Abstract—We evaluated habitat quality for juvenile California halibut (*Paralichthys californicus*) in a Pacific Coast estuary lacking in strong salinity gradients by examining density, recent otolith growth rates, and gut fullness levels of wild-caught and caged juveniles for one year. Juveniles <200 mm standard length were caught consistently in the inner, central, and outer sections of the estuary. The density of juveniles was two times higher in the inner estuary during most of the year, consistent with active habitat selection by part of the population. A generalized linear model indicated temperature, sampling time, and the interaction between salinity and temperature were significantly related to density. However, the model explained only 21% of the variance. Gut fullness levels of wild-caught juveniles were highest during the summer, but recent otolith growth rates were not related to temperature. The proportion of individuals feeding successfully indicated that seasonal differences in food availability are more important than spatial variation in prey abundance in driving feeding success. Feeding success of caged fishes was limited, precluding the use of growth rates as indicators of local habitat quality. However, marginal increment widths were reliable indicators of somatic growth at low growth rates over two-week periods. The relatively high growth rates and abundance of small wild-caught juveniles found throughout the estuary indicates that the entire estuary system has the potential for serving as nursery habitat.

Assessment of habitat quality for juvenile California halibut (*Paralichthys californicus*) in a seasonally arid estuary

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California halibut (*Paralichthys californicus*) is a species of commercial and recreational importance that is found in coastal waters from Washington, U.S.A., to Baja California Sur, Mexico (Sweatnam et al., 2007). Spawning occurs along coastal areas and planktonic larvae inhabit the continental shelf for about a month before settling in shallow protected areas along the coast or in the outer reaches of protected embayments (Allen and Herbinson, 1990; Moser and Watson, 1990). Juveniles make facultative use of protected embayments such as coastal lagoons, bays, and estuaries (Horn and Allen, 1985; Allen, 1988; Kramer, 1990; Fodrie and Mendoza, 2006). Recent studies indicate that both protected embayments and coastal habitats contribute to the production of adults, but that juvenile densities are substantially higher within embayments (Forrester and Swearer 2002; Fodrie and Mendoza, 2006; Fodrie and Levin, 2008). However, there are no studies where juvenile habitat quality has been assessed for California halibut on the intra-embayment level.

Juvenile flatfish occupying specific habitats or areas within embayments may exhibit considerable variability in abundance, growth, and mortality rates (Allen and Baltz, 1997; Gilliers et al., 2006). In addition, specific regions within embayments may contribute disproportionaly to the

production of recruits to the adult population (Beck et al., 2001). Sogard (1992) reasoned that if rapid growth during the juvenile stage offers an advantage in terms of increased survival, and if growth rates vary as a function of habitat quality, individuals will select habitats that offer the maximum growth potential, although biological interactions such as predation can influence habitat choice. Within this context, high-quality nursery habitats within embayments are those in which growth and survival rates are higher than the corresponding rates in coastal habitats (Gilliers et al., 2006).

In estuarine systems strongly influenced by freshwater inflow ("classical" estuaries), salinity exhibits strong spatial gradients from the mouth to the head of the estuary. Gradients in salinity have been related to the distribution of some species of flatfish (e.g., Allen and Baltz, 1997; Able et al., 2005). In contrast, estuaries in seasonally arid regions, such as the Pacific coast of Baja California and southern California, tend to receive freshwater inflow only during the rainy winter season or summer monsoon. These "Mediterranean-type" estuary systems are increasingly hypersaline with increasing distance from the river mouth during a large part of the year, and in the inner reaches of the estuaries the water exhibits high residence times, which influence nu-

trient availability and production (Largier et al., 1997). Hence, spatial patterns of habitat use and quality for juvenile flatfish in classical and "Mediterranean-type" estuaries may differ substantially.

Use of habitat by juvenile flatfish has been related mostly to temperature, salinity, dissolved oxygen, substrate type, and depth (Gibson, 1994; Able et al., 2005). The first three variables directly influence metabolic processes, and hence abundance and growth (Gibson, 1997). Substrate type can be used as a proxy for food availability, and is related to success in predator avoidance (Gibson, 1994; Amezcua and Nash, 2001). Differences in distribution as a function of depth may be due to habitat partitioning among life stages (Kramer, 1990; Gibson, 1997). Because a direct assessment of juvenile habitat quality is difficult, growth and density have served as proxies. These measures integrate the effect of biological factors and environmental conditions (Necaise et al., 2005; Gilliers et al., 2006). Specifically, estimates of recent otolith growth rates evaluated through the measurement of increment widths can be used as an integrative indicator of habitat quality and the suitability of environmental conditions over short time scales (Le Pape et al., 2003; Gilliers et al., 2006). The fine-scale temporal and spatial variation of growth rates can thus serve as indicators of habitat quality.

The use of otolith marginal increment widths as indicators of habitat quality relies on two premises. First, there must be a high correlation between somatic and otolith growth rates (Campana and Jones, 1992). This has been shown to be the case for juvenile California halibut (Kicklighter, 1990; Kramer, 1991). Secondly, differences in growth rates should reflect the quality of the habitat in which fish were captured (Sogard, 1992; Gilliers et al., 2006). The second premise can be rendered invalid if there is substantial movement to or from areas with different environmental conditions within the time interval used to evaluate growth. Haaker (1975) found little movement of tagged juvenile California halibut within Anaheim Bay in southern California. Tagging studies of age-0 winter flounder (*Pseudopleuronectes americanus*) and plaice (*Pleuronectes platessa*) have also indicated limited displacement on the scale of a few hundred meters (Saucerman and Deegan, 1991; Burrows et al., 2004). However, Fodrie and Herzka (2008) used otolith microchemistry to reconstruct movement patterns of juvenile California halibut within an arid estuary and found that 8 out of 14 (57%) individuals moved among sections of the estuary over a two-month period. Likewise, Herzka et al. (2009) examined length-frequency distributions and recapture locations of tagged individuals and found simultaneous evidence of estuarine emigration and residency. If juveniles move substantially within an estuary, the implicit assumption that an individual has remained in the vicinity of its capture location for the time period over which growth is evaluated may be violated. Caging experiments guarantee that an individual has remained at a given location under measurable environmental conditions (Sogard, 1992). However, confinement has the potential to influence natural growth rates (Guindon and Miller, 1995). Caging experiments and sampling of natural populations are thus complimentary approaches for using growth rates as proxies for habitat quality.

We evaluated nursery habitat quality for juvenile California halibut (*Paralichthys californicus*) in a seasonally arid estuary, Punta Banda Estuary in Baja California, Mexico, based on recent otolith growth rates and an index of feeding success in relation to feeding levels. To determine if specific sections of the estuary serve as preferred juvenile habitat, we assessed spatial and temporal variability in density and evaluated recent otolith growth rates in relation to environmental conditions. In addition, we tested the hypothesis that juvenile density is higher in areas that favor higher growth rates. We simultaneously performed caging experiments and sampled natural populations to assess growth rates in relation to environmental conditions.

Materials and methods

Study area

Punta Banda Estuary is a medium-size (11-km² at high tide, 5-km² at low tide) protected embayment located within the Southern California Bight. It is located 100 km south of the US-Mexico border on the Pacific side of Baja California, Mexico (Fig. 1). The estuary lies along the southeastern margin of Todos Santos Bay (31°42′–31°47′N lat and 116°37′–116°39′W long), a semiprotected coastal system. The L-shaped estuary is connected to the bay at its northern end through a 125-m inlet (Ortiz et al., 2003). The fastest current velocities are found within the main channel at the mouth (~1 m/s), where depths are 10–12 m (Pritchard et al., 1978). A channel runs along the main axis of the estuary and is flanked by shallow submerged or exposed flats at low tide. The depth of the main channel in the central and inner sections of the estuary is shallow (<3 m) compared to the outer section (approximately 8 m, see Ortiz et al., 2003 for a detailed bathymetry). Along the shorter axis, the main channel splits into different arms and the average depth is <1 m in relation to mean low water. Patches of eelgrass (*Zostera marina*) are found in the central estuaries and there are tidal marshes along most of the banks. The bottom is sandy towards the outer reaches of the system and becomes increasingly silty toward the head (Ortiz et al., 2003).

Because the estuary is located in a seasonally arid region, the estuary behaves mostly as a negative estuary, in that temperature and salinity increase from the mouth to the head, particularly during the warmer months (Álvarez-Borrego and Álvarez-Borrego, 1982). Temperature and salinity also exhibit variations associated with the semidiurnal tidal cycle because of the exchange of water with Todos Santos Bay. Maximum tidal range during spring tides is about 1.7 m.

Experimental design

Density, recent growth rates, and environmental parameters (temperature, salinity, dissolved oxygen and gut fullness levels as a proxy for food availability) were measured approximately every other month between October 2004 and October 2005. To evaluate growth and abundance over a gradient of environmental conditions, the inner, central and outer reaches of the estuary were chosen as sampling and caging locations (Fig. 1). Six 28-day caging experiments were performed throughout the year to evaluate recent otolith growth, somatic growth, and gut fullness levels (Table 1). Density of natural populations was evaluated at the beginning and end of each caging experiment. Juveniles collected at the beginning of each caging period were used for caging experiments, whereas those captured at the end were used for measuring otolith growth rates and evaluating gut fullness levels of natural populations. To minimize the range of sizes evaluated for growth and gut fullness levels and allow for direct comparison of otolith growth rates from natural populations and caged individuals, we limited the sizes of fish analyzed to between 50 and 160 mm standard length (SL).

Density and environmental variables

On each sampling date, five 10-minute tows were conducted in each section of the estuary with a 7.6-m wide otter trawl (headrope length 9.5 m, 2.0- and 0.5-cm mesh in the body and codend, respectively). The sampling gear was not efficient at catching fish <40 mm SL. For each section and sampling date, we sampled at a range of depths and areas to obtain a representative index of density. Sampling was mostly limited to the mid-to-high tidal range of spring tides because we needed to gain access to the cages during low tides. All tows were performed with the prevailing current at a target tow speed of 3 km/hr. For each tow, initial and final coordinates, mean current speed and the distance covered by the trawl (approximately 500 m) were registered by using a hand-held GPS. Temperature, salinity and dissolved oxygen (DO) were measured at the end of each tow with an YSI 85 dissolved oxygen and conductivity meter (Yellow Springs Intruments, Concord, CA). Because previous studies have reported a relationship between depth and abundance of juvenile California halibut in shallow estuarine systems (Kramer, 1990; Fodrie and Mendoza, 2006), a consistent depth was maintained during each tow. The depth of each tow was monitored and recorded with an onboard fish finder. To obtain a density estimate representative of each section of the estuary, tows were performed at a variety of depths and locations.

After capture, California halibut were immediately measured for standard length. Length-frequency distributions were constructed for each sampling period and section of the estuary by 10-mm size classes. Density on an area basis was calculated by assuming a 7.6-m
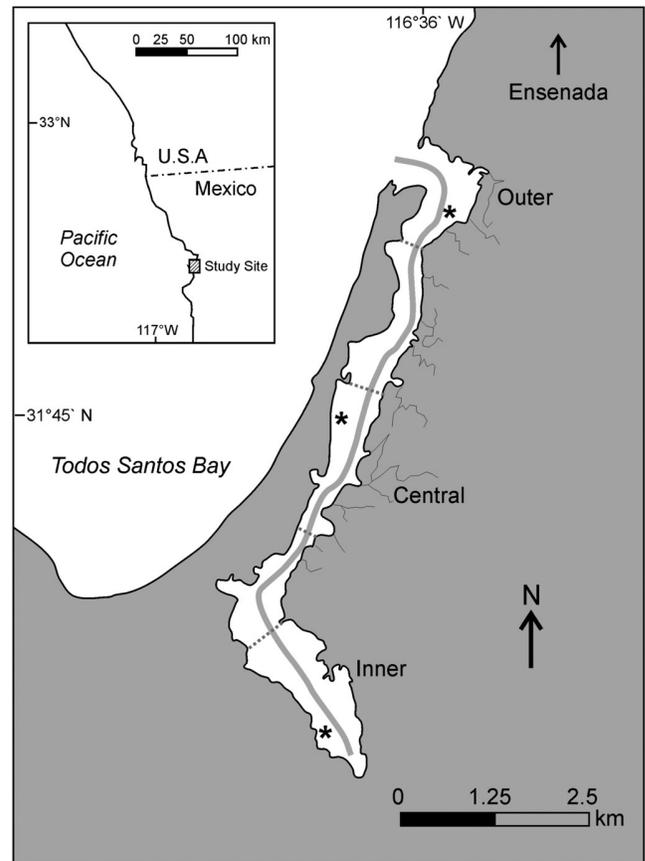

Figure 1
Map of Punta Banda Estuary, Baja California, Mexico where density and growth rates of California halibut (*Paralichthys californicus*) were assessed between October 2004 and October 2005. Black asterisks indicate locations where experiments were performed. Sampling for natural abundance and growth estimates was conducted in the outer, central, and inner sections of the estuary; the areas between these sections were not sampled. The gray solid line indicates the channel that runs along the main axis of the estuary.

trawl width and standardizing the tow to 1000 m^2 (reported as fish/1000 m^2). Estuarine emigration has been reported to occur during summer at lengths ranging from 140 to 200 mm (Haaker, 1975; Kramer, 1990; Hammann and Ramírez-González, 1990). Hence, mean density (±standard error [SE]) was calculated for fish ≤200 and >200 mm SL for each section of the estuary and sampling time.

Given that our primary interest was young juveniles, the densities of fish ≤200 mm SL were analyzed by two-way analysis of variance (ANOVA) with time and section of the estuary as fixed factors. Normality and homogeneity of variance were evaluated by using the Kolmogorov-Smirnov and Levene's tests, respectively. The data were log (x+1) transformed before we conducted the ANOVA to comply with the assumption of normality. A Tukey HSD test for unequal sample sizes was used to identify homogenous groups. The size-frequency

Table 1

Starting date, size range, and number of fish recovered in cages in the outer, central, and inner reaches of Punta Banda Estuary. Cages were recovered after 14 or 28 days; each row indicates a single cage (n=6 juveniles). Asterisks indicate locations in which cages were not recovered. No data (n. d.); cages were not seeded because of low capture rates.

Starting date	Section	14-day caging period		28-day caging period	
		Size range mm SL	Number of fish recovered (% mortality)	Size range mm SL	Number of fish recovered (% mortality)
28 Oct 2004	Outer	89–158	*	72–130	*
	Outer	70–102	*	69–85	*
	Central	96–159	6 (0)	55–103	6 (0)
	Central	79–135	6 (0)	67–146	4 (33)
	Inner	78–146	6 (0)	75–149	*
	Inner	75–150	4 (33)	67–148	*
12 Jan 2005	Outer	96–116	4 (33)	80–145	*
	Outer	84–104	0 (100)	82–143	*
	Central	88–115	5 (17)	90–122	6 (0)
	Central	90–113	6 (0)	62–146	5 (17)
	Inner	113–149	4 (33)	120–140	4 (33)
	Inner	95–112	4 (33)	85–119	2 (67)
28 Mar 2005	Outer	61–125	1 (83)	n.d.	—
	Outer	55–140	5 (17)	n.d.	—
10 Mar 2005	Central	62–138	4 (33)	54–150	4 (33)
	Central	52–136	5 (17)	n.d.	—
	Inner	80–150	6 (0)	118–156	6 (0)
	Inner	80–144	5 (17)	102–160	6 (0)
04 May 2005	Outer	114–140	4 (33)	63–132	*
	Outer	65–140	2 (67)	64–155	*
	Central	64–165	5 (17)	69–157	5 (17)
	Central	63–152	6 (0)	n.d.	—
	Inner	68–150	4 (33)	57–160	4 (33)
	Inner	56–139	4 (33)	56–146	4 (33)
16 Jun 2005	Outer	88–146	3 (50)	89–159	*
	Outer	n.d.	—	106–133	*
	Central	91–157	6 (0)	101–161	3 (50)
	Central	72–99	3 (50)	69–73	*
	Inner	65–170	4(33)	72–150	5 (17)
	Inner	n.d.	—	63–172	4 (33)
06 Sep 2005	Outer	75–122	4(33)	71–144	*
	Outer	73–141	6 (0)	71–143	6 (0)
	Central	53–146	4(33)	50–151	4 (33)
	Central	n.d.	—	110–129	4 (33)
	Inner	91–167	5 (17)	147	1 (83)
	Inner	n.d.	—	n.d.	—

distributions of California halibut ≤200 mm SL caught in different sections of the estuary were compared by using the nonparametric Kruskall-Wallis H test.

The relationship between density of fish ≤200 mm SL, environmental conditions, section of the estuary and sampling time was evaluated by using a general linear model (GLM). Densities were $\log(x+1)$ transformed to achieve normality. Temperature, salinity, DO, and depth were were included as continuous predictor vari-

ables. Section of the estuary and sampling time were included as categorical variables. Data corresponding to the beginning and end of each caging experiment were pooled for analysis and considered as a single point in time; the data from August 2005 were entered as a separate time point. Because there were significant correlations between salinity and tempreature (r=0.487) and salinity and DO (r=−0.633), the model was run to include an interaction term for these variables. Model

residuals were close to normally distributed (Shapiro Wilk's statistic=0.984, P=0.031).

Otolith growth rates of natural populations

Using measurements of daily increment widths as a proxy for somatic growth rate, we relied on two assumptions: 1) that growth increments in the form of ring formations in otoliths occurs daily, and 2) the increment widths of otoliths are proportional to somatic growth (i.e., there is a linear relationship between fish size and otolith size; Campana and Jones, 1992). Kramer (1991) and Kicklighter (1990) validated daily ring formation in larval and juvenile California halibut, respectively. Using caging experiments to evaluate otolith and somatic growth rates in juvenile California halibut, Kicklighter (1990) documented a strong linear relationship between SL and otolith length for juveniles ranging from 40 to 100 mm SL. Kicklighter (1990) also reported a linear relationship between mean recent otolith growth (14 days) and somatic growth (y=0.619x+0.093, r^2=0.55). Hence, the measurement of recent increment widths as a proxy for somatic growth rates in juvenile California halibut is justified.

Wild-caught juveniles were placed over ice in individual bags and later frozen in the laboratory. We chose five individuals from each of the following size classes for otolith analysis: 50–80, 81–120 and 121–160 mm SL (n=15 per date and section of the estuary). Sagittal otoliths were extracted, cleaned in a sonicator with a 10% bleach solution to remove tissue, rinsed with distilled water, dried, and mounted on slides sulcus-side-down with Krazy Glue (Industrias Kola Loka SA de CV, Mexico State, Mexico). The right or left sagittal otolith was chosen randomly. The percent difference in length between the sagittal otoliths dissected from the eyed or blind side of both right and left-eyed juveniles is small (mean ±standard deviation [SD] in relation to blind side=−1.7% ±3.0%, range −11.1% to 2.5%, n=20).

Polishing was necessary to reveal daily growth increments in the otolith posterior margin. Polishing cloths of several sizes (34.3, 22.1, 14.5, and 6.5 μm) were used depending on otolith size and visibility of daily increments. Otoliths were given a final polishing with a 0.3-μm aluminum powder and soaked in 5% EDTA to increase the visibility of daily growth increments.

We were interested in examining the relationship between recent growth rate and environmental conditions over a relatively short time period to minimize the possibility that individuals had moved substantially within the estuary. We measured the width of daily growth increments for the period corresponding to the 14 days before capture (corresponding to the second half of the caging experiment). Daily increments, consisting of an opaque and translucent ring, were viewed under 400× magnification. The width of each increment was measured parallel to the main growth axis of each otolith in the posterior margin (range of widths 3–15 μm; mean= 6 μm ±2 SD) by using an imagine analysis system consisting of a compound microscope and digital camera

connected to a computer loaded with Image J analysis software (National Institutes of Health, Bethesda, MD). We had difficulty distinguishing the interface between the opaque and translucent rings of the outermost increments with sufficient clarity to accurately measure the daily increment widths, although we could identify daily increments. We therefore counted the 14 increments deposited before capture and measured the width of those in which the interface between the opaque and translucent rings was clear to obtain an accurate measurement. The number of increments measured in a given otolith ranged from 5 to 12 (mean=9 ±3 SD). Otoliths for which we could not measure at least five increments were discarded (about 20%). In those cases, we prepared additional otoliths from fishes of the same size class. Each increment was measured three times and its average width was used in subsequent calculations. Recent growth rates are reported in μm/day.

The width of daily increments can vary as a function of fish size. Analysis of covariance (ANCOVA) has been used in previous studies to remove size-related differences in tests for differences in otolith growth rates among groups (e.g., Phelan et al., 2000). We evaluated whether recent otolith growth was correlated with SL within the 50–160 mm SL size range that we examined. Data from fishes collected in different sections of the estuary at a given time were pooled. Sampling periods were considered separately and six correlations were performed (n=45 fish per sampling period). Only one correlation was positive and significant (October 2004; P<0.001) and a second was slightly negative and marginally significant (January 2005; P=0.032). In both cases, the proportion of the variance in recent otolith growth rates explained by SL was very low (r^2=0.26 and r^2=0.10, respectively). Hence, we did not find a strong dependence of recent otolith growth rates on size within our target size range. Recent otolith growth rates of natural populations were thus analyzed withg two-way ANOVA and by using time and section of the estuary as fixed factors. Data were log (x+1) transformed to comply with the assumption of normality. Tukey HSD tests were used to test for specific differences between means after ANOVA.

We used correlation analysis to test the hypothesis that higher growth rates coincide with higher density of juveniles ≤200 mm SL and to examine the relationship between recent otolith growth rates of natural populations and temperature. Mean temperature during the 14 days before their capture was calculated by using data from thermographs deployed during caging experiments (see below). Correlation analysis was performed only for times and sections of the estuary for which both otolith and temperature data were available.

Somatic and otolith growth rates of caged fishes

Valle et al. (1999) examined the fine-scale distribution of juvenile California halibut in shallow (<1.1 m depth) waters of Alamitos Bay, CA, in relation to the presence or absence of eelgrass habitat. Juveniles were 2–6 times

more abundant in unvegetated habitats. Eelgrass is not found in the outer and inner sections of Punta Banda Estuary and only sparse eelgrass beds are found in the central section. We placed cages solely in unvegetated areas because eelgrass is not the preferred habitat of juvenile halibut. Cages were constructed with a PVC frame (1 m wide × 1 m long × 0.5 m high) wrapped in Vexar® low-density polyethylene netting of 0.5 × 0.5-cm mesh. Cages were closed on the bottom to prevent escapement. Similar designs have been used in other studies seeking to evaluate the growth of juvenile flatfish (Kicklighter, 1990; Sogard, 1992). Caging experiments began and ended during spring tides, allowing us access to subtidal habitat during lower low water. The day before starting each caging experiment, four cages were placed within a few meters of each other in the outer, central, and inner sections of the estuary (Fig. 1). Each cage was anchored by rebar fastened to the corners with cable ties. Temperature was measured continuously at each caging location by using thermographs placed in the vicinity of each caging location (HOBO Water Temperature Data Loggers model 856097, Onset Computer Corporation, Pocasset, MA). These thermographs were programmed to record every 30 minutes.

To supply the cages, individuals within the target size range (50–160 mm SL) were placed in ice chests filled with aerated seawater immediately after trawling. Seawater was exchanged frequently and mortality was minimal. Cages were seeded with juveniles caught in the same section of the estuary to avoid subjecting them to substantial changes in the environmental conditions to which they had been exposed.

The target number of fish to be placed within each cage was six. Other flatfish studies have used similar fish densities (Kicklighter, 1990). The number of fish introduced into each cage was held constant throughout the caging experiments. If we did not catch enough fish of the targeted size range in a given section of the estuary, fewer cages were seeded rather than altering fish density (Table 1). To evaluate somatic growth during the course of the experiment, each juvenile was marked by clipping the dorsal or anal fins, or both. Juveniles were then injected intramuscularly with tetracycline (0.05 mg/kg) to create an otolith mark indicative of the beginning of the caging period. To determine the correct dose for each individual, wet weights were estimated from SL measurements by using a relationship previously obtained for juveniles captured in Punta Banda Estuary (wet weight $(g) = 8.77 - 0.36SL + 0.0045SL^2$, $r^2 = 0.99$).

We were concerned about cage loss. Hence, half the cages were retrieved after 14 days during lower low tide ($n=2$ cages per section of the estuary) and the remainder were recovered after 28 days. Otolith growth rates were thus measured after a 14- or 28-day caging period. Following retrieval from the cages, juveniles were identified by their pattern of fin clippings, SL was measured, and the number of survivors was recorded. Fish were placed on ice in the field and frozen in the laboratory for subsequent analysis of otolith growth

rates and gut fullness levels. Otoliths were removed and prepared as described above. It was more difficult to visualize daily growth increments in caged individuals that in those from natural populations (see also Fodrie and Herzka, 2008). Hence, we measured the width of the otolith anterior margin from the tetracycline mark to the edge. Tetracycline marks were viewed under 400× magnification under ultraviolet light with a FlashUV2 flashlight (375 nm). Otolith growth rate was expressed as μm/day. Individual somatic growth rates of caged fishes were calculated as instantaneous growth coefficients (G, 1/d) with the folowing equation:

$$G = \left(\ln(SL_t) - \ln(SL_0)\right)/\Delta t,$$

where SL_t = standard lengths (mm) measured at the beginning of a caging period;
SL_0 = standard lengths (mm) measured at end of a caging period;
Δt = number of days fish remained within cages.

We used correlation analysis to examine the relationship between otolith and somatic growth rates (G) of caged juveniles retrieved after 14 days.

Gut fullness levels

Our main objectives were to evaluate whether food availability was related to seasonal patterns in recent growth rates and to compare the amount of food ingested by wild-caught and caged California halibut. We assessed the gut fullness level of all juveniles captured in the field ($n=456$) and those retrieved from cages ($n=214$). The complete digestive tract (esophagus, stomach, and intestine) was dissected whole and preserved in 80% ethanol. An index was developed to classify fish by their relative gut fullness: 1) empty; 2) 1–25% full; 3) 26–50% full; 4) 51–75% full; and 5) 76–100% full. Gut fullness assessment was performed by a single person to maintain consistency. The frequency of occurrence of different gut fullness levels for each section of the estuary and sampling period was calculated as a percentage of the total caged or wild-caught fish processed for a given date.

Results

Density and environmental variables

Mean density of juveniles ≤200 mm SL ranged from 0.36 ±0.36 to 9.68 ±2.71 fish/1000 m² (overall mean=3.31 ±1.07 fish/1000 m², Fig. 2A). It was roughly two times higher (~10 fish/1000 m²) in the innermost section of the estuary than in the central and outer sections (~4–5 fish/1000 m²) during the winter and spring. Although during summer densities were lower than during winter and spring, they were still twice as high in the inner estuary than in the central and outer sec-

tions (~3 vs. 1.5 fish/1000 m^2). ANOVA results indicated that density varied significantly as a function of time ($F_{12,154}$=3.97, P<0.005) and among sections of the estuary ($F_{2,154}$=4.77, P=0.009). The interaction between factors was not significant ($F_{24,154}$=1.33, P=0.154). *Post-hoc* multiple comparison tests indicated that density was significantly higher in the inner estuary (4.55 ±1.02 fish/1000 m^2) than in the central section (2.46 ±0.88 fish/1000 m^2). In addition, density was significantly higher during winter (November and February) than during most summer months (June through October).

The size distribution of juveniles varied as a function of time and section of the estuary. Recent recruits (<70 mm SL; Kramer, 1991) were relatively abundant throughout the estuary between October 2004 and February 2005, indicating that the peak in estuarine immigration occurred during winter. However, fish 60–80 mm SL were also captured between May 2005 and July 2005. In the outer section, a large proportion (79% of total) of juveniles <100 mm SL were caught between October 2004 and April 2005; few individuals were >200 mm SL (Fig. 2B). Between May 2005 and October 2005, a greater percentage of the fish caught were >200 mm SL (range 21 to 52%, Fig. 2C). In the central and inner sections, 87% and 85% of all fish caught were <200 mm SL. Throughout the estuary, juveniles <200 mm SL predominated between October 2004 and April 2005 (89% of total); fish >200 m SL were more frequent between June2005 and October 2005 (23% of total, Fig. 3).

The size-frequency distributions for the outer and central sections exhibited a single marked peak of 40–90 mm SL (51% of all fish caught) and 40–70 mm SL (32% of all fish caught), respectively (Fig. 4). In contrast, the size-frequency distribution of halibut caught in the inner section had a primary peak at 40–70 mm SL (21% of all fish caught) and a broad, secondary peak at 100–150 mm SL (28 % of the total catch). However, the size-frequency distributions of California halibut did not differ significantly among the outer, central, and inner sections of the estuary (Kruskall-Wallis H=1.35, P=0.51). The maximum SL found in the outer, central and internal sections of Punta Banda Estuary was 680, 788, and 784 mm, respectively.

Instantaneous measurements of temperature, salinity, DO, and depth taken during trawling varied throughout the year (range 15–24.0°C, 32–38‰, 3–11 mg/L; Fig. 5). The GLM results indicated that density was signicantly and negatively related to temperature (β=0.59, F=5.50, P=0.020), sampling time (F=2.264, P=0.039), and the interaction between temperature and salinity (β=0.016, F=4.906, P=0.0208). All other predictor variables were not significantly related to density, although there was a weak negative relationship with salinity (β=−0.302, F=3.274, P=0.072). The GLM explained a low proportion of the variance (multiple r^2=0.208).
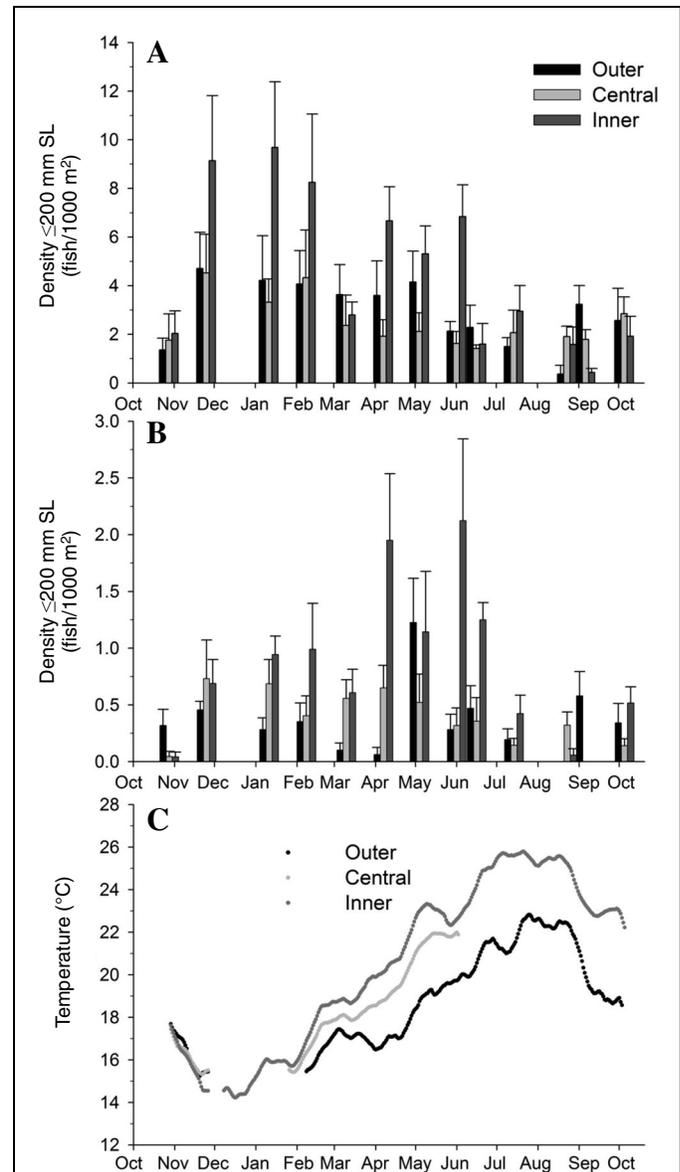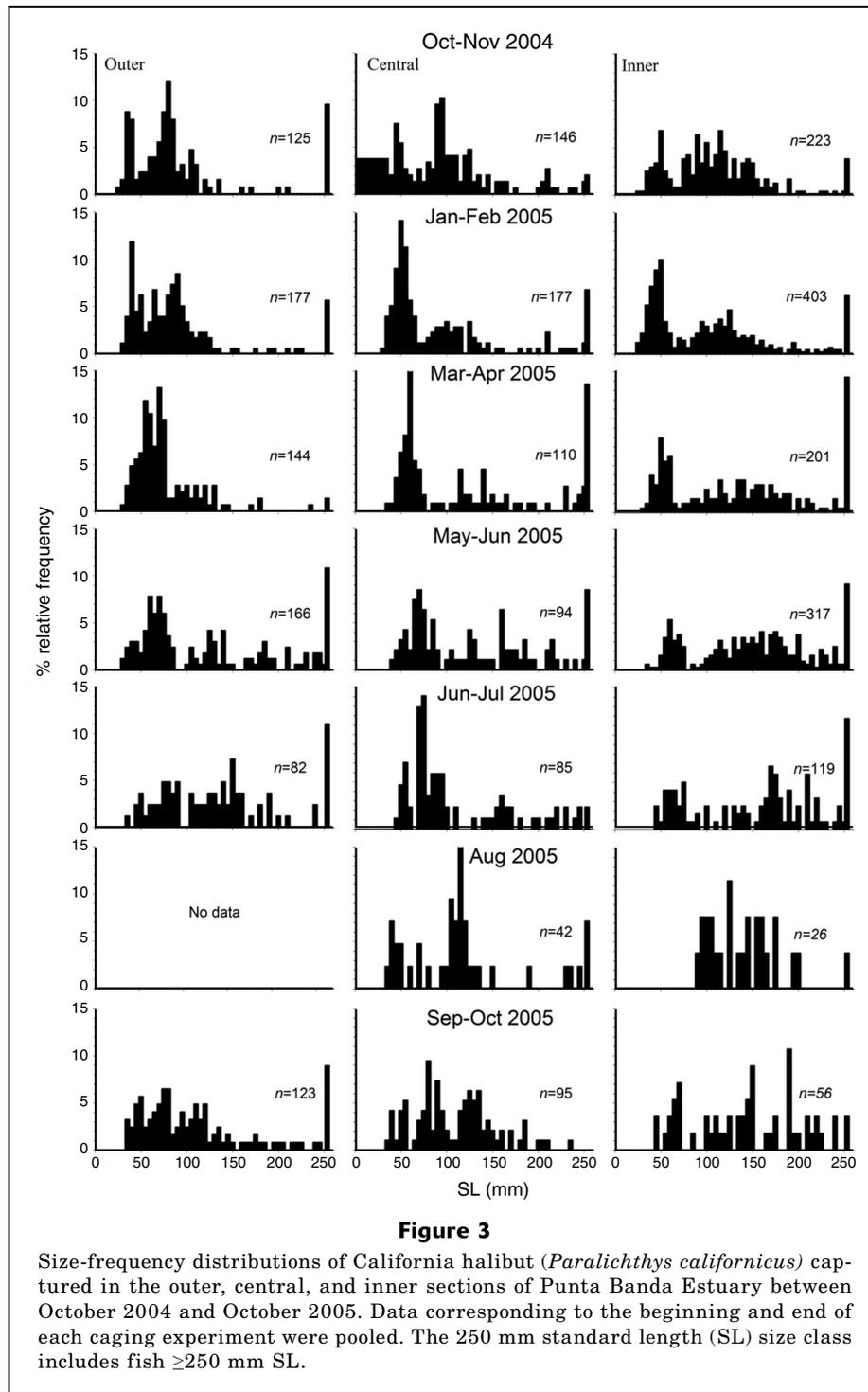

Figure 2

(**A**) Density of juveniles ≤200 mm standard length (SL) and (**B**) late juveniles >200 mm SL and adults of California halibut (*Paralichthys californicus)* captured in the outer, central, and inner sections of Punta Banda Estuary between October 2004 and October 2005. Values represent means ± standard error (SE). (**C**) Continuous temperature measurements made at locations in the outer, central and innermost sections of Punta Banda Estuary. Missing data reflect loss of thermographs.

Otolith growth rates of natural populations

Two-way ANOVA of log-transformed recent otolith growth rates indicated a significant interaction between time and section of the estuary ($F_{10,249}$=8.30, P<0.001). In the outer section, the highest mean growth

Figure 3

Size-frequency distributions of California halibut (*Paralichthys californicus*) captured in the outer, central, and inner sections of Punta Banda Estuary between October 2004 and October 2005. Data corresponding to the beginning and end of each caging experiment were pooled. The 250 mm standard length (SL) size class includes fish ≥250 mm SL.

rates were found in January 2005 and May 2005 (8.13 ±0.40 and 6.75 ±0.45 μm/d, respectively) and the lowest in September 2005 and March 2005 (4.52 ±0.16 and 5.47 ±0.35 μm/d, respectively; Fig. 6A). A similar pattern was observed for the central section. The highest growth rates in the inner section were found in October 2004 and May 2005 (8.40 ±0.32 and 7.78 ±0.41 μm/d, respectively), and the lowest in September 2005 and January 2005 (4.11 ±0.15 and 4.89 ±0.40 μm/d, respectively). Correlation analysis indicated that the relationship between recent otolith growth rates and mean temperature during the 14 days before capture was not significant ($r=0.31$, $F_{1,11}=1.20$, $P=0.295$), even though the mean temperature ranged between 15.8

and 25.7°C (Fig. 2B). There was a positive relationship between density and recent growth rates, but the relationship was not statistically significant ($r=0.43$, $P=0.074$).

Somatic and otolith growth rates of caged fishes

Throughout the caging experiments, two cages were lost in the outer section after the first two weeks. Another 12 cages were not recovered after 28 days (mostly from the outer section; Table 1). Excluding fish from cages that were not retrieved, 72.7% (131 juveniles) and 72.8% (83 juveniles) were recovered after 14 days and 28 days, respectively.

Recent otolith growth rates during the first 14 days were 5–6 times lower than those of wild-caught California halibut (1–2 μm/d, Fig. 6B). Minimum otolith growth was also detected during the second half of each caging period (Fig. 6C). Somatic growth rates measured after 14 and 28 days were very low, indicating that conditions within the cages did not favor growth (Fig. 6, D and E). We therefore concluded that the growth rates of caged individuals did not reflect habitat value and did not test for growth differences between sections or caging periods.

Despite the low growth rates, there was a significant positive correlation between somatic and recent otolith growth of caged fishes during the first 14 d of the experiments ($r=0.76$, $F_{1,127}=176.07$, $P<0.001$, Fig. 7). This finding indicates that otolith and somatic growth are coupled in California halibut juveniles, even at very low growth rates. There was also a significant negative correlation between somatic growth rates and mean temperature ($r=0.56$, $F_{1,11}=5.15$, $P =0.044$), although the correlation between otolith growth rates and temperature was not significant ($F_{1,11}=1.21$, $P=0.295$; data not shown).

Gut fullness levels

Most juveniles captured in the wild had at least some food in their digestive tract (62%, 60%, and 64% of total in the outer, central and inner sections of estuary, respectively; Fig. 8A). The percentage of individuals with gut fullness levels >50% ranged roughly between 40 and 80%, varying as a function of time and section of the estuary. In general, fewer fish exhibited empty guts during the early spring and summer. In contrast, most of the fishes recovered from the cages after 14 days exhibited empty stomachs (Fig. 8B). Only occasionally did some caged individuals have noticeable amounts of food in the digestive tract.

Discussion

Density and environmental variables

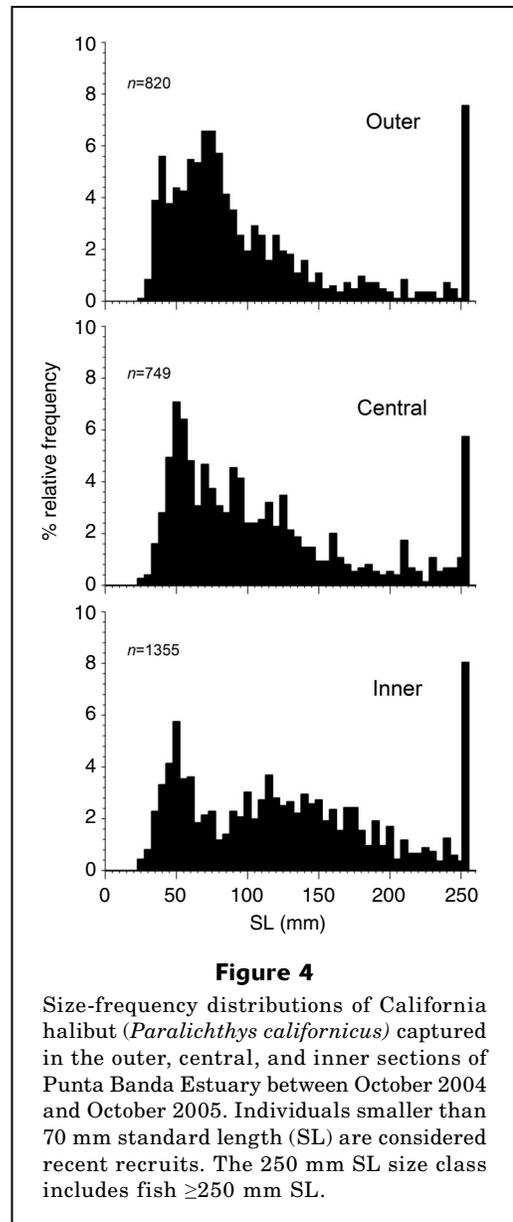California halibut ≤200 mm SL were consistently captured throughout Punta Banda Estuary, indicating the

Figure 4

Size-frequency distributions of California halibut (*Paralichthys californicus)* captured in the outer, central, and inner sections of Punta Banda Estuary between October 2004 and October 2005. Individuals smaller than 70 mm standard length (SL) are considered recent recruits. The 250 mm SL size class includes fish ≥250 mm SL.

entire system is used as juvenile habitat. Based on the relationship between daily otolith increment counts and SL reported by Rosales-Casián (2004) for juveniles caught in northern Baja California, and the age-length relationship reported by Hammann and Ramírez-Gonzáles (1990) for halibut captured in Todos Santos Bay (*TL* (cm) = 8.98+9.51*Age* (yr)) fish <180 mm SL are young-of-the-year (see also Haaker, 1975; Kramer, 1991). Maturity occurs at approximately 20–23 cm total length (TL) for males and 38–47 cm TL for females (Haaker 1975; Love and Brooks 1990). Hence, most of our catch was comprised of juveniles, although some adults were also caught.

The distribution of juveniles relative to the mouth of medium-sized estuaries in Baja California and southern California appears to vary among systems. We
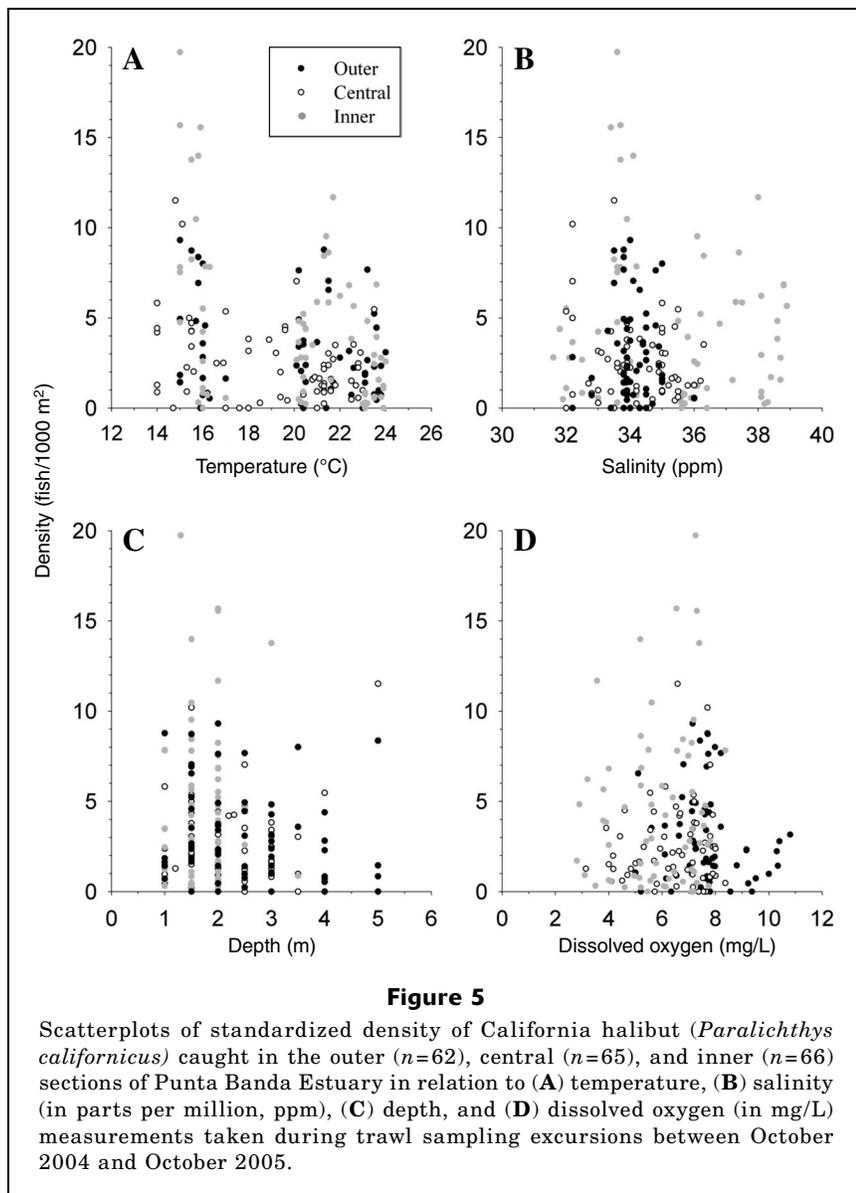
found the highest abundance of juveniles in the inner reaches of Punta Banda Estuary throughout most of the year. Based on an annual survey, Hammann and Ramírez-González (1990) reported higher abundance of juveniles in the central section of the same system between January and April. However, their sampling was limited to the main channel and did not include the inner reaches. Valle et al. (1999) reported that juvenile densities decreased from the mouth to the inner reaches of Alamitos Bay in southern California. In a fall survey, Fodrie and Mendoza (2006) found higher abundance of juveniles in the central and outer reaches of the systems in southern California most similar in size, shape, and depth to Punta Banda Estuary (Batiquitos, Agua Hedionda Lagoon, Buena Vista, and Mission Bay). The density of juveniles captured in Punta Banda estuary is toward the lower range of those reported by Fodrie and
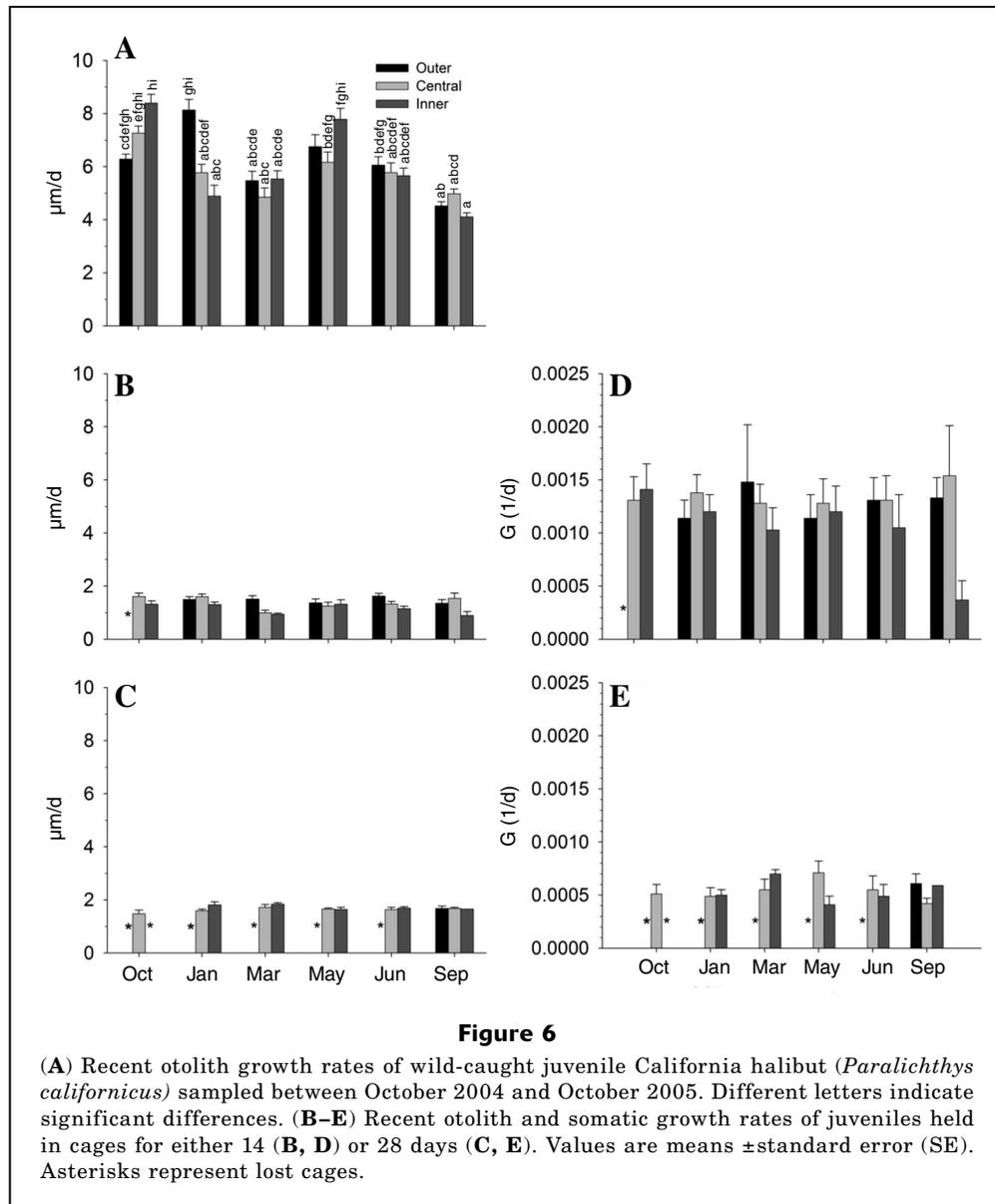
Mendoza (2006) for medium-size embayments (termed lagoons in their study, range 4–30 fish/1000m² after taking into account their gear efficiency corrections).

Juveniles were caught throughout the range of instantaneous temperatures measured in Punta Banda Estuary (15–24°C), although our GLM analysis indicated a weak but significant negative relationship between temperature and density. Likewise, other studies have also reported capturing juveniles at a broad range of temperatures (e.g., Allen 1988; Kramer 1990; Fodrie and Mendoza 2006). Madon (2002) conducted laboratory studies on juveniles ranging from 118–172 mm SL and found them tolerant to a broad range of temperatures (14–28°C) and salinities (8–34‰). Within this size range, growth and osmoregulation were positive at various combinations of temperatures and salinities, except when both were low and outside the range of those measured in this study (14°C and 8‰). Likewise, laboratory studies on California halibut between 40–50 mm TL acclimated to 15°, 18°, 21°, and 24°C indicate preferred temperatures are similar to acclimation temperatures (Esquer-Méndez, 2006). Further, juveniles acclimated to 15–24°C only avoid temperatures substantially above and below those of the acclimation interval (<10.8°C and >29.1°C). The broad temperature interval over which juveniles were captured in this and other studies is thus consistent with the high temperature tolerance of relatively small juveniles.

Figure 5

Scatterplots of standardized density of California halibut (*Paralichthys californicus*) caught in the outer (*n*=62), central (*n*=65), and inner (*n*=66) sections of Punta Banda Estuary in relation to (**A**) temperature, (**B**) salinity (in parts per million, ppm), (**C**) depth, and (**D**) dissolved oxygen (in mg/L) measurements taken during trawl sampling excursions between October 2004 and October 2005.

In a review of juvenile flatfish distribution in relation to environmental conditions, Gibson (1994) noted that salinity generally has a limited effect on growth of juvenile flatfish, and that its primary effect is on distribution and movement patterns, although others have noted that high salinities may imply a bioenergetic cost to juveniles (Wuenschel et al., 2005). Although the GLM analysis indicated a weak, non-significant relationship salinity and density, juveniles were captured in variable densities over a range of salinities (31.6–38.9‰). Further, we found higher densities of juvenile California halibut in the inner reaches of Punta Banda Estuary, where salinity is usually highest. Hence, it does not appear that the higher salinities we measured during our study limited habitat availability. Given that salinity gradients in seasonally arid estuaries are much more limited than in "classical" systems,

Figure 6

(**A**) Recent otolith growth rates of wild-caught juvenile California halibut (*Paralichthys californicus)* sampled between October 2004 and October 2005. Different letters indicate significant differences. (**B–E**) Recent otolith and somatic growth rates of juveniles held in cages for either 14 (**B, D**) or 28 days (**C, E**). Values are means ±standard error (SE). Asterisks represent lost cages.

tolerant species such as juvenile California halibut may utilize the entire embayment as juvenile habitat.

Various studies have reported that small juvenile California halibut are found in higher densities in shallow habitats (~<2 m; Allen and Herbinson, 1990; Fodrie and Mendoza, 2006). This is consistent with our results; the highest densities of juveniles in Punta Banda Estuary occurred at depths between 1–2 m. To our knowledge there are no studies examining the causes of underlying the depth-related distribution patterns in juvenile California halibut, but size-specific depth preferences have been associated with resource partitioning, avoidance of predation by conspecifics, and feeding excursions into shallow areas (Kramer 1990; Gibson, 1994; Able et al., 2005). In addition, the use of shallower habitats subject to stronger variations in temperature by smaller juveniles is consistent with the higher tolerance of smaller juveniles reported by Madon (2002).

The low proportion of the variance explained by the GLM analysis suggests other abiotic or biotic variables also influence juvenile density. The lack of a significant relationship between dissolved oxygen concentrations and density is probably due to the absence of low DO levels during our surveys; values <2 mg/L are typically associated with detrimental effects on growth and survival of fishes (Stickney, 2000). Abundance of juvenile flatfish has been negatively related to sediment grain size, although the relationship varies among species and with size (e.g., Drawbridge, 1990; Amezcua and Nash, 2001). This may be due to the influence of sediment grain size on prey availability, or related to the burial

behavior typically exhibit by flatfish in response to pre-dation pressure or as part of their ambush feeding be-havior (Haaker, 1975; Allen, 1990; Amezcua and Nash, 2001). We did not evaluate sediment grain size during our study. However, Ortiz et al., (2003) reported that in Punta Banda Estuary sediment grain size ranges from fine sand (0.19–0.93 mm) near the mouth of the to coarse silt (0.03 mm) near the head. We found that density was generally highest in the innermost reaches of the estuary, where sediments are finest. Hence, the higher abundance of juveniles in the inner estuary may be at least partially related to the characteristics of the substrate.

There is consistent evidence to suggest that the peak in estuarine immigration occurs primarily during win-ter and spring (Allen, 1988; Kramer, 1990; Hammann and Ramírez-González, 1990; Valle et al., 1999), al-though settlement can also take place during the sum-mer months (Allen et al., 1990). Based on analysis of the long-term larval surveys preformed as part of the California Cooperative Oceanic Fisheries Investiga-tions Program (CalCOFI), Moser and Watson (1990) reported that off the coast of northern Baja California and in southern California, the peak in larval abun-dance occurs between February and April, with a sec-ondary peak during summer. We observed the highest abundance of recent recruits (40–50 mm SL) during winter and spring. There was secondary peak of small juveniles during the summer, which could reflect either estuarine recruitment (the recent ingress of juveniles into the system) or growth of previous recruits that entered the estuary at a very small size.

The marked decrease in the density of juveniles >150 mm SL that we observed during the summer is strongly suggestive of estuarine emigration. Although size-selec-tive mortality of larger juveniles (Sogard, 1997) could also lead to a decrease in density, the decrease occurred primarily in the inner and central estuary and was ac-companied by an increase the in abundance of larger juveniles in the outer section, which is consistent with movement toward the mouth of the estuary. Given that estuarine emigration coincided with the onset of higher temperatures within Punta Banda Estuary, tempera-ture gradients may provide the cue for emigration.

Lastly, late juveniles >200 mm SL and adults were captured throughout Punta Banda Estuary, albeit in low numbers. Spawning only occurs in coastal areas (Haaker, 1975). The presence of late juveniles and adults within the estuary suggests that these systems may serve as feeding grounds for larger halibut, despite their predominantly coastal habits (Haaker, 1975; Al-len, 1990).

Otolith growth rates of natural populations and gut fullness

The daily otolith growth rates of the fastest (Octo-ber 2004; 7.32 μm/d) and slowest (September 2005; 4.54 μm/d) growing juveniles 50–160 mm SL varied approximately two-fold during the study. These values
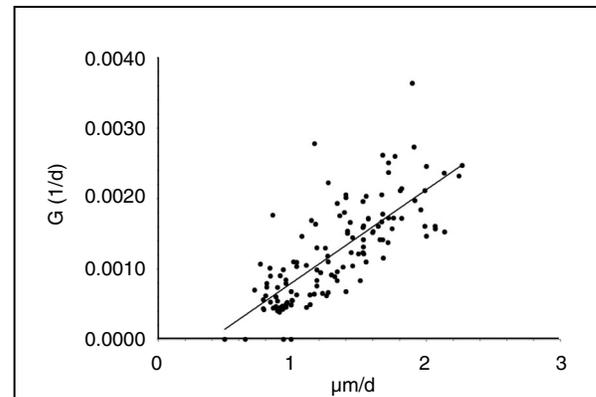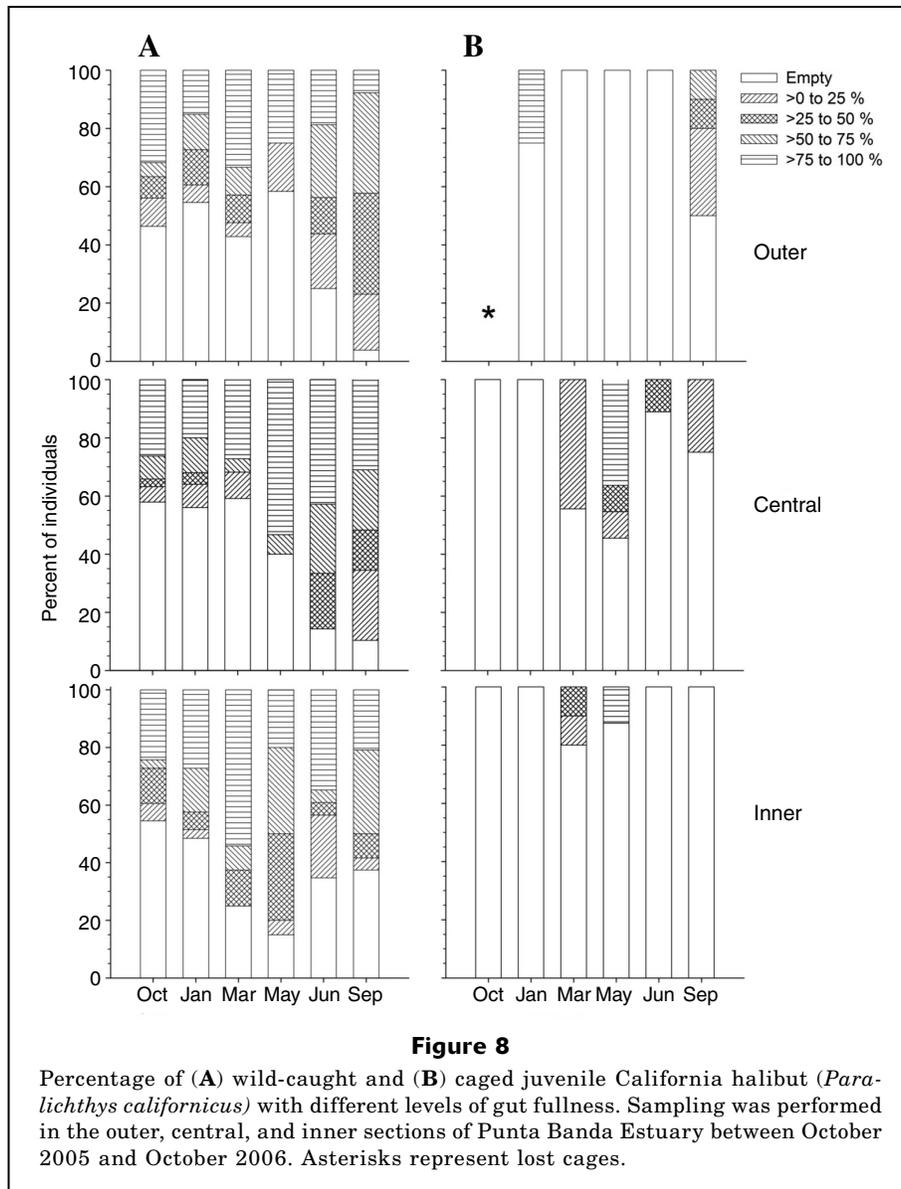

Figure 7

Linear regression between somatic and recent otolith growth rates of juvenile California halibut (*Paralichthys californicus*) held in cages for 14 days (G (1/d)$=-0.0005 + 0.0013*\mu$m/d, $r=0.76$, $n=129$).

are within the range of daily otolith growth rates reported for juvenile fishes (Sogard and Able, 2002; Gilliers et al., 2006). Recent otolith growth rates varied significantly as a function of time and section of the estuary, although juveniles grew throughout the year. This indicates spatial and temporal variability in the quality of juvenile habitat within the estuary (Sogard, 1992; Phelan et al., 2000; Necaise et al., 2005). Tem-perature, food availability and quality, size and preda-tion pressure are considered the most important factors influencing growth in juvenile flatfish (Gibson, 1994). We did not find a relationship between the average temperatures and recent otolith growth, although other studies on California halibut indicate that an increase in temperature from 20° to 23°C leads to higher somatic growth rates in the absence of food limitation (Haaker, 1975; Gadomski and Caddell, 1991). This could indi-cate that temperature does not substantially influence otolith growth rates (Campana and Jones, 1992). How-ever, Kicklighter (1990) reported a significant linear relationship ($r=0.69$, $P<0.001$) between temperature and otolith growth rates in caged juvenile California halibut held at a single site. We found a significant negative correlation between somatic growth rates and temperature in our caged fish, although the growth rates were very low. Hence, although there is evidence to suggest temperature does influence otolith growth in juvenile California halibut, for wild-caught juve-niles, other physical or biological factors play a more important role.

California halibut are primarily diurnal, visual feed-ers (Haaker, 1975). During our study, 40–85% of indi-viduals exhibited some degree of feeding (gut fullness levels >0%). Likewise, Plummer et al. (1983) found that 46% of juveniles and young adults (124–176 mm SL) captured in coastal waters using an otter trawl exhib-ited empty stomachs. Wertz and Domier (1997) reported that 69% of fish 156–1055 mm TL had empty stomachs.

Figure 8

Percentage of (**A**) wild-caught and (**B**) caged juvenile California halibut (*Paralichthys californicus)* with different levels of gut fullness. Sampling was performed in the outer, central, and inner sections of Punta Banda Estuary between October 2005 and October 2006. Asterisks represent lost cages.

Regurgitation of gut contents during trawling may partially explain the high incidence of empty stomachs in their studies and ours. However, Plummer et al. (1983) did not find significant diel and spatial differences in gut fullness levels. We have no way of correcting for the potential effect of regurgitation without a full study designed specifically for that purpose. Nevertheless, we find it likely that if regurgitation is frequent in juvenile California halibut, our data are likely to be biased systematically.

Seasonal patterns in gut fullness levels were evident: there was a high (up to 55%) percentage of empty stomachs in all sections of the estuary during the late fall and winter, when temperatures were lowest (~14–18°C). During the spring and summer, when temperatures were substantially higher (18–25°C), the incidence of empty stomachs was substantially

lower (10–40%, except for the outer estuary in March). Our qualitative observation that feeding levels are positively related to temperature is consistent with Madon's (2002) laboratory results; he observed an increase in food consumption and metabolic rates at higher temperature. Further, somatic growth rates of juveniles in his experimental treatments (14°, 20°, 25° and 28°C) did not differ significantly, suggesting that higher food consumption is a response to higher metabolic demand.

In contrast, qualitative comparison of the months and sections of the estuary with the highest otolith growth (central and inner sections October 2004, outer section January 2005 and outer and inner sections May 2005) with the proportion of individuals that exhibited evidence of feeding did not show a consistent relationship. Low growth rates (Septem-

ber 2005) did not coincide with a high proportion of empty stomachs. However, our study was not designed to directly relate recent otolith growth with feeding. Gut fullness levels are only a crude point-estimate of feeding success. Our recent otolith growth estimates represent the average daily growth over a 14 day period, whereas the time required to process ingested food is substantially shorter (1–2 days). Detailed studies of food availability and consumption rates (e.g., Sogard, 1992) are necessary to identify the factors underlying variation in otolith growth rates of juvenile California halibut.

Density dependent processes, such as competition for food or space and predation pressure, can also influence growth rates. We found a weak positive relationship between density and recent otolith growth rates of wild-caught juveniles, but the correlation was not significant (see also Fodrie and Levin, 2008). Hence, we did not find strong evidence to suggest limitation for food or space (negative density dependence) or the active selection of habitats supporting to higher growth rates (positive density dependence; Sogard, 1992). However, density-dependent growth regulation may occur at smaller spatial scales than those examined in this study, and cannot be conclusively ruled out.

Somatic and otolith growth rates of caged fishes

Due to the low growth rates of caged juveniles, we could not use our recent somatic and otolith growth measurements as proxies for habitat quality. Most caged juveniles had empty stomachs. This could be due to a variety of factors, including limited availability of prey within the cages, limited feeding success and foraging ability, competition for food resources due to high fish density, or as a result of a stress response in relation to handling (e.g., Guindon and Miller, 1995). A density of 6 fish/m^2 is much higher than densities of juvenile California halibut found within embayments (Fodrie and Mendoza, 2006).

During the first 14 days of caging, somatic growth rates of caged juveniles were very low (G=0.0003 to 0.0015 1/d). For fish 50 and 160 mm SL, this is equivalent to 0.01 to 0.12 mm/d, respectively, which is much lower than has been reported previously for wild-caught juveniles California halibut (0.13–1 mm/d, Haaker, 1975; Allen, 1988; Kramer, 1990; Kicklighter, 1990). Accordingly, recent otolith growth rates of caged juveniles were also three to six times lower than in wild-caught juveniles (equivalent to 0.89–1.63 μm/d, mean=1.32 μm/d). Kicklighter (1990) also found very low otolith growth rates during his caging experiments; daily increment widths along the main growth axis were 0.49 to 2.26 μm. Fodrie and Herzka (2008) also reported limited otolith growth in some juveniles held in cages in Punta Banda Estuary.

Somatic and otolith growth rates calculated over the 28 days caging period were substantially lower than over the first 14 days, implying little or no growth during the second half of the experiment. The significant positive relationship between somatic and otolith growth during first 14 days indicates marginal increment widths are reliable proxies for somatic growth at low growth rates, at least for a few days. However, uncoupling between otolith and somatic growth rates occurred during the second half of the experiment; there was virtually no difference in marginal increment widths between fish retrieved after 14 and 28 days. As discussed by Paperno et al. (1997), uncoupling between otolith and somatic growth rates tends to occur under extreme starvation conditions.

Conclusions

Our results indicate the entire Punta Banda Estuary serves as juvenile habitat for California halibut. This suggests that in arid or seasonally regions in which estuaries lack in strong environmental gradients, particularly in salinity, entire systems may provide suitable habitat for juvenile California halibut. Fodrie and Levin (2008) found evidence to suggest that juvenile abundance is an adequate proxy for recruitment to adult populations in this species. If so, the innermost section of Punta Banda Estuary, in which temperature and salinity is highest during most of the year, may contribute the most to the production of adults. In contrast, Fodrie and Herzka (2008) used otolith microchemistry to evaluate the nursery contribution of juveniles from different sections of Punta Banda Estuary to subadult production in the adjacent coastline, and found that the central and outer sections produced the majority of recruits. Considering that juveniles from the inner estuary must migrate through the central and outer sections of the estuary to emigrate from the system, it is possible that Fodrie and Herzka's (2008) estimates of subadult production are biased. If the abundance of juveniles is indeed a good proxy for production of adults, then the inner section of Punta Banda Estuary is probably the most important area in terms of juvenile California halibut habitat. Put together, these studies highlight the need for assessing juvenile habitat utilization and production on various spatial and temporal scales.

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