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Linking juvenile habitat utilization to population dynamics of California halibut

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Running Head: Nursery role of coastal finfish habitat

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Abstract

We investigated the nursery role of four coastal ecosystems for the California halibut (*Paralichthys californicus*) using the following metrics: (1) contribution in producing the fish that advance to older age classes, (2) connectivity of coastal systems resulting from migration of fish from juvenile to sub-adult habitats, and (3) effect of nursery habitat usage and availability on sub-adult population size, specifically evaluating the concentration hypothesis. Potential nurseries were grouped using a robust classification scheme that segregated exposed, bay, lagoon, and estuarine environments. Assignment of nursery origins for individual sub-adult fish via elemental fingerprinting indicated that exposed coasts, bays, lagoons, and estuaries contributed 31, 65, 1, and 3% of advancing juvenile halibut during 2003, versus 49, 33, 16, and 2% during 2004, respectively. These results were remarkably similar to "expected" nursery contribution derived from field surveys, suggesting that in this system juvenile distributions were a good indicator of unit-area productivity of juvenile habitats and that density-dependent mechanisms during the juvenile phase did not regulate recruitment pulses. Elemental fingerprinting also demonstrated that individuals egressing from bays did not migrate far from their nursery origins (< 10 km), resulting in reduced connectivity along the 110-km study region

over the time scale of ~ 1 generation. Consequently, we observed considerably higher sub-adult densities at sites near large bays, while populations distant from large bays appeared to be more influenced by nursery habitat limitation. Over large (~100 km) scales, the location and availability of nursery habitat alternatives had significant effects on the population dynamics of an important member of the ichthyofaunal community of southern California.

For coastal fish and invertebrate species, recruitment to an adult population is affected by a wide suite of spatially varying biotic and abiotic factors that operate throughout the pelagic larval phase (e.g., Checkley et al. 1988), at settlement (e.g., Allen 1988), or during advancement to older age classes (e.g., Modin and Pihl 1994). Many species are defined by life histories in which settled juveniles must select among nursery habitat alternatives that can affect the demography of adult populations through habitat- or site-specific growth or mortality (e.g., Sogard et al. 1992). Therefore, understanding the functional role that nursery habitats play in promoting population success is critically important for the proper management of coastal ecosystems and fish populations.

Estuaries and semi-enclosed bays have historically been considered essential nursery habitat for many economically and ecologically important fish and crustacean species (Beck et al. 2001; Gillanders et al. 2003). In many instances, distribution records have revealed above-average densities of juvenile fish within estuarine environments (e.g., Krygier and Pearcy 1986; Kramer 1991), and these data have been used by scientists, managers, and fishermen as verification of finfish reliance upon specific coastal habitats as nurseries. Juvenile fish distributions are valuable for generating first approximations of expected contribution from potential nursery habitats in producing new recruits that advance to adult populations (e.g., Le Pape et al. 2003). Nevertheless, these data alone are not rigorous tests of nursery habitat value because it is unclear how well local juvenile density relates to habitat productivity (Beck et al. 2001). At the ambit of juvenile fish, examinations of food resources, growth rates, ecophysiology, and survival (e.g. Sogard et al. 2001; Madon 2002; Heck et al. 2003) can be vital indicators of habitat quality. However, translating these data into estimates of overall habitat productivity for fish populations and species fitness remains difficult without knowing the nursery origin of adults. For many species, it remains largely unknown which specific nursery habitat types were used by those individuals that successfully recruit to adult populations (Beck et al. 2001).

Understanding the strength of linkages between nursery and adult habitats is greatly aided by the ability to track individuals throughout coastal environments. This is especially true for finfish with spatially separated juvenile and adult populations – a common life-history trait of the mobile megafauna of coastal environments (Gillanders et al. 2003). In recent years, trace element analyses of otoliths (teleost ear stones) have been employed to determine the trajectories of marine fishes egressing from putative nurseries (Gillanders 2002a; Brown 2006). Otoliths grow as daily and annual rings that are deposited around a central core. As rings accrete, trace elements are deposited into successive layers in some relation to the ambient environment (Campana 1999). Thus, provided that there are spatial gradients in environmental conditions (e.g., trace element concentrations), otoliths can carry a permanent record, or fingerprint, that allows researchers to retroactively track fish through time and space (e.g., Gillanders 2002b). This method represents an alternative to tracking fish by ID tags, radio telemetry and physical modeling, and is particularly advantageous because it is less susceptible to some of the dilution problems and tagging artifacts understood by marine scientists (sensu Levin 2006). Forrester and Swearer (2002) found that juvenile California halibut (*Paralichthys californicus*) collected within protected bays of California had otoliths that were enriched with Cu and Pb relative to the otoliths of juveniles collected from along the open coast. We built on their results to identify otolith chemical signals and nursery utilization at higher spatial resolution along the southern California coastline, as well as determine the nursery origin(s) and ontogenetic movement(s) of a large number of sub-adult halibut.

Key measures for assessing nursery “value” include: (1) determining the unit-area contribution of putative nurseries in terms of producing the individuals that recruit to adult populations (Beck et al. 2001), (2) understanding scales of population connectivity between juvenile and adult habitats that result from the ontogenetic migration of fish (Gillanders et al. 2003), and (3) identifying effects of nursery availability and usage on stock size, especially compensatory processes (Iles and Beverton 2000), or nursery habitat limitation (sensu Schmitt and Holbrook 2000). While these issues have received considerable attention over the last few decades, few studies have evaluated them collectively (Mumby 2005). We addressed these three population-level components of nursery “value” along the southern California coastline for the halibut. The tools available to investigate the nursery role of coastal habitats include a number of traditional (abundance and length-frequency distributions; age, feeding, growth, and mortality estimates; mark-recapture techniques)

and novel (elemental fingerprinting; stable isotopes; genetics; demographic or metapopulation modeling) techniques (see Gillanders et al. 2003). We combined orthogonal approaches that included both traditional (intensive field surveys) and new (elemental fingerprinting) methods in order to assess the ecological role of putative nurseries in supporting healthy finfish stocks.

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Materials and methods

Study species- The California halibut is an important member of the nearshore ichthyofauna community along the California coast. Adults of this species live in waters as deep as 100 m, but migrate into shallow (< 10 m) coastal waters to spawn throughout the spring and summer (Kramer and Sunada 1992). Larvae spend 20-30 d distributed across the continental shelf in surface waters prior to onshore transport and transformation to their benthic form (Moser and Pommeranz 1999). Following settlement, juveniles utilize exposed shorelines, coastal bays, lagoons, and estuaries as putative nurseries (e.g., Allen 1988; Kramer 1991; Fodrie and Mendoza 2006). After ~1-yr residency, halibut emigrate from these primary nursery habitats to sub-adult and adult habitats generally characterized by deeper water, typically along the exposed coastline (Kramer 1991). For clarity, we refer to all halibut from settlement until their first birthday as juveniles, halibut between their first and fourth (when ~50% maturity is reached) birthday as sub-adults, and halibut older that four as adults. The “nursery-generalist” life-history strategy exhibited by the halibut, in concert with the landscape of available habitats along the California coastline, makes this a model system for the application of elemental fingerprinting to address questions regarding the functional role of nurseries.

Study region- The San Diego County coastline is located at the southwestern-most corner of the continental United States, bounded by a narrow continental shelf along 112 km of shoreline (N 33.39, W 117.61 – N 32.54, W 117.13), and punctuated by a series of relatively small (< 1 km^2) or highly modified embayments. In order to sample all possible nursery habitats utilized by juvenile halibut from the international border to Oceanside, CA (a necessary component of elemental fingerprinting; Campana et al. 2000), the study area was divided into 14 sites for surveying and collecting fish (Fig. 1). Sites represented 4 distinct habitat types classified as: (1) exposed: Oceanside, La Jolla, Pacific Beach and Imperial Beach; (2) bay: Oceanside Harbor, Mission Bay and San Diego Bay; (3) lagoon: Buena Vista, Batiquitos and Agua Hedionda; and (4) estuary: San Elijo, San Dieguito, Penasquitos and Tijuana River (Fig. 1). Exposed habitats were defined as the narrow ribbon of bottom from 0-20-m depth adjacent to sandy beaches or rocky cliffs along the open coast. Embayment (bay, lagoon, and estuary) classification was supported by geomorphologic characteristics such as surface area and average depth (Table 1), as well as juvenile halibut densities (Fodrie and Mendoza 2006). Bays were > 0.84 km^2 in area, with average depths > 4 m. In San Diego County, bays are kept open and relatively deep to serve as harbors for shipping and recreational boating. Lagoons were distinguished by surface areas of 0.35-0.84 km^2 and average depths ~ 3 m. Estuaries were described as habitats covering < 0.25 km^2 with an average depth < 2.5 m. Estuaries were also characterized by high salt-marsh cover.

Expected contribution of nurseries- We assessed the potential contribution from each putative nursery by estimating the population sizes of juvenile halibut within all 14 of our sites. These results provided ecological baselines for the expected contribution of each juvenile habitat to adult halibut populations, assuming no growth or mortality differences among nursery alternatives. We made 234 and 293 collections in 2003 and 2004, respectively. All collections occurred in October and November, during daylight. Collections were made by otter trawling (doors 45x90 cm, headrope length 9.5 m, mesh 2.0 cm, bag mesh 0.5 cm) as well as block-net seining. Otter trawls were conducted from a 17’ research vessel traveling at 2.2-2.5 km h^{-1} and lasted for 10 min each. Block-net seining involved passing two nets (mesh 1.0 cm) across a channel or shallow body of water to trap fish, and subsequently dragging a beach seine (mesh 1.0 cm, bag mesh 0.5 cm) between the blocking nets until no halibut were collected on two consecutive drags. Distances covered during each collection event were recorded using a hand-held GPS so that sampling areas could be calculated. Buena Vista was not surveyed extensively because its inlet had remained closed since before 2001 and measured salinity was below the tolerance of juvenile halibut (< 10; Madon 2002).

It was necessary to employ two collection methods because of the drastically different habitats included in this study. Otter trawling was not feasible in estuaries characterized by channels less than 5 m in width and 1 m in depth, while block-net seining was not practical in the deeper waters of embayments and exposed coasts. In order to account for the different efficiencies of these gears, we conducted mark-recapture experiments to determine the relative juvenile halibut catch efficiencies for both gear types. First, we conducted a two-week mark-recapture study on halibut in the Punta Banda Estuary, Mexico, using our otter trawl and estimated the gear efficiency at 25.3% (Herzka unpubl). We also performed a smaller-scale mark-recapture experiment in San Elijo during the spring of 2003 to calculate the efficiency of block-net seining. Marked halibut were released into an area enclosed by blocking nets, and we attempted to recover fish from within the enclosure by seining (as above). This was replicated 4 times over 2 d and established a capture efficiency of 39.0% for our seines (Fodrie 2006).

To quantify the expected contribution of putative nurseries, only fish 50-250 mm SL were included in distribution analyses. Fish smaller than 50 mm were excluded because: (1) post-settlement migration among potential nurseries may continue for up to three months and confound distribution results (Kramer 1991), and (2) sampling gears used in this study had different mesh sizes and 50 mm proved a conservative measure to restrict potential gear bias. Fish larger than 250 mm were assumed to have grown out of the juvenile class (Kramer 1991).

Our georeferenced collection data were entered into a Geographic Information System database and juvenile halibut densities were mapped over each site. By integrating this density surface across each potential nursery, we were able to produce an estimate of total juvenile halibut occupying each of the 14 sites during 2003 and 2004. From these estimates we predicted a contribution from each site and habitat type (exposed, bay, lagoon, and estuary) to adult populations based solely on resident juvenile halibut population size (for more detail, see Fodrie and Mendoza 2006).

Realized contribution of nurseries- Elemental fingerprinting was employed to determine the nursery habitat origin of sub-adult halibut and quantify the realized contribution from putative nurseries in producing the fish that recruited to older classes. We used otolith signatures of juvenile halibut collected during the fall surveys in 2003 and 2004 from each site in San Diego County to generate a library of elemental fingerprints. Large embayments such as Mission and San Diego bays impart distinct chemical signals in the otoliths of fish occupying different zones along the long-axes of the bays (Fodrie 2006). We collected and analyzed fish from both the front and back of bays and lagoons in order to define all possible otolith signatures (sensu Gillanders 2002b). Halibut settle at approximately 10 mm SL and spend some period migrating among habitats (Allen 1988; Kramer 1991); therefore we only included otoliths from fish 50-200 mm SL to generate fingerprints. We assumed that these fish had been residents long enough to record local conditions in their otoliths and would provide nursery contribution data directly comparable to our field surveys.

During the spring of 2005, we collected fish that would have occupied local nurseries during 2003 (2-year-olds) and 2004 (1-year-olds) by means of 10-min otter trawls and timed hook-and-line fishing. Hook-and-line effort consisted of 2 fishermen each fishing over unstructured bottom using 1 circle hook baited with a live Pacific sardine (*Sardinops sagax*). Fishing always occurred between 0700 and 1100 hours to limit the influence of diel cycles in halibut feeding. We collected these sub-adult fish in all of our sites during 2005, except from Batiquitos and Penasquitos. To avoid uneven spatial sampling of sub-adult fish that could bias our contribution results, we divided trawling and fishing effort proportionally according to habitat availability. For example, because 15% of coastal habitat for sub-adult halibut in San Diego County is in San Diego Bay, 15% of our sampling effort occurred within the Bay during the spring of 2005.

Otolith analyses- All fish were frozen prior to otolith extraction. Saggital otoliths were dissected using sterile scalpels and ceramic forceps. Following removal, otoliths were placed in plastic vials after being rinsed in Milli-Q water and blotted with kimwipes to clean off attached organics. Samples were then sonicated in 15% H_2O_2 buffered with 0.05 mol L^{-1} NaOH and 3% HNO_3^- for 5 min each to further remove organics, and dried in a class 100 laminar flow hood. We mounted otoliths in crazy glue on petrographic slides, sanded them using 30- and 3-µm lapping paper, and polished them using a Milli-Q wetted microcloth. Otoliths were sanded and polished in the saggital plane to expose rings. Mounted otoliths were given additional 5-min rinses in both 15% H_2O_2 buffered with 0.05 mol L^{-1} NaOH and 3% HNO_3^-, and then rinsed three times with Milli-Q before being stored in the laminar flow hood. All reagents we used to prepare otoliths were rated as trace-metal grade. All plastic containers, glass slides, and forceps were leached in a 3% HNO_3^- solution and rinsed with Milli-Q before coming in contact with otoliths. Unlike other teleosts, flatfish are not bilaterally symmetrical, and there is the potential for left and right otoliths to sample different environmental signals in relation to proximity with the sediment interface. We only examined otoliths from the blind side of fish to ensure that all otoliths were recording from the same environment (nearer the sediment interface). Since halibut can be left- or right-eyed, the saggital otolith we selected varied between specimens.

Targeted growth rings of otoliths were excavated using a New Wave UP 213-nm laser ablation (LA) unit. All otoliths were sampled by ablating a 300-µm line along targeted rings at ~ 0.5-mJ laser energy, 15-µm s^{-1} scan speed, and 20-µm spot size. Post-run inspection revealed that ablations could range between 20-35 µm wide, and 8-14 µm deep (*n* = 10). Therefore, we sampled roughly 2 wk of growth with each laser track (Kramer 1991). For the juvenile fish collected in 2003 and 2004, ablations sampled the most recent growth rings laid down by fish. Ablations were begun adjacent to the apex of the post rostrum, and progressed ventrally along that edge. We attempted to position the ablations to leave a 5-10-µm band between the edge of the otolith and the ablation pit to avoid contamination from the otolith surface or glue. The mean distance from the otolith nucleus to the post rostrum was 1300 ± 450 µm (1 SD) for the juvenile fish we analyzed in 2003 and 2004.

For the sub-adult halibut collected in San Diego County during 2005, we sampled the rings deposited during the first year of the fish’s life for comparison to the signals from 2003-2004 juveniles in order to infer a nursery origin for each individual. On these fish, we ablated material at 1300 ± 300 µm outside the otolith nucleus in the direction of the post rostrum. This range allowed us to target what appeared to be fall growth using the opaque-hyaline banding for reference (Beckman and Wilson 1995). Successive rings appeared to have “elbows” indicating the approximate location of the post rostrum in earlier growth rings. We exploited these elbows to position our ablations.

Ablated material was transported in He gas (mixed with Ar before induction) to a Thermoquest Finnigan Element 2 double-focusing, single-collector, magnetic-sector Inductively Coupled Plasma Mass Spectrometer (ICP-MS). We sampled for the following isotopes: ^{26}Mg, ^{48}Ca, ^{55}Mn, ^{63}Cu, ^{88}Sr, ^{112}Cd, ^{138}Ba, ^{208}Pb, and ^{238}U (hereafter referred to by elemental abbreviation) to bolster our power to discriminate among habitats (Forrester and Swearer 2002; Becker et al. 2005). We eventually dropped cadmium from our analyses due to a lack of confidence in signal stability. Some juvenile fish from lagoons provided signals that were 10^3 times higher than other lagoon samples that were near detection limits. To determine element intensities, a chromatogram was generated for each element in each sample, and resulting peaks were analyzed individually. Detection limits for each element in each sample were defined as three standard deviations above the mean of the background (for average detection limits for each element, see Table 3). Any elemental “signal” below this threshold was deemed unreliable and, as a default, set to equal zero. For signals above detection limits, background signals (linearly extrapolated from pre- and post-signal data) were subtracted from sample signals in order to discount elemental counts not associated with our ablations. We then calculated the total counts (area under the chromatogram peak) for each element in each sample. The elemental counts were divided by the counts of Ca, which was used as an internal standard in order to account for the amount of otolith ablated. Element:Ca values were then multiplied by a correction factor generated from standards (below), using recorded run numbers and linear estimates of machine drift. These corrected ratios were used for all statistical analyses.

A glass standard spiked with trace elements (National Institute of Standards and Technology Standard Reference Material, NIST 612; Pearce et al. 1997) was analyzed at the beginning and end of each analysis day to account for machine drift. NIST 612 was analyzed using a 300-µm line sampled at 0.5-mJ laser energy, 10-µm s^{-1} line speed, and 50-µm spot size. Although calcium carbonate matrix-matched standards are preferable, NIST does provide good precision and intra-study consistency between samples (Vander Putten and Dehairs 2000).

Data analysis- Element ratios (X:Ca) recorded from the otoliths of juvenile fish were analyzed using linear Discriminant Function Analysis (DFA, Systat 9, © SPSS) to generate: (1) site, (2) regional (northern exposed, northern embayment, southern exposed, southern embayment; e.g., Becker et al. 2005), (3) habitat (exposed, bay, lagoon, and estuary), and (4) open coast versus embayment (bay, lagoon and estuary pooled) fingerprints. We ran DFAs with 2003 and 2004 juvenile signatures considered separately as well as combined. DFA is a data-reduction approach that uses multivariate data sets to generate a series of orthogonal algorithms (scores) that maximize variance among data groups. All DFAs were conducted stepwise, by running the analysis on all element ratios, and dropping the least significant variable as determined by the *F*-to-remove statistic. This procedure was repeated until all remaining element ratios scored *F*-to-remove values greater than 2. Distinct grouping in DFA space represented chemical difference in otoliths that were used to distinguish habitats. These fingerprints were used to assign a nursery habitat origin for 1- (relative to the 2004 library) and 2-year-old (relative to the 2003 library) sub-adults collected during 2005. By using the collection sites of sub-adults as an analog for recapture locations, and the nursery origin of individuals determined from elemental fingerprinting as release points, we were also able to quantify the connectivity of halibut populations as fish egressed from nursery habitats to join older age classes.

Ecologists are widely interested in the role that density-dependent processes in the early life histories of fish play in regulating population dynamics. The “concentration hypothesis” as defined by Iles and Beverton (2000) predicts that juveniles can concentrate into spatially limited nurseries far beyond carrying capacity, at which point density-dependent mortality or growth costs would limit the amount of contribution possible from those sites. We used model II regression (Sokal and Rohlf 2000) to examine the relationship between the change in realized and expected contribution, and juvenile halibut densities recorded during 2003 and 2004 in each nursery habitat type. Essentially, this is a means for evaluating habitat-specific survivorship against local juvenile density. To decompose the relative effects of habitat availability versus habitat usage (local density) on survivorship, we also regressed the change in realized/expected contribution against nursery habitat availability.

To examine if adult population size can be limited by the quantity of nursery habitat available to settling fish (Gibson 1994; Schmitt and Holbrook 2000), we regressed the catch rate (catch-per-unit-effort: CPUE) of sub-adult halibut during 10-min otter trawls in each of our four exposed sites during the spring of 2005 against the proportion of fish within each exposed site that utilized embayment vs. exposed habitats as nurseries (determined from elemental fingerprinting). We only considered exposed habitats since they are distributed along the entirety of the coastline and because all 4 exposed sites we included should have similar carrying capacities for sub-adult fish. Also, exposed habitats are where the majority of recreational and commercial fishing takes place for this species (Kramer and Sunada 1992). All regression analyses were completed in StatView 5.0.1 (SAS Institute Inc.).

Results

Nursery habitat contribution- Field surveys and GIS analyses produced estimates of approximately 789,000 juvenile halibut occupying nearshore habitats in San Diego County during the fall of 2003, and approximately 826,000 juveniles during the following fall (see also Fodrie and Mendoza 2006). Based on the distribution of juvenile fish, we expected the relative nursery contribution from exposed, bay, lagoon and estuarine habitats of new recruits for the adult population to be 31, 64, 4, and 1%, respectively, in 2003, and 42, 49, 4, and 5%, respectively, in 2004 (Fig. 2).

Our ability to distinguish otolith signals by individual sites was very low in both 2003 (33% success rate) and 2004 (29% success rate) based on resampling and reclassifying each individual data point in the DFA model. Success rates for individual sites ranged from 80% (Oceanside, 2003) to 0%

(La Jolla, both years; Mission Bay 2004). Mn, Sr, and Ba were used to discriminate among sites in 2003, while Mg, Cu, and Ba were included in the final DFA to distinguish sites in 2004. At the regional scale, northern exposed, northern embayment, southern exposed, and southern embayment were distinguished from one another only marginally better (44% success rate in 2003, and 54% success rate in 2004 based on resampling individual data points). Cu, Sr, and Pb were used to discriminate among regions in 2003, while Mn, Cu, and Ba were included in the final DFA to distinguish sites in 2004.

By grouping sites into four distinct habitat types, we improved our overall classification success rates to 66% in 2003 and 69% in 2004 (Table 2, Fig. 3A, C). These success rates were far better than the results for the same data with habitat designations randomized (35% success rate in 2003, 34% success rate in 2004; Table 2) (White and Ruttenberg 2007). Also, these success rates compared favorably with our ability to distinguish open-coast versus embayment signals, which could be correctly assigned with 70% accuracy in 2003 (open coast at 73%, embayments at 70%) and 63% accuracy in 2004 (open coast at 91%, embayments at 48%). Therefore, nursery origins of halibut were determined at the resolution of habitat ‘type’ (exposed, bay, lagoon, and estuary). At least 15 juvenile fish were analyzed from each habitat type during both 2003 and 2004. Our ability to classify nursery types was especially high for bay habitats (86% success rate in

2003; 93% success rate in 2004), and also good for exposed habitats (77% success rate in 2003; 65% success rate in 2004). Because lagoons exhibited chemical signatures similar to exposed and estuarine habitats, we recorded a success rate of only 18% for classifying lagoon fish signals in 2003, which was below the rate we could expect to obtain by random chance (Table 2). In 2004, lagoon fish scores again grouped with other habitats (exposed and estuary), but because of very tight clustering and tightened confidence intervals, lagoons were correctly resampled and classified at an 80% rate (Table 2). Otoliths of estuarine fish were correctly classified at roughly a 50% rate in both years, with about half the misclassifications attributed to exposed sites and the other half to bays in 2003 and lagoons in 2004 (Table 2). In both years, exposed and estuarine habitats were characterized by higher Ba concentrations than were recorded in lagoons and bays (Table 3, Fig. 3B, D). Bay signals were separated from other habitats by low Mg and Ba, and by higher Pb (2003) and Cu (2004) in the otoliths of juvenile fish (Table 3, Fig. 3B, D). On average, U was an order of magnitude higher in the otoliths of fish collected in estuaries during 2003 and could be used to distinguish some of the fish from that habitat during that year (Table 3).

Combining 2003 and 2004 data to generate DFA scores resulted in lower (48%) overall correct classifications for habitat signals (Table 2). These “smudged” fingerprints indicated that there is significant interannual variability in habitat signals. For instance, Mg concentrations in the otoliths of estuarine fish were 30-fold greater in 2003 than in 2004, while Mg concentrations only increased by a factor of 2 in fish from exposed habitats during the same period. As a result, Mg levels were roughly equal between 2003 estuary fish and 2004 exposed fish (Table 3). Also, Cu concentrations were higher in all habitats during 2003 than in 2004 (Table 3). Therefore, we kept the 2003 and 2004 libraries of habitat fingerprints separate, and used only the 2003 library to assess the nursery origin of 2-year-old fish collected in 2005, and only the 2004 library for resolving nursery origins of 1-year-olds.

Each sub-adult halibut we collected in 2005 was assigned to a nursery origin using the DFA fingerprints generated from juvenile fish. Based on the 75 two-year-old halibut collected in 2005, exposed, bay, lagoon, and estuary habitats were determined to have contributed 31, 65, 1, and 3%, of the successful recruits (advancing halibut) during 2003, respectively (Fig. 2). From the 129 one-year-old fish we analyzed, contributions were 49, 42, 16, and 2%, respectively, from the same four habitats during 2004 (Fig. 2).

Nursery-adult habitat connectivity- We were able to exploit an asymmetry in embayment location along the coastline to examine the ontogenetic migrations of fish from nursery to sub-adult habitats. Over 98% of bay habitat in San Diego County occurs within the southern one-third of the study region. Conversely, 100% of lagoon habitat is found along the northern one-third of coastline. Three of the four estuaries occur centrally within the study region, although Tijuana River is the southernmost embayment we included (Fig. 1). Of the sub-adult fish we collected in the southern one-half of the county, there were large and nearly equal contributions from exposed and bay habitats (Fig. 4). Meanwhile, lagoons and estuaries accounted for only 6% of the nursery contribution in that half of the county. The sub-adult fish we collected in San Diego Bay during 2005 were dominated by fish with bay (nursery) origins, while sub-adult fish in Mission Bay, Pacific Beach, and Imperial Beach had apparently utilized bay and exposed nurseries in about equal numbers. We collected only one fish from Tijuana River and determined it also had a bay origin. In the northern half of the county, the most common nursery origin was exposed habitat (Fig. 4). Even inside northern embayments, over 55% of the fish had migrated from exposed nurseries. Only in Oceanside Harbor (a bay) and La Jolla (the farthest south of the northern group) did we collect more than 1 bay-derived fish. These results suggest that fish egressing from bays in the southern half of the County did not move farther than ~10 km while migrating to sub-adult habitats (Fig. 4). Unlike those from bays, fish egressing from lagoons migrated all over the study system and were collected in equal likelihood from as far north as Oceanside Harbor and as far south as San Diego Bay (Fig. 5).

Juvenile concentrations and population regulation- Realized contributions of nursery habitats in San Diego County, in terms of producing the individual juvenile fish that successfully recruit to older age classes, were markedly similar to the expected contributions we calculated from distribution results ($r^2 = 0.900$, $p < 0.001$; Fig. 2, 6A). The agreement between expected and realized contribution was especially strong in 2003, whereas in 2004 exposed and lagoon habitats produced more recruits than expected, and bays and estuaries produced fewer than expected (Fig. 6A). There was no statistically significant relationship ($r^2 = 0.012$, $p = 0.789$) between local juvenile halibut density and the offset between realized and expected contribution from nursery habitats (Fig. 6B). This finding suggests that relative survivorship among habitats did not vary strongly as a function of local juvenile density. There was also no statistically significant relationship between the change in realized and expected contribution, and nursery habitat availability (area) ($r^2 = 0.047$, $p = 0.604$; Fig. 6C). We did observe a suggestive, but nonsignificant relationship ($r^2 = 0.792$, $p = 0.150$) between CPUE of sub-adult fish from exposed sites along San Diego County and the proportion of fish at each site that had utilized embayments (bays, lagoons or estuaries) as nursery habitat (Fig. 7). Latitude and CPUE within exposed sites were inversely related, with the lowest catch rate at the northernmost exposed site (Oceanside) and highest catch rate at the southernmost site (Imperial Beach).

Discussion

Nursery habitat contribution- Field survey and elemental fingerprinting results indicated that all coastal juvenile habitats contributed to older age classes of California halibut. These data also indicated that the halibut is facultatively dependent on estuarine habitats, but not an obligate user (sensu Able and Fahay 1998). Still, approximately 58% of juvenile halibut were determined to have embayment origins in 2003 and 2004 (*n* = 204; Fig. 2) even though only 15% of the potential nursery habitat area occurred within embayments (bays, lagoons, and estuaries; Fodrie and Mendoza 2006). The majority of these fish utilized Mission and San Diego bays as nurseries. Our findings parallel the results of Forrester and Swearer (2002), who reconstructed the nursery origin of 19 adult halibut and concluded that approximately 57% of those fish had utilized protected embayments as nursery habitats, while the remainder spent their juvenile periods in the shallows of the open coast.

Otolith chemistry could be used to discriminate among nurseries approximately 70% of the time when we used a classification scheme that delineated exposed coasts, bays, lagoons, and estuaries. This is a lower classification success than has been reported previously along the California coastline to distinguish otoliths taken from fish either along the open coast or within protected embayments (Forrester and Swearer 2002; Brown 2006), although we defined (more) habitats at a higher resolution than earlier studies. The most useful elements in distinguishing habitats during 2003 and 2004 were Ba, Mg, Pb, U (2003), and Cu (2004). Forrester and Swearer (2002) also found that Pb and Cu were enriched in the otoliths of juveniles collected within bays, but like them we found that Pb and Cu concentrations in halibut otoliths collected from embayments were not consistent between years. Studies in central California working with flatfish (Brown 2006) and southern California working with fish (Swearer et al. 2003) or invertebrates (Becker et al. 2005) have routinely shown that Sr and Mn can be useful markers for distinguishing between coastal and estuarine habitats. Neither of these elements was particularly valuable in our analyses, which was surprising to us initially. However, Fodrie (2006) found that Mn was highly variable along the primary axis of large embayments and therefore confounded inter-embayment signals. Also, Sr uptake is highly dependent on water temperature, salinity, physiological processes, as well as the rate and magnitude of environmental instability (e.g. Bath Martin and Wuenschel 2006), all of which could decouple habitat-specific environmental conditions and halibut otolith microchemistry.

We were concerned that our overall classification success could lead to a number of incorrect assignments of nursery origin(s) for the sub-adult fish we collected in 2005. However, reconstructed nursery origins based on DFA agreed very well with what the relative contribution from nurseries should have been based on field surveys. Based on available juvenile growth and mortality data that suggest relatively small differences among habitats (Kramer 1991), our overall results seem very reasonable. As a check for our DFA approach, we also defined nursery habitat fingerprints and assigned the nursery origin of sub-adult fish using Classification Trees (Breiman et al. 1984). Like DFA, Classification Trees can be used as a clustering analysis to explain variation in a response variable using a multivariate dataset. However, whereas DFA uses general linear models to generate distinct scores that distinguish groups, Classification Trees repeatedly partition groups by creating binary divisions in explanatory variables (elemental concentrations in this case) so as to sequentially reduce the largest amount of variation in a response variable (nursery type identification in this case).

Using these “decision trees”, we examined the chemistry of sub-adult fish to determine their nursery origin. Although the mechanics of these two approaches are very different, both statistics (DFA and Classification Trees) resulted in very similar results for the contribution of nursery habitats and their role in regulating halibut population dynamics. Therefore, we expect that any errors with DFA algorithms would not change our broader conclusions. The most likely error resulting from low classification efficiency was overestimation of lagoon contribution during 2004 (16% of total) because of the relatively tight grouping of lagoon signals within a larger pool of exposed habitat scores (Fig. 3C). As a result, the connectivity among lagoon nurseries and sub-adult habitats throughout the study region may have also been overestimated.

Quantifying nursery habitat value is essential for effective management of coastal ecosystems and finfish populations, particularly given the need to prioritize where to devote limited conservation resources. One problem in setting conservation priorities, however, is that the concept of nursery habitat has rarely been defined clearly, even in research studies that purport to test it. Beck et al. (2001) formulated a rigorous definition of the nursery-role concept that stressed per-unit-area production to the adult population in order to evaluate juvenile habitat value. This approach has provided an important framework of habitat classification for conservation and management efforts. According to Beck et al. (2001), nurseries are those habitats with above-average unit-area production of adult biomass. In our system, bay habitats contributed the largest number of recruits, but exhibited low unit-area production relative to lagoons and estuaries (Fig. 2). Unit-area production along exposed coasts was significantly lower than for all embayment types, yet exposed habitats contributed roughly 42% of advancing juveniles available to join older age classes. Conversely, habitats with highest unit-area production (lagoons and estuaries) were distinguished by producing far fewer successful recruits on an absolute scale because of their limited size. Using Beck et al.'s nursery-role concept, only lagoons and estuaries would achieve nursery status even though they constituted only 13% of total realized contribution. In fact, ranking nursery habitat value according to both the nursery-role concept (unit-area production) and absolute production (Gibson 1994) results in an almost complete reversal of trends for quantifying nursery “value” for this species. Dahlgren et al. (2006) recently reviewed this issue and coined the term “Effective Juvenile Habitat” (EJH) for sites that make high overall contribution to adult populations (exposed and bay habitats here), but at a low unit-area rate. Selection between these alternative ranking schemes could have significant effects on the priorities for nearshore habitat conservation along southern California.

Nursery-adult habitat connectivity- There is mounting evidence that fish egressing from nurseries either remain near their nursery origin, or demonstrate site fidelity during the course of their movement patterns and can return to specific habitats periodically. For instance, snapper (*Pagrus auratus*) exiting coastal nurseries along the southeast coast of Australia remained within several kilometers of their nursery origin (Gillanders 2002a). In tropical systems, fishery production has decreased on coral reefs where adjacent mangrove nurseries have been removed (Mumby 2005). Moreover, the largest herbivorous species in the tropical Atlantic (*Scarus guacamaia*) suffered local extinction at sites where mangrove nurseries were removed (Mumby et al. 2004). Some species, such as juvenile sole (*Solea solea*), simply remain in nursery sites for extended periods (Rogers 1993). Even for species with life histories that include a large seasonal migration (e.g., *Cynoscion regalis*), elemental fingerprinting has indicated that fish have an ability to return to their natal habitats and regions (Thorrold et al. 2001). Tracking halibut via elemental fingerprinting demonstrated that individuals egressing from bay habitats along southern California did not migrate very far from their nursery origin (< 10 km). This fidelity appears to have resulted in little exchange between ontogenetically migrating halibut from the northern and southern halves of the study region over the time scale of ~ 1 generation. Mark-recapture studies of halibut have indicated that the majority of halibut remain with a few kilometers of their release point over the course of several years (e.g., Tupen 1990). These mark-recapture results were based on movements of large, sub-adult and adult fish, and our data fill a gap in tracking the movements of post-settlement individuals and indicate little migration of halibut across latitudes once fish have settled. Since we sampled a single location (single growth period in time) on the otoliths of sub-adult halibut, we are unable to say if these fish made one migration from nursery to sub-adult (collection) habitats, or made repeated migrations between habitats in order to periodically exploit feeding, breeding, and wintering grounds.

Limited connectivity among ontogenetically migrating halibut populations should result in highly variable patterns of nursery habitat contribution along the coastline. As a result, local nursery contribution to adult stocks will be tightly linked to local nursery habitat availability and usage. For instance, within Todos Santos Bay, Baja California, Mexico, embayments (Ensendada Harbor and Punta Banda Estuary) produced 89% of successful recruits that advanced to the sub-adult classes during 2002 and 2003 (Fodrie 2006). Semi-exposed beaches were responsible for only 11% of recruits. These results are very different than reported for central and southern California, possibly because Todos Santos has relatively more (undisturbed) embayment habitat as compared with southern California.

Juvenile concentrations and population regulation- For many species, it remains unclear how availability and usage of nursery habitat alternatives affects adult population size and population fitness. This ambiguity is largely the result of difficulties related to tracking fish from juvenile to adult habitats, and scaling individual growth or survivorship rates, that vary between habitats, up to population-level fitness (Gillanders et al. 2003). Iles and Beverton (2000) have proposed that, for species whose juveniles concentrate into spatially limited nurseries, local populations can approach carrying capacity thus limiting the contribution possible from those habitats. Several studies have reported that growth or mortality can vary among successive year classes characterized by an order-of-magnitude difference in settlement (e.g. Modin and Pihl 1994). However, we observed no relationship between relative survivorship and local density for juvenile halibut in the nearshore habitats of southern California (Fig. 6B).

Our data contribute to the debate over the regulating mechanisms of finfish stock size, and suggest that for this species nursery-ground processes via density dependence do not dampen variability of recruitment pulses to adult stocks. In fact, local densities of juveniles were observed to be good predictors of unit-area contribution from individual nurseries for up to two years based on elemental fingerprinting results that retroactively tracked fish nursery origins (apparent because we combined survey and elemental fingerprinting approaches; Fig. 6A). These data suggest macroscopic density-independence in nursery productivity once fish reach ~ 30 mm SL. We do recognize that our sampling gear would not allow us to have detected density-dependent mortality of fish smaller than 30 mm (fish smaller than our gears could reliably collect), a period when larval and juvenile halibut may be especially vulnerable to density-related mortality (e.g., Kramer

1991). Consequently, either larval supply or very early post-settlement processes may still control population structure.

Although juvenile, density-dependent mortality was not observed to regulate recruitment pulses to sub-adult populations, we found strong evidence that halibut populations along the southern California coastline could be nursery-habitat limited and that catch-per-unit-effort (CPUE), a proxy for local density, was linked to the relative contribution from embayment habitats (bays, lagoons or estuaries). The term habitat limitation was originally applied to spatial resources required during settlement (Schmitt and Holbrook 2000), but is equally suitable for linking recruitment pulses to nursery habitat availability: The number of fish available to recruit to an adult population is ultimately determined by both nursery habitat quality and quantity (Gibson 1994). In San Diego County, embayment habitats can contribute 5-30 times more halibut recruits per unit area than exposed habitats. However, since these habitats are generally small and fragmented, the total number of recruits that they can contribute is limited. For instance, embayments make up only about 2% of the available habitat in the northern half of the county (Fodrie and Mendoza 2006), and therefore the overall contribution they make in terms of new recruits to the sub-adult population is small. Population regulation via nursery habitat limitation does not require density-dependent growth or mortality cost during the juvenile phase, but could be generated by density-dependent settlement or juvenile emigration from already occupied nurseries (Schmitt and Holbrook 2000).

CPUE from exposed habitats in the northern half of the study region was considerably lower (less than half) than along the southern half, even though these are similar sub-adult habitats separated by only tens of kilometers. This result suggests that recruitment subsidies to local halibut stocks will not come from the nurseries of neighboring stretches of coastline at generation time scales. Therefore, CPUE along the northern half of San Diego County (or similar stretches of coastline) could likely be elevated by large-scale juvenile habitat conservation or restoration only in the adjacent nearshore and embayment habitats. Although fishing effort confounds any direct conclusion, there appears to be clear “hotspots” of commercial take along the Alto and Baja California coastlines in close proximity to large tracts of nursery habitat such as Humboldt Bay, Half-Moon Bay (adjacent to San Francisco Bay), the Santa Barbara Flats, and Bahia Magdalena (J. Hunter pers. comm.).

Despite the variable effects that larval supply and adult mortality can have, nursery habitat availability and utilization also have clear effects on local population size and patterns of connectivity for the California halibut, and presumably other coastal finfish species. Our data indicate that exposed habitats should be valued for contributing far more recruits to replenish adult populations than was previously realized, while at the same time coastal embayments indeed function as productivity “hotspots” for this species. Because halibut remain close to their nursery origins, disturbance to coastal habitats could have effects for halibut stocks that are highly localized rather than wide ranging. Targeted management and conservation efforts will require these metrics regarding the nursery role of nearshore ecosystems to optimize habitat productivity, which is particularly important as coastal systems continue to experience significant change (Kennish 2002).

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Table 1. Summary table of geomorphologic characteristics and juvenile halibut distributions within putative nursery habitats in San Diego County. Nursery habitat types indicated with EX (exposed), B (bay), L (lagoon), and ES (estuary).

	North San Diego Coast	Oceanside Harbor	Buena Vista	Agua Hedionda	Bati-quitos	San Elijo	San Dieguito	Penas-quitos	South San Diego Coast	Mission Bay	San Diego Bay	Tijuana Estuary	Total
Habitat classification	EX	B	L	L	L	ES	ES	ES	EX	B	B	ES	-
Low-tide bottom area (km^2)	145.35	0.85	0.35	0.84	0.74	0.10	0.24	0.06	132.66	8.52	41.74	0.17	331.62
Low-tide perimeter of bottom (km)	-	8.4	14.9	10.0	11.8	12.2	13.4	6.9	-	55.7	107.0	21.1	-
Average depth (m)	-	6.0	2.5	3.1	2.8	1.4	1.7	2.2	-	4.7	12.4	1.3	-
2003 resident halibut (no.)	137654	6516	0	20502	6783	2468	6092	730	112408	78876	413137	3355	788522
2004 resident halibut (no.)	162314	11489	0	28022	7528	5369	9213	4382	182134	85901	305397	24497	826247

Table 2. Classification matrix of assignments for otolith signals from juvenile halibut collected within 14 putative nurseries along San Diego County, CA, using Discriminant Function Analysis (DFA) to generate assignment algorithms. Rows list the actual collection site, and columns list the predicted site of collection using DFA algorithms, with replacement. The success rates are presented for individual habitat types, grouped as: Exposed = Oceanside, La Jolla, Pacific Beach, and Imperial Beach; bay = Oceanside Harbor, Mission Bay, and San Diego Bay; lagoon = Agua Hedionda and Batiquitos; and estuary = San Elijo, San Dieguito, Penasquitos, and Tijuana

Classification

nbined.

2003	Predicted site					% correct random
	Exposed	Bay	Lagoon	Estuary	% correct	
Actual site						
Exposed	23	6	0	1	77	10
Bay	9	62	0	1	86	28
Lagoon	7	6	3	1	18	29
Estuary	12	10	2	19	44	65
Total	51	84	5	22	66	35

2004	Predicted site					% correct random
	Exposed	Bay	Lagoon	Estuary	% correct	
Actual site						
Exposed	46	2	15	8	65	24
Bay	0	51	4	0	93	38
Lagoon	3	0	12	0	80	47
Estuary	12	3	11	23	47	41
Total	61	56	42	31	69	34

2003 and 2004	Predicted site					% correct random
	Exposed	Bay	Lagoon	Estuary	% correct	
Actual site						
Exposed	62	36	1	2	61	46
Bay	36	88	0	3	69	21
Lagoon	11	18	1	2	3	17
Estuary	38	34	3	17	18	26
Total	147	176	5	24	48	31

Table 3. Means (± 1 SE) of element:Ca ratios in juvenile halibut otoliths collected in San Diego County, grouped by habitat type. Exposed = Oceanside, La Jolla, Pacific Beach, and Imperial Beach; bay = Oceanside Harbor, Mission Bay, and San Diego Bay; lagoon = Agua Hedionda and Batiquitos; and estuary = San Elijo, San Dieguito, Penasquitos, and Tijuana River.

	Samples (*n*)	Mg:Ca (mmol mol^{-1})	Mn:Ca (mmol mol^{-1})	Cu:Ca ($^{x}10^{2}$) (mmol mol^{-1})	Sr:Ca (mmol mol^{-1})	Ba:Ca (mmol mol^{-1})	Pb:Ca ($^{x}10^{1}$) (mmol mol^{-1})	U:Ca ($^{x}10^{5}$) (mmol mol^{-1})
Detection limit		0.02	<0.01	<0.01	0.01	<0.01	0.01	0.09
2003								
Exposed	30	0.79 ± 0.76	0.01 ± 0.01	0.01 ± 0.01	6.36 ± 0.82	0.03 ± 0.02	0.01 ± 0.01	3.83 ± 0.01
Bay	72	0.03 ± 0.02	0.02 ± 0.01	0.14 ± 0.05	6.06 ± 0.53	0.01 ± 0.01	0.18 ± 0.01	1.91 ± 0.02
Lagoon	17	0.10 ± 0.07	0.03 ± 0.01	0.01 ± 0.01	7.50 ± 0.49	0.01 ± 0.01	0.04 ± 0.01	1.91 ± 0.01
Estuary	43	1.50 ± 1.24	0.07 ± 0.02	0.63 ± 0.33	12.22 ± 1.41	0.37 ± 0.17	0.91 ± 0.04	57.42 ± 0.04
2004								
Exposed	71	1.54 ± 1.19	0.03 ± 0.02	0.01 ± 0.01	5.39 ± 0.10	0.05 ± 0.03	0.01 ± 0.01	9.20 ± 0.01
Bay	55	0.03 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	5.09 ± 0.11	0.01 ± 0.01	0.00 ± 0.00	0.19 ± 0.01
Lagoon	15	0.03 ± 0.02	0.01 ± 0.01	0.00 ± 0.00	5.14 ± 0.20	0.01 ± 0.01	0.00 ± 0.00	0.19 ± 0.01
Estuary	49	0.05 ± 0.02	0.02 ± 0.01	0.01 ± 0.01	6.20 ± 0.43	0.02 ± 0.01	0.07 ± 0.01	0.77 ± 0.01

Figure 1. San Diego County Coastline study region highlighting the 14 sites sampled to generate halibut distribution data and provide samples for trace element fingerprinting. Sites included: 1. Oceanside (EX), 2. La Jolla (EX), 3. Pacific Beach (EX), 4. Imperial Beach (EX), 5. Oceanside Harbor (B), 6. Buena Vista (L), 7. Agua Hedionda (L), 8. Batiquitos (L), 9. San Elijo (ES), 10. San Dieguito (ES), 11. Penasquitos (ES), 12. Mission Bay (B), 13. San Diego Bay (B), and 14. Tijuana River (ES). Letters following each site indicate: Exposed (EX), bay (B), lagoon (L), and estuary (ES) habitats.

Figure 2. Expected and realized contributions (expressed as a percentage of total) of nursery habitats along San Diego County from 2003 and 2004 in producing the juvenile halibut that successfully advanced to the sub-adult population sampled in 2005. Expected contributions are based on 2003 (estimated 788,500 juveniles) and 2004 (estimated 826,500 juveniles) field surveys of juvenile halibut distributions and nursery habitat availability. Realized contributions are based on elemental fingerprinting results for 75 individuals that utilized nurseries in 2003 and 129 individuals that used nurseries in 2004. Nurseries are classified as: Exposed = Oceanside, La Jolla, Pacific Beach, and Imperial Beach; bay = Oceanside Harbor, Mission Bay,

and San Diego Bay; lagoon = Agua Hedionda and Batiquitos; and estuary = San Elijo, San Dieguito, Penasquitos, and Tijuana River.

Figure 3. Discriminant scores of element ratios to Ca in otoliths of juvenile halibut collected during the fall from all putative nursery sites in San Diego County during 2003 (A-B; Mg, Ba, Pb and U) and 2004 (C-D; Mg, Cu, Ba and Pb). Data are grouped as: Exposed = Oceanside, La Jolla, Pacific Beach, and Imperial Beach; bay = Oceanside Harbor, Mission Bay, and San Diego Bay; lagoon = Agua Hedionda and Batiquitos; and estuary = San Elijo, San Dieguito, Penasquitos, and Tijuana River. (A, C) Scatterplot of DFA scores; and (B, D) Discriminant functions, standardized by within-habitat variances, for the element ratios used to create the DFA. Vectors represent the relative contribution of each element ratio to the resulting scores.

Figure 4. Nursery origins of sub-adult halibut collected in 2005 within San Diego County with respect to their eventual collection sites. Sites positioned along the left margin represent locations where 1- and 2-year-old fish were collected, and the patterns of the bars indicate the nursery origins of individual fish. The thin, horizontal line represents the division between northern (N) and southern (S) halves of the study region.

Figure 5. Recipient sites for advancing juveniles egressing from each of the 4 potential nursery types (exposed, bay, lagoon, and estuary) considered in

this study. Nursery habitats are positioned along the left margin and eventual collection sites of 1- and 2-year-old fish are represented by unique bar patterns (expressed as a percentage of total).

Figure 6. (A) The relationship between expected and realized contributions from putative nursery habitats along San Diego County. Dashed line represents the one-to-one line. Also shown are the relative changes in realized contribution (determined via elemental fingerprinting) versus expected contribution (from field surveys of juvenile halibut distributions and habitat availability) plotted in relation to (B) local 0-age halibut densities and (C) habitat availability in San Diego County (± 1 SE). Local juvenile densities are taken from Fodrie and Mendoza (2006). Eight data points are included for the change in expected and realized contribution representing the 4 habitats considered in this study (exposed, bay, lagoon, and estuary) from both 2003 and 2004.

Figure 7. Catch-per-unit-effort (CPUE: fish collected per 10-min tow ± 1 SE) of sub-adult halibut along the 4 exposed study sites (Oceanside, La Jolla, Pacific Beach, and Imperial Beach) during 2005 plotted against the % of fish collected from each exposed site retroactively determined via elemental fingerprinting to have utilized embayments (bay, lagoon, or estuary) as nursery habitat in 2003 or 2004.

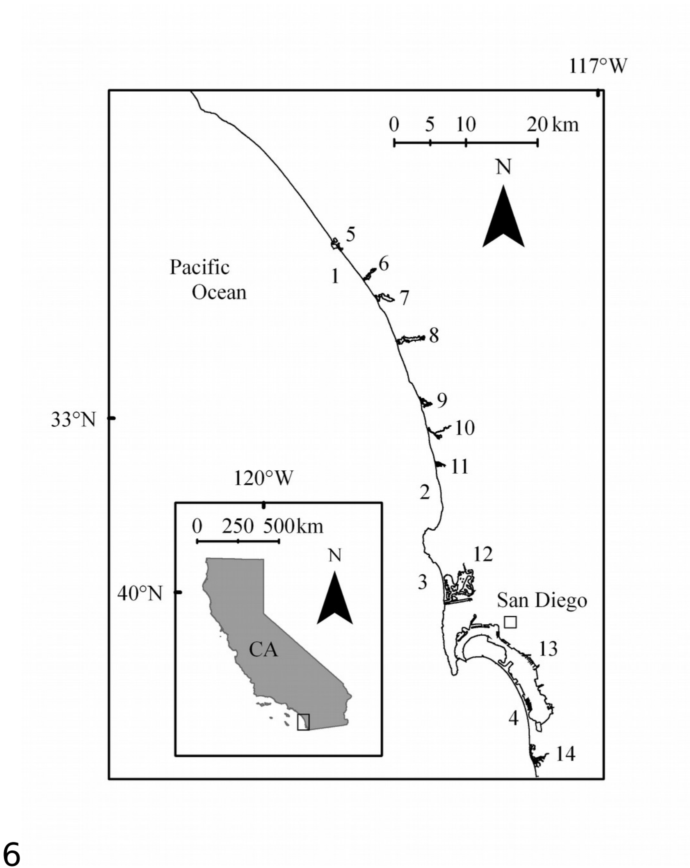
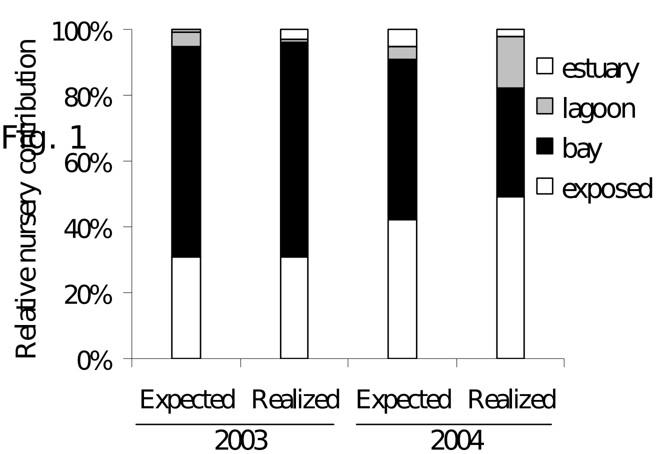
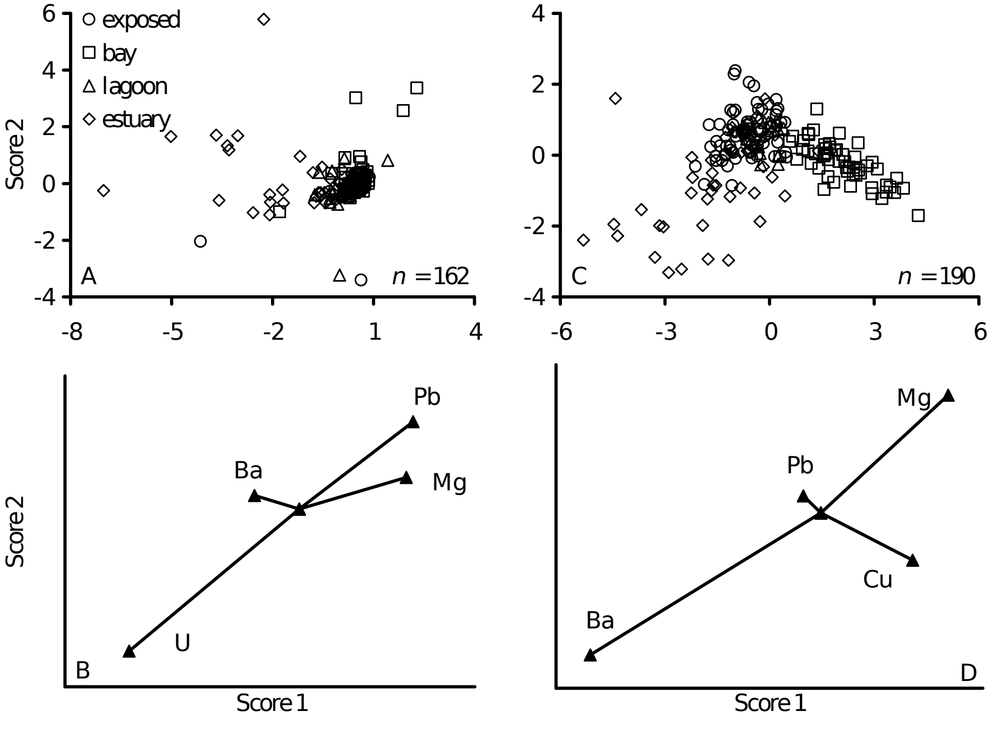
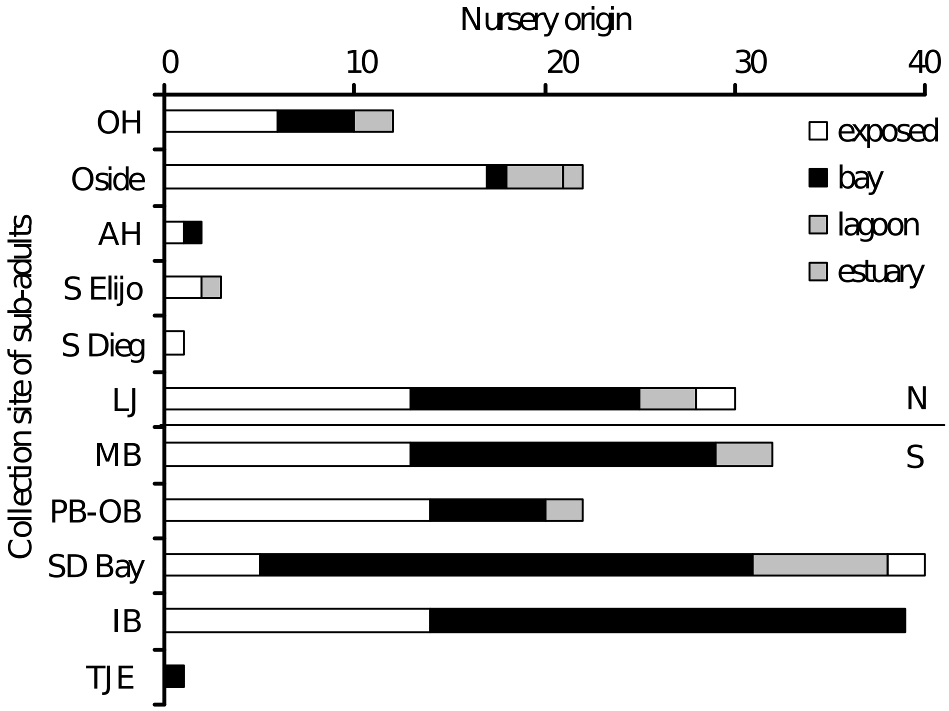
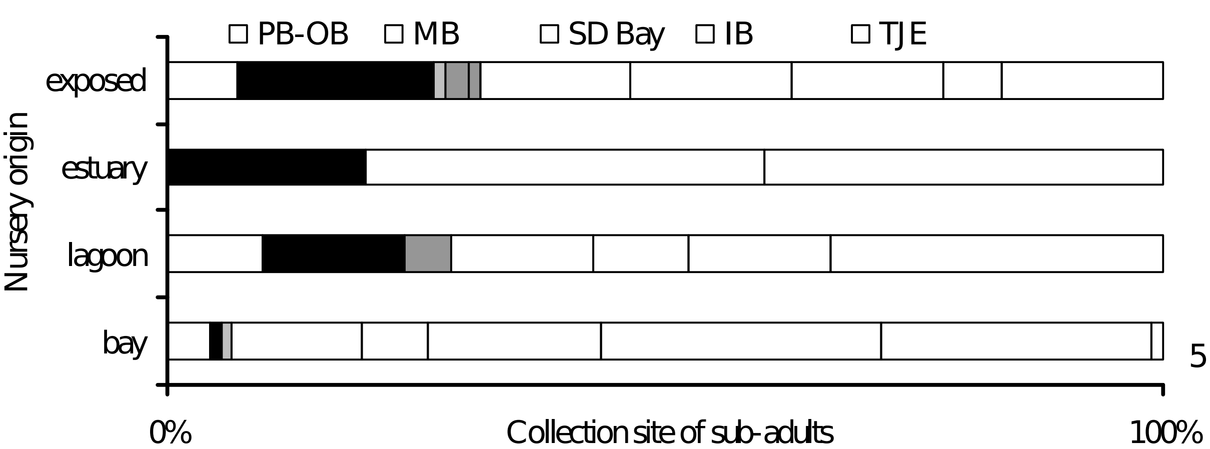

117°W
0 5 10 20 km
N
5
6
1
7
8
Pacific Ocean
9
33°N
10
11
120°W
2
0 250 500km
N
12
40°N
3
San Diego
CA
13
4
14

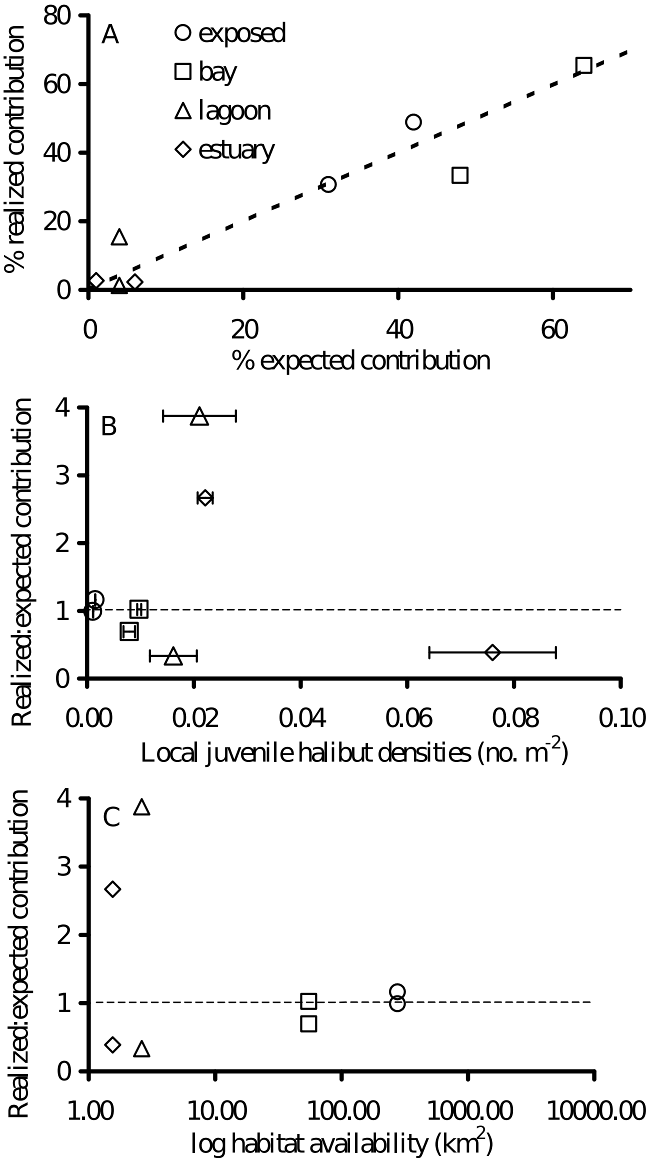
Fig. 1


Relative nursery contribution
100%
80%
60%
40%
20%
0%
Expected
Realized
Expected
Realized
2003
2004
☐ estuary
▨ lagoon
■ bay
☐ exposed

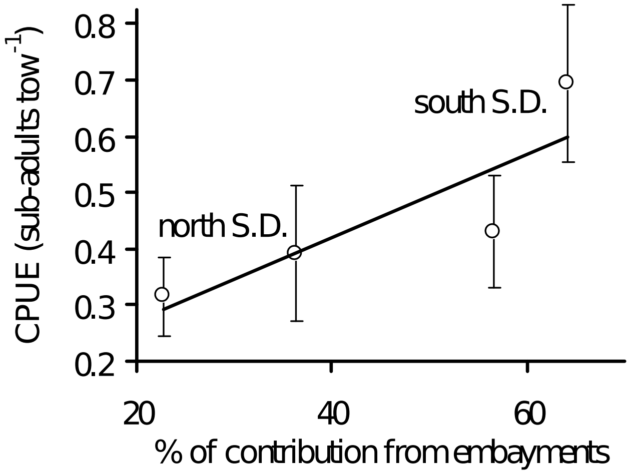

exposed
bay
lagoon
estuary
Score 2
6
4
2
0
-2
-4
A
n = 162
-8
-5
-2
1
4
4
2
0
-2
-4
C
n = 190
-6
-3
0
3
6
Score 2
Pb
Ba
Mg
U
B
Score 1
Mg
Pb
Cu
Ba
D
Score 1


Nursery origin
0
10
20
30
40
OH
Oside
AH
S Elijo
S Dieg
LJ
MB
PB-OB
SD Bay
IB
TJE
Collection site of sub-adults
□ exposed
■ bay
▨ lagoon
▨ estuary
N
S


OH
Oside
AH
S Elijo
S Dieg
LJ
PB-OB
MB
SD Bay
IB
TJE
exposed
estuary
lagoon
bay
Nursery origin
0%
Collection site of sub-adults
100%


A
exposed
bay
lagoon
estuary
% realized contribution
80
60
40
20
0
0
20
40
60
% expected contribution
B
Realized:expected contribution
4
3
2
1
0
0.00
0.02
0.04
0.06
0.08
0.10
Local juvenile halibut densities (no. m^{-2})
C
Realized:expected contribution
4
3
2
1
0
1.00
10.00
100.00
1000.00
10000.00
log habitat availability (km^2)

F



CPUE (sub-adults tow^{-1})
0.8
0.7
0.6
0.5
0.4
0.3
0.2
south S.D.
north S.D.
20
40
60
% of contribution from embayments

Fig. 7

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