Growth, Mortality, and Movements of Juvenile California Halibut *Paralichthys californicus* in Shallow Coastal and Bay Habitats of San Diego County, California

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Abstract.– Growth and mortality rates were compared for juvenile California halibut *Paralichthys californicus* from bay and open coast habitats. Growth was estimated by determination of size-at-age using daily increments in otoliths. No significant difference was observed in size-at-age for juvenile halibut between 6 and 41 mm from the bays and open coast. However, age-specific mortality rates estimated for halibut <70 days were highest for newly-settled halibut on the open coast. California halibut settled either in bays or on the open coast, but ultimately nearly all of the halibut that settled on the coast entered and used the bays as nursery areas during their first year of life or else they died. The advantages of bays as nursery areas may be a decrease in risk of mortality of newly-settled halibut and an increase in growth of larger juveniles that feed upon the abundant small fishes in the bays.

The utilization of specialized nursery habitats by juvenile fish is a common phenomenon (Boehlert and Mundy 1988, Miller et al. 1986). Many of the fish species that utilize bays as nursery areas spawn in offshore waters, and move into bays as late larvae and early juveniles (Boehlert and Mundy 1988, Miller et al. 1986). The migration, location, and entry of larvae and juveniles into the bays involve complex behaviors that are particularly important on the Pacific coast of North America, where only 10–20% of the coastal habitat consists of estuaries and lagoons, compared with 80–90% on the Atlantic and Gulf coasts (Emery 1967). Possible consequences of the use of bays as nursery areas include faster growth because of high food production, warm temperatures, and decreased predation (Miller et al. 1986, Kneib 1987, Krygier and Pearcy 1986).

The California halibut *Paralichthys californicus* is a commercially important flatfish found in southern California coastal waters and bays (Frey 1971, Haaker 1975, Allen 1988, Love et al. 1986, Plummer et al. 1983). Eggs and larvae occur over the shelf and seaward, with greatest densities in waters less than 75 m deep and within 6 km of shore (Frey 1971, Gruber et al. 1982, Barnett et al. 1984, Lavenberg et al. 1986, Walker et al. 1987, Moser and Watson 1990). In past studies juvenile halibut rarely were taken on the open coast, suggesting that bays and lagoons might be the only significant nursery habitat (Plummer et al. 1983, Allen 1982, Kramer 1990).

The objective of this study was to determine the relative importance of bays as nursery areas and to evaluate the movements between bay and open coast habitats. To meet these objectives, I estimated habitat-specific distribution, abundance, and growth and mortality rates of juvenile halibut from both bay and open coast habitats.

Materials and methods

Distribution and abundance

California halibut were collected during a 2-year survey (September 1986–September 1988) of the open coast between Mission Bay and San Onofre, and two bays, Mission Bay and Agua Hedionda Lagoon (Fig. 1). A stratified random sampling design was used, consisting of four open coast blocks each with three depth strata (5–8 m, 9–11 m, and 12–14 m), and five blocks in Mission Bay and three blocks in Agua Hedionda Lagoon, each with three depth strata (0–1 m, 1–2 m, and 2–4 m) (Fig. 1).

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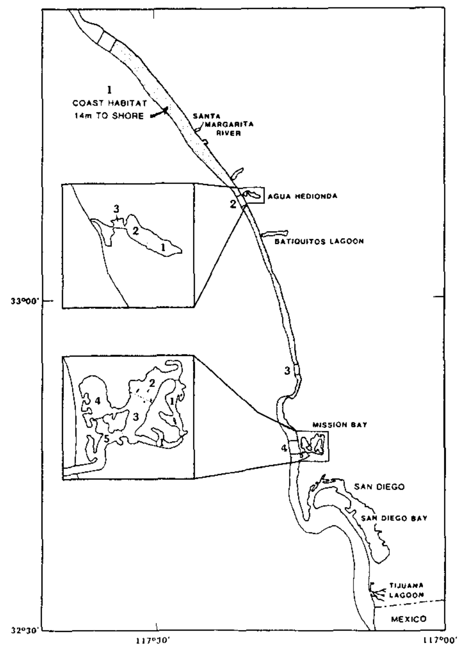

Figure 1

Location of sampling blocks. Open coast blocks are (1) San Onofre, (2) adjacent to Agua Hedionda Lagoon, (3) Torrey Pines, and (4) adjacent to Mission Bay. The two bays sampled are Agua Hedionda Lagoon and Mission Bay, with sampling blocks denoted.

For further description of the sampling design and the habitats see Kramer (1990).

Three gear types were used, all lined or made of 3-mm mesh: a 1.0-m wide beam trawl, a 1.6-m wide beam trawl, and a 1 x 6-m beach seine. The 1.6-m beam trawl, set from a 15-m research vessel, was used to sample the open coast and Mission Bay (Fig. 1). I sampled Agua Hedionda Lagoon and the areas of Mission Bay that were inaccessible to the larger vessel with the 1.0-m beam trawl, set from a 6-m skiff. The 1.0-m beam trawl and the beach seine were pulled along the bottom by two people to sample the shallow shoreline (<1 m) in the bays. The trawls were fitted with a wheel and revolution counter to determine the distance traveled by the trawl along the bottom, allowing a quantitative assessment of fish density since the trawls had a fixed mouth opening (Krygier and Horton 1975). All trawls and seines were fished during the day.

Table 1

Gear weighting coefficients and their variances by length-class for conversion of shoreline collections by beach seine and 1-m beam trawl. Coefficients determined by 3-way ANOVA between gear types, blocks, and months of sample on density for each length-class. Correction terms are given for length-classes with significant gear effects ($P \leqslant 0.05$). There were no significant gear effects in the 1.0–1.6 m beam trawls for open water tows.

Length class (SL, mm)	Correction term	Variance
26–30	3.291	0.124
31–35	4.398	0.319
36–40	2.752	0.099
41–45	4.699	0.359

All flatfishes taken in trawls and seines were measured to standard length (SL) in mm. Density of halibut in 5-mm standard length-classes was determined for juveniles ≤70 mm SL. The thirteen length-classes used were: SL≤10 mm, 11–15 mm, 16–20 mm, continuing to 66–70 mm SL. Abundance was determined by multiplying the mean density for each habitat by the area of each habitat.

Gear comparison

Densities based on the 1.0-m beam trawl collections did not differ significantly from those of the 1.6-m beam trawl for any length class (ANOVA, $P>0.05$, n 826). However, the beach seine captured significantly fewer small halibut (26–45 mm SL) than the 1.0-m beam trawl (Table 1). Since significant biases existed, density and abundance estimates of halibut were corrected for the differences in gear efficiency by weighting the mean density and variance for each length class where significant differences in catchability were found (Table 1).

The weighted mean density for each gear type was calculated as

$$d_w = (d_1 + gd_2)/(1 + g)$$

where d_1 = unweighted density, d_2 = weighted density, and g = weighting coefficient.

Estimated variance of the weighted mean d_w was calculated as

$$V(d_w) = V(d_1) + g^2V(d_2) + d_2{}^2V(g) + V(g)V(d_2)$$

where $V(d_1)$ = variance of unweighted density, $V(d_2)$ = variance of weighted density, and $V(g)$ = variance of weighting coefficient. Variance of the weighted mean was underestimated because the covariance terms were not included. Resampling techniques to estimate variance (e.g., bootstrap) were impractical because of the large size of the database.

Age validation and determination

Laboratory-reared halibut larvae of known age were measured to standard length in mm and their sagittae excised and mounted in resin (Eukitt, O. Kindler, West Germany) on a microscope slide. Age was estimated using the methods of Methot (1981) and Butler (1987). A microcomputer interfaced to an electronic digitizer was used to measure and count increments on a projected image of the otolith from a high-resolution video camera mounted on a compound microscope. Increment counts of 45 larvae (3.1–9.1 mm SL) that were reared at 16–20°C in the laboratory were regressed against the known age of the larvae to establish a relationship between estimated and known age. Increments were formed daily: the slope of the relationship (0.969) did not differ significantly from unity ($P>0.05$). The regression of the number of increments on age of halibut larvae (5–29 days) was

$$\text{Age (days)} = 3.496 + 0.969 \times (\text{no. increments})$$

where $r^2 = 0.981$, SE constant = 1.055, SE slope = 0.018, and range of increment counts = 1–26) (Fig. 2). Daily formation of rings has also been found in juveniles 30–70 mm SL (Kicklighter 1990). The first increment is deposited about 3.5 days after hatching, coinciding with the day of first feeding (Gadomski and Peterson 1988). I added 3.5 to the number of increments counted on the otolith so that age was equivalent to the number of days from hatching.

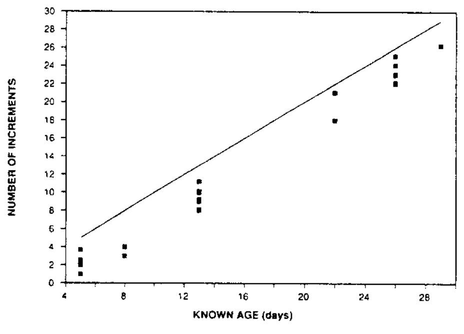

Figure 2
Age validation of California halibut sagittae. Number of increments counted on the sagittae are compared with the known age of laboratory-reared larval halibut (*n* 45). Straight line represents a one-to-one relationship of increment number and known age.

Ageing of field-caught halibut

Juvenile halibut from field collections were measured alive and either frozen or preserved in 80% ethanol. Sagittae were dissected and increments counted using the techniques described above. Sagittae from juveniles >20 mm SL were polished with 400- and 600-grit wet sandpaper before counting.

A total of 120 field-caught halibut were aged: 50 from Mission Bay, 19 from Agua Hedionda Lagoon, and 51 from the open coast. Larval sagittae are symmetrical and nearly circular (Fig. 3A), but after metamorphosis additional foci develop and the sagittae became asymmetrical, with maxiumum deposition along the rostral axis (Karakiri et al. 1989) (Fig. 3B). This shift in the axis of sagittal growth produces areas that are difficult to interpret (Fig. 3). These areas correspond to a period of about 7 days after metamorphosis. I estimated the number of increments in regions of transition between foci by counting the number of increments that occurred in an adjacent area on a different axis (Fig. 3). The relationship between standard length (mm) and otolith radius (μm) was linear for halibut >10 mm SL (Fig. 4).

Mortality estimates

I did not use data from the 1987 survey for estimating mortality because nearly all of the 1987 year-class occurred in bays and comparisons of mortality between bay and coast habitats were an essential step in the analysis. The relationship between abundance and age (estimated from the length-at-age relationship) of the 1988 year-class was used to estimate age-specific mortality rates.

I used seven different models to estimate age-specific instantaneous mortality rates. Three of the models were estimates based on the following assumptions regarding the relationship between survival rates and age (Barlow 1982): (1) Age-specific survival rates increase linearly with age; (2) age-specific survival rates increase exponentially with age; and (3) age-specific survival rates approach an asymptote with age. The two daily production models estimated age-specific instantaneous mortality rates based on the relationship between daily production (abundance of length class/duration of length class) and age (Lo 1985). The last

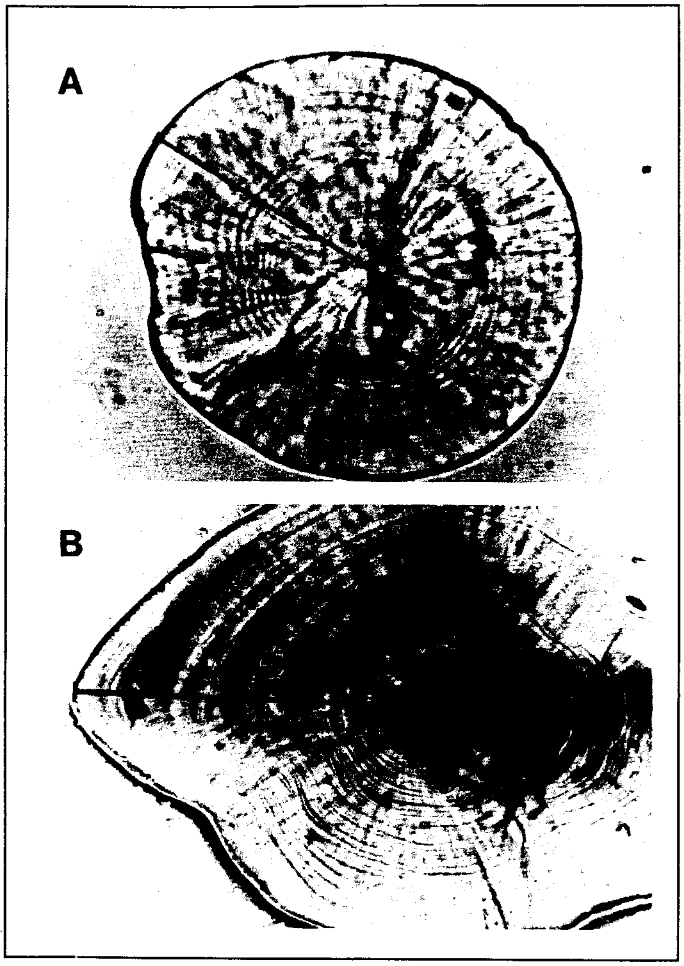

Figure 3
Photomicrographs of California halibut otoliths. (A) Sagitta from halibut 6.94 mm SL, estimated age 22 days. Distance of drawn radius, 70 µm. (B) Sagitta from halibut 48 mm SL, estimated age 109 days. Distance of drawn radius, 890 µm.

two models were simple linear estimates, using a linear regression of ln-transformed abundance-at-age on age (constant mortality rate with age) and on ln(age) (age-specific mortality rates). The sum of squared deviations of observed abundance-at-age from the calculated or transformed abundance-at-age predicted by each model was used to determine the model that best fit the data.

Mortality estimates for halibut from the open coast include loss of juveniles from the open coast population due to emigration into the bays. These estimates are used to calculate age-specific emigration rates by comparing the apparent mortality (= mortality + emigration) on the open coast to the total mortality calculated for the population on the open coast and in the bays.

Results

Effects of season and location on size-at-age

Relationships between halibut length and age did not vary significantly between seasons or between habitats. Analysis of covariance indicated no significant difference in length-at-age between fish that had birthdates in the spring and those with birthdates in the late summer and fall, but the sample size was small for fall fish (*n* 9) (Table 2). The common slope was 0.6206 (SE 0.0905).

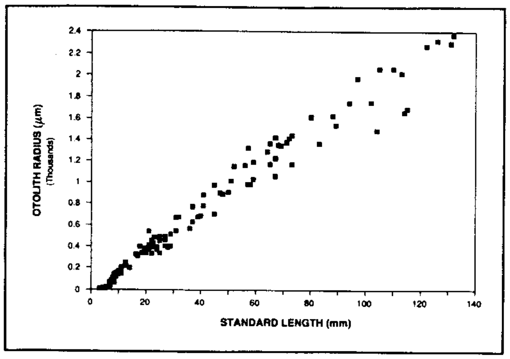

Figure 4
Relationship between otolith radius (µm) and standard length (mm) of California halibut (*n* 120).

Analysis of covariance also indicated no significant difference between juveniles from the bays and the open coast in the relationship between length and age (Table 2). The comparison was made between fish from the bays and the open coast. The common slope was 0.471 (SE 0.0238). Therefore, I used the pooled data for all estimates of growth (*n* 120).

Table 2

Regression analysis and analysis of covariance (ANCOVA) of size-at-age by season and by habitat. Slopes and intercepts were compared using ANCOVA; all tests were not significant at $P > 0.05$.

Covariates	*N*	Size range (mm)	Equality of Intercept	Equality of Slope	*F*-statistic Intercept	*F*-statistic Slope
Seasons						
Spring	26	27–80	−7.6	0.637	1.68	0.051
Fall	9	27–83	−8.6	0.594		
Habitats						
Coast	51	6.8–41	−7.2	0.468	3.87	0.035
Bays	26	8.3–41	−4.7	0.478		

Length-at-age

The relationship between standard length (mm) and age (days) was best described with the Gompertz growth function,

$$\text{Length} = P_1 \times \exp(P_2(1 - \exp(-P_3 \times \text{age})))$$

with $P_1 = 2.13$, $P_2 = 4.77$, and $P_3 = 0.011$, and an estimated mean square error of 0.99 ($2SE_{P_1} = 0.34$, $2SE_{P_2} = 0.137$, $2SE_{P_3} = 0.0013$) (Fig. 5A). The parameter P_1 closely estimates the length-at-hatching, which is 2.0 for halibut (Ahlstrom et al. 1984).

The relationship of age-at-length was determined with the function,

$$\text{Age} =$$

$$-88.347 \times \ln(\ln(\text{standard length} \times 251.07) / -4.769)$$

derived from the Gompertz relationship for size-at-age (Methot 1981) (Fig. 5B). The variance in the estimate of age-at-length increases with increasing length; the 95% confidence interval (CI) for a halibut age 25 days is ± 6 days, but for a 90-day-old halibut the 95% CI is ± 19 days (Fig. 5). This relationship was used to convert length-classes into age-classes using the mean of each length-class (Lo 1985).

I used the method outlined by Methot (1981, equations 1–5) to compute the age-specific daily growth rates. Length-specific daily rate of growth and the variability in growth rate increased with increasing length: the slowest growth occurred just after transformation (SL 6–10 mm), with daily growth <0.3 mm/day, and maximum growth rates of about 1 mm/day occurred in juveniles 70–120 mm SL (between 110 and 160 days) (Fig. 6). These growth rates are similar to those measured by Allen (1988) who estimated that juveniles 21–29 mm SL grew at 0.36 mm/day, and juveniles 19–47 mm SL grew at 0.99 mm/day.

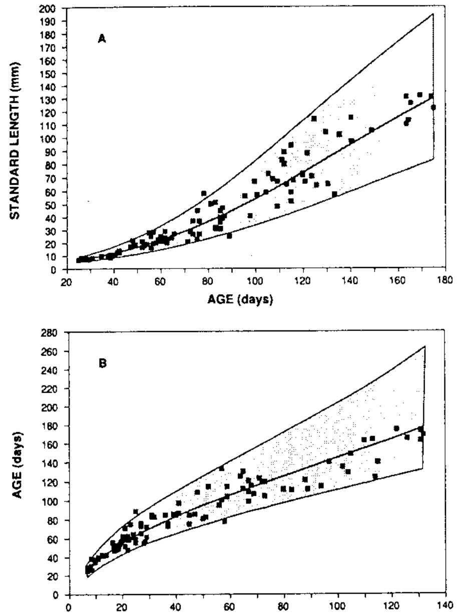

Figure 5

Gompertz relationship with 95% confidence intervals fitted to length-at-age of California halibut. (A) Standard length-at-age; (B) estimated age-at-length (mm).

Distribution and abundance

Juvenile California halibut 16–70 mm SL were present in the bays during January–July 1987 and March–September 1988, and on the open coast between May and September 1988. The distribution of transforming larvae and juveniles on the open coast differed for the 1987 and 1988 year-classes, with very few larvae and no small juveniles taken on the open coast in 1987

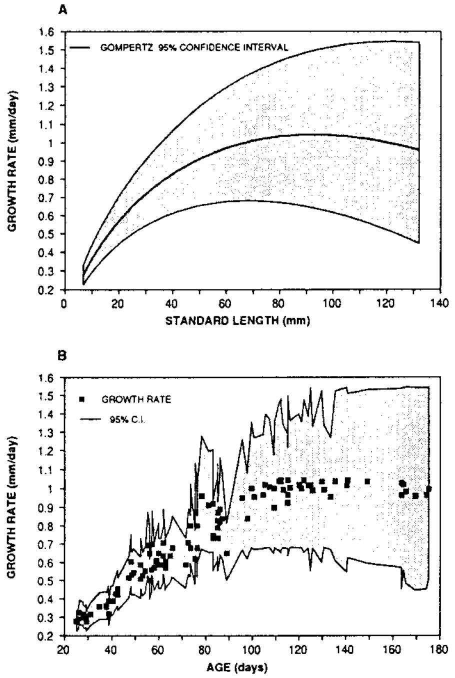

Figure 6

Growth rates of juvenile California halibut estimated from the Gompertz parameters for length-at-age, shown with 95% confidence intervals. (A) Relationship between growth rate (mm/day) and length (mm); (B) relationship between growth rate (mm/day) and age (days).

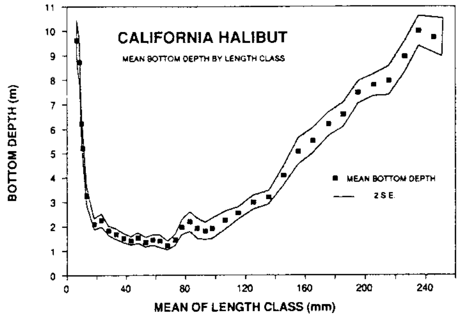

Figure 7

Mean depth of capture of California halibut by standard length-class (mm). Length-classes (mm) were ≤7 (*n* 54), 8 (52), 9 (47), 10 (38), 11–15 (116), 16–20 (198), 21–25 (161), 26–30 (161), 31–35 (116), 36–40 (116), 41–45 (138), 46–50 (127), 51–55 (124), 56–60 (92), 61–65 (81), 66–70 (92), 71–75 (74), 76–80 (45), 81–85 (53), 86–90 (50), 91–95 (42), 96–100 (53), 101–110 (74), 111–120 (103), 121–130 (101), 131–140 (154), 141–150 (154), 151–160 (109), 161–170 (129), 171–180 (143), 181–190 (121), 191–200 (135), 201–210 (128), 211–220 (88), 221–230 (73), 231–240 (60), and 241–250 (47).

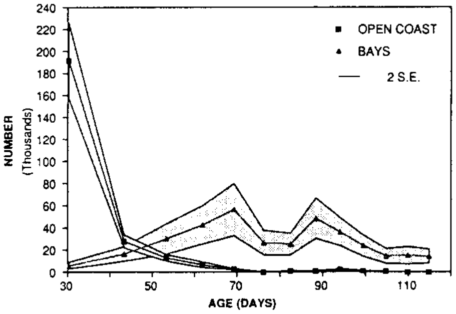

Figure 8

Abundance of juvenile California halibut by age-class for open coast and bay habitats in 1988.

whereas transforming larvae and newly-settled juveniles were common in 1988. Only the 1988 year-class was used to compare growth and mortality rates for juvenile halibut in bays and on the open coast. Further information on the distribution patterns of juvenile California halibut can be found in Kramer (1990).

The length distribution of transforming larval and juvenile halibut varied with depth. The smallest length-class of halibut (≤7 mm SL) was taken at an average depth of 9.6 m (SD 3.08, *N* 54). The mean depth of occurrence decreased with increasing length up to a mean length of 67.8 mm SL (Fig. 7). At this size, the trend reversed, with mean depth of occurrence increasing with increasing length (Fig. 7). This pattern of length-at-depth indicates that transforming and newly-settled halibut move into shallower water along the open coast and into the bays, and halibut >70 mm SL move into deeper water habitats within the bays (maximum bay depths were <5 m) and eventually move out of the bays to the open coast (Fig. 7) (Plummer et al. 1983).

The age of peak abundance of juvenile halibut in the bays in 1988 was equivalent to the average time required for newly-hatched larvae to move from the continental shelf to the bays. Peak abundance was at about 70 days in both Mission Bay and Agua Hedionda

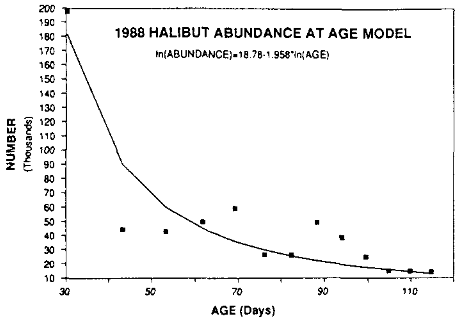

Figure 9
Total abundance of juvenile California halibut by age-class summed over both open coast and bay habitats, with the fitted model used to estimate mortality rates.

Table 3
Sum of squared deviations (SS) between observed and calculated or transformed abundance-at-age predicted from seven regression models applied to abundance-at-age for juvenile California halibut from 1988.

Model	Residual SS ($\times 10^9$)
1 Survival rate (SR) increases linearly SR = 0.264 + 0.0072 • age	6.48
2 Survival rate increases exponentially SR = 0.174 • exp((0.0070 • age) + 1.0035)	7.99
3 Survival rate asymptotic SR = 0.025 • age • exp(−0.897)	7.49
4 Daily production ln(daily production) = 17.1 − 1.54 • ln(age)	12.09
5 Daily production ln(daily production) = 9.55 − 0.0123 • age	12.60
6 Log-transformed abundance on age ln(abundance) = 12.3 − 0.0229 • age	10.87
7 Log-transformed abundance on ln(age) ln(abundance) = 18.78 − 1.958 • ln(age)	4.38

Lagoon ($N_{\text{Mission Bay}}$ 42,067, SE 8543; $N_{\text{Agua Hedionda Lagoon}}$ 14,432, SE 3312), but there was a second large peak in Mission Bay for individuals at about 90 days (N 43,697, SE 7850) (Fig. 8).

The class composed of transforming larvae (age 30 days) was the most abundant age class on the open coast in 1988 (N 191,553, SE 17,339) (Fig. 8). Abundance rapidly decreased with age on the open coast, with essentially no halibut 70–180 days of age present on the open coast (Fig. 8). The decline in abundance of halibut on the open coast corresponded to an increase in the bays (Fig. 8).

Mortality

Total age-specific abundance was determined by combining data from the bay and open coast habitats (Fig. 9). In the survey area, the total loss of juvenile halibut ages 30–115 days was estimated at 183,250 (95% CL of 148,800 and 210,350) (Fig. 9).

Instantaneous mortality rates ($z_{(t)}$) were calculated by age-class using abundance-at-age, with age obtained from the linear regression of ln-transformed abundance on ln(age) (Table 3, Fig. 9), and the duration of each age-class calculated from the age-at-size relationship (Table 4) (Lo 1985). Instantaneous mortality rates ($z_{(t)}$) were highest (0.044) for the youngest juveniles, and decreased with increasing age but became constant ($\bar{x}$ 0.0124, SD 0.001) for juveniles 70 days of age and older (Table 4).

I also calculated habitat-specific instantaneous mortality rates ($z_{(t)}$) for juveniles $\leqslant$70 days of age that were taken only on the open coast, and for those 88–115 days of age taken only in the bays (i.e., immigration completed (Table 5).

The apparent mortality in bays was much higher than that predicted from the combined bay and coast data, ranging from 0.043 to 0.037 for the bay model and from 0.011 to 0.014 for the total mortality model (Tables 4, 5). The age-specific mortality of halibut from the bays declined with increasing age, and was not constant as predicted by the total mortality model (Tables 4, 5).

To test for differences between the age-specific instantaneous mortality rates ($z_{(t)}$) of the total population, and of the open coast and bays, I used ANCOVA on the age-specific mortality coefficient, Beta. Beta is related to the instantaneous mortality rate ($z_{(t)}$) by the equation: $z_{(t)}$ = Beta/t (Lo 1985). The Beta coefficients for the total population (1.94, SE 0.22) and the open coast juveniles (ages $\leqslant$70 days, Beta 3.58, SE 1.10) were significantly different ($P \leqslant 0.01$) (Table 6). The difference in the Beta coefficient between juvenile halibut on the open coast and the total halibut abundance-at-age is probably due to movement of halibut from the coast to the bays. Nearly half of the decline in abundance of juveniles along the coast could be caused by their movement into the bays (1.94/3.58 = 0.54). The Beta coefficients for the total population and the bay juveniles (ages 94–115 days) also differed significantly ($P \leqslant 0.05$), with a Beta of 0.69 (SE 0.77) for the total population, and 2.96 (SE 0.65) for the juveniles from the bays (Table 6). Mortality rates in the bays appear to be underestimated by the abundance-at-age model for the total halibut population.

Table 4

Instantaneous mortality rates for the 1988 year-class of juvenile halibut <115 days ($z(t_i)$) by age in days (t_i) computed from daily juvenile production estimates (P_{ti}) and age (t_i) for 1988. Daily production estimates were obtained from log-linear model estimates of abundance-in-age classes adjusted for the number of days juveniles remained in the age-class. Percent of the total population in the bays by age-class is also given.

Length-class (SL, mm)	Age-class (t_i) (days)	Estimated abundance (*n*)	Percent in bays	Estimated daily production				
				P_{ti}	$P_{ti-1} - P_{ti}$	$t_i - t_{i-1}$	$t_i = (t_i + t_{i-1})/2$	$z(t_i)$
≤10	30.3	181385.1	3.08	18138.5				
11–15	43.3	90161.8	40.37	7706.1	10432.4	13.0	36.8	0.044
16–20	53.3	60025.3	69.92	6454.3	1251.8	10.0	48.3	0.016
21–25	61.8	44927.3	86.16	5615.9	838.4	8.5	57.5	0.015
26–30	69.3	35901.3	95.24	5056.5	559.4	7.5	65.5	0.013
31–35	76.2	29812.5	100.00	4586.5	469.9	6.9	72.7	0.013
36–40	82.5	25518.1	95.93	4183.3	403.2	6.3	79.3	0.013
41–45	88.4	22290.1	98.13	3910.5	272.7	5.9	85.4	0.011
46–50	94.1	19723.2	93.30	3586.0	324.5	5.7	91.2	0.014
51–55	99.5	17681.8	95.68	3336.2	249.8	5.4	96.8	0.012
56–60	104.8	15973.4	96.17	3132.0	204.2	5.3	102.1	0.011
61–65	109.9	14554.3	100.00	2910.8	221.2	5.1	107.3	0.013
66–70	114.9	13340.1	100.00	2722.4	188.4	5.0	112.4	0.012

Table 5

Habitat-specific instantaneous mortality rates of juvenile halibut <115 days ($z(t_i)$) by age in days (t_i) computed from daily juvenile production estimates (P_{ti}) and age (t_i) for 1988. Halibut 30.3–69.3 days of age were from the open coast habitat, and halibut ≥88.4 days were from the bays. Daily production estimates were obtained from log-linear model estimates of abundance by habitat adjusted for the number of days juveniles remained in each age-class.

Habitat	Age-class (t_i) (days)	Estimated abundance (*n*)	Estimated daily production				
			P_{ti}	$P_{ti-1} - P_{ti}$	$t_i - t_{i-1}$	$t_i = (t_i + t_{i-1})/2$	$z(t_i)$
Open coast	30.3	185384.8	18538.5				
	43.3	32540.9	2781.3	15757.2	13.0	36.8	0.065
	53.3	11820.4	1271.0	1510.3	10.0	48.3	0.054
	61.8	5746.9	718.4	552.6	8.5	57.5	0.051
	69.3	3288.5	463.2	255.2	7.5	65.5	0.048
	76.2						
	82.5						
Bays	88.4	45824.8	8039.4				
	94.1	33279.7	6050.9	1988.6	5.7	91.2	0.043
	99.5	25010.6	4718.9	1331.9	5.4	96.8	0.041
	104.8	19175.6	3759.9	959.1	5.3	102.1	0.038
	109.9	15035.1	3007.0	752.9	5.1	107.3	0.039
	114.9	11972.7	2443.4	563.6	5.0	112.4	0.037

Bay abundance-at-age estimate: $\ln(\text{abundance}) = 33.68 - 5.12 * \ln(\text{age})$ (residual SS = 4.567×10^7).
Open coast abundance-at-age estimate: $\ln(\text{abundance}) = 28.76 - 4.87 * \ln(\text{age})$ (residual SS = 6.219×10^7).

Table 6

Analysis of covariance (ANCOVA) on the age-specific mortality rate Beta by habitat, where Beta is defined by the relationship between the instantaneous mortality rate and age (z_t = Beta/t).

Covariates	*N*	Age range (days)	Beta	SE	*F*	*P*
Total population	4	43–69	1.94	0.22	19.62	<0.01
Coast population	4	43–69	3.58	1.10		
Total population	5	94–115	0.69	0.76	8.31	<0.05
Bay population	5	94–115	2.96	0.65		

Rate of movements into bays

I estimated the proportion of the population by age-class emigrating each day from the open coast to the bays by calculating the difference between the percentage of juvenile halibut lost daily from the total population and from the open coast using age-specific instantaneous mortality rates (Tables 4, 5) in the following equation:

$$\% \text{ emigrating/day } =$$

$$((1 - e^{-z(\text{total population})} - (1 - e^{-z(\text{open coast})})) \times 100.$$

The decline in abundance of juvenile halibut on the open coast between days 30 and 70 was 182,100, and for the total population was 145,500 (Tables 4, 5). During this time, the daily emigration rate increased from 1.99% for juveniles from age 30–43 days, to 3.67% from age 43–53 days, then declined slightly to 3.35% by 70 days.

Discussion

Extent of bay utilization

Juvenile halibut appear to be dependent upon bays as nursery areas, since nearly all halibut between 76 and 115 days of age occurred in the bays rather than the open coast (Fig. 8). Transforming larvae and newly-settled juvenile halibut ≤70 days old occurred on the open coast (97% of the transforming larvae were on the open coast), but over 95% of the total population of halibut >70 days were in the bays (Table 4).

An alternative explanation for the decline in abundance of juvenile halibut on the open coast is that they move somewhere other than the bays, or suffer heavy mortality. If halibut moved offshore, one would expect a positive relationship between size of juvenile halibut (31–70 mm SL, or 76–115 days) and bottom depth. This is contrary to the observed size-structured distribution pattern (Fig. 7). The decrease in abundance of juvenile halibut on the open coast may have included higher in situ mortality rates, but the corresponding increase in abundance in the bays suggests that movement from the coast to the bays probably accounts for about half of the coastal decline.

Advantage of bays as nursery areas

Growth The potential advantages of using bays as nursery areas are increased growth and decreased mortality. Increased growth was not observed for juvenile English sole *Parophrys vetulus* in Oregon estuaries: they grow at about the same rate as juveniles on the Oregon coast, but were more variable in size-at-age than those on the coast (Rosenberg 1982). Similarly, growth rates of juvenile California halibut ≤40 mm SL on the coast and in the bays were not significantly different.

California halibut 70–120 mm SL grew faster than all other length-classes with rates approaching 1 mm/day (Fig. 6). These fast and variable growth rates occurred during the period when juvenile halibut occurred only in the bays (>115 days of age). Unfortunately, comparisons could not be made between open coast and bay habitats during this period of fast growth, which coincides approximately with a change in the food habits of halibut >55 mm SL, from a diet composed primarily of small crustaceans (copepods, amphipods, mysids, and cumaceans) to one composed of an increasing proportion of fish by weight (mostly gobies) (Haaker 1975, Allen 1988, Drawbridge 1990). Juvenile halibut feeding on gobies in the laboratory remain partially buried in the substrate, only striking at gobies passing within a distance of three headlengths (Haaker 1975). Gobies are abundant in bays (mean density of *Ilypnus gilberti* in Mission Bay, 8.1/m^2), but not in shallow coastal waters <30 m (Brothers 1975, Allen 1985, Plummer et al. 1983). The diet of larger juvenile halibut becomes increasingly piscivorous: juvenile halibut >150 mm SL on the open coast eat primarily northern anchovies by weight (Plummer et al. 1983, Allen 1982).

Predation risk Predation risk may be higher for small halibut on the open coast than in the bays. At least six fish species on the open coast are known to eat flatfishes: these include California halibut, thornback ray *Platyrhinoidis triseriata*, fantail sole *Xystreurys liolepis*, bigmouth sole *Hippoglossina stomata*, speckled sanddab *Citharichthys stigmaeus*, and California lizardfish *Synodus lucioceps* (Ford 1965, Allen 1982). Ford (1965) found many small halibut (TL <10 mm) in the stomach contents of thornback rays, with a maximum of 15 newly-settled halibut in the stomach of one ray alone. The combined density of rays *Platyrhinoidis triseriata*, *Urolophus halleri*, and *Gymnura marmorata*) on the shallow open coast (<10 m) is about 100/hectare (Ford 1965). Speckled sanddab is the most abundant flatfish in shallow open coast waters, with a mean density of 950/hectare at Torrey Pines (Ford 1965, Allen 1982, Love et al. 1986, DeMartini and Allen 1984, Kramer 1990). Although the diet of speckled sanddab is composed primarily of mysids, they are probably capable of eating newly-settled halibut, since small unidentified flatfish juveniles have been found in their stomachs (Ford 1965).

In the bays, two potential predators include the round stingray *Urolophus halleri*, and the staghorn sculpin *Leptocottus armatus* (Allen 1985, Tasto 1975, Babel

1967). Both occur along the shallow open coast as well, but are most abundant in bays (Allen 1985). Staghorn sculpin feed primarily on crustaceans (>50% by weight), but small diamond turbot *Hypsopsetta guttulata* have also been found in their stomachs (frequency of occurrence 0.5%) (Tasto 1975). Over 94% of the diet by volume of round stingray is composed of molluscs, polychaetes, and crustaceans, but gobies also have been found in their stomachs (Babel 1967).

Other predators found both in the bays and on the open coast include barred sand bass *Paralabrax nebulifer*, spotted sand bass *P. maculatofasciatus*, and kelp bass *P. clathratus*. Spotted sand bass occur predominantly in bay habitats, barred sand bass occur ubiquitously in the bays and on the open coast, and kelp bass are associated with rock reef and kelp bed habitats on the open coast, but also have been taken as juveniles in bays (Allen 1985, Lane 1975). Kelp bass on the open coast feed mostly on northern anchovies and crabs, and have been found occasionally with flatfishes in their stomachs (Quast 1968). The diet of barred sand bass taken from bottom depths of 8–30 m on the open coast indicates that they forage close to the substrate, feeding on brachyuran crabs, mysids, pelecypods, and epibenthic fishes (mostly *Porichthys notatus*) (Roberts et al. 1984, Feder et al. 1974). Spotted sand bass occur predominantly in bay habitats, feeding on crabs and other crustaceans, and on small kelpfish (Feder et al. 1974, Allen 1985). The juveniles of all three species are found commonly in Mission Bay, and are considered highly probable goby predators (Brothers 1975). The sand basses probably eat juvenile halibut also, as gobies and halibut share the same habitats.

Comparison of predation risk must also include a measure of abundance or biomass of predators by habitat. The estimated density of the potential bay predators (round stingray, *Paralabrax* spp., and staghorn sculpin) based on otter trawl surveys is 61/hectare in Agua Hedionda Lagoon, and only 3/hectare on the open coast (San Diego Gas and Electric 1980). The estimated density of two open-coast predators, the speckled sanddab and the thornback ray, is >1000/hectare (Ford 1965). Based on this scanty information, it appears that predators are more abundant on the open coast than in the bays.

Thus the possible advantages of using bays as nursery areas by juvenile halibut appear to be at least twofold: (1) Decreased risk of predation on newly-settled juveniles, since fewer predators are known to occur there; and (2) increased potential for faster growth of juveniles >55 mm SL because small fishes (gobies) are more abundant in bays than on the open coast (Haaker 1975, Allen 1985).

Migration to bays

The migration of larvae from spawning areas over the continental shelf to their juvenile nursery areas in embayments is thought to consist of two phases (Boehlert and Mundy 1988): Accumulation of larvae in the nearshore zone (Boehlert and Mundy 1988, Miller et al. 1986), and location and entering of the bays by transforming larvae and juveniles (Boehlert and Mundy 1988). The nearshore accumulation of larvae prior to movement to the bays is probably facilitated by the timing of spawning, the short duration of pelagic stages, and the vertical distributions of the postflexion and transforming larval stages. California halibut spawn throughout the year, with peak spawning during the winter and spring (Lavenberg et al. 1986, Walker et al. 1987). The spawning peak coincides with the period of minimum offshore transport of surface water in the Southern California Bight (Parrish et al. 1981, Jackson 1986). Offshore transport increases in late spring and summer due to increasing upwelling activity (Parrish et al. 1981, Jackson 1986). The seasonal shift in upwelling activity has been correlated with a seasonal cross-shelf shift in the zooplankton assemblage off San Onofre: from February to early April the community was shifted onshore, and from mid-April to July the shift was offshore, corresponding to the period of increased upwelling (Barnett and Jahn 1987).

The size distribution of California halibut larvae taken in plankton tows indicates that they move inshore as they approach metamorphosis. Preflexion and flexion larvae (~2–6 mm SL) occur in midwater >2 km offshore, whereas transforming larvae occur at night in the neuston within 1 km of shore (Moser and Watson 1990). My collections indicated that transforming larvae occur on the bottom during the day; thus transforming larvae appear to undergo a daily vertical migration, occurring at the surface at night and at the bottom during the day. Larvae of other *Paralichthys* species, yellowtail flounder *Limanda ferruginea*, stone flounder *Kareius bicoloratus*, and the larval stages of several crustacean taxa have similar diurnal activity patterns (Weinstein et al 1980, Tsuruta 1978, Shanks 1988, Penn 1975, Smith et al. 1978).

Postflexion and transforming halibut larvae may be transported shoreward by internal waves at night when they are in the neuston, with very little movement during the day while they are on the bottom, resulting in accumulation of larvae nearshore (Moser and Watson 1990). Surface slicks associated with internal waves may transport neustonic larval fishes and crustaceans onshore (Shanks 1988, Kingsford and Choat 1986). Recovery of drift bottles released <20 miles offshore in the Southern California Bight region is greatest between March and October, also suggesting increased onshore transport of surface water (Schwartzlose 1963).

Once nearshore, transforming larvae or settled juveniles may search for bays by using longshore transport (Boehlert and Mundy 1988). Net longshore transport of shallow shelf waters in the Southern California Bight is to the south (Winant and Bratkovich 1981). Longshore current speed measured in shallow water (15m) averages less than 5cm/second; at this speed, after 12 hours longshore movement could be as great as 2km (Winant and Bratovich 1981).

My data on the abundance of transforming larvae and newly-settled juveniles provide an estimate of the time required for halibut to locate and enter the bays from the open coast. The time required can be considered to be equivalent to the difference in the age of peak abundance between the coast and the bays. Halibut reached peak abundance in the bays at an age of about 70 days in 1988, whereas they were most abundant at age 30 days (transformation) on the open coast (Fig. 8). Thus the time required to locate and enter the bays was about 40 days in 1988 (70–30 = 40 days) (Fig. 8). Over a 40-day period, halibut potentially could be transported about 80km alongshore (40 days × (2km at 12 hours in the neuston)), which is greater than the total distance between the northern sampling block at San Onofre and Mission Bay (64km) (Fig. 1). I measured the maximum distance between adjacent bays in southern California at less than 60km, thus larvae using this transport mechanism would probably encounter a bay within 30 days of reaching the shallow-water coastal environment.

The potential cues used to find the entrances to bays include temperature, currents, odor, turbidity, and bottom substrate (Boehlert and Mundy 1988). A probable cue in southern California is temperature: during spring and summer, when larvae and juveniles are moving into the bays, the temperature is as much as 5°C warmer in the bays than on the open coast (Kramer 1990).

Once a bay entrance is located, the mechanism used to migrate into the bay probably is tidal transport, using incoming tidal currents to aid movement into the bay, and remaining at the bottom to avoid transport out of the bay (Weinstein et al. 1980, Boehlert and Mundy 1988, Fujii et. al. 1989, Tsuruta 1978, Weihs 1978, Runsdorp et al. 1985). To use tidal stream transport to move into bays, individuals must be able to orient to currents, control vertical movements, and remain on the bottom during unfavorable currents. These abilities probably develop by the time larvae reach transformation (Boehlert and Mundy 1988, Weinstein et al. 1980). Only a few tidal cycles may be required for halibut to move from the entrance into the bay. Larval flounder (*Paralichthys* sp.) on the North Carolina coast use tides to augment movement into marshes, migrating to the surface during night flood tides and remaining on the bottom during ebb tides and during the day (Weinstein et al. 1980).

In conclusion, California halibut settle either in bays or on the open coast, but ultimately nearly all halibut settling on the coast enter and use the bays as nursery areas during their first year of life. The advantages of bays as nursery areas may be a decrease in risk of mortality of newly-settled halibut, and an increase in growth of larger juveniles that feed upon the abundant small fishes in the bays.

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