GROWTH, MORTALITY, AND REPRODUCTIVE SEASONALITY OF CALIFORNIA HALIBUT (*PARALICHTHYS CALIFORNICUS*): A BIOGEOGRAPHIC APPROACH

CHERYL L. BARNES
Moss Landing Marine Laboratories
8272 Moss Landing Road
Moss Landing, CA 95039
ph: (831) 515-8232
cheryl.barnes@alaska.edu

RICHARD M. STARR
California Sea Grant
Moss Landing Marine Laboratories
8272 Moss Landing Road
Moss Landing, CA 95039

PAUL N. REILLY
California Dept. of Fish and Wildlife
20 Lower Ragsdale Drive, Suite 100
Monterey, CA 93940

ABSTRACT

Differences in key biological processes, such as growth and reproduction, can greatly influence localized population dynamics. Thus, it is important to characterize spatial variation in life history traits of harvested species to develop management plans that maximize fishery sustainability. We estimated sex- and region-specific growth, total mortality, and reproductive seasonality to assess biogeographic differences in California Halibut life history. We found that central California Halibut grew faster but attained smaller maximum sizes than those from southern California. Catch curve analysis illustrated no difference in total mortality by sex or region, though females lived longer than males. Year-class frequency distributions suggested greater recruitment variability in central California, where abiotic factors (e.g., upwelling strength, sea surface temperature) are likely drivers. Reproductive data indicated that summer spawning seasons peak earliest in Mexico, followed by southern and central California. These results demonstrate a need to assess and manage California Halibut at the regional scale.

INTRODUCTION

Biogeographic differences in growth, mortality, and reproduction can result in disproportionate effects of fishing (Rice et al. 2005). However, fisheries are often managed at relatively broad (e.g., statewide/nationwide) spatial scales. Although averaging the condition of a species across its range simplifies resource management, spatiotemporal changes in key biological processes can result in localized over- or under-utilization of the resource (Prince 2010). This is because many fish stocks consist of metapopulations (i.e., groups of individuals that are interconnected through larval dispersal, yet exhibit distinct population dynamics), which are differentially affected by fishing pressure (Levins 1969; Adams 1980; Orensanz et al. 2005; Pascoe et al. 2009). Thus, it is important to understand spatial variation in the life history traits of harvested species, especially those that exhibit widespread distributions spanning multiple biogeographic regions.

California Halibut, *Paralichthys californicus* (family Paralichthyidae), is an economically important species that can be found as far north as the Quillayute River in Washington and as far south as Magdalena Bay in Baja California Sur, Mexico (Allen 1990). However, most individuals in U.S. waters are encountered between Bodega Bay, California and the US-Mexico border. After a short larval duration of 20 to 29 d, juveniles settle into bays, estuaries, and shallow waters of the open coast (Allen 1988; Kramer 1990). Adults are primarily found nearshore (typically less than 60 m water depth) over sandy habitats that are adjacent to hard substrate or biogenic structures (e.g., sand dollar, *Dendraster excentricus*, beds) (Allen 1988; Allen 1990). Female California Halibut grow faster and mature later than male conspecifics (Haaker 1975; MacNair et al. 2001). Males reach sexual maturity between 19 and 32 cm (1 to 3 yr), whereas females mature between 36 and 59 cm (2 to 7 yr) (Love and Brooks 1990). California Halibut are multiple, broadcast spawners that have been noted as living to 30 yr, though recent data have demonstrated a lifespan of only 23 yr (CDFW unpublished data [2007 to 2014]).

In 2011, the California Department of Fish and Wildlife (CDFW, formerly California Department of Fish and Game) conducted its first comprehensive stock assessment for California Halibut to determine population size and the effectiveness of existing management actions (Maunder et al. 2011). As part of the assessment, fishery-independent and –dependent data were synthesized and incorporated into statistical models developed for two separate stocks, one north and one south of Point Conception (a well-known biogeographic boundary between central and southern California). Although substantial amounts of biological information were made available during the assessment, life history data pertained primarily to fish collected off southern California (e.g., Allen 1988; Allen and Herbinson 1990; Allen et al. 1990; Kramer 1990; Domeier and Chun 1995; Valle et al. 1998; MacNair et al. 2001). This forced assessment scientists to parameterize both stock models based primarily on the southern California population. To assess the effect of biogeography on California Halibut life history characteristics, we estimated sex-specific growth and instantaneous total mortality for fish collected both north and south of Point Conception. We also compared
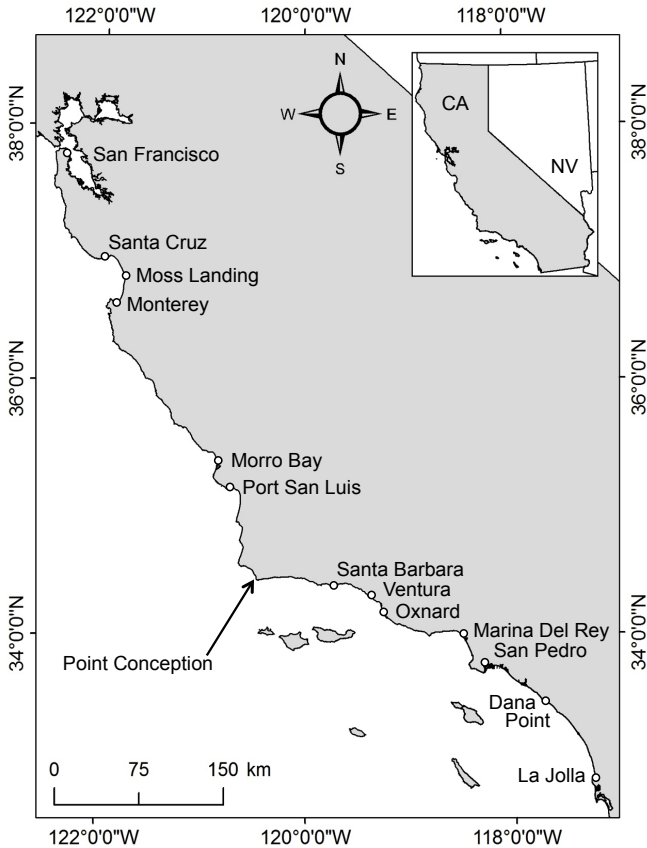
Figure 1. Primary locations used to sample California Halibut, *Paralichthys californicus*. Point Conception (indicated by the black arrow) denotes the boundary between central and southern California sites.

TABLE 1
Sample Sizes of California Halibut Collected by Region, Sex, and Fishery.

	Central California		Southern California	
	Female (n = 743)	Male (n = 556)	Female (n = 615)	Male (n = 145)
Commercial	293	269	571	134
Recreational	359	219	19	1
Research	72	53	23	10
Incidental	19	15	2	0

ity of fish from southern California were obtained from commercial fisheries (table 1).

Date, location, fishery (i.e., commercial or recreational), gear type, sex, fork length (mm), and wet body weight (kg) were recorded in the field. The majority of fork lengths were obtained from whole fish sampled at shore-based facilities. However, a number of California Halibut were received from recreational fishers as filleted carcasses. Fork lengths for filleted fish were recorded and converted to pre-fillet lengths using the relationship y = 1.37 + 0.99x (R² = 0.999, p < 0.001), where x represents post-fillet fork length (mm) and y represents pre-fillet fork length (mm).

In the laboratory, sagittal otoliths were extracted and thin-sectioned according to procedures outlined by the Committee of Age Reading Experts (CARE 2006). Because eyed-side otoliths tended to exhibit distorted patterns of growth, blind-side otoliths were selected for ageing whenever possible. Without prior knowledge of size or sex, two or three readers independently aged each fish to the nearest year. Rounding decisions were based upon the amount of marginal growth relative to immediately adjacent annuli (i.e., otoliths with a margin representing greater than half the distance between neighboring annuli were rounded up and margins representing less than half the distance between neighboring annuli were rounded down). From 2007 to 2011 and again in 2014, two CDFW staff independently read each otolith until a minimum of two identical (within-reader) age estimates were made. If age determinations by the two readers did not agree, a digital image of the thin section was prepared and both readers discussed the various aspects of the otolith until a final age was agreed upon or they decided to exclude the otolith from analyses due to issues associated with poor readability. In 2012 and 2013, one CDFW and one MLML reader followed the same procedures detailed above. However, if reader-specific age determinations conflicted with one another during these years, a third (CDFW) reader was introduced to settle the disagreement. If the third reader did not agree with either of the other two readers, a digital image of the thin section was prepared and all readers either came to a unanimous agreement or

region-specific estimates of reproductive seasonality by evaluating temporal changes in gonadosomatic index for females collected off central California and corrected larval density data obtained by California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys along southern California and Mexico.

MATERIALS AND METHODS

California Halibut were collected between San Francisco Bay, CA and the US–Mexico border from 2007 to 2014 (fig. 1). Fish were collected using both fishery-independent and fishery-dependent sampling methods. A diversity of gear types (i.e., hook and line, trawl, gill net, seine, and spear) was used to collect fishes of both sexes and from various size classes. Although fishery-independent methods were used, we (CDFW [2007 to 2014] and Moss Landing Marine Laboratories [MLML, 2012 and 2013]) procured most specimens from commercial and recreational fisheries using a combination of stratified random and opportunistic sampling designs (CDFW 2013; Barnes 2015). Fish from central California were collected in nearly equal proportions from commercial and recreational fisheries, whereas the major-

decided to exclude the otolith from analyses. Finally, age estimates and capture dates were used to assign a year-class to all fish.

Growth

Sex- and region-specific growth rates were estimated using length-at-age data and the von Bertalanffy growth equation $L_t = L_\infty(1-e^{-K(t-t_0)})$, where L_t is the predicted length at age t, L_∞ represents the theoretical maximum length, K is the growth coefficient, and t_0 indicates the predicted age at a length equal to zero (von Bertalanffy 1938). Parameters L_∞ and K were estimated using least-squares regression techniques and the Excel add-in "Solver." Because our collection methods yielded few fish under 200 mm, we fixed the parameter t_0 at zero (e.g., Robertson et al. 2005; Caselle et al. 2011). Maximum likelihood techniques described by Kimura (1980) were then used to estimate and compare 95% confidence intervals surrounding the intersection of K and L_∞ (R 3.1.1). Statistical significance was determined by evaluating spatial overlap between sex- and region-specific confidence intervals (i.e., overlapping confidence intervals indicated no difference in growth and spatially explicit confidence intervals demonstrated a significant difference).

Mortality

Catch curve analysis was employed to estimate instantaneous total mortality (Z) using the equation $N(t) = N_0 e^{-Zt}$, where $N(t)$ is the number of individuals collected within a particular year-class at age t and N_0 represents the number of individuals from the same year-class at age zero (Ricker 1975). This equation was rewritten as $\ln N(t) = \ln N_0 - Zt$, enabling the use of linear regression on log-transformed age frequency data to solve for N_0 (y intercept) and Z (slope). Because we could not sample the entire range of California Halibut ages (e.g., due to size-based gear selectivity, release of fish measuring less than the minimum legal size, ontogenetic shifts in habitat use or spatial distributions), only data from age classes greater than or equal to the mode were included. ANCOVA (Model III), using age as a covariate, was used to test for differences in slopes and y-intercepts (SPSS 22.0).

We also evaluated differences in year-class frequency distributions to gain a basic understanding of spatio-temporal variation in the survival of young California Halibut. A two-sample Kolmogorov-Smirnov (KS) test was used to compare region-specific differences in year-class strength, a proxy for recruitment (SPSS 22.0). Measures of kurtosis and skewness were also calculated to quantitatively characterize the shape (i.e., peakedness and degree of symmetry) of year-class frequency distributions for each region. Years with the greatest number of fish

sampled in each region were selected for these analyses (i.e., 2013 for central California [n = 587] and 2012 for southern California [n = 265]). Year-class frequencies between 1993 and 2007 were analyzed.

Reproductive Seasonality

Duration and peak of the summer spawning season were estimated for central California females using reproductive data collected in 2012 and 2013 (Barnes 2015). Ovaries from sampled fish were removed and weighed to calculate gonadosomatic index (GSI), represented by the equation

$$GSI = \frac{\text{ovary mass (g)}}{\text{body mass (g)} - \text{ovary mass (g)}} * 100$$

(Le Cren 1951; Delahunty and de Vlaming 1980; de Vlaming et al. 1982). Ovaries were then preserved in 10% formalin, stored in 70% ethanol, and processed using histological methods described by Luna (1968). Microscopic maturity stages were determined based, in part, upon descriptions by Murua et al. (2003). The incidence of spawning females (i.e., those possessing hydrated oocytes and/or new postovulatory follicles) was used to estimate the duration of the spawning season, whereas peaks in reproductive activity were identified by fluctuations in GSI (Le Cren 1951; Delahunty and de Vlaming 1980; Almatar et al. 2004).

Reproductive data similar to those described above were not available south of Point Conception. Therefore, temporal changes in larval densities obtained from CalCOFI ichthyoplankton surveys (1980 to 2011) were used to approximate peaks in reproductive activity off of southern California and Mexico. Additionally, we applied a one-month correction to CalCOFI data to account for California Halibut's 20 to 29 d larval duration and approximate the time at which spawning occurred. Because California Halibut spawn in shallow waters, exhibit a relatively short larval duration, and settle into nearshore environments (Allen 1988), the farther offshore and more infrequent CalCOFI surveys conducted north of Point Conception were not appropriate for assessing the reproductive patterns of this species. Therefore, spatiotemporal trends in reproductive activity were assessed by plotting mean monthly GSI for fish collected off of central California and corrected mean monthly larval densities from southern California and Mexico.

RESULTS

In total, 2059 California Halibut (1299 central California, 760 southern California) were collected as part of this study. Fork lengths ranged from 85 to 1346 mm and ages ranged from 1 to 23 yr (tables 2 and 3). The overall mean length (± SE) was 680 ± 4.3 mm and the overall mean age (± SE) was 6.5 ± 0.1 yr. The sex ratio

TABLE 2
Minimum, Mean (Standard Error), and Maximum Fork Lengths (mm) for California Halibut, by Region and Sex. Sample Sizes are Indicated for Each Group.

	Central California		Southern California	
	Female (n = 743)	Male (n = 556)	Female (n = 615)	Male (n = 145)
Minimum	186	130	85	152
Mean (SE)	748 (7)	634 (6)	679 (8)	518 (17)
Maximum	1171	1047	1346	1065

TABLE 3
Minimum, Mean (Standard Error), and Maximum Ages (yr) for California Halibut, by Region and Sex. Sample Sizes are Indicated for Each Group.

	Central California		Southern California	
	Female (n = 743)	Male (n = 556)	Female (n = 614)	Male (n = 145)
Minimum	1	1	1	1
Mean (SE)	6.8 (0.1)	6.7 (0.1)	6.4 (0.1)	4.9 (0.2)
Maximum	19	16	23	14

TABLE 4
Von Bertalanffy Growth Parameters L_∞ and K for California Halibut, by Sex and Region. Standard Errors are Shown in Parentheses.

Growth Parameter	Female		Male	
	Central CA	Southern CA	Central CA	Southern CA
L_∞	1049 (15)	1304 (35)	820 (14)	1048 (60)
K	0.21 (0.01)	0.12 (0.01)	0.25 (0.01)	0.15 (0.01)

was skewed toward females in both regions and was calculated at 1.4:1 (X^2_{11297} = 26.290, p < 0.001) in central California and 4.3:1 (X^2_{1759} = 291.512, p < 0.001) in southern California. Additionally, contingency table results demonstrated a significant difference in sex ratio between the two regions (X^2_1 = 12.556, p < 0.001).

Growth

Sex-specific von Bertalanffy growth equations were estimated to be $L(t)_{female} = 1049 (1 - e^{-0.21t})$ and $L(t)_{male} = 820 (1 - e^{-0.25t})$ for central California and $L(t)_{female} = 1304 (1 - e^{-0.12t})$ and $L(t)_{male} = 1048 (1 - e^{-0.15t})$ for southern California (table 4). Lifetime growth curves and 95% confidence intervals surrounding parameters K and L_∞ indicate that females grow faster and attain

larger maximum sizes than males, and that central California Halibut grow faster but smaller maximum sizes than southern California Halibut (figs. 2 and 3). Based upon the von Bertalanffy growth equations above, central California Halibut typically recruit to the fishery (i.e., reach the minimum legal size limit of 559 mm) at 3.7 yr for females and 4.6 yr for males. In southern California, females recruit to the fishery at 4.6 yr and males recruit to the fishery at 5.0 yr.

Mortality

Statistical comparisons of catch-at-age data indicated no difference in instantaneous total mortality (Z) between male and female California Halibut (central California: $F_{1,12}$ = 0.166, p = 0.691; southern California: $F_{1,13}$ = 0.006, p = 0.937). Sex-specific estimates of Z for southern California Halibut were very similar to one another (Z_{male} = 0.35, Z_{female} = 0.36). In central California, however, the total mortality estimate for males (Z = 0.42) was considerably greater than that of females (Z = 0.34). When comparing sex-specific estimates of total mortality by region, we found no significant difference between females collected from central and southern California ($F_{1,16}$ = 0.035, p = 0.854) and an apparent, but nonsignificant difference between males ($F_{1,9}$ = 0.123, p = 0.734) (fig. 4). Additionally, the number of
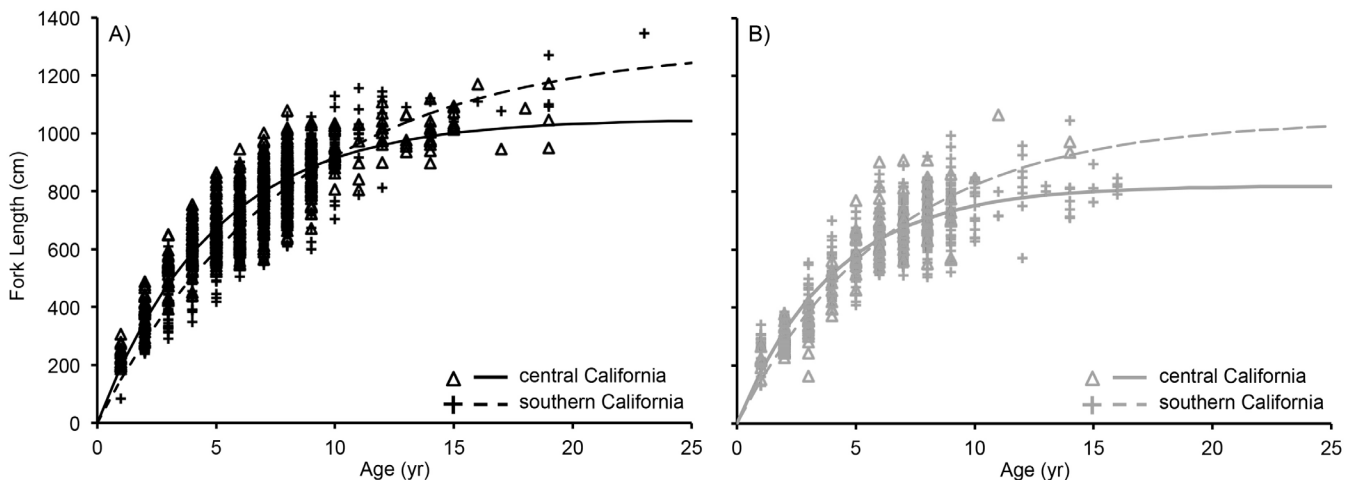

Figure 2. Length-at-age data and von Bertalanffy growth curves for female (A) and male (B) California Halibut. Fish from central California are indicated by open triangles (observed) and solid lines (predicted), whereas fish from southern California are indicated by crosses (observed) and dashed lines (predicted).
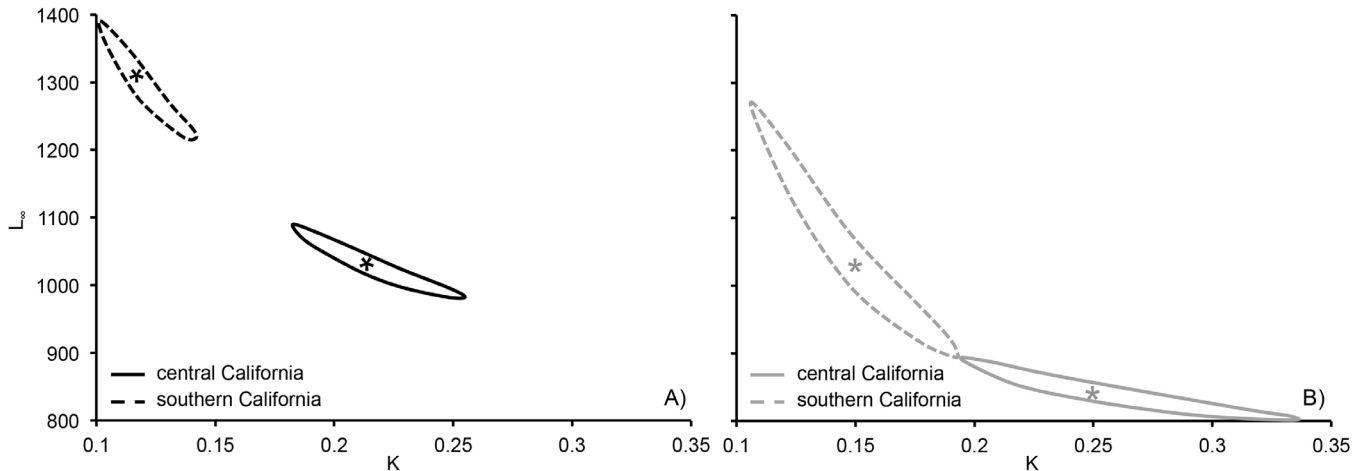
Figure 3. Von Bertalanffy growth parameters K and L_∞ for female (A) and male (B) California Halibut. Ellipses represent sex- and region-specific 95% confidence intervals. Fish from central California are indicated by solid lines and fish from southern California are indicated by dashed lines.
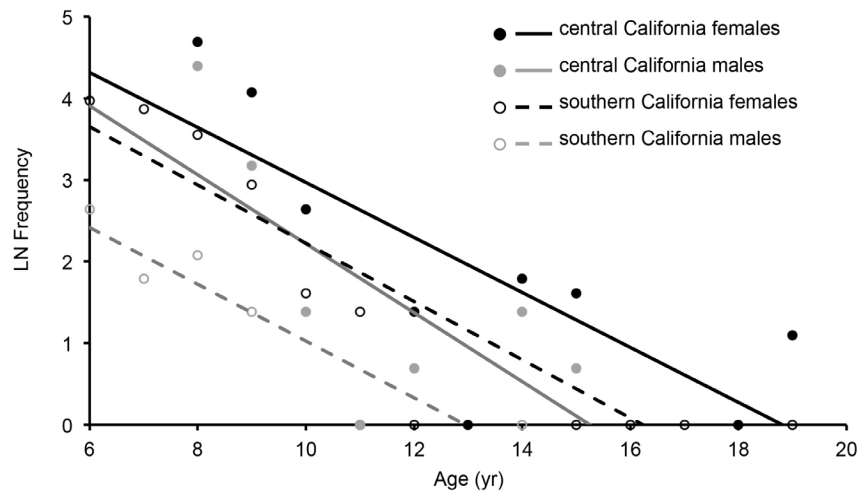

Figure 4. Instantaneous total mortality for California Halibut collected from central California in 2013 (solid) and southern California in 2012 (dashed). Females are shown in black and males are shown in gray.

southern California males sampled was significantly less (as indicated by a difference in the y-intercept) than females from the same region ($F_{1,14} = 69.150$, p = 0.004).

When comparing region-specific year-class frequency distributions, we found no significant difference between central and southern California Halibut (D = 0.250, p = 0.847). However, there were noticeable peaks in year-class frequencies (a proxy for recruitment) in central California in 1998, 1999, and 2005 (fig. 5). Corresponding peaks were absent from southern California, where we observed a relatively normal distribution surrounding the 2006 year-class. The central California year-class frequency distribution (n = 12) was leptokurtic (kurtosis = 3.195 ± 1.23), denoting the presence of a sharper than normal peak in the 2005 year-class. Conversely, the year-class frequency distribution for southern California (n = 12) was platykurtic (kurtosis = - 0.515 ± 1.23), which indicates a broader than normal shape lacking any significant peaks. Both populations were skewed to the right

(skewness$_{central}$ = 1.899 ± 0.64, skewness$_{southern}$ = 0.970 ± 0.64), though the central California Halibut year-class frequency distribution exhibited a greater probability of encountering relatively old fish.

Reproductive Seasonality

We observed spawning females in central California from mid-June to the beginning of September in 2012 and 2013. From these data, we estimated the duration of the summer spawning season to be 79 ± 3 d (SE). This duration was also supported by relatively low mean GSI of mature females (2.9 ± 0.5 [SE]) in May and September. Additionally, increases in mean GSI to 4.7 ± 0.3 (SE) demonstrated a peak in reproductive effort in central California in July. Because large quantities of California Halibut are not caught between October and April north of Point Conception (CDFW 2014), we have no data with which to evaluate reproductive activity in central California outside of the summer months.
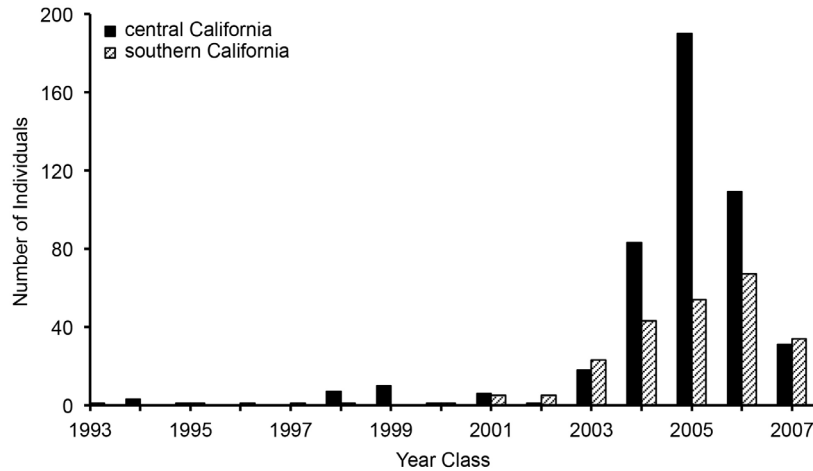
Figure 5.   Year-class frequency distributions for central (solid) and southern (dashed) California Halibut, 1993 to 2007.
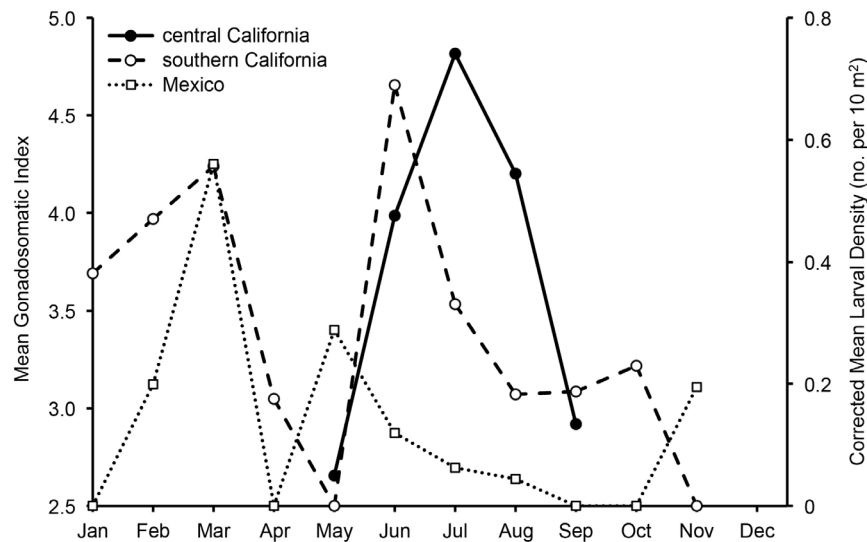

Figure 6.   Mean gonadosomatic index for mature California Halibut females collected from central California in 2013 (closed circles, solid line) and corrected mean larval densities (number per 10 m², wet displacement volume) for southern California (open circles, dashed line) and Mexico (open squares, dotted line) by month. Larval density data were collected by CalCOFI from 1980 to 2011. Error bars have been omitted for clarity.

Based upon the incidence of larvae obtained from CalCOFI ichthyoplankton surveys in nearshore waters, we know that California Halibut spawn year-round in southern California and Mexico. The greatest larval densities (number of larvae per 10 m²) of California Halibut can be found in April (0.56 ± 0.19 [SE]) and June (0.29 ± 0.15 [SE]) in Mexico and in April (0.56 ± 0.18 [SE]) and July (0.69 ± 0.20 [SE]) in southern California (CalCOFI 2014). Given the approximate one-month lag between spawning and late larval phase, we inferred that peak spring spawning occurs in Mexico and southern California in March. Additionally, corrected larval density data indicate that peak summer spawning takes place in Mexico in May and in southern California in June. When comparing this information with our observed

peak spawning in central California in July, we found that California Halibut display a latitudinal gradient in timing of reproduction, with spawning taking place earlier to the south and later to the north (fig. 6).

DISCUSSION

Our estimated female to male sex ratios of 1.4:1 for central California and 4.3:1 for southern California differ from previous approximations for smaller fish from the same regions (1.1:1 and 1:2.2, respectively; MacNair et al. 2001). However, the 4.3:1 sex ratio for southern California Halibut matches a previous estimate obtained from similarly sized individuals (Sunada et al. 1990). The relatively greater difference in the number of males and females collected off of southern California Halibut may

be a result of sampling bias from fishing activities that target larger (typically female) fish. It may also be due to sampling fish within an area where there are sex-structured spatial distributions (e.g., more females found nearshore, as indicated by Sunada et al. 1990). Investigations into sex-specific habitat associations and movement patterns of California Halibut may elucidate potential mechanisms for the observed difference in sex ratio by region.

Growth

Consistent with the scientific literature, female California Halibut collected as part of this study grew faster and to larger sizes than male conspecifics (Haaker 1975; Hammann and Ramirez-Gonzalez 1990; Sunada et al. 1990; MacNair et al. 2001). However, contrary to the only other regional comparison of California Halibut growth (MacNair et al. 2001), our data show that central California Halibut grow faster, but attain smaller maximum sizes than those from southern California. Conflicting results between MacNair et al. (2001) and our study are likely due to different size and age ranges of fish sampled. MacNair et al. (2001) used a single gear type (i.e., trawl with a 8.5 cm mesh cod end), which resulted in the collection of smaller sex- and region-specific median sizes (ranging from 387 to 544 mm) and younger maximum ages (from 12 to 13 yr) of California Halibut. Because our study incorporated numerous gear types (i.e., trawl, gill net, hook and line, spear, seine), we were able to sample a wider size range of fish, with larger sex- and region–specific median sizes (ranging from 559 to 780) and older maximum ages (between 14 and 23 yr) of California Halibut. The truncated size and age distributions of fish collected by MacNair et al. (2001) generated estimates of L_∞ and K that were more theoretical, whereas our estimates were corroborated by length-at-age data for a wider age range of fish, including older fish. Additionally, without having sampled large quantities of small (<200 mm) fish, we found that it was more appropriate to fix t_0 at zero for our study because doing so produced more biologically realistic growth curves that intersected at the origin.

Mortality

Despite observing sex- and region-specific differences in growth, statistical analyses indicated no differences in instantaneous total mortality. Although we did not detect statistical differences, estimates of Z suggested greater mortality for male California Halibut found north of Point Conception (Z = 0.42) as compared to females from the same region (Z = 0.34) and males from southern California (Z = 0.35). Greater calculations of Z for central California males may be due to a combination of several factors. First, catch curve analysis is limited to fish greater than or equal to the mode age sampled. Because

of issues associated with selective fishing imposed by a minimum size limit of 559 mm and a sampling scheme that was primarily fishery-dependent, we were limited to fish greater than 6 yr. Additionally, a strong 2005 year-class in central California shifted the mode of age frequencies to the right, preventing catch curve analysis for 6 and 7 yr old fish north of Point Conception. Finally, male California Halibut exhibit a shorter lifespan than females, further reducing the number of data points used in catch curve analysis of this sex. It is probable that each of these factors compounded upon one another to increase the variation in our age frequency data for central California males. As such, continued sampling is necessary to improve our understanding of Z for male California Halibut caught north of Point Conception.

Our estimate of instantaneous total mortality for southern California Halibut females (Z = 0.36) was much less than the only other estimate (Z = 0.53), which was calculated for fish collected between 1985 and 1988 (Reilly et al. 2008). The greater estimate of total mortality for southern California females may be attributed to the inclusion of particularly strong year-classes resulting from the 1982–83 El Niño event. This, along with some uncertainty surrounding our estimates of Z for central California males, reiterates the need to conduct catch curve analysis over longer time series that account for various levels of year-class strength.

When evaluating spatiotemporal variation in survival of young California Halibut, we observed greater variation in year-class frequency distributions (i.e., recruitment) north of Point Conception. With a pelagic larval phase, young California Halibut are susceptible to advection offshore during periods of intense and persistent upwelling, as has been found in other species resident to eastern boundary currents (e.g., Parrish et al. 1981; Cury and Roy 1989; Gibson 1994; Wilderbuer et al. 2002). Additionally, periods of strong upwelling may decrease sea surface temperatures below a threshold at which young California Halibut can survive. We observed stronger recruitment for California Halibut during weaker upwelling years (1998, 1999, and 2005) and weaker recruitment during stronger upwelling years (2000 to 2002) in central California (Auth 2008; Caselle et al. 2010; Ralston et al. 2013). This variation in California Halibut recruitment is out of synchrony with rockfish recruitment north of Point Conception, which is strongest during colder SST and stronger upwelling (Caselle et al. 2010; Ralston et al. 2013). The opposing patterns of California Halibut and rockfish recruitment in central California may have implications for the nearshore ecosystem as a whole (e.g., California Halibut and similarly influenced species serving as important food sources during periods of poor rockfish recruitment) and, therefore, are important to better understand.

In southern California, a change in current direction produces relatively weak upwelling year-round. This more static upwelling state, combined with generally warmer sea surface temperatures, can offer an explanation for regular recruitment of California Halibut (as evidenced by a more normal distribution of year-classes) south of Point Conception. With more favorable abiotic conditions, it is probable that density dependent processes (e.g., competition, predation) are more important for recruitment of southern California Halibut (Lasker 1981; Cushing 1990; Searcy and Sponaugle 2001). Although we believe that these regional differences in California Halibut recruitment are real, longer time series of year-class frequency data would enhance our understanding about potential environmental and ecological drivers.

Reproductive Seasonality

California Halibut have previously been described as exhibiting year-round reproduction, with peak activity in late winter and spring (Haaker 1975; Lavenberg et al. 1986; Love and Brooks 1990). Recent ichthyoplankton surveys confirmed year-round reproduction south of Point Conception, with greatest densities of California Halibut larvae occurring in April, June, and July (CalCOFI 2014). However, in analyzing GSI data obtained north of Point Conception, we found that California Halibut spawn later and likely for a shorter duration in central California.

Limited quantities of commercially or recreationally caught fish between October and April precluded reproductive analyses outside of the summer months in central California (CDFW 2014). The absence of halibut caught during winter may be indicative of seasonal migrations related to spawning, though movement data are necessary in order to evaluate this hypothesis. Nevertheless, reproductive effort from all three regions (i.e., corrected larval densities from southern California and Mexico and GSI from central California) illustrated a latitudinal gradient in summer spawning. Although this pattern matches that of other West Coast flatfishes (e.g., *Citharichthys* spp., Chamberlain 1979), it opposes temporal trends observed for other *Paralichthys* spp. studied along the east coast of the United States, where spawning takes place earliest in northerly regions (e.g., *Paralichthys dentatus*, Smith 1973).

Temperature and photoperiod have been implicated as potentially important factors in California Halibut reproduction (Caddell et al. 1990). In a laboratory study, Caddell et al. (1990) observed spawning activity at temperatures between 15.0° and 16.5°C and during day lengths greater than or equal to 10.5 hr. Our results indicated that spawning occurs in waters as cold as 13.0°C in central California, though day lengths are comparable to the laboratory

study. This indicates that temperature thresholds for reproduction are lower than previously estimated for California Halibut and that some other factor (e.g., planktonic food supply) effects the timing of spawning.

The estimates of growth, total mortality, and reproductive seasonality that we have provided not only enhance our understanding about spatiotemporal effects on the life history traits of nearshore fish species, they also provide sex- and region-specific data for reparameterization of the stock models developed specifically for California Halibut. As such, incorporation of our results into future stock assessments should improve model outputs and reduce uncertainty concerning the sustainability of California Halibut within state waters.

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