Abstract-California halibut, Paralichthys californicus, collected by a 400mesh eastern trawl in southern (Mexican border to Point Conception) and central (Point Conception to Tomales Bay) California were aged by using whole and sectioned otoliths (sagittae) to determine age, growth, and mortality. Males represented 69% of the sample from southern California and 53% of the sample from central California. A higher proportion of California halibut were older in southern California than in central California. Although California halibut can live as long as 30 years, the oldest fish found in our study was 13 years old. For southern California, the von Bertalanffy growth function (VBGF) was L_t =925.3(1- $e^{-0.08(t+2.2)}$) for males and $L_t=1367.7(1-e^{-0.08(t+1.2)})$ for females. For central California, the VBGF was L_t =956.7(1- $e^{-0.10(t+2.1)}$) for males and $L_t=1477.1(1-e^{-0.10(t+0.2)})$ for females. The VBGF showed that at the same age, females on average were larger than males in both southern and central California. The VGBF also showed that both male and female halibut in central areas on average were larger than halibut from southern California. Instantaneous mortality rates of halibut in southern California were estimated at 0.91 for males and 0.68 for females. Mortality estimates for central California could not be calculated because of small sample sizes.

Age, growth, and mortality of California halibut, Paralichthys californicus, along southern and central California

Leslie S. MacNair Michael L. Domeier Calvin S. Y. Chun

California Department of Fish and Game 4665 Lampson Avenue, Suite C Los Alamitos, California 90720 E-mail address (for C. S. Y. Chun, contact author): cchun@dfg.ca.gov

California halibut, *Paralichthys californicus*, is an important flatfish species for sport and commercial fisheries in nearshore waters off central and southern California (Frey, 1971). The gear most commonly used commercially to harvest California halibut are otter trawls, gill nets, and trammel nets, whereas hook-and-line or spear are used mostly in the recreational fishery (Kramer and Sunada, 1992).

Information on age, growth, and mortality of California halibut are important to the management of both the sport and commercial halibut fisheries. Previous studies have addressed these issues to a limited extent. Pattison and McAllister (1990) studied techniques to age halibut and determined length-atage of halibut along the California coast, but most of the fish were taken south of Point Conception and they did not do separate analyses for southern and central California. Sunada et al. (1990) analyzed age, size, and sex composition of commercial landings in southern California. Haaker (1975) studied the biology of California halibut in Anaheim Bay, including age and growth, but the fish he used were generally less than three years of age, immature, and included fish only to 510 mm total length. In contrast to other studies, our study provides information on age and growth for central and southern California separately. Mortality for southern California was also calculated.

Methods

Southern California was defined as the area between the U.S.-Mexico border

and Point Conception, and central California as the area between Point Conception and Tomales Bay. Bottom trawl surveys were conducted off central California from 8 July through 3 August 1993 and off southern California from 14 February through 18 March 1994. California halibut were caught with a 400-mesh eastern trawl (15 m wide × 1.5 m high; 9.8 cm mesh body, 8.5 cm mesh codend). For both areas, sampling effort was stratified by depth: 0-20 fathoms (fm), 21-40 fm, and 41-60 fm. Fifty stations within each depth stratum were randomly selected for sampling by trawling parallel to isobaths at each station. The sample sizes were not proportional to the estimated area of the strata (Table 1).

An additional ten California halibut were collected with the same 400-mesh eastern trawl gear in southern California from July 1994 to June 1995. These were included in the age and growth determinations. However, they were not used for mortality estimates because they were collected at a different time period from the other halibut collected off southern California.

Each halibut was measured to the nearest millimeter for total length (TL) and standard length (SL). Gonads were examined visually to determine the sex of the fish. Sagittal otoliths were removed and stored dry in vials for age determination. Pattison and McAllister (1990) determined that when compared with other fish structures, otoliths provided the most reliable ages for California halibut. They found that in an otolith, an opaque band was formed during spring and summer (from April to October) and a translucent band was

Manuscript accepted 9 March 2001. Fish. Bull. 99:588–600 (2001).

Table 1
Number of trawls and number of California halibut used in age and growth analyses by depth strata and region. Asterisk (*)
indicates that these fish were not used in the mortality estimates because they were caught at a later date.

		Southe	ern California			Central California	
Stratum	Depth (fm)	No. of trawls	No. of halibut used	Area (nmi²)	No. of trawls	No. of halibut used	Area (nmi²)
1	0-20	58	913 +3*	575	47	254	587
2	21-40	46	165 +2*	495	39	22	905
3	41-60	45	13 +1*	425	40	0	1124
Total			1091 +6*			276	

deposited in winter (from November to March). A combination of an inner opaque and adjacent outer translucent zone represents an annular growth ring or annulus (Casselman, 1983). This growth ring was validated by Pattison and McAllister (1990) with oxytetracycline-marked otoliths; they found that only one complete ring (opaque and translucent) was formed each year.

Pattison and McAllister suggested that age estimates of older fish (age 11 or older) may be underestimated when whole otoliths, rather than sectioned otoliths, are read. In the preliminary analysis in our study, to test if a significant difference existed between estimating age with whole otoliths and estimating age with sectioned otoliths, an otolith from each of 80 randomly selected fish (10 fish from each 100-mm size class from 200 to 900 mm TL) was viewed both whole and sectioned to estimate age. A mutually determined age (an age agreed upon by the two readers) was established for the whole otolith, as well as for the sectioned version of the otolith. If the age readings were identical for each reader, then that age was considered the correct age. Otherwise, the two readers

discussed the readings and agreed upon an age. The nonparametric, paired Wilcoxon test was applied to the pairs of whole and sectioned otolith ages for each fish. In addition, a paired Wilcoxon test was applied to otoliths for fish restricted to 8 years and older (*n*=32).

In addition to determining whether to use whole or sectioned otoliths, the preliminary analysis also involved determining how halibut age was to be estimated: either by using the mutually determined age, as already described, or an averaged age. The averaged age was a single value calculated as the mean of the four independent readings (whole or sectioned version of an otolith read by two readers on two different occasions) and rounded to the nearest integer. Sample means generally have the same type of sampling distribution as individual observations, but with a smaller variance. Hence, we applied the nonparametric paired Wilcoxon test to the pairs of averaged and mutually determined ages for each otolith (*n*=80). The results from the preliminary analysis determined how we conducted the process of age determination in the main part of the study.

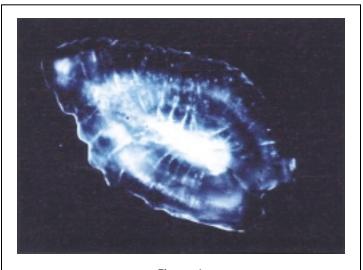
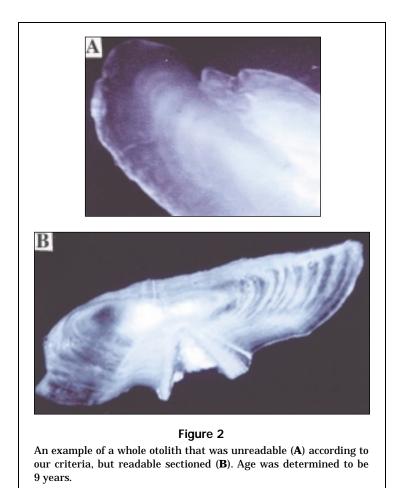


Figure 1 An example of an otolith viewed whole. Age was determined to be 3 years.

We acknowledge that using sectioned otoliths is the recommended procedure when analyzing long-lived fish. Although individual California halibut may live as long as 30 years (Frey, 1971; Pattison and McAllister, 1990), all the fish in our study were relatively young (less than 14 years old). Because of our preliminary analysis and because sectioning a large number of otoliths (potentially over 1300) would have entailed considerable costs, all otoliths were initially read whole. We did use sectioned otoliths when the variability in the age readings for that otolith seemed to be unacceptably high and when the whole otolith was judged unreadable because of the anise oil residue.

Before recording ages, two readers consulted with each other to standardize their technique for counting annuli. Each otolith was initially read whole, that is, the surface of the uncut otolith was read for the number of annuli present. The whole otolith was submerged in water, illuminated with fiber optic light transmitted from the sides, and viewed against a dark background with a dissecting microscope (16× to 25×). Figure 1 is an example of an otolith



viewed whole. Some whole otoliths from central California were soaked in anise oil during initial handling to facilitate viewing annuli. The anise oil, however, left a residue that later caused problems in reading the otoliths. Therefore, these otoliths had to be sectioned before they could be read. For each otolith (either whole or sectioned), the two readers counted the annuli twice at different times, for a total of four independent readings. The birth date for a halibut was assigned to 1 January (Williams and Bedford, 1974).

The mean and standard deviation of the four age determinations for each whole otolith were calculated. Because of our preliminary analysis, if the standard deviation was less than 1.5 years, the mean, rounded to the nearest integer, was the estimated age for that halibut. A standard deviation of 1.5 years was arbitrarily chosen as the upper limit for acceptance of an age determination. This deviation represented a difference in ages of 3 years or more among readings. If the standard deviation was 1.5 years or larger the whole otolith was judged unreadable. These otoliths were cut laterally through the nucleus with a diamond blade on a Buehler low-speed Isomet saw. Three sections, approximately 0.38 mm thick, were cut from each otolith and mounted on a glass slide with Eukitt clear mounting medium. These sections were viewed with a compound microscope (25× to 100×) with transmitted light. The best of three sections on a slide was chosen for age determination. Figure 2 is an example of a whole otolith that was unreadable, but readable when sectioned.

The mean and standard deviation of the four age determinations for each sectioned otolith were calculated. In accordance with our preliminary analysis, if the standard deviation was less than 1.5 years, the rounded mean was considered the estimated age. If the standard deviation was 1.5 years or larger, the otolith was not used in the analysis because it was felt to be unreadable. The index of average percent error was calculated to compare within-reader precision (Beamish and Fournier, 1981) for both whole and sectioned otoliths.

Several analyses were made on total lengths and ages by sex and region. Comparisons of both length and age distributions between sexes for each region were made by using the two-sample Kolmogorov-Smirnov test (Hollander and Wolfe, 1973). Length-at-age data for females were compared with those for males sampled from the same region by using the nonparametric Mann-Whitney test. The Mann-Whitney test was also used to compare the length-at-age data between regions for each sex separately.

The von Bertalanffy growth function was fitted to the length-at-age data for individual fish (Ricker, 1975); parameters were estimated by nonlinear least squares by us-

ing the Gauss-Newton method in the program NLIN from SAS (1990). Outliers were removed when the von Bertalanffy growth function was fitted to the data. Outliers were data points that clearly stood apart in scatter plots of individual total length versus age. Means and standard deviations of observed length-at-age, and the theoretical von Bertalanffy growth function (VBGF) were plotted for females and males by region.

Hotelling's T^2 test (Bernard, 1981) compared growth parameters between male and female halibut in each region. This test was also used to determine if growth in southern California was different from growth in central California, for each sex separately.

The estimated annual survival rate, S, was calculated for males and females separately by region by using Robson and Chapman's method (1961). Total annual mortality, A, was calculated by using the complement of annual survival, A = 1 - S. The instantaneous mortality rate, Z, was estimated by using $-\ln(S)$ (Ricker, 1975). All statistical analyses were performed at the 0.05 level of significance.

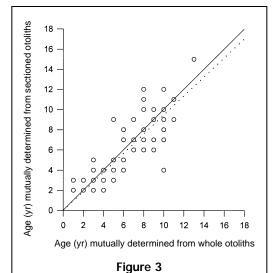
Results

In our preliminary analysis, a subsample of whole otoliths from 80 fish were read and then sectioned to determine the best method for reading otoliths for age determination. In Figure 3 is a plot of the mutually determined ages from sectioned and whole otoliths, along with a 45 degree line and a linear regression. No significant difference was found between ages from whole and sectioned otoliths when using all 80 fish (paired Wilcoxon test, P=0.21), and when using only older fish (8 years and older) (paired Wilcoxon test, P=0.11).

Also, as part of the preliminary analysis, in the comparison of averaged ages with mutually determined ages for the estimation of halibut age, we found no significant differences for both whole (paired Wilcoxon test, mean difference=0.15, P=0.23) and sectioned ototliths (paired Wilcoxon test, mean difference=0.16, P=0.06). Therefore, ages were estimated for each individual by calculating an average of four independent readings from whole or sectioned otoliths because an average of several readings is considered a more reliable measurement than a single reading (Fleiss, 1986).

The total number of trawls conducted by strata and region are listed in Table 1. The original intent was to perform 50 trawls at each depth stratum for both southern and central California. However, substrate obstructions and other problems limited the number of successful tows at most strata. A total of 58 trawls were successfully completed in stratum 1 in southern California.

Because most of the halibut were collected in a single stratum (stratum 1), comparisons among strata were not made (Table 1). In southern California, a total of 916 individuals were collected from stratum 1 (84% of total), 167 individuals from stratum 2, and only 14 individuals from stratum 3. In central California, a total of 254 individuals were collected from stratum 1 (92% of total), 22 individuals from stratum 2, and none from stratum 3.



A scatter plot of mutually determined ages for sectioned otoliths and whole otoliths. The dotted line is the linear regression through the origin (slope is 0.947); solid line is the 45 degree line.

For southern California, pairs of whole otoliths from 1109 individuals were initially examined to estimate age. Twenty-two pairs of whole otoliths were unreadable, six pairs had no discernible opaque and translucent zones, and sixteen pairs had large variations in the four age readings (SD ≥1.5). These 22 pairs of whole otoliths were sectioned to determine age. Of these, two were eliminated because of large variations in the four age readings (SD ≥1.5). An additional ten were eliminated as outliers because lengths were anomalously small or large for the estimated age when the von Bertalanffy growth function was fitted to the data. Thus, a total of 1097 individuals were used to evaluate age and growth for halibut in southern California. The sample consisted of 69% males (761 individuals) and 31% females (336 individuals). Tables 2 and 3 provide counts of total length versus age for males and females, respectively, in southern California.

In central California, pairs of whole otoliths from 292 individuals were initially examined to estimate age. Otoliths from 28 halibut had no discernible opaque and translucent zones and 49 had large variations in the four age readings (SD \geq 1.5), resulting in a total of 77 otoliths that were sectioned to estimate age. Of these, fourteen otolith pairs were eliminated because of large variations in readings (SD \geq 1.5). An additional two became outliers that were removed when the von Bertalanffy growth function was fitted to the data. Thus, a total of 276 individuals were used to evaluate age and growth for halibut in central California. The sample consisted of 53% (147 individuals) males and 47% (129 individuals) females. Counts of total length versus age for males and females, respectively, in central California are shown in Tables 4 and 5.

Within-reader index of average percent error for whole otoliths ranged from 8.1% to 13.2%. For sectioned otoliths,

							A	Age (yr)					
TL (mm)	1	2	3	4	5	6	7	8	9	10	11	12	Mean age
201–225		2	1										2.3
226-250	2	5	2										2.0
251–275	1	20	14										2.4
276-300	1	51	59	4	1								2.6
301-325		14	33	4	2								2.9
326-350		7	21	18	5								3.4
351–375		4	32	34	17	3							3.8
376-400			11	25	16	6	1						4.3
401–425			5	10	25	8	12	2					5.3
426-450				8	15	15	11	2					5.7
451-500				6	14	26	21	6	6				6.3
501-525				1	7	14	17	5	2				6.5

9

9

7

506

8

9

1

5

1

1

538

4

3

3

2

2

1

552

2

1

n

578

7.5

7.2

7.6

8.0

7.5

0.0

0.0

8.5

1

2

1

417

5

9

4

1

482

within-reader average percent error ranged from 4.7% to

289

319

377

259

Median length of distribution: 387 mm TL

526-550

551 - 575

576-600

601 - 625

626-650

651 - 675

676-700

701-725

Mean length

In southern California, significant differences between males and females were found in comparisons of length distributions (Kolmogorov-Smirnov: D=0.42, P=0.0001). A higher proportion of males were smaller than females (Fig. 4). The median length for males was 387 mm TL (range: 210-707 mm TL); the median length for females was 544 mm TL (range: 241-987 mm TL) (Tables 2, 3, and 6). Females on average were significantly larger than males for ages 3 through 10 (Mann-Whitney tests, Table 6).

Some differences in lengths were also found between males and females in central California. Most of the larger fish were females (Fig. 4). However, the length distributions of males and females in central California were not significantly different (Kolmogorov-Smirnov: *D*=0.14, *P*=0.12). The median length for males was 437 mm TL (range: 285-781 mm TL); the median length for females was 444 mm TL (range: 262-1039 mm TL) (Tables 4, 5, and 7). Females on average were significantly larger than males for ages 3 and 5 through 8 (Mann-Whitney tests, Table 7).

In addition, comparisons were made between regions for each sex separately. In comparisons of mean length at ages, the males in central California on average were significantly larger than those in southern California for ages

2 through 9, except age 8 (Mann-Whitney tests, Table 8). The females in central California on average were significantly larger than those in southern California for only ages 5, 7, and 8 (Mann-Whitney tests, Table 8). However, the median length of females in southern California (544 mm) was greater than the median length for those in central California (444 mm).

577

586

In southern California, age distributions were significantly different for males and females (Kolmogorov-Smirnov: D=0.18, P=0.0001). A higher proportion of females were older fish compared with males. The primary age mode for females was age 6 and for males it was age 3 (Fig. 5). In central California, age distributions were also different for males and females (Kolmogorov: *D*=0.20, P=0.008). Males had a higher percentage in the 6 to 8 year range and a lower percentage in the 3 to 5 year range compared with females (Fig. 5). In central California, the primary mode for both males and females was age 3. With both regions combined, females were found up to age 13 and males up to age 12. In comparisons of age distributions between regions, we found that a higher proportion of halibut in southern California was older than halibut in central California (Fig. 5).

Because differences in length-at-age were found between sexes, von Bertalanffy growth parameters were cal-

Table 3
Female California halibut total length versus age (mostly whole otoliths, some sectioned) in southern California.

								Age (y	/r)					
TL (mm)	1	2	3	4	5	6	7	8	9	10	11	12	13	Mean ag
201-225														0.0
226-250		3												2.0
251-275	1	5	4											2.3
276-300		7	7											2.5
301-325		1	2											2.7
326-350		3	6	5										3.1
351-375		2	4	2										3.0
376-400			4	5	2									3.8
401-425			6	12	3	1								4.0
426-450			5	5	3	1								4.0
451-500			4	9	10	4	3	1						4.9
501-525				1	17	5	1							5.3
526-550				3	9	8	1	1	1					5.6
551-575				4	3	10	6	2						6.0
576-600				4	3	8	4	4	1					6.2
601-625				2	4	8	6	2						6.1
626-650					3	10	9	4	1					6.6
651-675				2	1	10	6	3	2					6.5
676-700						3	1	1	0	0	1			7.3
701-725							3	1	1	1				8.0
726-750						2	0	2						7.0
751-775							1							7.0
776-800								1	1	3				9.4
801-825								1	1	1				9.0
826-850								1	1	1				9.0
851-875								2	0	1				8.7
876-900														0.0
901-925									1	1				9.5
926-950									1	1				9.5
951-975													1	13.0
976-1000											1			11.0
Mean length Median length		292	364	463	520	591	616	666	736	828	836	000	964	

culated separately for males and females for both regions (Table 9). Outliers were removed when the von Bertalanffy growth function was fitted to the data. With outliers removed, the standard errors of the asymptotic mean length, L_{∞} , became considerably smaller. Graphs of the von Bertalanffy growth function are shown in Figure 6 (where females and males are compared by region) and Figure 7 (where southern and central California are compared by sex).

Significant differences between males and females in southern California were found for all three growth parameters (Hotelling's T^2 tests, P<0.0001). For central California, two of the three growth parameters were signifi-

cantly different between males and females (Hotelling's T^2 tests, P<0.0001). Females grew faster and on average were larger than males at the same age in both regions (Fig. 6).

Similar comparisons were made between regions for each sex separately (Fig. 7). For females, all three growth parameters were significantly different between southern and central California (Hotelling's T^2 tests, $P \le 0.003$). In contrast, the only significant difference between regions for males was in K, the Brody growth coefficient (Hotelling's T^2 tests, P < 0.0001).

In southern California, survival rates were based on ages 7 to 12 years for males and ages 6 to 11 years for females. The estimated annual survival rates, *S*, for halibut from south-

Table 4
$\label{thm:male} \mbox{Male California halibut total length versus age (mostly whole otoliths, some sectioned) in central California.}$

							A	Age (yr)					
TL (mm)	1	2	3	4	5	6	7	8	9	10	11	12	Mean ag
201–225													0.0
226-250													0.0
251-275													0.0
276-300		4	1										2.2
301-325		4	3										2.4
326-350		5	4										2.4
351-375			9										3.0
376-400		2	15	8									3.2
401-425			9	1	1								3.3
426-450			2	7	2								4.0
451-500			3	6	2	4	1	1					4.8
501-525				2	1	5	1	3					6.2
526-550				1	1	7	1	1					6.0
551-575					1	2	4	1					6.6
576-600					1	0	0	2					7.0
601–625							1	1	1				8.0
626-650						1	2	2	1				7.5
651-675				1	0	0	2						6.0
676–700						1	0	1	1				7.7
701–725								1					8.0
726-750							1	0	0	0	1		9.0
776-800										1			10.0
Mean length	000	326	385	448	493	539	596	582	649	781	737	000	
Median length o	f distribu	tion: 437	7 mm TI	_									

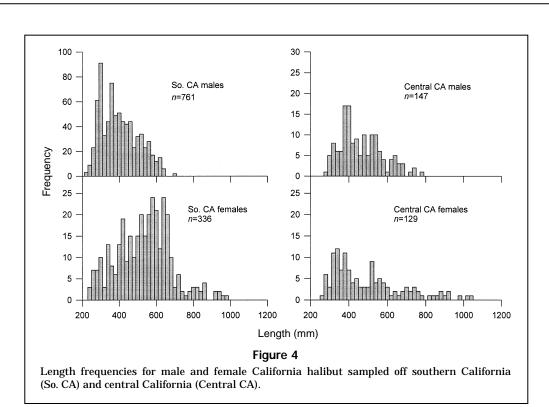


Table 5
Female California halibut total length versus age (mostly whole otoliths, some sectioned) in central California.

								Age (y	yr)					
TL (mm)	1	2	3	4	5	6	7	8	9	10	11	12	13	Mean ag
201-225														0.0
226-250														0.0
251-275		1												2.0
276-300		3	4											2.6
301-325		5	7											2.6
326-350		2	10	2										3.0
351-375		1	7											2.9
376-400			8	5										3.4
401-425			3	2										3.4
426-450			2	6										3.8
451-500			1	3	2									4.2
501-525				7	2									4.2
526-550			2	1	3									4.2
551-575			1	3	1									4.0
576-600			1	2	2	1								4.5
601-625				1										4.0
626-650					1	1	0	0	1					6.7
651-675				1	1									4.5
676-700				1	0	1	1	1						6.3
701-725					1	0	0	1						6.5
726-750					3									5.0
751-775					1	0	1							6.0
776-800						1								6.0
801-825				1										4.0
826-850								1						8.0
851-875									1					9.0
876-900								1	1					8.5
901-925								1	2					8.7
926-950														0.0
951-975										1				10.0
976-1000														0.0
1001-1025												1		12.0
1026-1050												1		12.0
Mean length	000	313	373	493	606	672	726	810	842	970	000	1027	000	
Median lengtl														

ern California were 0.40 (95% confidence interval=0.34, 0.46) for males and 0.51 (95% confidence interval=0.45, 0.57) for females. Estimated annual mortality rates, A, were 0.60 for males and 0.49 for females. Instantaneous mortalities, Z, were estimated at 0.91 for males and 0.68 for females. We were unable to calculate survival rates and mortalities for central California halibut because the sample sizes were too small.

Discussion

The California halibut can be a long-lived species, living as long as 30 years (Frey, 1971; Pattison and McAllister,

1990). However, none of the fish in our study was older than 13 years, and most of the fish were less than 11 years old (Fig. 5). We feel that the low average percent error in our study showed that both whole and sectioned otoliths were reliable methods for aging California halibut for the age range of our study.

Pattison and McAllister (1990) suggested that because of the asymmetrical growth of the sagittae in larger fish, ages assigned to older fish (age 11 or older) may be underestimated if whole otoliths, rather than sectioned otoliths, were read. Manooch and Potts (1997) in a growth study of greater amberjack also did not find whole otoliths useful in aging fish. In contrast, we found that age estimates from whole and sectioned otoliths were not sig-

nificantly different, even when the analysis was limited to ages 8 to 13 years. However, our conclusions are limited to primarily younger fish because most of the fish in our study were less than 11 years old. Pattison and McAllister recommended sectioned otoliths for fish aged 11 years or older. Nonetheless, we concur that use of sectioned otoliths in older individuals may reduce the variation in assigned ages.

We feel that the larger percentage of unreadable whole otoliths in central California versus southern California was due primarily to the preparation techniques used for age determination. The anise oil used in the initial handling of some central California otoliths created a white film that precluded the otoliths from being read at a later time. Because of problems encountered with anise oil, we do not recommend applying it to otoliths until one is ready to age them.

 Table 6

 Mean total length (mm) and standard deviation for male and female California halibut by age group in southern California. Mann-Whitney comparisons of male and female halibut for mean length at age. Asterisk (*) indicates statistical significance.

			Male					3.6 3371.4			
Age (yr)	n	Mean	SD	Min	Max	n	Mean	SD	Min	Max	Mann-Whitney <i>P</i> -value
1	4	259.3	25.0	232	290	1	252.0	_	252	252	_
2	103	289.4	28.4	210	369	21	291.9	38.4	241	368	0.77
3	178	319.3	39.3	220	411	42	364.4	63.9	254	477	0.0001*
4	110	377.3	42.2	291	501	54	462.6	86.7	342	660	0.0001*
5	106	417.2	55.0	294	561	58	520.5	64.3	389	671	0.0001*
6	92	481.7	61.9	362	646	70	591.2	67.7	401	735	0.0001*
7	97	505.6	65.1	399	645	41	616.1	60.5	493	758	0.0001*
8	40	538.3	62.6	403	707	26	666.0	101.4	492	859	0.0001*
9	23	551.5	68.0	451	707	11	736.2	131.9	534	934	0.0002*
10	6	578.2	34.5	542	619	9	828.3	67.4	720	937	0.002*
11	1	577.0	_	577	577	2	836.0	213.5	685	987	_
12	1	586.0	_	586	586	_	_	_	_	_	_
13		_	_	_	_	1	964.0	_	964	964	_
Total	761					336					

Table 7

Mean total length (mm) and standard deviation for male and female California halibut by age-group in central California. Mann-Whitney comparisons of male and female halibut for mean length at age. Asterisk (*) indicates statistical significance.

			Male					Female			
Age (yr)	n	Mean	SD	Min	Max	n	Mean	SD	Min	Max	Mann-Whitney <i>P</i> -value
2	15	325.9	29.8	285	381	12	312.9	28.7	262	367	0.29
3	46	384.8	38.1	293	472	46	373.4	70.0	279	593	0.02*
4	26	447.8	60.5	380	660	35	493.5	102.3	328	820	0.07
5	9	492.8	59.0	424	582	17	606.2	101.4	474	758	0.007*
6	20	538.6	49.4	479	680	4	672.0	87.0	582	782	0.006*
7	13	595.6	72.7	490	748	2	725.5	43.1	695	756	0.05*
8	13	582.5	74.4	475	719	5	810.4	99.3	694	925	0.002*
9	3	648.7	29.5	619	678	5	842.0	112.2	547	923	_
10	1	781.0	_	781	781	1	970.0	_	970	970	_
11	1	737.0	_	737	737	_	_	_	_	_	_
12	_	_	_	_	_	2	1026.5	17.7	1014	1039	_
Total	147					129					

The data in our study confirmed that females grow faster than males, as found in previous studies (Pattison and McAllister, 1990; Sunada et al., 1990), and that growth was different between males and females for each region. Females in both regions had larger asymptotic mean lengths, L_{∞} , than males (Table 9).

Growth curves for males and females crossed between ages 1 and 2 for southern California and at age 3 for central California (Fig. 6). This finding suggests that young male and female halibut are of similar size until about ages 2 and 3 in southern and central California, respectively. However, Haaker (1975) found that juvenile female halibut in Anaheim Bay grew faster than males. The crossover in growth curves may be due to the small sample sizes for ages 1 and 2 in our study. The growth curves also involved some extrapolation for very young ages.

Our study showed lower mean length-at-age than that obtained by Pattison and McAllister (1990); however, the differences for females were slight. These differences may partly be attributed to different environmental conditions in the years prior to each study. Pattison and McAllister used otoliths collected from 1955-66 and 1984-88, whereas we used otoliths collected from 1993 to 1995. Manooch and Potts (1997) in a study of greater amberjack in the Gulf of Mexico also cited temporal changes as one of the factors that may have contributed to differences in growth between greater amberjack in southern Florida and northern Gulf of Mexico. The geographic range of the samples may also have affected the results because we found growth differences between southern and central California. Pattison and McAllister's study encompassed samples from central and southern California, but they did not separate the two regions in their analysis. In addition, gear selectivity may have contributed to the differences found between our two studies. Pattison and McAllister used halibut that were collected with several gear types (trawl, gill net, beach seine, hook and line, and spear), whereas our study sampled halibut with only trawl gear of a specific mesh size. Potts et al. (1998) found while studying vermillion snapper from the southeastern United States that the different gear types used in sample collection may bias growth results.

Sunada et al. (1990) found that for commercial halibut landings in southern California the asymptotic mean length, L_{∞} , was 909 mm TL for males and 1445 mm TL for females. In comparison, our study showed for southern

California. Length is given in mm TL.

Table 8

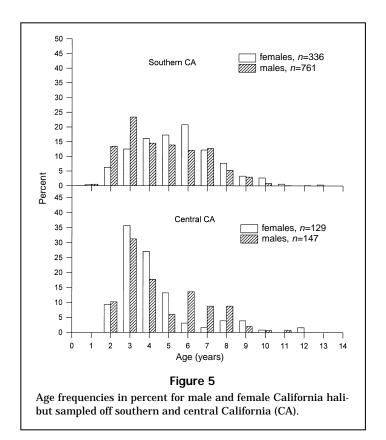
Mann-Whitney comparisons of California halibut from southern and central California for mean length at age. Asterisk (*) indicates statistical significance.

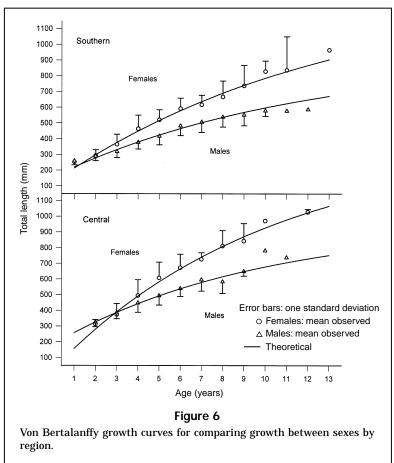
	Mean ol total leng		Sampl n		Mann-	
Age (yr)	Southern	Central	Southern	Central	Whitney <i>P</i> -value	
Males	s					
2	289.4	325.9	103	15	0.0001*	
3	319.3	384.8	178	46	0.0001*	
4	377.3	447.8	110	26	0.0001*	
5	417.2	492.8	106	9	0.0006*	
6	481.7	538.6	92	20	0.0002*	
7	505.6	595.6	97	13	0.0002*	
8	538.3	582.5	40	13	0.08	
9	551.5	648.7	23	3	0.03*	
Fema	les					
2	291.9	312.9	21	12	0.10	
3	364.4	373.4	42	46	0.92	
4	462.6	493.5	54	35	0.21	
5	520.5	606.2	58	17	0.002*	
6	591.2	672.0	70	4	0.07	
7	616.1	725.5	41	2	0.04*	
8	666.0	810.4	26	5	0.01*	
9	736.2	842.0	11	5	0.17	

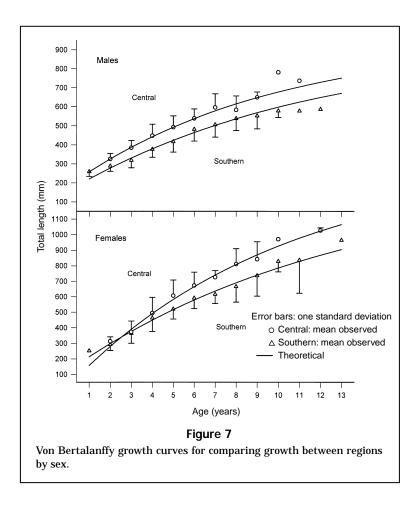
California a slightly higher L_{∞} for males at 925 mm TL, and a lower L_{∞} for females at 1368 mm TL. The asymptotic mean length for females may be lower because fewer large females were collected in our study. Although our study had different growth parameters than those of Sunada et al. (1990), the differences were only slight. The differences may have been due to gear vulnerability. Sunada et al. (1990) collected halibut from both trawl nets and gill nets and found that fewer females were collected in trawl nets, which may be attributed to trawl gear being restricted to offshore areas during spawning season. Also

Table 9 Von Bertalanffy growth parameters with asymptotic standard errors (SE) for California halibut by sex in southern and central

Region	Sex	n	$L_{\scriptscriptstyle \infty}$	SE	K	SE	t_0	SE
Southern	male	761	925.3	121.4	0.08	0.02	-2.2	0.41
	female	336	1367.7	273.4	0.08	0.03	-1.2	0.48
Central	male	147	956.7	211.9	0.10	0.05	-2.1	0.91
	female	129	1477.1	308.1	0.10	0.04	-0.2	0.43







females, which are generally larger, may be more capable of escaping a trawl net than males. Other factors that may have affected the growth parameters include the following: method of collection, time periods of sampling, and different environmental conditions in the years prior to each study.

Many factors can affect growth rates of fish including differences in the seasonality of spawning, environmental factors, amount and size of food, and genetics (Weatherly and Gill, 1987; Moyle and Cech, 1988). Southern and central California are biogeographically different. Differences between central and southern California coastal waters include temperature, water circulation patterns, bottom topography, and substrate. In particular, Jow (1990) noted differences in bottom topography and substrate between the trawl areas for California halibut in southern and northern (San Francisco Bay area) California. The biogeographical differences among these regions could possibly cause growth rates of the same species to differ. Studies of other fish species have shown differences in growth between geographical regions. For example, Parrish et al. (1985) found latitudinal differences in the growth of northern anchovy, *Engraulis mordax*. They found that the growth rate of juvenile northern anchovy in central California was greater than that of juvenile northern anchovy in southern California. Butler et al. (1996) found differences in maturation and length at age of Pacific sardine

between latitudinal regions. Sardine appeared to mature at a younger age off both southern and Baja California than off Monterey; one-, two-, and three-year old fish were smaller at age off Baja and larger off Monterey. Deriso et al. (1996) confirmed the findings of sardine growth differences by Butler et al. (1996). The exact mechanism for latitudinal differences in growth rates of California halibut is still unclear and further research is needed to clarify this phenomenon.

Acknowledgments

We wish to express our appreciation to Larry Jacobson with the National Marine Fisheries Service, for his detailed review of an earlier draft of the paper. We appreciate the efforts of Steve Wertz, Sandra Owen, and Paul Gregory who helped with various aspects of this study. We also thank the reviewers for their comments and suggestions that improved the paper.

Literature cited

Beamish, R. J., and D. A. Fournier.

1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38: 982–983.

Bernard, D. R.

1981. Multivariate analysis as a means of comparing growth in fish. Can. J. Fish. Aquat. Sci. 38:233–236.

Butler, J. L., M. L. Granados G., J. T. Barnes, M. Yaremko, and B. J. Macewicz..

1996. Age composition, growth, and maturation of the Pacific sardine (*Sardinops sagax*) during 1994. Calif. Coop. Oceanic Fish Invest. Rep. 37:152–159.

Casselman, J. M.

1983. Age and growth assessment of fish from their calcified structures-techniques and tools. *In* Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, sharks (E. Prince and L. Pulos, eds.) p. 1–17. U.S. Dep. Commer, NOAA Tech. Report 8.

Deriso, R. B., J. T. Barnes, L. D. Jacobson, and P. R. Arenas.

1996. Catch-at-age analysis for Pacific sardine (Sardinops sagax) 1983–1995. Calif. Coop. Oceanic Fish Invest. Rep. 37:175–187.

Fleiss, J. L.

1986. The design and analysis of clinical experiments. John Wiley and Sons, New York, NY, 432 p.

Frev. H. W., ed.

1971. California's living marine resources and their utilization. Calif. Dep. Fish Game, Sacramento, CA, 148 p.

Haaker, P. L

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

Hollander, M., and D. A. Wolfe.

1973. Nonparametric statistical methods. John Wiley and Sons, New York, NY, 503 p.

Jow. T.

1990. The California halibut trawl fishery. In The California halibut, Paralichthys californicus, resources and fisheries (C. W. Haugen, ed.), p. 229–241. Calif. Dep. Fish Game, Fish Bull. 174.

Kramer, S. H., and J. S. Sunada.

1992. California halibut. In California's living marine resources and their utilization (W. S. Leet, C. M. Dewess, and C. W. Haugen, eds.), p. 94–97. California Sea Grant, Univ. Calif., Davis, CA.

Manooch, C. S. III. and J. C. Potts.

1997. Age, growth, and mortality of greater amberjack, Seriola dumerili, from the U.S. Gulf of Mexico headboat fishery. Bull. Mar. Sci. 61:671–683.

Moyle, P. B., and J. J. Cech Jr.

1988. Fishes: an introduction to ichthyology, 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, NJ, p. 593

Parrish, R. H., D. L. Mallicoate, and K. F. Mais.

1985. Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax*. Fish. Bull. 83:483–496.

Pattison, C. A. and R. D. McAllister.

1990. Age determination of California halibut, *Paralichthys californicus*. *In* The California halibut, *Paralichthys californicus*, resources and fisheries (C. W. Haugen, ed.), p. 207–216. Calif. Dep. Fish Game, Fish Bull. 174.

Potts, J. C., C. S. Manooch III, and D. S. Vaughan.

1998. Age and growth of vermillion snapper from the southeastern United States. Trans. Am. Fish. Soc. 127:787–

Ricker, W. E.

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

Robson, D. S., and D. G. Chapman.

1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181–189.

SAS.

1990. SAS/STAT user's guide, version 6, fourth ed., vol. 2. SAS Institute, Inc., Cary, NC, 846 p.

Sunada, J. S., P. V. Velez, and C. A. Pattison.

1990. Age, size, and sex composition of California halibut from southern California commercial fishery landings, 1983–1988. *In* The California halibut, *Paralichthys californicus*, resources and fisheries (C.W. Haugen, ed.), p. 303–319. Calif. Dep. Fish Game, Fish Bull. 174.

Weatherly, A. H., and H. S. Gill.

1987. The biology of fish growth. Academic Press, Orlando, FL, 443 p.

Williams, T., and B. C. Bedford.

1974. The use of otoliths for age determination. *In* Aging of fish: proceedings of an international symposium, p. 114–123. Unwin Brothers Ltd., Surrey, England.