole occur in the intertidal zone, speckled sanddab in deeper channels (Toole 1980).

California halibut and fantail sole are morphologically similar yet eat different prey. Larger juveniles (>200 mm) occur together on the open coast, but halibut eat fish and mysids, and fantail sole eat primarily decapods and other crustaceans (Ford 1965; Allen 1982; Plummer et al. 1983). Newly settled juveniles do not occur together; fantail sole settle in much deeper water (12–15 m; Moser and Watson 1990) than halibut.

Large juvenile and adult spotted turbot, hornyhead turbot, diamond turbot, and English sole occur together on the open coast, but have different diets: all of them eat polychaetes, but each eats different species. About 40% of the hornyhead turbot's diet by weight is the polychaete *Owenia fusiforma*, and 50% of spotted turbot's diet is anemones that are attached to the basal disc of the sand tube of polychaetes (Ford 1965; Luckinbill 1969). Diamond turbot also eat polychaetes, but clam siphons compose nearly 40% of the diet by weight (Ford 1965; Lane 1975; Peterson and Quammen 1982). English sole also eat polychaetes, but brittle stars compose 16% of the diet by volume (Ford 1965; Allen 1982). Although these species coexist, they partition the habitat by eating different prey.

Dietary overlap is probably greatest between newly settled and small juvenile stages of flatfish; food resources are partitioned during later juvenile and adult stages. Newly settled juveniles were found in different habitats, with very little overlap in distribution. Most species, including fantail sole, tonguefish, hornyhead turbot, and spotted turbot, probably settle at depths greater than those surveyed (>14 m). Speckled sanddab settled deeper than halibut, and both settled deeper than diamond turbot. Time of settlement also differed, with diamond turbot settling primarily in winter, halibut in spring, and speckled sanddab in late spring and summer (figure 5). Small juvenile stages (<50 mm) were also found in different habitats: diamond turbot in back bays, halibut in the middle sections of bays out to the open coast at depths <8 m, and speckled sanddab on the open coast at greater bottom depths (figure 4).

In conclusion, the flatfish species found in shallow-water habitats (≤14 m) do not occur together during early juvenile stages; they settle at different depths, have ontogenetic depth distributions, and settle at different times of the year. Older juveniles and adults partition the habitat by partitioning food resources and by living at different depths and locations. Life histories of nearshore flatfishes vary widely, from that of speckled sanddab, which settle at a large size on the open coast and mature rapidly, to that of California halibut, which settle at a small size, use bays as nurseries, and delay maturity.

ACKNOWLEDGMENTS

This paper represents part of a dissertation submitted to the University of California, San Diego, Scripps Institution of Oceanography. The research was supported by funds provided by the Habitat Program of the National Marine Fisheries Service and by the Southwest Fisheries Science Center of the National Marine Fisheries Service. I thank John Hunter, Richard Rosenblatt, Michael Mullin, and Clint Winant for their support and comments. Mike Davis, Steve Swailes, Kevin George, Dennis Gruber, and many others were invaluable in the field. I also thank Geoffrey Moser, William Watson, Barbara MacCall, Elizabeth Stevens, and Elaine Acuna for sharing their expertise in identification of flatfish larvae. Richard Charter and Carol Kimbrell provided technical guidance with analysis and management of the data base. Comments from Jim Allen and two anonymous reviewers improved the manuscript. MBC Applied Environmental Sciences generously provided support during the time this paper was being prepared for publication.

LITERATURE CITED

Ahlstrom, E. H., K. Amaoka, D. A. Hensley, H. G. Moser, and B. J. Sumida. 1984. Pleuronectiformes: development. *In* Ontogeny and systematics of fishes, H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds. Spec. Publ. Am. Soc. Ichthyol. Herpet. No. 1, pp. 640–670.

Allen, L. G. 1988. Recruitment, distribution, and feeding habits of young-of-the-year California halibut (*Paralichthys californicus*) in the vicinity of Alamitos Bay—Long Beach Harbor, California, 1983–1985. Bull. South. Calif. Acad. Sci. 87:19–30.

Allen, M. J. 1982. Functional structure of soft-bottom fish communities of the southern California shelf. Ph.D. thesis, Univ. Calif., San Diego, 577 pp.

Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. 1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. Fish. Bull., U.S. 82:92–111.

Boehlert, G. W., and B. C. Mundy. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Amer. Fish. Soc. Symp. 3:51–67.

Cowen, R. K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications. J. Mar. Res. 43:719–742.

DeMartini, E. E., and L. G. Allen. 1984. Diel variation in catch parameters for fishes sampled by a 7.6-m otter trawl in southern California coastal waters. Calif. Coop. Oceanic Fish. Invest. Rep. 15:119–134.

Drawbridge, M. A. 1990. Feeding relationships, feeding activity and substrate preference of juvenile California halibut, *Paralichthys californicus*, in coastal and bay habitats. M.S. thesis, San Diego State Univ. 214 pp.

Ford, R. E. 1965. Distribution, population dynamics and behavior of a bothid flatfish, *Citharichthys stigmaeus*. Ph.D. thesis, Univ. Calif., San Diego, 243 pp.

Goldberg, S. R. 1981. Seasonal spawning cycle of the California tonguefish, *Symphurus atricauda* (Cynoglossidae). Copeia 1981:472–473.

———. 1982a. Seasonal spawning cycles of two California flatfishes, *Pleuronichthys verticalis* (Pleuronectidae) and *Hippoglossina stomata* (Bothidae). Bull. Mar. Sci. 32:347–350.

———. 1982b. Seasonal spawning cycle of the longfin sanddab, *Citharichthys xanthostigma* (Bothidae). Fish. Bull., U.S. 80:906–907.

———. 1987. Seasonal spawning cycle of the speckled sanddab, *Citharichthys stigmaeus* (Bothidae). Bull. South. Calif. Acad. Sci. 86:164–166.

Gruber, D., E. H. Ahlstrom, and M. M. Mullin. 1982. Distribution of ichthyoplankton in the Southern California Bight. Calif. Coop. Oceanic Fish. Invest. Rep. 23:172–179.

Haaker, P. L. 1975. The biology of the California halibut, *Paralichthys californicus* (Ayres) in Anaheim Bay. *In* The marine resources of Anaheim Bay, E. D. Lane and C. W. Hill, eds. Calif. Dept. Fish Game, Fish. Bull. 165, pp. 137–151.

Hensley, D. A., and E. H. Ahlstrom. 1984. Pleuronectiformes: relationships. *In* Ontogeny and systematics of fishes, H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds. Spec. Publ. Am. Soc. Ichthyol. Herpet. No. 1, pp. 670–687.

Hobson, E. S., and J. R. Chess. 1986. Relationships among fishes and their prey in a nearshore sand community off southern California. Environ. Biol. Fishes 17:201–226.

Hosie, M. J., and H. F. Horton. 1977. Biology of the rex sole, *Glyptocephalus zachirus*, in waters off Oregon. Fish. Bull., U.S. 75:51–60.

Klein-MacPhee, G. 1978. Synopsis of the biological data for the winter flounder, *Pseudopleuronectes americanus* (Walbaum). U.S. Dept. Comm. NOAA Tech. Rep. NMFS Circ. 414, 43 pp.

Kramer, S. H. 1990a. Distribution and abundance of juvenile California halibut (*Paralichthys californicus*) in shallow waters of San Diego County. Calif. Dept. Fish Game. Fish. Bull. 174.

———. 1990b. Habitat specificity and ontogenetic movements of juvenile California halibut, *Paralichthys californicus*, and other flatfishes in shallow waters of southern California. Ph.D. dissertation, Univ. Calif. San Diego, 266 pp. (also available as Southwest Fisheries Center Administrative Report LJ-90-22, National Marine Fisheries Service, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038)

Krygier, E. E., and H. F. Horton. 1975. Distribution, reproduction, and growth of *Crangon nigricauda* and *Crangon franciscorum* in Yaquina Bay, Oregon. Northwest Sci. 49:216–240.

Krygier, E. E., and W. G. Pearcy. 1986. The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, of Oregon. Fish. Bull., U.S. 84:119–132.

Lane, E. D. 1975. Quantitative aspects of the life history of the diamond turbot, *Hypsopsetta guttulata* (Girard) in Anaheim Bay. *In* The marine resources of Anaheim Bay, E. D. Lane and C. W. Hill, eds. Calif. Dept. Fish Game, Fish. Bull. 165, pp. 153–173.

Lavenberg, R. J., G. E. McGowen, A. E. Jahn, J. H. Petersen, and T. C. Sciarrotta. 1986. Abundance of southern California nearshore ichthyoplankton: 1978–1984. Calif. Coop. Oceanic Fish. Invest. Rep. 27:53–64.

Love, M. S., J. S. Stephens, Jr., P. A. Morris, M. M. Singer, M. Sandhu, and T. C. Sciarrotta. 1986. Inshore soft substrata fishes in the Southern California Bight: an overview. Calif. Coop. Oceanic Fish. Invest. Rep. 27:84–106.

Luckinbill, L. S. 1969. Distribution and feeding relationships of the flatfishes *Pleuronichthys verticalis* and *P. ritteri*. M.S. thesis, Calif. State Univ., San Diego, 81 pp.

Mearns, A. J. 1979. Abundance, composition, and recruitment of nearshore fish assemblages on the southern California mainland shelf. Calif. Coop. Oceanic Fish. Invest. Rep. 20:111–119.

Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dept. Fish Game, Fish. Bull. 157, 235 pp.

Moser, H. G. 1981. Morphological and functional aspects of marine fish larvae. *In* Marine fish larvae. Morphology, ecology, and relation to fisheries, R. Lasker, ed. Univ. Wash. Press, Seattle, pp. 89–131.

Moser, H. G., and W. Watson. 1990. Distribution and abundance of early life history stages of the California halibut, *Paralichthys californicus*, and comparisons with the fantail sole, *Xystreurys liolepis*. Calif. Dept. Fish Game, Fish Bull. 174.

Nelson, W. R., M. C. Ingham, and W. E. Schaaf. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull., U.S. 75:23–41.

Orcutt, H. G. 1950. The life history of the starry flounder *Platichthys stellatus* (Pallus). Calif. Dept. Fish Game, Fish. Bull. 78, 64 pp.

Owen, R. W. 1980. Eddies of the California Current system: physical and ecological characteristics. *In* The California islands: proceedings of a multidisciplinary symposium, D. M. Power, ed. Santa Barbara Museum of Natural History, Santa Barbara, pp. 237–263.

Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175–203.

Peterson, C. H., and M. L. Quammen. 1982. Siphon nipping: its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* (Conrad). J. Exp. Mar. Biol. Ecol. 63:249–268.

Plummer, K. M., E. E. DeMartini, and D. A. Roberts. 1983. The feeding habits and distribution of juvenile-small adult California halibut (*Paralichthys californicus*) in coastal waters off northern San Diego County. Calif. Coop. Oceanic Fish. Invest. Rep. 24:194–201.

Roff, D. A. 1981. Reproductive uncertainty and the evolution of iteroparity: Why don't flatfish put all their eggs in one basket? Can. J. Fish. Aquat. Sci. 38:968–977.

———. 1982. Reproductive strategies in flatfish: a first synthesis. Can. J. Fish. Aquat. Sci. 39:1686–1698.

Rogers, C. W., D. R. Gunderson, and D. A. Armstrong. 1988. Utilization of a Washington estuary by juvenile English sole, *Parophrys vetulus*. Fish. Bull., U.S. 86:823–831.

Royce, W. F., R. J. Butler, and E. D. Premetz. 1959. Decline of the yellowtail flounder (*Limanda ferruginea*) off New England. Fish. Bull., U.S. 146:169–267.

Shanks, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13:311–315.

———. 1988. Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish. Fish. Bull., U.S. 86:703–714.

Smith, R. W., and F. C. Daiber. 1977. Biology of the summer flounder, *Paralichthys dentatus*, in Delaware Bay. Fish. Bull., U.S. 75:823–830.

Toole, C. L. 1980. Intertidal recruitment and feeding in relation to optimal utilization of nursery areas by juvenile English sole (*Parophrys vetulus*: Pleuronectidae). Environ. Biol. Fishes 5:383–390.

Winant, C. D., and A. W. Bratkovich. 1981. Temperature and currents on the southern California shelf: a description of the variability. J. Phys. Oceanogr. 11:73–86.