Title

Quantifying nursery habitat value for the California halibut, Paralichthys californicus : distribution, elemental fingerprinting and demographic approaches

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Quantifying nursery habitat value for the California halibut, *Paralichthys californicus*: distribution, elemental fingerprinting and demographic approaches

A dissertation submitted in partial satisfaction of the requirements
for the degree of Doctor of Philosophy
in
Oceanography

by

Fredrick Joel Fodrie

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Professor John Hunter
Professor Russ Lande
Professor Enric Sala
Professor Clint Winant

2006

The dissertation of Fredrick Joel Fodrie is approved, and it is acceptable in quality and form for publication on microfilm:

Chair

University of California, San Diego

2006

DEDICATION

In loving memory of my mother, Freda G. Fodrie, whose devotion to education and steadfast parental care, along with my father, James E. Fodrie II, provided me with the foundation to succeed. It was excellent nursery habitat.

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Chapter 2 of this dissertation, in full, is reprinted with permission from an article in the journal Estuarine, Coastal and Shelf Science (Fodrie, F.J. and G. Mendoza. 2006. Availability, usage and expected contribution of potential nursery habitats for the California halibut. Est. Coast. Shelf Sci. **68**: 149-164.). The dissertation author was the primary investigator and author of this paper.

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VITA

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Fodrie, FJ and SH Herzka (submitted) Tracking juvenile fish movement and nursery contribution within arid coastal embayments via otolith microchemistry

Becker, BJ, LA Levin, **FJ Fodrie** and PA McMillan (submitted) Population connectivity patterns differ in closely related coastal bivalve species.

Fodrie, FJ and LA Levin (submitted) Linking habitat utilization to population dynamics of a coastal finfish: nursery contribution, connectivity and compensation

Fodrie, FJ, LA Levin and AJ Lucas (in prep) Consequences of nursery habitat selection for the demography of California halibut populations

PRESENTATIONS

“Three ‘seas’ of nursery habitat utilization: contribution, concentration and connectivity” Invited Talk, Dauphin Island Sea Lab, Dauphin Island, AL. 2006

“A generalist nursery habitat strategy by the California halibut connects southern California seascapes” (Poster) ASLO, Honolulu, HI. 2006.

“Availability, suitability and contribution of potential nursery habitats for the California halibut” (Oral) CAERS, Santa Barbara, CA. 2005

“Trace element fingerprinting to infer larval trajectories: implications and benefits of high- frequency field collections” (Oral) International Larval Biology Meetings, Hong Kong, China. 2004.

“Metapopulation Dynamics in the Bay Scallop: Mechanisms Creating Population Sinks Where Least Expected” (Oral) Benthic Ecology Meetings, Wilmington, NC. 2000.

ABSTRACT OF THE DISSERTATION

Quantifying nursery habitat value for the California halibut, *Paralichthys californicus*: Distribution, elemental fingerprinting and demographic approaches

by

Fredrick Joel Fodrie
Doctor of Philosophy in Oceanography
University of California, San Diego, 2006
Professor Lisa A. Levin, Chair

To determine the linkages between nursery habitat utilization and the population dynamics of a coastal finfish of southern California, the California halibut, *Paralichthys californicus*, the following questions were asked: (1) What are the habitat associations (distribution patterns) of juvenile halibut among nearshore ecosystems (2) What are the nursery habitat origins for the individual fish that successfully recruit to the adult population, and can the contributions from individual nursery types be predicted from distribution data? (3) Over what spatial scale are nursery contributions realized? (4) What role do nurseries play in regulating population size? and (5) What are the demographic consequences (population growth) related to utilization of nursery habitat alternatives? Potential nurseries in San Diego County, California, were grouped using a novel classification scheme that delineated exposed, bay, lagoon and estuarine environments.

Retroactive assignment of nursery origin for individual fish via elemental fingerprinting indicated that exposed coasted, bays, lagoons and estuaries contributed 42%, 45%, 11% and 2% of advancing juvenile California halibut during 2003 and 2004, respectively. These results were remarkably similar to the expected contribution from nursery habitats based on field surveys, indicating that in this system juvenile distributions are a good indicator of unit-area productivity of nurseries. Over smaller scales, unique chemical fingerprints were observed along the main-axis of coastal embayments (Punta Banda Estuary, Baja California, Mexico and Mission Bay, California) and were used to document the contribution of individual embayment zones. Results from the Punta Banda Estuary indicated that the majority of embayment contribution is derived from the lower two-thirds of the embayment system, and that individual zones within the embayment are utilized differently throughout the year by juvenile halibut. Elemental fingerprinting also revealed that individuals egressing from bays did not migrate far from their nursery origin (<10 km), and this resulted in reduced connectivity between the northern and southern halves of the San Diego County coastline over the timescale of ~ 1 generation. Because of this, coastal sites far from large embayments appeared to have smaller sub-adult population sizes due to nursery habitat limitation. Juvenile cohort analyses and nursery contribution results indicate that density-dependent juvenile mortality does not limit nursery contribution for this species. However, mortality rates were considerably higher in exposed habitats, and because of this at least 38% of recruits to the adult stage must originate from embayment nurseries to produce stable or positive population growth based on population projection matrix model simulations that included four years (1987-1988, 2002-2003) of nursery habitat-specific vital rate data. Together, these results generate a number of valuable metrics for evaluating nursery habitat value, including: (1) unit-area contribution of recruits to replenish adult populations, (2) raw contribution of recruits to replenish adult populations, and (3) impacts on population growth rate. These data should be of considerable value for management and conservation of coastal ecosystems by expanding our understanding of what defines the nursery-role of coastal habitats.

I.

Introduction

Nursery habitat

The importance of high-quality habitats for finfish and invertebrate species has been recognized by scientists, managers, and fishermen (Magnuson-Stevens Act 1996; Public Law 94-265). However, quantitative measures for evaluating the role that habitats such as nurseries play in determining the population dynamics of marine species remain elusive (Peters and Cross 1992). As a result, there remains ambiguity about the value of particular habitats in sustaining ecologically and economically important fishery populations. Improving conservation and management strategies for nearshore ecosystems depends on data that link nursery habitat utilization to fishery productivity and overall population health. The unifying theme of the research presented has been to tease apart those linkages for one species, the California halibut (*Paralichthys californicus*).

Not all habitats occupied by juvenile organisms (defined as post-settlement individuals prior to sexual maturity) in the marine environment are nurseries. First, nurseries represent fundamentally different settings, or only a portion of the environments occupied by older life-history stages (Gunter 1967; Gillanders et al. 2003). Because of this habitat partitioning among life-history stages, it is necessary to consider what processes regulate population size and population growth rate, and if those processes occur pre- or post-recruitment to an adult stock. Second, nurseries must contribute to the strength of recruitment to adult stocks (e.g. Mumby et al. 1998). There are two contrasting frameworks for evaluating nursery contribution: (1) Beck et al. (2001) formulated the nursery-role hypothesis for distinguishing nurseries. This concept stresses the unit-area contribution to adult biomass, and suggests that only those habitats with above-average contribution are nurseries. Alternatively, (2) Gibson (1994) has stated that the number of fish available to recruit to adult stocks is ultimately determined by both nursery habitat quality (implicit in Beck et al.'s definition) and quantity. Therefore, Gibson's definition focuses more on raw contribution rather that unit-area productivity. Data generated in this thesis were used to evaluate the merits of these alternative descriptions of nurseries for a coastal finfish of southern California. Additionally, a new metric of nursery "value" was generated by considering the impacts of nursery habitat selection on the overall growth rate of California halibut populations.

Brief history of nursery habitat research

*"**Estuarine nursery habitat use is an extremely important phenomenon and constitutes a general law** regarding most of the large motile estuarine organisms of the south Atlantic and Gulf coast of the U.S. However, recognition of this phenomenon was so slow that no one deserves full credit for it, and **appreciation of it came about so gradually that it stands as an example of how important generalizations are brought to light through the long laborious field work of a number of workers**."* Gunter (1967)

The first data to suggest that coastal habitats played an accentuated role for the early life-history stages of coastal species was generated by C.J.J. Petersen in the 1890s. Petersen (1896) documented the immigration of young-of-the-year plaice into fjords adjacent to the German Sea. He also suggested that young plaice could be transplanted to particular coastal habitats in order to increase the productivity of the plaice fishery. Even today, the small discs used to tag flatfish bear Petersen' name. Soon after Petersen, Hay (1905) began working with blue crab in Chesapeake Bay and documented the ontogenetic migratory cycle that blue crabs make; females exit coastal estuaries to spawn, and young crabs utilize the innermost portions of those estuaries. Similar patterns were later observed for shrimp (Viosca 1920), mullet and drum (Hildebrand and Scroeder 1928). It may have been Pearson (1929) who first appreciated the importance of coastal habitats as a secondary "bottleneck" in the life history of fish. Based on the data sets he generated for habitat use by juvenile Sciaenids in Gulf Coast estuaries, Pearson spoke about the value of conserving seagrass habitat necessary for the health of nearshore drum fisheries. Until the 1980s, research continued to focus on the "estuary" as the nursery unit, and, as Gunter (1967) observed, documented the prevalence of estuarine nursery use by almost all of the large, mobile fauna of nearshore waters. Recently, focus has shifted to documenting small-scale, habitat-specific (e.g, seagrass versus mudflat) differences in growth and survivorship experienced by juvenile fish and invertebrates within alternative putative nurseries (e.g., Sogard 1992).

Study system and specific problem

The California halibut (Appendix 1), *Paralichthys californicus*, is a key member of the nearshore ichtyofauna community along western North America. Halibut hold special stature in southern California fisheries management as the major fisheries species considered to be estuarine dependent (along a coastline where the availability of estuarine-type habitats is minimal in comparison to East Coast environments). Juvenile distribution data indicate the species is reliant upon shallow exposed shores, coastal bays, lagoons, and estuaries (Figure 1.1) as nursery grounds (e.g., Kramer 1990). Despite measures of local density, growth of survival, the relative importance of specific habitats (e.g., protected embayment vs. exposed coastline) as productive nursery grounds for the California halibut remains uncertain without knowledge of: (1) the nursery origin of those fish that successfully recruit to adult stocks, and (2) the demographic (population growth) consequences of spending the juvenile period in particular habitat types. Put another way, I asked if the protected wetlands, shallow lagoons, and estuaries that are so limited spatially along the California coastline could contribute 50% of the juveniles that recruit to adult stocks? 90%? 10%? Given an answer, what were the expected consequences for halibut populations in the face of continued coastal change?

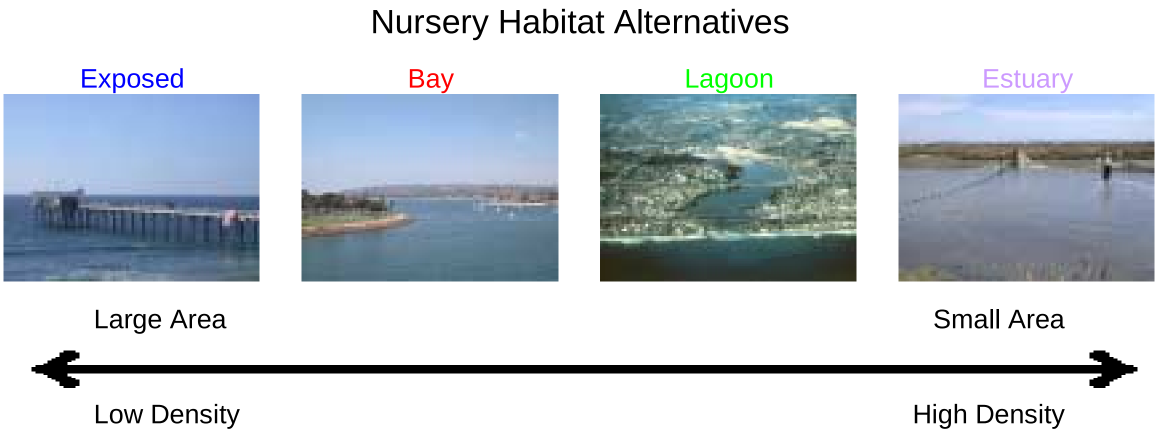

Figure 1.1 Potential nursery habitats available to juvenile halbut along the southern California coastline.

The United States has experienced a 54% loss of its wetland habitats (Chambers 1992), and California has been particularly impacted with >80% losses of coastal wetlands (California State Costal Conservancy, 1989). The continued alteration of the coastal zone due to human needs and land-use changes only amplifies the need for information to quantify the importance of specific coastal habitat types along southern California in promoting the health of fisheries resources. It also should be known if threshold levels of nursery habitat must be conserved to maintain viable populations (Scheffer et al. 2001).

Questions and objectives

The overall goal of this research was to determine the linkages between nursery habitat utilization and the population dynamics of the California halibut. The impacts of nursery utilization on population size, connectivity and growth rate were measured to provide metrics of habitat value. A number of orthogonal approaches were applied to quantify nursery value, including distribution surveys with cohort analysis, elemental fingerprinting and demographic modeling. Specifically, I asked the following questions: (1) What are the nursery habitat origins for the individual fish that successfully recruit to the adult stock? Could overall contributions from individual nursery types be predicted from distribution data? In Chapter II, detailed distribution maps were generated to explore habitat availability and utilization, as well as generate a first-order approximation for what individual nurseries should contribute in terms of recruits to adult populations, assuming no growth or survivorship differences among habitats. Additionally, the distribution of juvenile halibut in relation to several abiotic factors (depth, temperature, salinity, bottom characteristics) was examined. In Chapter III and Chapter IV, the actual contributions from specific nurseries were determined using an elemental fingerprinting approach. Chapter III focuses on contribution from zones within specific embayments, while Chapter IV utilizes a novel habitat classification scheme for evaluating nursery contribution from all potential nurseries in San Diego County, CA (Figure 1.1). (2) Over what spatial scales are contribution impacts realized? In Chapter IV, elemental fingerprinting results revealed the spatial scale of migration that individual fish make from juvenile to adult habitats. (3) What role do nurseries play in regulating stock size?

Analyses of juvenile cohorts (Chapter II, Chapter V) and nursery contribution (Chapter IV) were used to test for density-dependent regulation of juvenile mortality within putative nursery habitats, as well as for whether or not halibut populations appear to be limited by nursery habitat availability. (4) What are the demographic consequences related to utilization of nursery habitat alternatives? Juvenile halibut may experience quite different growth and survival conditions among nursery types. As a result, some habitats may serve as demographic “sources” or “sinks”. In Chapter V, population projection matrix models were employed to examine the consequences of different nursery-habitat conditions on population growth rate (λ) (Caswell 2001). I also explored which demographic transitions (stage-specific growth, survivorship and fertility) have the greatest influence in determining λ, with specific focus on the role of juvenile vital rates in the demography of halibut subpopulations that utilize alternative nursery habitat types. Demographic results were combined with the contribution data (Question 1) to suggest goals and priorities for habitat management and conservation of California halibut population along southern California.

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II.

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Availability, usage and expected contribution of potential nursery habitats for the California halibut

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Abstract

Coastal ecosystems have been identified as important nursery habitats for many of the world's fishery species. Beyond this, there remain many questions about what exactly constitutes high-value, even critical, habitat for juvenile fish. A first step in investigating nursery habitat value should be to catalogue the spatial coverage (availability) of all potential nursery habitats as well as the distribution (usage) of juvenile fish within those habitats. We conducted two years of fall surveys in the nearshore areas of San Diego County, CA, examining the spatial distribution of 0-group California halibut, *Paralichthys californicus*. The database generated by 527 otter trawls and block-net seine collections was used to produce a series of models employing regression trees to study the abiotic factors (water column and bottom features) that affect juvenile distributions. Along the exposed coast, highest 0-group densities (0.002–0.008 individuals/m^2 (indiv/m^2)) occurred where temperatures exceeded 21.5 °C (2003), and at depths between 3.3 and 5.2 m (2004). Within protected embayments, densities were higher at depths less than 1.5 m (0.054–0.430 indiv/m^2) and, in 2004, inside channeled marsh estuaries (0.156 indiv/m^2). The spatial coverage of potential nursery habitats was calculated using a Geographic Information System (GIS) database, and the total number of resident 0-group halibut within each site was estimated (habitat area × juvenile halibut density) as a proxy for expected contribution of halibut advancing to the adult stock from each nursery. Although 85% of the potential nursery habitat area occurred along the exposed coastline, 69% (2003) to 58% (2004) of 0-group halibut resided in protected embayments. Embayment contribution is much greater in the southern half of the study region, largely due to Mission and San Diego bays. We conclude that all nursery habitat types demonstrate the potential to contribute significantly to stock fitness, and that in general, shallow and better-protected habitats are highly utilized nurseries for 0-group halibut and deserve special attention in management or conservation efforts.

Keywords: nursery habitat; expected contribution (EC); California halibut; *Paralichthys californicus*; Geographic Information System (GIS); regression trees

1. Introduction

Coastal habitats such as estuaries and semi-enclosed bays have historically been considered essential nursery habitat for many economically and ecologically important fish and crustacean species (Petersen, 1896; Pearson, 1929; Gunter, 1967). Roughly 75% of the United States' commercial landings are made up of estuarine-dependent species (Chambers, 1992). For many of these species, it is the juvenile phase that is often considered to be most dependent on nearshore habitats for use as nurseries.

Evidence for finfish reliance upon specific coastal habitats as nurseries comes from studies of juvenile distributions (Krygier and Pearcy, 1986; Parrish et al., 1997), food resources (Drawbridge, 1990; Burke, 1995; Wertz and Domeier, 1997), growth rates (Sogard, 1992; Phelan et al., 2000; Sogard et al., 2001; Ross, 2003), ecophysiology (Yamashita et al., 2000; Madon, 2002) and mortality (Pihl and Van der Veer, 1992; Modin and Pihl, 1994). Nevertheless, data concerning the functional role of specific nursery habitat types in

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sustaining fish stocks remain ambiguous, largely because it is unclear how these factors contribute to the productivity of a stock and affect species fitness. Most importantly, it remains largely unknown for many species which specific nursery habitat types were used by those individuals that successfully recruit to adult stocks (Beck et al., 2001). This is especially true for species with spatially separated juvenile and adult populations such as red drum, speckled sea trout, bluefish, summer flounder, southern flounder, English sole and California halibut (Gillanders and Kingsford, 2000).

The California halibut, *Paralichthys californicus*, holds special status in southern California fisheries management as the major fisheries species considered to be facultatively dependent (Able and Fahay, 1998) on estuaries for nursery habitat. Adults of this species live in nearshore waters ranging from 1 to 100 m deep (Kramer and Sunada, 1992). Pulsed spawning occurs in shallow water habitats year round with peaks in February, July and October (Moser and Watson, 1990). Following spawning, larvae spend 3–4 weeks in surface waters distributed across the continental shelf (Moser and Watson, 1990) before transport shoreward and settlement in shallow coastal environments at 7–9 mm standard length (Allen, 1988). Data regarding the distribution of juveniles indicate they are reliant upon coastal bays, lagoons, estuaries and shallow exposed waters as nursery habitats (Allen and Herbinson, 1990; Allen et al., 1990; Allen, 1992). Kramer (1991a) hypothesized that small halibut may have evolved to be nursery habitat generalists since "optimal" nursery habitats in southern California are periodically unavailable due to inlet closures. This life-history strategy, in which multiple nursery habitats can be utilized, potentially means that no single habitat type is critical for maintaining halibut stocks. This generalist strategy also makes the halibut an ideal model species for examining the functional relationship of nursery habitat utilization and stock regulation.

Beck et al. (2001) have stated:

> *A habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur…even if a habitat is small in area.*

Kramer (1990), among others, observed that juvenile halibut densities inside protected environments (when open to the ocean) are 5–10 times higher than densities observed along exposed coasts. These distribution data, viewed through the framework laid out by Beck et al., have led managers and scientists to designate the halibut as estuarine dependent for nursery habitat (assuming local density as a proxy for per unit area contribution). Gibson (1994), however, advised that the number of fish available to recruit to adult stocks is ultimately determined by both nursery habitat quality (implicit in Beck et al.'s definition) and quantity. Consequently, we ask if it is appropriate to consider a habitat with lower than average per unit area contribution to adult stocks, but extremely high spatial cover, as an unimportant nursery for management of nearshore habitats along southern California?

A first step in investigating nursery habitat value for presumably estuarine-dependent species such as the halibut should be to catalogue the spatial coverage (availability) of all potential nursery habitats as well as the distribution of juvenile fish (usage) within those habitats. In this study, we first evaluated the availability of potential nursery habitats for the California halibut along the San Diego County, CA, coastline (Fig. 1). Second, we examined the distribution of 0-group halibut in relation to key abiotic features measured within each nursery habitat type. Third, we used juvenile distribution survey data from San Diego County's nearshore habitats to estimate the total number of juvenile halibut occupying each nursery habitat type. This generated a first approximation for the expected contribution of potential nursery habitats in producing new recruits that advance to adult stocks (Le Pape et al., 2003a,b). These results should provide null hypotheses for the expected value of nursery habitat types for halibut stocks, against which field tests of juvenile growth and survival or tracking studies to assess marine connectivity can

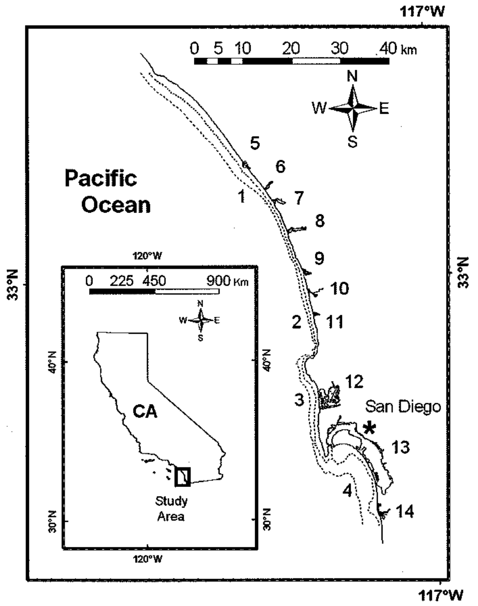

Fig. 1. San Diego County coastline study region highlighting the 14 sectors sampled to generate halibut distribution data. Sectors are: 1. Oceanside (EX), 2. La Jolla (EX), 3. Pacific Beach (EX), 4. Imperial Beach (EX), 5. Oceanside Harbor (B), 6. Buena Vista (L), 7. Agua Hedionda (L), 8. Batiquitos (L), 9. San Elijo (E), 10. San Dieguito (E), 11. Penasquitos (E), 12. Mission Bay (B), 13. San Diego Bay (B), and 14. Tijuana River (E). Letters following each site indicate exposed (EX), bay (B), lagoon (L) and estuary (E) habitats. Coastline and 10 m, 20 m bathymetry contours are shown with solid and dashed lines, respectively (Data source: California Department of Fish and Game Marine GIS office). Blow-ups of each sector are provided in Fig. 5.

be weighed to more meaningfully define nursery habitat value. Another practical application is to weight the results of demographic models (based on nursery habitat-specific growth and survivorship terms) by the expected contribution of each nursery to obtain an improved forecast of population fitness. This approach should benefit management and conservation efforts to ensure "no net loss" of habitat productivity (Minns, 1997), which is particularly important as coastal systems continue to experience significant change (Peters and Cross, 1992; Brown and McLachlan, 2002; Kennish, 2002).

2. Methods

2.1. Study region

The San Diego County coastline (Fig. 1) was chosen for this study because: (1) it is located in the geographic center of the California halibut species distribution (Kramer and Sunada, 1992), (2) there is pre-existing literature on juvenile halibut settlement and distribution patterns in the region (Kramer, 1990, 1991a,b), and (3) this segment of coastline comprises four (as we define them below) potential nursery habitat types. San Diego County is located in the southwestern-most corner of the continental United States, adjacent to Mexico, and flanked by the Pacific Ocean along 112 km of coastline (N 33.39, W 117.61–N 32.54, W 117.13). Typical of the region, the coastline is underlain by a narrow shelf, and is punctuated by a series of relatively small (<25 ha) or highly modified embayments (Fig. 1).

The study region was divided into 14 sectors representing potential nursery habitats for 0-group halibut (fish <one year old). We located three sectors (Oceanside, La Jolla, Pacific Beach) along the exposed coastline adjacent to sandy beach faces using the zones established by Kramer (1991b), and we included an additional sector off Imperial Beach in order to extend the sampling region farther south. Exposed sectors were defined as waters 0–20 m deep in order to bracket the depths at which juvenile halibut are known to occur (Kramer, 1990). All embayments with open inlets within San Diego County were included in the study. However, Buena Vista was not extensively surveyed as the inlet mouth has remained closed since before 2002 and salinity levels within the lagoon were <10 during 2003 and 2004. Although southern California embayments have many forms and may function very differently, no standardized classification system exists for describing them as fish habitat. For this study, embayments were classified either as bays, lagoons or estuaries. We classified embayments using basic geomorphologic characteristics such as low-tide surface area, average depth and surface area to perimeter (A/P) ratio (Table 1). Bays were characterized by low-tide surface areas >84 ha, average depths >4 m, and A/P ratios >10. Bays included Oceanside Harbor, Mission Bay and San Diego Bay. These bays are kept open and relatively deep to serve as harbors for shipping and recreational boating. Lagoons were characterized by low-tide surface areas of 35–84 ha, average depths ~3 m, and A/P ratios between 2.4 and 8.4. Using this criterion Buena Vista, Agua Hedionda and Batiquitos were classified as lagoons. Estuaries were described by low-tide surface areas <25 ha and average depth <2.5 m. Estuaries were also characterized by high wetland (saltmarsh) cover that resulted in low A/P ratios (<2). San Elijo, San Dieguito, Penasquitos and Tijuana River were all classified as estuaries. Using these criteria, we achieved 100% jackknifed classification success using Discriminant Function Analysis to distinguish embayment types. Our scale for defining a nursery habitat is similar to that of early work, which often focused on the entire estuary as the nursery unit (although we do consider smaller-scale habitat features). More recently, great advances have been made in evaluating landscape-level distinctions between habitats (Beck et al., 2001).

2.2. Nursery habitat area calculations

Digitized orthophotos and bathymetry data of the nearshore habitats of San Diego County were provided by the California Department of Fish and Game Marine Region Geographic Information System (GIS) Unit and imported into a GIS database. All GIS data processing and analyses were done using ArcGIS 8.3 (©ESRI), and using the NAD27 coordinate system and the Albers Equal-Area Conic projection. Working with aerial images collected at both high and low tides, we created polygon features to represent each of the 14 study sectors. The Oceanside and La Jolla, as well as the Pacific Beach and Imperial Beach sectors were combined to create two polygons (North and South) representing exposed habitat. No 0-group halibut were observed during four years of recent dive surveys over structured bottoms (kelp forest, understory algae, rocky benches and surfgrass (*Phyllospadix* spp.) covered soft bottom) along the exposed coast of San Diego (M. Craig, J. Hyde and E. Parnell, personal communications). Therefore, we constructed polygons for each bottom type along the exposed coastline (0–20 m deep), but only used unvegetated soft bottom to determine exposed coastline habitat availability in subsequent analyses. Vegetation and bottom cover data for exposed coast sectors were acquired from the San Diego Nearshore Program website (http://nearshore.ucsd.edu/). Juvenile halibut densities were also expected to be dramatically different between eelgrass, *Zostera marina*, and unvegetated bottoms within protected embayments (Valle et al., 1999). For that reason, polygon features were produced that differentiated eelgrass-dominated and unvegetated soft bottom. Eelgrass distribution data for San Diego County were provided by Merkle and Associates, San Diego, CA. During their surveys, seagrass was found in Oceanside Harbor, Agua Hedionda, Batiquitos, Mission Bay and San Diego Bay. Sediment grain-size data were provided by Coastal Environments, La Jolla, CA, for the nearshore habitats of San Diego County. We used a visual basic (VB) script provided in the ArcMap software to calculate the areas and perimeters for each sector and bottom type (polygons) that comprised the habitat available to 0-group halibut.

Table 1

Summary table for GIS-based area, as well as 0-group halibut density and abundance estimates for each of the potential nursery habitats in San Diego County, CA. Oceanside and La Jolla sectors are combined as North San Diego Coast, and Pacific Beach and Imperial Beach sectors are combined as South San Diego Coast. Geomorphologic characteristics used to classify embayments included surface area, average depth and surface area to perimeter ratios

	North San Diego Coast	South San Diego Coast	Oceanside Harbor	Buena Vista	Agua Hedionda	Batiquitos	San Elijo	San Dieguito	Penasquitos	Mission Bay	San Diego Bay	Tijuana River	Total
Mouth location (DD)	–	–	33.21– 117.40	33.16– 117.36	33.15– 117.34	33.09– 117.31	33.02– 117.28	32.98– 117.27	32.93– 117.26	32.76– 117.25	32.68– 117.23	32.56– 117.13	–
High-tide bottom area (ha)	14,535.4	13,266.1	86.1	35.5	95.0	143.1	57.7	40.3	16.4	912.5	4517.0	40.8	33,734.6
Low-tide bottom area (ha)	14,535.4	13,266.1	84.5	35.5	83.9	73.9	10.3	24.3	5.7	851.9	4174.0	16.9	33,162.4
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	–
Low-tide area/perimeter	–	–	10.1	2.4	8.4	6.3	0.8	1.8	0.8	15.3	39.0	0.8	–
Surface area change, low tide/high-tide	–	–	0.98	1.00	0.88	0.52	0.18	0.60	0.35	0.93	0.92	0.41	–
Average depth (m)	–	–	6.0	~2.5	3.1	2.8	1.4	1.7	2.2	4.7	12.4	1.3	–
Zostera marina area (ha)	–	0.3	0.5	–	28.6	14.7	–	–	–	324.6	661.7	–	1030.4
Kelp area 0–20 m depth (ha)	1560.7	2525.4	–	–	–	–	–	–	–	–	–	–	4086.2
Understory algae 0–20 m depth (ha)	575.4	977.2	–	–	–	–	–	–	–	–	–	–	1552.6
Phyllospadix spp. area 0–20 m depth (ha)	53.3	105.0	–	–	–	–	–	–	–	–	–	–	158.2
Unvegetated soft-bottom area	12,562.4	10,110.6	84.1	35.5	66.4	59.2	10.3	24.3	5.7	527.3	3512.3	16.9	27,015.0
2003 Sampling nodes (*n*)	55	20	10	–	9	12	11	7	10	41	34	25	234
2003 Halibut density (#/ha)	10.96	11.12	77.07	0.00	215.72	91.76	240.30	250.90	127.10	92.58	98.98	198.70	–
2003 Resident halibut (#)	137,654	112,408	6516	0	20,502	6783	2468	6092	730	78,876	413,137	3355	788,522
2004 Sampling nodes (*n*)	55	47	13	–	11	12	6	15	15	45	54	20	293
2004 Halibut density (#/ha)	12.92	18.01	135.89	0.00	294.85	101.84	524.40	379.40	763.20	100.83	73.17	1450.70	–
2004 Resident halibut (#)	162,314	182,134	11,489	0	28,022	7528	5369	9213	4382	85,901	305,397	24,497	826,247

2.3. Distribution surveys

We made 234 and 293 collections in 2003 and 2004, respectively. All collections occurred in October and November, during daylight hours. Sampling in lagoons and estuaries was performed when tidal levels were below +0.33 m mean lower-low water. Collections were made by otter trawling (doors 45 × 90 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 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 of the seine. Distances covered during each collection event were recorded using a hand-held GPS so that sampling areas could be calculated.

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 (Kjelson and Johnson, 1978; Parsley et al., 1989; Kuipers et al., 1992), we conducted mark-recapture experiments to determine the relative juvenile halibut catch efficiencies for both gear types. Griffiths et al. (submitted for publication) conducted a two-week mark-recapture study on California halibut in Punta Banda Estuary, Mexico, using our otter trawl and estimated the gear efficiency at 25.3%. We performed a smaller-scale mark-recapture experiment in San Elijo during the spring of 2003 to calculate the efficiency of block-net seining. This involved collecting small halibut (<200 mm standard length, SL) within San Elijo by seining and injecting them with 0.2 cc of red acrylic paint under the epidermis, beneath the dorsal fin on the blind (white) side. Marked fish were released into an area enclosed by blocking nets, except one fish (per trial) that was held in a 5 gallon bucket to observe tag retention and mortality. Fish within the enclosure were then collected by seining (as above) and recapture rates were calculated for marked fish. This was replicated four times over 2 days (recapture rates: 33%, 50%, 20% and 66% for the four trials) and established a capture efficiency of 39%.

During each collection event, depth, surface temperature, and surface salinity were recorded. During otter trawls, depth and temperature were recorded from an onboard fishfinder equipped with a sonar and temperature-sensing transducer. While seining, depth was recorded using a tape measure placed at the center of the enclosed area, and temperature was recorded using a portable thermometer. Surface salinity was measured using a hand-held refractometer. Qualitative data on bottom type were recorded at each collection based upon the contents of the catch (presence/absence of seagrass and community composition of catch). In the laboratory, bottom type was checked by visually comparing the location of collection events to the mapped distribution of bottom habitats in the GIS database. If bottom type could not be determined conclusively, data were used in density extrapolations for both vegetated and unvegetated soft bottoms (see below). However, when we tested for the significance of abiotic effects on juvenile density, data in which bottom type was uncertain were excluded.

Halibut were counted and measured (SL) immediately following each collection event. For this study, only fish 50–250 mm SL were included in subsequent distribution analyses. Fish smaller than 50 mm were not included because: (1) post-settlement migration among potential nurseries may continue for up to three months and confound distribution results (Kramer, 1990), and (2) sampling gears used in this study had different mesh sizes and 50 mm proved a conservative measure to minimize potential gear bias. Fish larger than 250 mm were assumed to have grown out of the 0-group class (MacNair et al., 2001). For each collection, an uncorrected density estimate of 0-group halibut was calculated by dividing the number of 50–250 mm SL halibut caught by the area covered during each sampling. These unadjusted densities were then corrected using the gear efficiency factors to estimate local density.

2.4. Survey data analysis

The independent factors used to test for significant ($\alpha = 0.05$) differences in the density of 0-group halibut were year (2003 vs. 2004), habitat exposure (exposed coast vs. embayment), geomorphologic habitat type (exposed coast, bay, lagoon and estuary), bottom type (vegetated vs. unvegetated) and mean sediment grain size (Coarse Sand, Medium Sand, Fine Sand, Very Fine Sand, Coarse Silt, Medium Silt). In all cases, raw and transformed ($\log(X+1)$, $\sqrt{X}$) data failed the assumptions of normality and homoscedasticity (F_{MAX}-test). Therefore, we employed the non-parametric Mann–Whitney *U* and Kruskal–Wallis tests for between- and among-group comparisons, respectively. All analyses were conducted using StatView 5.0.1 (©SAS Institute Inc.). Scatterplots were created to illustrate trends of juvenile densities in relation to depth, surface temperature and surface salinity.

We also modeled the density of 0-group halibut as a function of abiotic factors using regression trees (Breiman et al., 1984). Regression trees are a clustering analysis used to explain variation in a response variable as a function of several independent variables (Merler et al., 1996). This procedure repeatedly partitions data by creating binary divisions in explanatory variables so as to sequentially reduce the largest amount of variation in a response variable. We used Systat 8.0 (©SPSS Inc.) to construct regression trees. Surveyed densities were modeled in relation to depth, surface temperature, surface salinity, nursery habitat geomorphology and bottom type (vegetation and sediment grain size). Regression trees are ideally suited to this type of analysis because they: (1) are not based upon parametric assumptions, (2) can handle multiple data types (numerical, categorical, other), (3) are relatively easy to construct and interpret, and (4) produce usable, binary results for classifying habitats (De'ath and Fabricius, 2000). For our analysis, data were divided by year (2003, 2004) and habitat exposure (exposed, embayment) prior to creating trees. This resulted in four separate analyses. To construct trees, the least squares method was used for reducing within-group variability (node impurity). Trees were grown until one of the terminal nodes contained only two data points. Trees were then pruned to optimal size using the cross-validation method proposed by Breiman et al. (1984) in order to minimize prediction error. To accomplish this, a random subset of the data was selected to build a sequence of nested trees. Then, we determined the predicted classification of the remaining data using the explanatory variables and calculated the error (total sum of squares) between the predicted and observed juvenile halibut densities. This was done for each tree size. The tree with the smallest prediction error was selected.

2.5. Distribution extrapolations and contribution estimates

To assess patterns of habitat usage, 0-group density survey data were split by year (2003, 2004), habitat sector (Oceanside-La Jolla, and Pacific-Imperial Beach data were pooled, while all other sectors were considered individually), and bottom type (eelgrass, unvegetated). These data were imported into ArcMap, and using the spatial analyst extension, density surfaces over each habitat polygon were created using the Inverse Distance Weighted (IDW) method (Beckler et al., 2004; but see Riou et al., 2001 for potential disadvantages). Since collections were conducted during low tides in locations with moderate to large changes in surface cover between spring high and low tides, density surfaces were created using the area polygon features created from low-tide images. Our density surfaces were designed to consider 12 neighbor data points and were weighted by a power of 2 to create a grid of densities over the entire polygon that defined the spatial extent of each nursery habitat sector. Grids covering exposed habitats were constructed with 10 × 10 m cells, grids covering lagoons and bays were constructed with 5 × 5 m cells and grids covering estuaries were made from a series of 2 × 2 m cells. The number of juveniles within each habitat (J_i) was then estimated, using the equation:

$$J_i = A_i D_i \qquad (1)$$

where A_i is the area of habitat type i, and D_i is the density of halibut within habitat type i. The total number of juvenile halibut in the study region (J_t) was calculated by summing the estimates of resident halibut from all potential nursery habitats (H), such that:

$$J_t = \sum_{i=1}^{H} J_i \qquad (2)$$

Last, we calculated the expected contribution (EC) of juveniles available to recruit to the adult stock from each nursery habitat as:

$$\mathrm{EC} = (J_i/J_t)100 \qquad (3)$$

3. Results

3.1. Habitat cover

In total, 33,174 ha (from low-tide estimates) of nursery habitat were available to juvenile California halibut within the San Diego County region during our study. Exposed coasts comprised 84% of the available habitat for juvenile halibut, bays made up almost 16% of accessible nursery habitat, and lagoons and estuaries accounted for <1% of potential nursery habitat (Table 1). Altogether, 81% of the nearshore habitat (<20 m deep) was unvegetated soft bottom while 3% was eelgrass bottom (within protected embayments, eelgrass occurred over 19% of the bottom). The remaining 16% of the benthos (all in exposed waters 0–20 m deep) was covered by kelp forest, understory algae, or surfgrass (Table 1), and is avoided by halibut <250 mm SL.

3.2. Halibut surveys

Densities of 0-group halibut varied as a function of habitat exposure (Mann–Whitney U; $p < 0.0001$) and nursery habitat type (Kruskal–Wallis; $p < 0.0001$). Densities were lowest along exposed habitats, were 5–10 times higher in bays, and 20–30 times higher in lagoons and estuaries (Fig. 2). Overall densities were not significantly different between years (Mann–Whitney U; $p = 0.1504$), but this is likely a result of pooling density data from all potential nurseries. All study sectors, with the exception of San Diego Bay, exhibited higher average densities in 2004 (Table 1). Survey data from each of the five embayments containing seagrass were used to test for bottom vegetation effects. Embayments included in the analysis were Oceanside Harbor, Agua Hedionda, Batiquitos, Mission Bay and San Diego Bay. Densities between vegetated and unvegetated bottoms were significantly different, although it is unclear how much of this result was influenced by changes

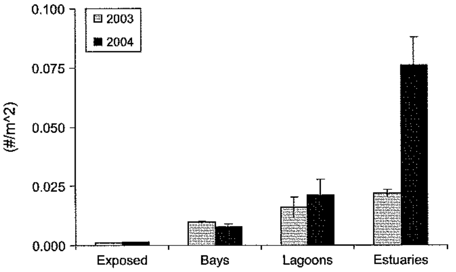

Fig. 2. Mean 0-group halibut densities (±1 SE) from each of the four nursery habitat types in San Diego County, CA, in 2003 (gray bars) and 2004 (black bars). Means are based on density surfaces interpolated in ArcMap 8.3 from field surveys in each of the 14 study sectors. Coast 0–20 m habitat = North and South San Diego Open Coast. Bay/Harbor habitat = Oceanside Harbor, Mission Bay and San Diego Bay. Lagoon habitat = Agua Hedionda and Batiquitos. Estuary habitat = San Elijo, San Dieguito, Penasquitos and Tijuana River. The closed embayment, Buena Vista, was not included in the analysis.

in gear efficiency over the two bottom types (Mann–Whitney U; $p < 0.0001$, Table 2). Overall, sediment grain size had no significant effect on the distribution of 0-group halibut (Kruskal–Wallis; $p = 0.9545$, but see Stranski, 1998), although there did appear to be a general trend toward increasing density with decreasing grain size down to 0.25–0.01 mm mean diameter sediments (fine sand to coarse silt, Table 2).

Along exposed coasts, densities reached a maximum of 0.023 indiv/m^2 between depths of 4.5–5 m (Fig. 3A), while within protected embayments, highest juvenile halibut densities ($\sim$0.9 indiv/m^2) were recorded in depths less than 2 m (Fig. 3D). When plotted along a temperature gradient, highest halibut densities were observed at 19 °C along exposed habitats and 21 °C within protected habitats (Fig. 3B, E). Plotted along a salinity gradient, 0-group halibut densities were highest at 34 (Fig. 3C, F).

Several abiotic factors appear important in describing halibut density variation based upon regression tree results, and key abiotic factors change with year and habitat exposure. Along exposed habitats in 2003, temperature was the key explanatory variable in partitioning halibut density variation. Higher temperatures were positively associated with increasing halibut densities, with highest average densities (0.008 indiv/m^2) recorded where surface temperature exceeded 21.5 °C and lowest average densities (0.001 indiv/m^2) found where surface temperatures were below 19.2 °C (Fig. 4A). In protected embayments in 2003, depth explained the largest amount of variation in halibut densities. Depths less than 1.5 m exhibited highest average densities (0.054 indiv/m^2). Within these shallow waters, temperatures above 23.5 °C and salinities exceeding 33.0 yielded higher abundances of halibut, with highest mean densities reaching 0.111 indiv/m^2 (Fig. 4B). In the following year, depth was the most important variable for explaining variance in 0-group halibut densities along exposed coasts. Lowest densities (0.001 indiv/m^2) occurred at depths > 5.2 m, while highest average densities (0.005 indiv/m^2) occurred between 3.3 and 5.2 m. Within this latter depth range, juvenile halibut appeared aggregated where surface water temperatures exceeded 19.0 °C with a mean density of 0.012 indiv/m^2 (Fig. 4C). Inside protected embayments during 2004, the largest amount of variation in density was explained by delimiting the type of nursery. Estuaries exhibited average densities considerably higher than those observed in bays and lagoons (0.156 indiv/m^2 compared to 0.013 indiv/m^2). Within estuaries, binary splits in salinity (at 34) and depth (at 0.75 m) also helped to partition a considerable amount of variation in density measures, as 0-group halibut were extremely abundant (0.430 indiv/m^2) in more saline, shallow waters (Fig. 4D). Overall, regression trees accounted for 54.1% (2003, exposed), 48.0% (2003, protected), 52.8% (2004, exposed) and 47.1% (2004, protected) of the variance in densities observed during fall surveys.

3.3. Juvenile distributions and expected contribution (of nursery habitats) to adult stocks

Even though the densities of 0-group halibut increased in 2004 in all but one of the habitat sectors, the centers of distribution within each sector appeared to remain constant between years (Fig. 5). In estuaries, highest densities occurred near the mouths in both years, while in bays and lagoons, densities were more concentrated in regions that were more central (although multiple density centers were observed). Generally, densities were low near the back of embayments. Along exposed coasts, densities were highest near La Jolla and Pacific Beach. One notable exception was a shift from low (2003) to high (2004) relative densities off Imperial Beach adjacent to the mouth of San Diego Bay (Fig. 5).

In 2003, we estimated $\sim$788,522 0-group halibut (from Eq. (2)) resided in the nearshore waters of San Diego County (Table 1). The following year, we estimated a population size of $\sim$826,247 0-group halibut. Average densities were higher in each of the 14 habitat sectors in 2004 (Tijuana River exhibited densities eight times higher in 2004), except San Diego Bay, which contained the single largest population of halibut in both years (Table 1). As a result, we estimated that twice as

Table 2

Mean 0-group halibut densities (SE) calculated from otter trawl and block-net seine collections. Data are broken down by year and habitat features. Also included are significance test results for between- (Mann–Whitney U) and among-group (Kruskal–Wallis) comparisons. Unlike letters denote significant differences using pair-wise comparisons (Mann–Whitney U, $\alpha < 0.05$) between nursery types. Sediment grain sizes were classified as coarse sand (1.0–0.5 mm), medium sand (0.5–0.25 mm, but $n = 0$), fine sand (0.25–0.125 mm), very fine sand (0.125–0.063 mm), coarse silt (0.063–0.032 mm) and medium silt (0.032–0.016 mm) based on mean grain diameter

Factor						p-Value
Year	2003 (n 183) 0.021 (0.003)	2004 (n 277) 0.033 (0.006)				0.1504
Site exposure	Exposed (n 163) 0.003 (0.0003)	Protected (n 297) 0.043 (0.006)				<0.0001
Nursery type	Exposed (n 163) 0.003 (0.0003)*	Bay (n 190) 0.016 (0.002)*	Lagoon (n 27) 0.073 (0.016)**	Estuary (n 80) 0.094 (0.018)**		<0.0001
Bottom structure	Vegetated (n 33) 0.003 (0.001)	Unvegetated (n 184) 0.027 (0.003)				<0.0001
Sediment grain size	Coarse sand (n 22) 0.019 (0.007)	Fine sand (n 262) 0.028 (0.006)	Very fine sand (n 128) 0.031 (0.005)	Coarse silt (n 12) 0.04 (0.027)	Medium silt (n 2) 0.012 (0.012)	0.9545

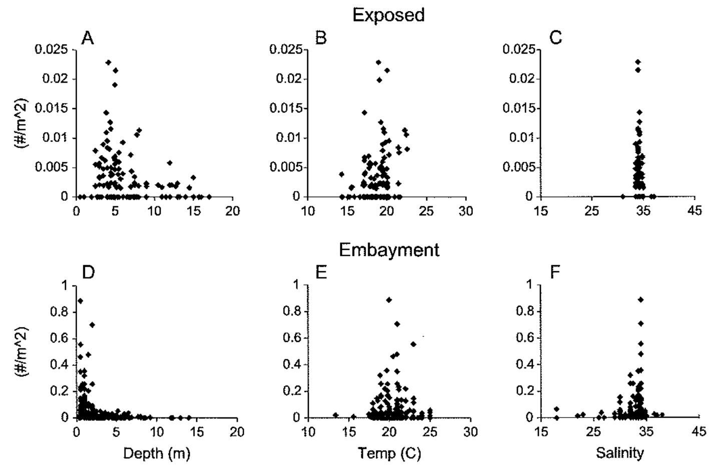

Fig. 3. Scatterplots of 0-group halibut density in relation to depth, temperature and salinity gradients. Data (pooled from 2003 and 2004) represent halibut densities estimated from trawls and block-net seining obtained concurrently with environmental data. Panels A–C show trends along exposed habitats ($N = 163$), while panels D–F show patterns within protected embayments ($N = 297$). Data from collection events in which bottom type could not be positively determined were excluded from the plots.

many halibut resided in bays as along the exposed coast in 2003, while nearly equal numbers of halibut resided within these habitats during 2004. Still, our calculations indicate that ~58,000 more 0-group halibut resided in bays than along the exposed coastline even in 2004 (Table 1). In 2003, ~250,000 0-group halibut (31%, EC from Eq. (3)) resided off exposed beaches, while ~538,500 halibut (69%) were located in protected embayments (bays, lagoons and estuaries). The following year, ~344,500 0-group halibut (42%) were located in exposed coastal waters, and ~481,800 juvenile halibut (58%) resided in protected embayments (Fig. 6). In the fall of 2003, we estimated that lagoons and estuaries contained ~39,900 0-group halibut, which represented only 5% of the study population (Fig. 6A). In 2004, the resident populations in lagoons and estuaries were nearly twice as large (~79,000 individuals), which made up 10% of the San Diego County population (Fig. 6B). The higher relative expected contribution (EC) of these habitats was due to greater abundances in estuaries (Table 1). If years are considered together, exposed coasts, bays, lagoons, and estuaries are expected to contribute 37%, 56%, 4% and 3%, respectively, of the juvenile halibut available to advance to adulthood (EC) from these two cohorts.

Because halibut exhibit limited migrations parallel to the coastline (Tupen, 1990; Posner and Lavenberg, 1999), it is reasonable to consider latitudinal differences in nursery habitat contribution. We bisected the San Diego coastline at Point La Jolla, where rocky substrate serves as a natural barrier for juvenile halibut passage. This created two regions (North and South) each ~55 km in length. In North San Diego County, 75% of 0-group halibut resided in exposed habitats, while the remaining 25% of halibut resided within protected embayments on average during 2003 and 2004. Along the South San Diego County coastline, the opposite was observed: only 24% of 0-group halibut resided along exposed habitats, while the remaining 76% were located in protected embayments (mostly in San Diego Bay). Consequently, the 0-group population was 3-fold larger in the southern half of the county.

4. Discussion

4.1. Distribution of 0-group fish among nursery habitat alternatives

Our survey and mapping results indicate that all coastal habitat types demonstrate the potential to contribute significantly to stock success of California halibut. Although 85% of the potential nursery habitat area occurred along the exposed coastline, 69% (2003) to 58% (2004) of 0-group halibut resided in protected embayments (Fig. 6). The majority of fish within embayments were in Mission and San Diego bays. Our findings concerning nursery habitat contribution show general agreement with the results of Forrester and Swearer (2002), who employed an elemental fingerprinting approach along a 300 km section of southern California to determine nursery habitat utilization. They concluded that approximately 50% of adult halibut had utilized protected embayments as nursery habitats, while the remaining 50% spent their juvenile period in the shallows of the exposed coastline. Experimental work in other systems has reproduced this 50/50 relationship of contribution from estuary/embayment vs. marine/exposed

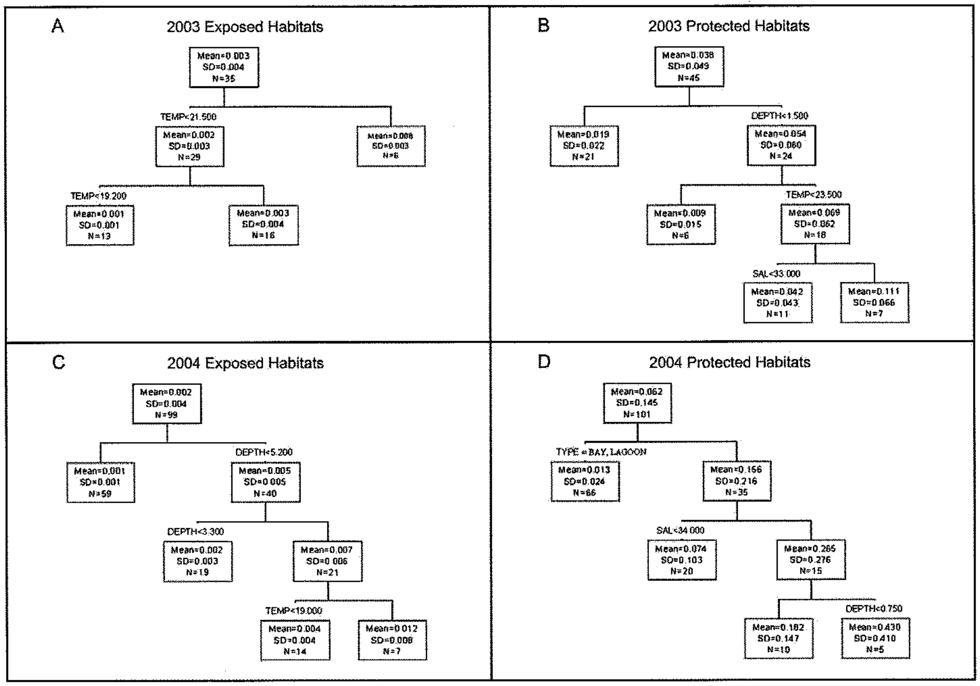

Fig. 4. Regression tree analysis for 0-group halibut density in 2003 (A&B) and 2004 (C&D) in Exposed (A&C) and Protected (B&D) habitats. Data represent halibut densities estimated from trawls and block-net seining obtained concurrently with environmental data. Potential explanatory variables used in the analysis were habitat type, depth, surface temp, surface salinity and sediment grain size. Variables important in explaining variation in halibut densities appear at terminal nodes along with the value that determines where density splits occur. Explanatory variables nearer the tree root explain a larger amount of variation in density. Nodes are labeled with the mean and standard deviation of halibut density as well as the number of observations in the group. Trees explained 54.1% (A), 48.0% (B), 52.8% (C) and 47.1% (D) of the variance in density. Relative importance of explanatory variables changed with year and habitat type. Data from collection events in which bottom type could not be positively determined were excluded from the analyses.

habitats. Therefore, this may be a good first null hypothesis for the expected contribution (EC) of temperate-region flatfish from each habitat type, at least for those species that demonstrate the ability to use both habitats as nurseries. For instance, Yamashita et al. (2000) also used elemental concentrations in the otoliths of stone flounder to determine that 20 of 42 individual adults had utilized estuaries as nursery habitat in the Sendai Bay region of northeastern Japan. In the Bay of Biscay, expected contribution of juvenile common sole, *Solea solea*, from estuarine waters ranged between 24% and 87% over 15 years. During this period a mean of 48% of all juveniles were found in estuarine, as opposed to fully marine, waters (Le Pape et al., 2003a). Although our study focused on a flatfish in southern California (a dramatically different coastal system), the common sole and stone flounder results are comparable to ours, in which an average of 63% of 0-group halibut resided in embayments and between-year variability was 10%.

Within embayments, halibut distributions appeared to be remarkably stable between years even as environmental conditions and local densities fluctuated (Fig. 5). For example, halibut tended to favor sites near the mouths of estuaries in both years, while avoiding habitat deeper within these embayments. Areas in the back of bays and lagoons were avoided by 0-group halibut during 2003 and again in 2004. This pattern of habitat use in San Diego Bay was also observed from 1994 to 1999 by Allen et al. (2002). The fact that juveniles do not shift their distributions within embayments year after year may simply demonstrate the environmental tolerances known to characterize small halibut (Madon, 2002), but also suggests that halibut did not spread out into new, potentially marginal, habitat as local densities increased from 2003 to 2004 (Table 1). We consider two alternative hypotheses to explain the stability in 0-group halibut distributions between years: (1) juvenile halibut do not experience strong density-dependent regulation related to growth or mortality at the densities we observed, and 0-group halibut selected nursery habitats regardless of intra-specific densities (Rodgers, 1994), or (2) halibut are habitat limited and must pack into specific habitat areas

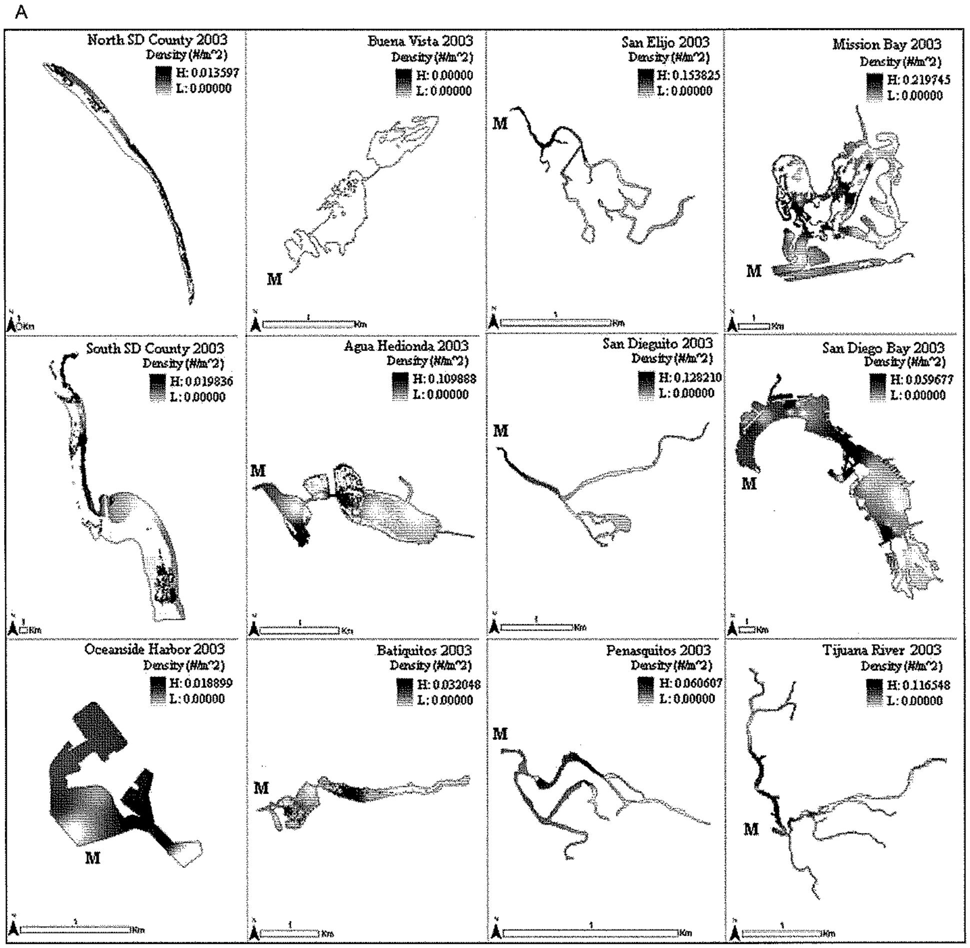

Fig. 5. The 2003 (A) and 2004 (B) distribution of 0-group halibut in the nearshore habitats of San Diego County, CA. Maps are interpolations of 234 (2003) and 293 (2004) data observations taken during fall 2003 and 2004. Density grids were generated using the Inverse Distance Weighting (IDW) spatial analyst tool in ArcMap 8.3. Maps have individual scale bars and density scales. Embayment mouths are denoted with M.

despite the consequences of local density (Holbrook et al., 2000). Subsequently, there are growth or mortality costs following high settlement that reduce interannual variation in recruitment via density-dependent mechanisms during the juvenile phase (Van der Veer et al., 1991; Modin and Pihl, 1994). Because halibut do show wide environmental tolerances and the ability to reside in multiple nursery habitat types, it seems unlikely that juveniles would be habitat limited given our distribution results. But ultimately, our data cannot arbitrate between these competing hypotheses. Instead, tests for density-dependent growth and survivorship are needed. One of the benefits of documenting the distribution of juvenile fish and calculating expected contribution is that this provides a prospective estimate for recruitment to adult stocks from each habitat. These data can be compared to retrospective analyses of actual contribution from each habitat to infer relative growth/survival rates. Given differences in juvenile densities among habitats, these prospective and retrospective assessments can be used to search for density-dependent regulation of contribution to adult stocks. For instance, when our results (approximately 63% of EC from protected embayments) are compared with those of Forrester and Swearer

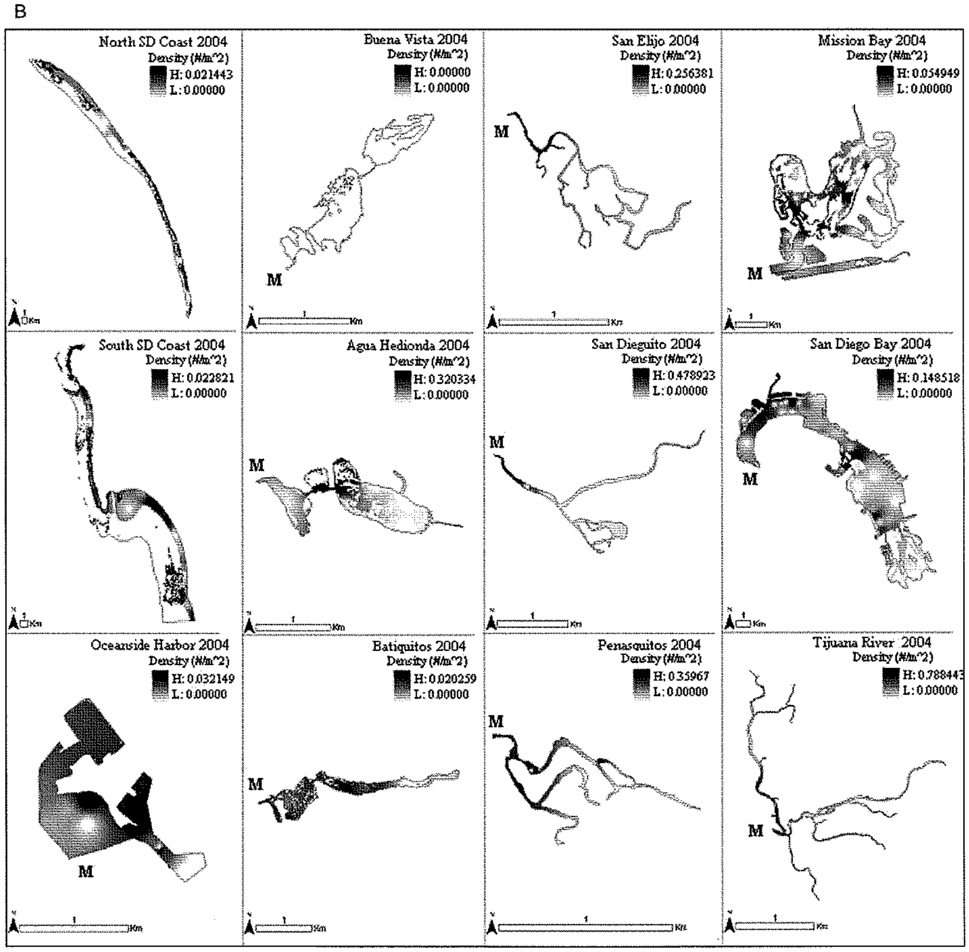

Fig. 5 (*continued*).

(2002), who estimated nearly 50/50 contribution from exposed/embayment nurseries using an elemental fingerprinting tracking method, one could infer that survivorship is elevated in exposed habitats, where densities are depressed relative to those observed in embayment habitats. Unfortunately, this example is only illustrative as the study periods and sites between experiments do not overlap. Also, examination of the stock-recruitment relationship for this species could indicate if density-dependent regulation during the juvenile phase moderates adult population sizes when high densities of juvenile fish concentrate into spatially limited nurseries (Iles and Beverton, 2000). Under either scenario, halibut stocks may experience diminished density-dependent regulation as a result of being nursery-habitat generalists.

The distribution data we generated are comparable to previous studies of juvenile halibut habitat use within San Diego County. Kramer (1990) produced estimates from beam trawl surveys and aerial estimates for halibut abundances in Mission Bay, Agua Hedionda and along the exposed coastline from 1987 to 1988 that were all within 20% of our more recent estimates. These data imply that over a two-decade period, there may have been muted temporal variability in resident juvenile halibut population sizes within these habitats. More than 20 years before our study, Zedler (1982) suggested that 30,000

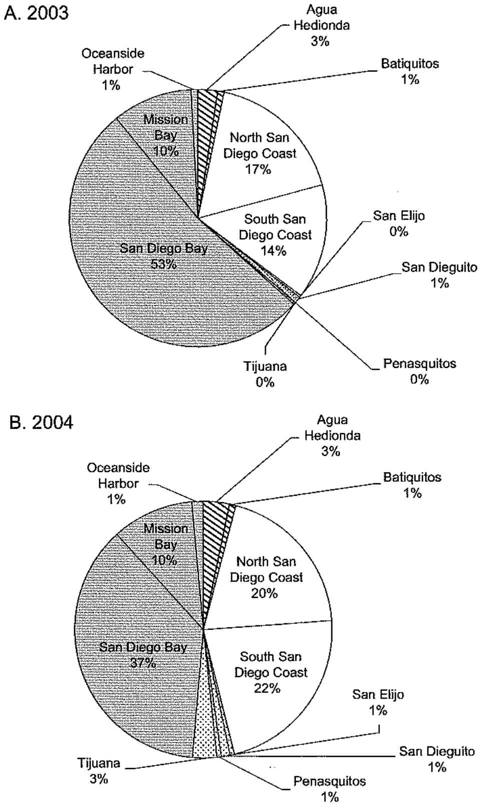

Fig. 6. Resident 0-group halibut in each of the potential nursery habitat types in San Diego County, CA, in 2003 (A) and 2004 (B). Percentages represent expected contribution (EC) from each habitat type based upon fish occupying each nursery site at time of study available to recruit to older age classes. Resident 0-group halibut in each site were calculated using the IDW spatial analyst tool in ArcMap 8.3. Exposed coast, bays/harbors, lagoons and estuaries are shown in white, gray, striped and spotted patterns, respectively.

juvenile halibut could reside within Tijuana River Estuary each year, although it was not evident how this estimate was produced. Our J_i (Eq. (1)) results for the Tijuana River Estuary indicate that Zedler's estimate is a good approximation in some years, but potentially an order-of-magnitude overestimation in other years (Table 1).

4.2. Evaluating nursery-role concept for 0-group California halibut

Beck et al. (2001) formulated a rigorous definition of the nursery-role concept that stressed unit-area production to the adult stock in order to evaluate juvenile habitat value. This has provided a clearer framework of habitat classification for conservation or management efforts. According to Beck et al. (2001), nurseries are those habitats with above average unit-area production of adults. In our study system, bay habitats contained the largest pool of potential recruits, but exhibited low densities relative to lagoons and estuaries. Densities along exposed coasts were significantly lower than in protected embayments, yet exposed habitats had an EC between 31% and 42%. Conversely, habitats with highest local densities (lagoons and estuaries) were characterized by an EC of 5–10% (Fig. 6). Using Beck et al.'s nursery-role concept (and assuming density is an adequate proxy for production), only lagoons and estuaries would achieve nursery status even though they comprised less than 1/10 of total EC. In fact, ranking nursery habitat value according to both the nursery-role concept (using density as a proxy) and expected contribution (EC) results in an almost complete reversal of trends (Unit-area production, estuary > lagoon > bay > exposed; EC, bay > exposed > lagoon > estuary). Kraus and Secor (2005) determined that there could also be reversals in nursery value rankings of freshwater and brackish habitats across years, and that dominant year classes of white perch, *Morone americana*, utilized juvenile habitat differently than all other year classes. These data present complications for applying the nursery-role concept of Beck et al. (2001), but do not negate its worth as an objective metric of habitat value.

The structural isolation and nature of disturbance impacting coastal embayments in southern California results in management decisions operating at the scale of entire bays, lagoons and estuaries. For instance, the decision to artificially open or close an inlet will have impacts for fishery production of halibut that are integrated over the entire embayment, regardless if the embayment is large or small and supports dense or sparse juvenile fish populations. Consequentially, we conclude Gibson (1994) provided a more useful framework for the halibut, and the goal of managers should be to evaluate the product of habitat quality and quantity when managing coastal habitats to maximize production. For the California halibut, Beck et al.'s nursery-role concept is most valuable for directing restoration projects that operate on smaller (acres) spatial scales. Our regression tree results clearly indicate shallow, warm-water habitats are associated with high local density of 0-group halibut (Fig. 4). Within the northern (front) section of San Diego Bay, and multiple sections of Mission Bay, there is considerable opportunity to create shallow subtidal habitat to promote higher local 0-group halibut densities. To measure the effectiveness of these manipulations, the unit-area production metric would be best for ranking habitat value between restored and adjacent, unrestored sites.

The spatial extent of top-quality habitat for fish and crustacean species may often be limited (Peterson et al., 2001). Therefore, habitats with lower per unit area carrying capacity but high spatial coverage can contribute significantly to the health of fish and invertebrate stocks. Even these, seemingly common habitats, can be dramatically altered over decadal and longer timescales (Chambers, 1992). For management purposes, these habitats should not be overlooked as important nurseries. Recently, Kareiva and Marvier (2003) pointed out the hazards of focusing too much effort on conserving biodiversity hotspots and neglecting what they termed "coldspots". They argue coldspots are worth protecting to insure a diversity of ecosystem functions in addition to a diversity of distinct genetic lineages. Analogously, utilizing multiple nursery habitat types may provide benefits for halibut other than maximal unit-area production of adults. Kramer (1991a) hypothesized that small halibut may have evolved to be nursery habitat generalists as a bet-hedging strategy since "optimal" nursery habitats in southern California are periodically unavailable due to inlet closures. Also, populations with juveniles spread across multiple habitat types may express a higher diversity of environmental adaptations or tolerances, and this could promote species persistence in the face of ecological perturbations.

4.3. Environmental influence on juvenile distributions

Juvenile halibut were generally concentrated in shallow, warm-water, unvegetated, high-salinity habitats (Table 2; Figs. 2–4). These are areas where food resources (mysids, amphipods, gobies) are relatively high (Haaker, 1975), metabolism and conversion efficiencies are high (Madon, 2002) and predation pressure is low (Allen and Herbinson, 1990). Other mapping studies have described similar habitat associations for juvenile flatfish. Eastwood et al. (2003) found that common sole in the English Channel favored shallow depths (3–10 m), temperatures between 16 and 18 °C, and salinities greater than 34. Likewise, Stoner et al. (2001) found that young-of-the-year winter flounder, *Pseudopleuronectes americanus*, in New Jersey estuaries concentrated themselves in waters less than 2 m, and warmer than 22 °C. Notably, our distribution results support the classification of embayments into distinct habitat types (termed bay, lagoon and estuary in this study). These classifications were originally generated using general geomorphologic characteristics, but based on density estimates these habitats appear to function very differently as nursery habitat for the California halibut and may have dramatically different carrying capacities (Fig. 2). Because juvenile fish are relatively mobile and are destined to undergo ontogenetic migrations, more specific habitat associations for 0-group halibut may be lacking (Sogard and Able, 1994; Able and Fahay, 1998). Our data represent a seasonal snapshot of habitat use by juvenile halibut, but Kramer (1990) has produced a data set demonstrating that shallow habitats have a higher proportion of very small halibut. These small halibut migrate to deeper, open waters throughout the summer and fall as they grow larger. Since these ontogenetic migrations occur over 10–100 m, we do not expect these movements would impact our conclusions regarding expected contribution from nursery habitat alternatives.

Nursery habitat availability and usage has been linked to the dynamics of fluvial discharge in previous studies employing similar mapping approaches to evaluate nursery habitat value for flatfish. These studies focused on the common sole, *Solea solea*, in coastal areas of the Bay of Biscay where interannual variation in river inputs can dramatically impact the nature of benthic habitats over large spatial scales (Le Pape et al., 2003a,b). In southern California, fluvial discharge should not have the same mechanistic effects on halibut distributions due to the spatially static nature of embayment and exposed habitats. Moreover, southern California is characterized by a Mediterranean-type climate where evaporation exceeds precipitation in almost all months (Zedler et al., 1992). Even in years with considerable precipitation, juvenile halibut 118–172 mm (TL) show wide tolerances to salinity (17–34) fluctuations (Madon, 2002). Our results indicate that average halibut densities were not significantly lower in polyhaline (18–30) waters relative to euhaline waters (30–40), and salinity was useful in predicting 0-group densities only in very shallow (<1 m depth) water (Fig. 4).

4.4. Impacts of coastal development and inlet closures

Due to the mechanisms of coastal habitat loss and degradation in southern California (e.g., inlet closures, non-point source pollution, historic wetlands loss), management decisions are often made at the scale of entire bays, lagoons and estuaries. This is the same scale we used to delineate nursery types for the purposes of estimating nursery habitat availability, usage and expected contribution to adult halibut stocks. In 1996, Batiquitos was dredged and the mouth jettied as part of a large-scale enhancement project. As a result, the area available to 0-group halibut has greatly increased. Subsequently, halibut utilization of this site has risen from zero (Appy, 1999) to roughly 7000 juvenile halibut each year (or 1% of the 0-group population in the study region, according to our estimates). Another example of dramatic change has occurred in Mission Bay, which has been modified over the last 150 years by diverting the San Diego River, removing large tracts of saltmarsh wetlands and constructing marinas and boating access. These modifications have changed the amount and nature of nursery habitat available to 0-group halibut in San Diego County (California State Costal Conservancy, 1989). Based on our J_i findings in other bay and estuarine habitats within the study region, it seems likely that these changes in Mission Bay have resulted in increased halibut abundances within the embayment (although we stop short of extrapolating to system wide halibut productivity).

Although fluvial discharge is not expected to directly impact the distribution of juvenile halibut, it can impact nursery habitat availability by modulating the periodicity of inlet closures and openings in southern California (Elwany et al., 1998). Inlet closures can seal off whole estuaries or lagoons that otherwise would serve as productive nurseries. This is especially important for the halibut if protected embayments do offer growth or survivorship benefits, and the ability to locate and pass through inlets acts as a (secondary) bottleneck for halibut populations, as is the case for red drum, *Sciaenops ocellatus*, along the southeastern United States (Pearson, 1929). In San Diego County, five embayments (Oceanside Harbor, Agua Hedionda, Batiquitos, Mission Bay and San Diego Bay) are jettied and remain constantly open, while five others (Buena Vista, San Elijo, San Dieguito, Penasquitos and Tijuana River) can experience periodic closures. Currently, Buena Vista is closed, while San Dieguito was reopened in 2003 following an 18-month closure. Based on our estimates, a closure to any of these lagoons or estuaries forces roughly 1–2% of the 0-group halibut population to either find other suitable nursery habitat or suffer growth or mortality costs.

4.5. Utility of mapping nursery habitat availability and use

The Magnuson–Stevens Act passed by congress in 1996 required that guidelines be established to identify essential fish habitat such as nursery grounds, and research be performed to investigate the impacts of anthropogenic habitat alteration on fish stocks. An obvious first step in meeting these requirements is to catalogue the availability and usage of potential nursery habitats. This, along with technological advances, has led to an increased demand for data maps on habitat and species distributions.

Geographic Information System databases that allow integration of multiple data layers provide a powerful means for quantifying nursery habitat availability and usage related to the population dynamics of coastal fish and crustacean species. To date, this spatially explicit approach has been used in combination with Generalized Linear Models (Riou et al., 2001), Generalized Additive Models (Stoner et al., 2001), regression quantiles (Eastwood et al., 2003) and regression trees (this study) to achieve three basic goals: (1) quantify the spatial extent of nursery habitat types, (2) relate finfish densities to key environmental factors that vary among nursery habitat types, and (3) produce estimates for nursery habitat productivity in terms of 0-group individuals available to recruit to adult stocks. In our study, we employed regression trees (to evaluate #2) and an IDW interpolation method (to assess #1,3) separately, as opposed to modeling the distribution of environmental factors within a GIS to infer habitat usage. We chose this approach because the spatial and temporal scales over which environmental factors vary in our system would have made it exceedingly difficult to generate maps of nursery habitat suitability indices that could be used to infer EC. Still, we are faced with several limitations related to our approach. The most striking is the assumption that density is a proper metric for habitat value (Van Horne, 1983). Previously, it has been demonstrated that fish abundance on artificial reefs (Bohnsack, 1989), and scallop density within specific eelgrass beds (Peterson et al., 2001) were poor indicators of productivity or population fitness. In this regard, Beck et al. (2001) were correct to ignore local density in favor of unit-area production to the adult stock when assessing the connectivity of habitats across life stages. Additionally, this study focused on abiotic factors, and did not consider the relationship between the distribution of 0-group halibut and their prey, competitors and predators. In the future, these data could be included as layers in a GIS database or in regression trees to more fully tease apart the causative agents behind observed halibut distributions. Our sampling design also produced collections only during daylight and, in lagoons and estuaries, low tides. Had collections been made during both day and night, and during all tidal conditions, our conclusions regarding habitat use may have been very different (e.g., Sogard and Able, 1994). At the very least, many of the small-scale (in time and space) habitat linkages could not be evaluated given our design.

Ultimately, our results on the distribution of 0-group halibut offer a valuable hypothesis for what nursery habitat contribution to adult stocks should be if there are no habitat-specific feeding, growth, survivorship, or reproductive benefits. In this study, we found 0-group halibut densities were generally elevated in protected embayments and in shallow, warm water. However, all nursery types we considered demonstrated the potential to contribute to adult halibut stocks, and this has significant implications for the design of management strategies. Our data are most useful when used as a lens to interpret additional field tests of juvenile growth and survival, demographic modeling, or tracking studies to assess marine connectivity.

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III.

Tracking juvenile fish movement and nursery contribution within arid coastal embayments via otolith microchemistry

Abstract

An increasingly common approach for examining the movement of fish is the application of elemental fingerprinting, which exploits variation in the chemical composition of otoliths induced by environmental gradients. We assessed the elemental signatures of otoliths from fish collected in multiple zones along the main-axis of coastal bays and estuaries of Alto and Baja California to test if there are unique chemical signals within embayments. Juvenile California halibut, *Paralichthys californicus*, were collected for three years (2001-2003) along two segments of coastline that included 4 embayment and 3 exposed habitats. Juvenile collections were supplemented by outplanting small halibut and incubating these fish in enclosures in the Punta Banda Estuary, Baja California, Mexico, and Mission Bay, CA. The chemical composition of otoliths was determined via laser ablation inductively coupled plasma mass spectrometry. A general pattern was observed for increasing ^{55}Mn and ^{138}Ba concentrations in the otoliths of wild-caught and outplanted juveniles collected further within embayments. We exploited this intra-embayment variability of otolith microchemistry to chart two forms of migration of

juvenile halibut within the Punta Banda Estuary. First, the within-embayment movements of juvenile fish over several weeks were examined, and an up-axis migration of young-of –the-year halibut was observed during the spring of 2004. Second, the contribution from embayment zones in producing the individual fish that successfully recruited to older age classes was determined. The vast majority of juvenile fish that advanced to older age classes from 2002 and 2003 occupied the middle and lower zones of Punta Banda during the fall of those years. Recognition of intra-embayment variability in otolith signals from Alto and Baja California should allow for finer-scale analyses of habitat utilization, and more thorough examination of connectivity of nearshore habitats resulting from the ontogenetic migration of fish from juvenile to adult habitats.

Introduction

The ability to track movements of fishes through complex life stages in which larvae, juveniles and adults exploit different habitats is necessary for estimating habitat "value" in terms of fishery production (Beck et al. 2001). Furthermore, calculating the extent of connectivity between habitats, or among spatially-separated juvenile and adult populations, has direct implications for stock and habitat conservation, as well as metapopulation and evolutionary processes (Secor and Rooker 2005). Perhaps one of the most important forms of immigration that connects coastal ecosystems is the ontogentic migration of fish and invertebrates from nearshore habitats occupied during the juvenile phase to offshore habitats occupied during sub-adult and adult life-history stages (Gunter 1967, Chambers 1992, Peters and Cross 1993). In recent years, trace element analyses have been employed to determine the nursery origin of marine fishes egressing from putative nurseries (Gillanders and Kingsford 1996, Yamashita et al. 2000, Gillanders 2002a). Because trace elements are incorporated into teleost otoliths during growth in a manner that reflects the ambient environment experienced by individuals, they serve as natural markers of residence and movement over a variety of spatial scales (Campana 1999). Ultimately, the capacity to identify the appropriate spatial and temporal scales over which to exploit elemental signal variation in otoliths will determine the resolution of these tracking studies.

Broadly, elemental fingerprinting studies seeking to assess fish movement and nursery origins have typically occurred along two distinct types of coastline. A number of studies have examined nursery utilization along coastlines that receive large amounts of freshwater input and hence exhibit complex wetland and estuarine habitats extending over hundreds of square kilometers (e.g., Secor 1992, Thorrold et al. 1998a, Kraus and Secor 2005). These habitats dominate along the east coast of North America, and to a lesser extent, the Pacific Northwest. Researchers working in these systems have taken great care to document the incorporation of trace elements into otoliths as a function of elemental concentrations in seawater, salinity, temperature and fish growth rate (e.g., Fowler et al. 1995, Secor et al. 1995). Investigators in these systems have also been careful to assess intra-embayment variability in signals in order to ensure reliability of inter-embayment signal variability (e.g., Thorrold et al. 1998b). Alternatively, wetlands and estuarine habitats along the southwest coast of North America are highly fragmented, modified, hypersaline, and often small in size (Zedler 1982). Studies of nursery contribution along this type of coastline have considered entire embayments as the nursery unit, and have not reported on intra-embayment variability in otolith microchemistry or nursery contribution (e.g., Forrester and Swearer 2002, Brown 2006a).

Our overall goal was to evaluate the feasibility of exploiting small-scale, within-embayment variation in otolith microchemistry to track the movements of juvenile fishes inside arid embayments of the Pacific Coast of North America. We attempted to track the movement of juvenile fishes at two scales: (1) within-embayment dispersal over several weeks, and (2) the movement of individual recruits from specific zones within an embayment to adult populations along the exposed coastline (as a measure of nursery role function; Beck et al. 2001). A requisite for this investigation was documenting the spatial patterns of signal variation inside coastal embayments.

Libraries of chemical fingerprints that represent potential nursery habitats are typically generated by collecting resident fish and sacrificing these specimens for otoliths (e.g. Gillanders 2002b, Hanson et al. 2004, Brown 2006b). An implicit assumption made in these studies is that captured fishes have resided near collection sites for sufficiently long to reflect local conditions. This may be a safe assumption in studies where collection sites are separated by 10 – 100 km (as with the studies listed above, but see discussion in Brown 2006a), but may be violated if collection sites are separated by only a few kilometers or less. One way to assure that fish are not migrating between closely spaced sites immediately prior to collection is to outplant and incubate specimens in enclosures, as Becker (2005) did for invertebrate larvae. Likewise, Forrester (2005) successfully demonstrated with reciprocal field transplants that gobies, *Gillichthys mirabilis*, could be held in small field cages for 1 month during which time they record local conditions.

We tested the utility of incubating fish in cages over monthly timescales in order to generate a series of small-scale, site-specific chemical signals within embayments. Our major goals were to: 1) compare the elemental signals from wild-caught and outplanted fish to examine the potential for caging effects on otolith microchemistry, and 2) where feasible, compared otolith chemical signals derived from caged fishes to those of wild-caught individuals of uncertain residence history in order to infer the short-term, within-embaymnet movements of resident juveniles.

Model species. The California halibut, *Paralichthys californicus*, is a flatfish found in the coastal waters of western North America. Within protected embayments, juvenile California halibut distributions can peak either near the mouth of small embayments, or more centrally within larger embayments (Fodrie and Mendoza 2006). Kramer (1991) found that juvenile halibut tended to move from shallow to deep water within embayments as they age, but recent tagging work by Griffiths et al. (submitted) in the Punta Banda Estuary suggests there is little movement of fish up- or down-axis of the embayment over 2-week periods. Together, these data suggest that halibut may utilize zones within individual embayments quite differently throughout the juvenile phase. Therefore, understanding intra-embayment variability in otolith microchemistry may greatly benefit assessment of nursery habitat utilization for this species.

Methods

Field work

Study system. Our primary study embayments were the Punta Banda Estuary (PBE) in Baja California, Mexico, and Mission Bay (MB) and San Diego Bay (SDB) in southern California (Figure 3.1). In both regions, we also evaluated sites in nearby semi-exposed or exposed habitats to serve as “embayment outliers”. The Punta Banda Estuary is located within Todos Santos Bay (TSB), a semi-enclosed coastal system 150 km south of the USA-Mexico border (31 ° 45' N, –116 ° 37' W). Immediately north and south of Todos Santos Bay, the coastline is rocky, highly exposed and unsuitable for juvenile halibut (Fodrie and Mendoza 2006). In TSB, there is suitable habitat for juvenile California halibut along an 8 km long, semi-exposed beach with sandy, sub-tidal habitat and within the Port of Ensenada, a small port in the northeast corner of the bay that was artificially created by long rock jetties. The Punta Banda Estuary is connected to Todos Santos Bay by a narrow inlet. It has a main channel 7.6 km long, a median depth of 5 m, and a simple L-shaped footprint (Ortiz et al. 2003).

In San Diego, CA, USA (32 ° 57' N, –117 ° 15" W; to 32 ° 43' N, –117 ° 14' W), we focused on two embayments (Mission an San Diego bays) and two exposed habitats (La Jolla and Imperial beaches) that provide suitable habitat for juvenile halibut. Mission Bay is roughly a 3 x 3 km square with an average depth of 5 m. There are several large dredge islands that divide the bay into multiple sections and several marinas and side basins (Largier 2003, Fodrie and Mendoza 2006). San Diego Bay covers over 4500 hectares with a mean depth of 12 m and has a J-shaped footprint. Outer San Diego Bay is deeper and serves as the major commercial and military port/harbor in the region, while the inner Bay is shallower and is host to less boating and shipping activity (U.S. Department of the Navy, Southwest Division and San Diego Unified Port District 2000).

Intra-embayment variability of otolith microchemistry. To test the coherence of otolith microchemical signals among zones within embayments, we collected and analyzed the otoliths of wild-caught fish, in addition to outplanted juveniles reared for several weeks in cages. Wild-caught fish were collected from the Todos Santos system in 2002-2003 and from San Diego in 2001. For these collections we divided Punta Banda into three zones representing the inner, middle and outer estuary, and bisected Mission and San Diego bays into inner and outer halves. Collections were made in October and November of all three years using an otter trawl. We were able to include at least 10 fish from every site in our analyses, except from the semi-exposed beach in TSB (N = 6) and Port of Ensenada (N = 7) sites in 2002.

During the spring and fall of 2003 and 2004, we also outplanted fish inside PBE and MB. During these caging experiments each embayment was divided into three zones: outer (zone 1), middle (zone 2) and inner (zone 3) (Figure 3.1). Outside each embayment we deployed cages to serve as “outliers” (at CICESE for Punta Banda, SIO for Mission Bay; Figure 3.1). Two ½-m^3 cages were deployed at each caging site during every trial, except at SIO where three cages were deployed. Cages were constructed with 6-mm

VEXAR mesh, 1" PVC piping, and marine cable ties. We avoided using metal in cages and leached all the components in seawater tanks for 2 months to reduce potential contamination of otoliths. Several sand bags filled with sediment from the caging sites were used to stabilize cages during deployment. Cages were sited sub-tidally, and allowed to settle for several days before juvenile fish were added.

Juvenile fish (80-120 mm Standard Length, SL) used for caging were collected from zone 2 of the Punta Banda Estuary (PBE cages) and the Tijuana River Estuary (MB cages) and held in laboratory tanks for 2-3 days. One day before placing them inside cages, the fishes' otoliths were marked by exposing juvenile halibut to alizarin complexone blue (ACB) dye (>30 ppb) for 12 hr (e.g., Elsdon and Gillanders 2005). Fish were then returned to the field, 4 juvenile fish were placed in each cage, and cages were sewn shut. Cages were regularly checked for debris and positioning, but not disturbed until fish were recovered at the end of 2 months. Several cages were lost because of the high flow-rates within the embayments, and absence of metal components to anchor or strengthen cages (for recaptures, see Table 3.1). As a result, we only recovered enough fish to examine intra-embayment variability using outplanted fish in Punta Banda during March-April of 2004, and in Mission Bay during September-October of 2003 and 2004. We present results from Punta Banda, spring 2004, and Mission Bay, fall 2003.

Comparison of outplanted vs. wild-caught otolith microchemical signals to infer recent movements. Due to their fixed position within cages, we also used outplanted fish to provide reference material for investigating the small-scale movements of wild-caught juvenile halibut within embayments. This was accomplished by collecting wild-caught juveniles via otter trawling adjacent to cages simultaneously to recovery of outplanted fish and making direct comparisons of otolith microchemistry between the two groups. All outplanted and wild-caught fish included in these comparisons were 80-120 mm SL.

Nursery contribution of embayment zones. The juvenile halibut collected in the TSB system in 2002 and 2003 to test for embayment-scale coherence of otolith signals were also used to generate a reference set of habitat-specific chemical fingerprints that represented all potential nurseries for juvenile halibut in the area. In 2005, we collected sub-adult halibut from the TSB system directly from local fishermen, who captured fishes by hook-and-line fishing. By comparing the otolith signals from 2- and 3-year-old fish collected from fishermen to the reference set generated from the 2002 and 2003 juvenile collections, nursery habitat origins could be inferred for individual 2- and 3-year-old fish.

Otolith analyses

Preparation and analyses. Sagittal otoliths were dissected using sterile scalpels and ceramic forceps. Otoliths were then sonicated for 5 min in 15% H_2O_2 buffered with 0.05 mol L^{-1} NaOH and 3% HNO_3^- to completely remove organics. We mounted otoliths in crazy glue on petrographic slides, sanded them along the sagittal plane using 30-µm and 3-µm lapping paper, and polished them using a rock cloth wetted with Milli-Q water (Secor et al. 1991). Mounted otoliths were given a 5 min rinse in 15% H_2O_2 and 3%

HNO_3^-, and then rinsed three times with Milli-Q before being dried and stored in a laminar flow hood. All plastic containers, glass slides and forceps were rinsed with a 3% HNO_3^- solution before contact with otoliths. We only examined otoliths from the blind side of fish to ensure that all otoliths were recording from the same environment (sediment interface). Since this species can be left-or right-eyed, the sagittal otolith we selected varied among individuals.

We sampled specific growth rings using a New Wave UP 213 nm laser ablation (LA) unit. Otoliths were sampled by ablating a 300-µm line along targeted rings at 50% intensity, 15-µm s^{-1} scan speed and a 20-µm spot size. Post-run inspection of 10 haphazardly selected otoliths revealed that ablations could range between 20-35 µm in width and 8-14 µm in depth. Given that the average daily increment width in juveniles measures ca. 1-3 µm, we sampled roughly 1-2 weeks of growth per abalation (Kramer 1990). Ablated material was transported using He gas (mixed with Ar) to a Thermoquest Finnigan Element 2 double focusing, single collector, magnetic sector Inductively Coupled Plasma Mass Spectrometer (ICPMS). Based on previous results of elemental fingerprinting of mussels collected from San Diego County (Becker et al. 2005), we sampled for the following isotopes to maximize spatial discrimination: ^{26}Mg, ^{48}Ca, ^{55}Mn, ^{63}Cu, ^{88}Sr, ^{65}Cd, ^{135}Ba, ^{208}Pb, and ^{238}U. Data processing to generate isotopic counts standardized to calcium ($X{:}^{48}Ca$) also followed Becker et al. (2005).

Glass standards spiked with trace elements (National Institute of Standards and Technology Standard Reference Material 612, 614, and 616; NIST 612: Pearce et al

1997; NIST 614 and 616: Horn et. al. 1997) were analyzed at the beginning and end of each day to account for machine drift. Unfortunately, calcium carbonate matrix-matched standards were not available at the time of our analyses. However, NIST provides good precision and allows for intra-study consistency between samples (Putten et al. 1999).

Intra-embayment variability of otolith microchemistry. We ablated rings from the post rostrum margin (PRM) of each juvenile otolith collected during the fall surveys in Todos Santos Bay (2002-2003) and San Diego (2001). These ablations sampled the most recent growth rings laid down by these fish. Ablations were begun as close to the post rostrum apex as possible, and progressed ventrally along the margin. The mean distance from the otolith nucleus to the PRM was 1250 μm.

Comparison of outplanted vs. wild-caught otolith microchemical signals to infer recent movements. The outplanted fish that were marked with alizarin complexone blue (ACB) exhibited three distinct growth patterns during caging: (1) 80-100 μm of normal growth increments from the ACB mark to the otolith margin, (2) 80-100 μm of growth from the ACB mark to the otolith margin without visible ring increments, and (3) no apparent growth following the ACB mark. We excluded the third class from elemental analyses, but did include the otoliths without visible increments. On these otoliths, we sampled along the PRM as described above, but sampled again adjacent to the ACB mark (using the same laser settings) at ~ 80 μm inside the otolith edge. Hence, we obtained chemical signals corresponding to the period immediately before retrieval (e.g., along the PRM) as well as the period of time shortly after the caging began (PRM - 80 μm). The same rings (PRM and PRM - 80 μm) were sampled from the wild-caught fish (14 individuals in which we were able to count growth increments clearly) collected in conjunction with the caging experiments.

Nursery contribution of embayment zones. On the 2- and 3-year-old halibut otoliths collected from Todos Santos Bay in 2005, we ablated material 1250 ± 300 μm (the range allowed us to target what appeared to be fall growth) outside the otolith nucleus in the direction of the PRM. These represent the rings laid down during the first year of the fish's life, and could be compared to the signals from 2002-2003 juveniles (see above) to infer nursery habitat origin. Successive rings appeared to have "elbows" indicating the approximate location of the PRM apex in earlier growth rings which we used to position our ablations.

Statistical analyses

Isotope to calcium ratios (X:^{48}Ca) were analyzed using linear Discriminant Function Analysis (DFA; Systat 9, © SPSS). DFA is a data reduction approach that utilizes multivariate datasets to generate a series of orthogonal algorithms (scores) that maximize variance among data groups. Distinct groups in DFA space represent unique spatial fingerprints that can be compared to data from samples of unknown origin and movement history. Cross-validation of each DFA model was achieved following their creation by re-classifying each sample using just its individual score without it's a priori grouping.

Intra-embayment variability of otolith microchemistry. Location-specific fingerprints were generated from the otoliths of juvenile halibut collected from Todos Santos (5 sites in 2002-2003) and San Diego County (6 sites in 2001) to examine the inter- and intra-embayment variability in chemical signals. For the San Diego collections, we also examined the ability of DFA algorithms to distinguish among putative nurseries by pooling the bay sites according to individual embayments (Mission Bay vs. San Diego Bay), and regions of bays (inner vs. outer). These data were supplemented by DFA models generated from the otolith signals of outplanted fishes in the Punta Banda Estuary (spring 2004) and Mission Bay (fall 2004).

Comparison of outplanted vs. wild-caught otolith microchemical signals to infer recent movements. In order for caged fishes to serve as useful proxies of site-specific signals that can be employed to infer movement of non-caged fishes over small distances, two requirements must be met. First, there must be general agreement in the X:^{48}Ca ratios of the most recently deposited growth increments in otoliths from outplanted and wild-caught fishes collected from the same place and time. Second, there must be differences in the X:^{48}Ca ratios in the otoliths of outplanted fishes incubated in different zones within an embayment. We used two-factor ANOVAs (StatView 5.0.1, © SAS Institute Inc.) to test for similarities between the elemental composition measured in the PRM of caged and wild-caught fishes collected simultaneously and from each zone within PBE and MB in order to evaluate the effects of caging and embayment zone on otolith signals. Separate analyses were conducted for PBE and MB, and only isotopes included in the DFAs generated from post rostrum ablations on outplanted fishes were considered to test for the significance of main effects. Parametric tests were used as F-tests revealed no heteroscedasticity among groups.

To reconstruct the recent movement history of wild-caught juveniles captured in the vicinity of the cages inside the Punta Banda Estuary, separate DFA models were generated from the PRM – 80-µm data sets obtained from outplanted fishes. We compared the PRM – 80-µm data from wild-caught fish to the DFA model generated from PRM – 80-µm ablations on outplanted fish. We used these data to infer the movement patterns of wild-caught halibut over a 2 month period.

Nursery contribution of embayment zones. The juvenile halibut collected in Todos Santos Bay system in 2002 and 2003 from the semi-exposed beach, Port of Ensenada and Punta Banda Estuary (inner, middle and outer zones) were used to generate a reference set of habitat-specific chemical fingerprints that represented all potential nurseries for juvenile halibut in the area (assuming a closed system). These algorithms were used to assign nursery habitat origin to 2-year-old (relative to the 2003 library) and 3-year-old (relative to the 2002 library) sub-adults collected in 2005 within the system.

Results

Intra-embayment variability of otolith microchemistry. For fishes collected in 2002 and 2003 in PBE and TSB, we generated distinct fingerprints representative of individual collection sites (Figure 3.2A, B). Overall classification success for the five sites was above 70% in both years (Table 3.2). After stepwise elimination of isotope ratios, ^{26}Mg:, ^{55}Mn:, ^{88}Sr: and ^{135}Ba:^{48}Ca remained in the final DFA model for the 2002 data set and ^{55}Mn:, ^{63}Cu: and ^{135}Ba:^{48}Ca for the DFA corresponding to 2003 (Figure 3.2C, D). In both years, PBE3 was distinguishable from all other sites by high ^{55}Mn:^{48}Ca ratios, and in 2002 we also detected high ^{135}Ba:^{48}Ca in the innermost zone of PBE. PBE2 also separated from other sites but appeared to be transitional in elemental composition between PBE3 and PBE1. In 2002, PBE1 signals overlapped with Todos Santos and the Port of Ensenada, but in 2003 PBE1 was distinct from all other sites.

In San Diego, otolith signals from La Jolla and inner Mission Bay were clearly distinct from all other sites we considered (Figure 3.3A; Table 3.3). Conversely, signals from Imperial Beach and the other 3 embayment sites showed considerable overlap. Stepwise elimination of isotope ratios left ^{55}Mn: and ^{88}Sr:^{48}Ca in the final DFA model (Figure 3.3B). Between the exposed habitats, La Jolla and Imperial Beach, we observed a notable difference in ^{88}Sr:^{48}Ca. Notably, pooling bay sites according to zones (inner vs. outer) was equally effective in maximizing overall classification success as classifying sites by individual bays (Table 3.3). For instance, Mission and San Diego bay samples were correctly classified 83 % and 44 % of the time (63% overall), respectively. Alternatively, inner and outer zones were classified with success rates of 91 % and 44 %, respectively (61% overall).

Analyses of outplanted fish also indicated considerable signal variability in chemical signals within embayments. The different zones of the Punta Banda Estuary ere well separated by PRM-based signals of outplanted fish (Figure 3.4A, C). PBE3 was most clearly distinguishable from the other zones, driven mainly by high ^{55}Mn: and ^{135}Ba:^{48}Ca. PBE2 also appeared to have higher ^{55}Mn: and ^{135}Ba :^{48}Ca ratios than PBE1 and the site in Todos Santos Bay, while PBE1 fish were distinguishable in DFA space from Todos Santos Bay fishes by higher ^{135}Ba:^{48}Ca (Figure 3.4A, C). Overall classification success was high (96%); only 1 out of 24 fishes was classified to an incorrect zone (a PBE1 fish was scored as being from Todos Santos Bay; Table 3.4A).

In Mission Bay, discriminant algorithms were generated using ^{55}Mn:, ^{63}Cu:, ^{88}Sr: and ^{238}U:^{48}Ca isotope ratios from otoliths of outplanted fish (Figure 3.4D). Although only two fishes from MB3 were analyzed for elemental composition (based on recapture rates and the evidence of otolith growth during caging), both chemical signals were well separated from fish captured in other zones within the Bay due to high ^{55}Mn: and ^{63}Cu:^{48}Ca ratios (Figure 3.4B). MB1 and MB2 fish demonstrated overlapping signals characterized by high ^{88}Sr: ^{48}Ca ratios. All Mission Bay signals separated from the exposed site (SIO) due to relatively low ^{238}U:^{48}Ca and high ^{55}Mn: and ^{63}Cu:^{48}Ca ratios. Specimens were correctly assigned to caging sites 76 % of the time in Mission Bay (Table 3.4B).

Comparison of outplanted vs. wild-caught otolith microchemical signals to infer recent movements. There were no significant differences in the ^{55}Mn: or ^{135}Ba :^{48}Ca ratios between outplanted and wild-caught fishes collected in the Punta Banda Estuary (Table 3.5). Alternatively, there was a significant effect ($p < 0.05$) of embayment zone on both isotopes, indicating that the elemental composition of the otoliths differed between zones. The ^{55}Mn: ^{48}Ca ratios observed in PBE1 and PBE2 for outplanted and wild-caught fish were similar (although a little higher for outplanted fish in both zones). However, ^{55}Mn: ^{48}Ca values were twice as large in PBE3, where the signals from wild-caught fish were more enriched in ^{55}Mn (Figure 3.5A). As for ^{55}Mn: ^{48}Ca, ^{135}Ba:^{48}Ca ratios were almost double in PBE3 fishes relative to those from PBE1 and PBE2 (Figure 3.5B). Outplanted and wild-caught specimens from PBE1 and PBE3 showed a high degree of similarity in ^{135}Ba:^{48}Ca ratios, but wild-caught fishes from PBE2 had about one-third the ^{135}Ba:^{48}Ca as recorded in the otoliths of outplanted fishes from the same location. No interaction between zone and caging was observed for any of the isotope ratios. The difference in the elemental composition of wild-caught California halibut captured in the various zones of the Punta Banda Estuary, and the lack of a difference in the signals originating from wild-caught and caged fishes, implies elemental analysis can be used to infer the movement of individuals within the system.

In Mission Bay, none of the isotope ratios (^{55}Mn:, ^{63}Cu:, ^{88}Sr: and ^{238}U:^{48}Ca) included in the DFA of outplanted fish demonstrated significant differences among zones (Table 3.5). Alternatively, ^{55}Mn:, ^{88}Sr:, and ^{238}U:^{48}Ca ratios were all significantly different between outplanted and wild-caught fishes (Table 3.5). ^{55}Mn and ^{238}U:^{48}Ca ratios were lower in outplanted fishes relative to wild-caught individuals in almost all zone-specific comparisons, while the reverse was observed for ^{88}Sr:^{48}Ca (Figure 3.5C, E, F). Only ^{63}Cu demonstrated no significant difference in outplanted vs. wild-caught fishes ($p = 0.993$) (Table 3.5, Figure 3.5D). No interaction between zone and caging was observed. These results precluded the use of outplanted fish as proxies for tracking the small-scale movements of juvenile halibut in Mission Bay.

The fingerprints generated from outplanted fish in the Punta Banda Estuary were used to generate a reference set of zone-specific signals to chart the small-scale movements of juvenile halibut. DFA models were generated from the PRM – 80-μm ablations on otoliths of outplanted fish. Chemical signals from these ablations reflected ca. 2 months prior to the date of collection. We selected ^{55}Mn: and ^{135}Ba:^{48}Ca ratios for generating the DFA model because they had been used in the DFA model generated from PRM ablations and had passed the tests regarding “zone” and “caging” effects. Based on the otolith chemistry (^{55}Mn: and ^{135}Ba:^{48}Ca ratios) from the 14 wild-caught individuals that we analyzed, 8 had moved among zones during the two months prior to capture, with a slight trend toward fishes moving up-estuary during the spring 2004. Of the 8 individuals collected in PBE1, 1 appeared to have recently moved into the estuary from Todos Santos Bay, while 3 fish appeared to have moved from PBE2 toward the mouth PBE2 (Table 3.6). Four other fishes had elemental compositions that suggested they resided in zone 1 throughout the experiment. Of the 3 fish collected in PBE2, 1 had occupied PBE1 at the start of the caging, and the other 2 had remained in PBE2 over the course of 2 months (Table 3.6). None of the 3 wild-caught fish we analyzed that were taken from PBE3 were long-term residents. Two had immigrated to zone 3 from zone 1, and the other had moved from PBE2 (Table 3.6).

Nursery contribution of embayment zones. Twenty-seven subadults (N = 14 two-year old and N = 13 three-year old) were captured in Todos Santos Bay and the Punta Banda Estuary to infer past habitat utilization patterns. Based on otolith microchemistry, 9 of the 2-year-old fish were assigned to a nursery origin inside the estuary (Figure 3.6). The remaining 5 two-year-old fishes were assigned to Todos Santos Bay (3) and Port of Ensenada (2) nurseries. All 3-year-old fishes were classified as having resided in the Punta Banda Estuary during the fall of 2002. Overall, Punta Banda accounted for 82% of the 0-group fish that advanced to older age classes, while Todos Santos and Port of Ensenada accounted for the remaining 11 % and 7 % of the advancing juveniles, respectively. All production from the estuary was assigned to zones 1 and 2. None of the fishes appeared to have occupied PBE3 during October-November of 2002 or 2003.

Discussion

Intra-embayment variability of otolith microchemistry. We observed distinct chemical fingerprints among habitats and zones within embayments along two segments of the Alto and Baja California coastline (Figure 3.2, 3.3, 3.4). Chemical fingerprints from these embayments and the adjacent exposed coast are better represented as a following a gradient, rather than a step change between two habitat types. Because coastal systems are classically recognized as biogeochemical transformers located between terrestrial and marine ecosystems, this result could have been expected (Mitsch and Gosselink 2000). In both juvenile surveys and outplanting experiments, the isotopes that were most useful in distinguishing embayment zones were ^{55}Mn, ^{88}Sr and ^{135}Ba (Figures 3.2, 3.3, 3.4). These elements have consistently been applied in embayment contribution studies, and should be considered valuable markers for attempts to unify environmental trends across regions (e.g., Gillanders and Kingsford 2003, Hanson et al. 2004, Forrester 2005).

Gillanders and Kingsford (2000), working along southeast Australia, were the first to examine if zones within an embayment of similar size and isolation to those found along the west coast of North America could demonstrate differences in otolith microchemistry, but results have been mixed. Kingsford and Gillanders (2000) found that nearby sites could exhibit significant variability in otolith microchemistry, while a related study found that intra-estuary variability was much less important than inter-estuary differences in otolith signals for snapper species (Gillanders and Kingsford 2003). Our data suggest that in order to accurately classify habitat signals along the Alto and Baja California coastline, future experiments must also consider the coherence of fingerprints within individual embayments. For example, intra-embayment variability was as powerful in distinguishing habitat-specific otolith microchemical signals as inter-embayment variability in San Diego during the fall of 2001 (Table 3.3). To insure that all important fingerprints are included in the library of nursery habitat signals, a necessary component of elemental fingerprinting studies to determine past habitat utilization

(Campana et al. 2000), researchers should either sample multiple zones within embayments that are potential nurseries (e.g., Gillanders and Kingsford 2003), or systematically survey each putative nursery embayment to locate the centers of juvenile fish distributions before collecting specimens to catalogue the fingerprints of all potential nurseries (e.g., Fodrie and Mendoza 2006).

In both Punta Banda Estuary and Mission Bay, fingerprints from the outer and middle thirds of the embayments tended to be more chemically similar (Figure 3.2, 3.4), while the innermost third was much more distinct because of high ^{55}Mn and ^{135}Ba :^{48}Ca ratios in halibut otoliths. Becker et al. (2005) reported similar zones for distinguishing mussel shell chemistry. Two likely, interacting mechanisms responsible for this are: 1) sediment redox cycles, and 2) tidal excursions within embayments. Within southern California embayments, manganese availability in near-bottom water is dominated by the reduction-oxidation reactions that occur in the sediments and overlying water column (J Gieskes, personal communication). Within San Diego Bay, there is a nearly linear trend in Mn seawater concentration moving from the mouth (< 1 ppb) to the head (> 30 ppb) (Esser and Volpe 2001). In muddy, anoxic sediments found in the inner regions of embayments, dissolved manganese is released (net transport) into the water column and becomes bioavailable for incorporation into the calcium carbonate matrix of growing otoliths (Hanson et al. 1993). Because most embayments are characterized by sandy sediments near the mouth that are constantly reworked by tidal flow, Mn efflux from the sediment is low near the mouth.

For protected embayments the size of Punta Banda Estuary, Mission Bay and San Diego Bay, excursions of “coastal” water during high tides typically reach only about half to two-thirds up the embayment. Largier et al. (2003), using dye and float traces, observed that over the course of several days, a water particle released from the back of the bay would typically remain within 500 m of the original release point, remaining near our MB3 cages (for San Diego Bay circulation see, Largier et al. 1999). As a result, inner embayment water masses potentially carry trace element loads surprisingly different from the water only a few km closer to the embayment mouth.

Arid coastline embayments. Our results should have greatest impact for research along similarly arid coastlines such as the west coasts of Australia and southern Africa (Largier et al. 1997, Potter et al. 1990). Embayments in these regions are characterized by small size and hypersalinity (Zedler 1982). These systems differ from the large estuarine habitats that dominate along the east coast of North America, or fjord systems of high-latitude coasts, in a number of important ways that will contribute to spatial gradients in chemical signals. For example, Li and O’Donnell (2005) modeled the residual circulation of embayments and determined that estuaries with a long-axis greater than 50 km could experience highly retentive flow (in the inner estuary) if circulation was tidally dominated. While Long Island Sound, Chesapeake Bay and Neuse River Estuary may all be large enough to experience these dynamics, there are no embayments in southern California large enough to experience similar residual circulation based upon Li and O’Donnell’s (2005) results.

Another critical difference between coastal regions is the amount of freshwater input that embayments receive. Even the coastal habitats along the southeast coast of Australia studied by Gillanders and Kingsford (2000) to document the intra-embayment variability in otolith signals receive 4 times the annual rainfall as occurs in southern California (www.weather.com) As a result, oxygen, carbon, and strontium isotope ratios may be of greater use in these lagoons and estuaries that in the less freshwater-impacted embayments of southern California, western Africa and western Australia. This hypothesis, however, remains largely untested.

Comparison of outplanted vs. wild-caught otolith microchemical signals to infer recent movements. Outplanting specimens in field enclosures offers a novel but untested method for obtaining site signals such that spatial variability in fingerprints and recent fish migrations can be discerned from one another. Fish outplanted in several zones along the axis of an estuary can record environmental differences that, at least in Punta Banda, are consistent with the trends obtained from wild-caught fish (Table 3.5, Figure 3.4, 3.5). Using caged fish to generate a reference set of zone-specific signals for Punta Banda, PRM – 80-µm results suggested that the further up-estuary we collected specimens, the farther they had migrated up-estuary during the caging period (Table 3.6). These data correspond to the spring immigration of newly-settled halibut into coastal embayments (Kramer 1991), and suggest that juvenile halibut are capable of considerable movement over relatively short (2 month) timescales.

Although the PRM signals from outplanted and wild-caught fish in Punta Banda were deemed similar enough to use outplanted fish for generating zone-specific elemental fingerprints, an equally interesting result was that outplanted and wild-caught juveniles did not map perfectly on one another. The differences we observed may have been generated by the immigration of wild-caught fish immediately prior to collection. This is especially interesting given that our caging sites were only separated by 100s of meters to several kilometers. It remains unclear why outplanting appeared to work much better in Punta Banda, but perhaps the more complex footprint of Mission Bay may have resulted in fish being able to more readily migrate shortly before fish were collected to caging sites from nearby sites characterized by distinct, undocumented fingerprints. As a result, we were comparing fingerprints of outplanted to wild-caught fish that had recorded environments within the bay that we did not sample, and this produced the disconnect in the otolith signals of outplanted and wild-caught fish inside Mission Bay. Brown (2006b) generated habitat-specific fingerprints for English sole along the central California coastline, and observed that many of the fish that were misclassified in discriminant models had values that were intermediate between habitats types. She hypothesized that fish may have recently migrated between sites, or that fish regularly moved between habitat types and integrated both signals. Because Punta Banda is characterized by a simple L-shaped morphology, the potential for recent immigration may have been dampened in the Estuary relative to Mission Bay. Over small spatial-scales, the assumption that fish collected at a site have been residents long enough to have incorporated local signals may be routinely violated.

Alternatively, caging can alter flow, feeding rates and induce physiologic stress (sensu Peterson and Black 1994). These effects may interact with caging site to generate artifacts in the elemental signals observed in the otoliths of outplanted fish, and make the data useless in documenting smaller-scale (spatial or temporal) signal variability relevant for tracking wild-caught fish. Caged fish collected for growth rate analyses in a related study had very different stomach contents than wild-caught fish from the same locations (Herzka unpublished). Because some of our outplanted fish demonstrated no or altered growth increments during caging, feeding changes or physiologic stress may have played a key role in the difference we observed between outplanted and wild-caught fish, although it remains unclear how much impact these factors have in determining uptake rates in otoliths for this species (Campana 1999). Ultimately, more work is needed before caging can routinely be used to generate proxies for habitat or site signals.

Nursery contribution of embayment zones. By exploiting small-scale variability in otolith signals, we have begun to tease apart the role of embayment zones in promoting stock success for the California halibut, as well as further resolve the connectivity between estuarine and marine populations. Elemental fingerprinting indicated a large majority (82%) of halibut production from nursery habitats within Todos Santos Bay originated from the Punta Banda Estuary during 2002 and 2003, assuming that Todos Santos is a closed system. By considering small-scale variability in site fingerprints, we were also able to demonstrate that all of the halibut that had advanced from Punta Banda had occupied the middle and outer zones of the estuary in the fall of 2002 and 2003. Conversely, the productivity of the inner Punta Banda Estuary for older halibut stocks was essentially zero during this same period. This is a somewhat surprising result since Griffiths et al. (submitted) collected a considerable number of juvenile fish from all three zones during the summer of 2004, with a peak in densities in the zone we defined as PBE2 (middle). Our contribution results may be sensitive to collection season, and had we collected fish during the summer in this study to generate nursery habitat chemical fingerprints, and then analyzed the growth rings of 2- and 3-year-old fish deposited during the summer, we might have recorded more zone 3 contribution. Swearer at el (2004) have demonstrated that there is considerable seasonable variability in the chemical signals of halibut otoliths, and we hesitated to use the fingerprints from fish collected in the fall to generate predictions of nursery habitat utilization during the summer.

Still, our results of juvenile migrations and nursery habitat contribution indicate that there are important differences in the way embayment zones are utilized by juvenile halibut along the California coastline. At the very least, juvenile halibut appear to use inner regions of embayments for much shorter periods of the season than sites closer to the mouth. Beck et al. (2001) formulated a definition of the nursery-role concept that stressed per unit area production to the adult stock in order to evaluate juvenile habitat value. This has provided a clearer framework of habitat classification for conservation or management efforts. According to Beck et al. (2001), nurseries are those habitats with above average unit-area production of adults. Applying the nursery-role concept to Punta Banda would mean that zones 1 and 2 are important nurseries, and zone 3 is not. The ability to evaluate habitat use and movement patterns at spatial scales smaller than entire embayments via elemental fingerprinting has direct implications for the management of coastal embayments, specifically whether environmental perturbations in embayments should be expected to have impacts that are highly localized or spatially cascading.

Figures and tables

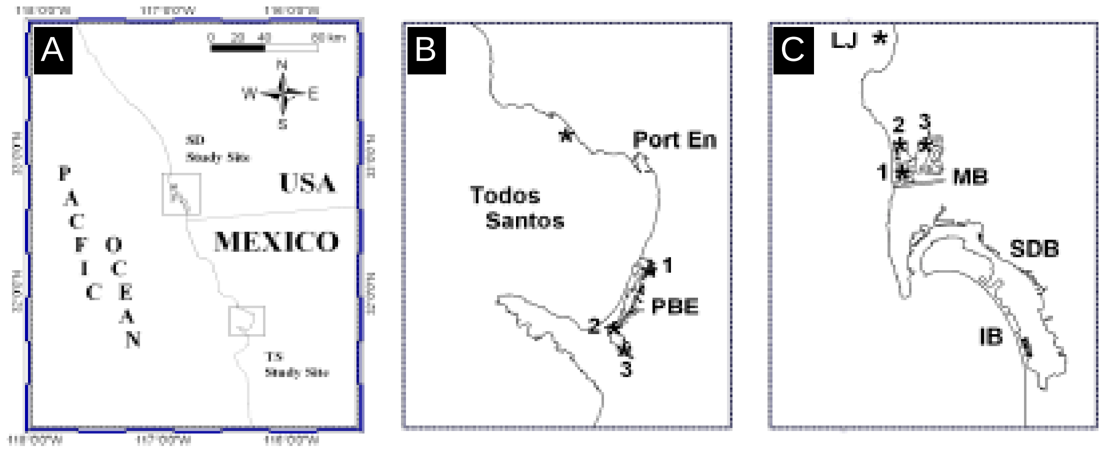

Figure 3.1. (A) Map of juvenile halibut collections and caging experiments in Todos Santos (Mexico) and San Diego (USA). (B) and (C) are blow-ups of Todos Santos and San Diego, respectively. Port En = Port of Ensenada; PBE = Punta Banda Estuary; MB = Mission Bay; SDB = San Diego Bay; LJ = La Jolla; IB = Imperial Beach. Cages were outplanted semi-annually during 2003 and 2004 within the Punta Banda Estuary (Mexico) and Mission Bay (USA) with locations denoted by "*".

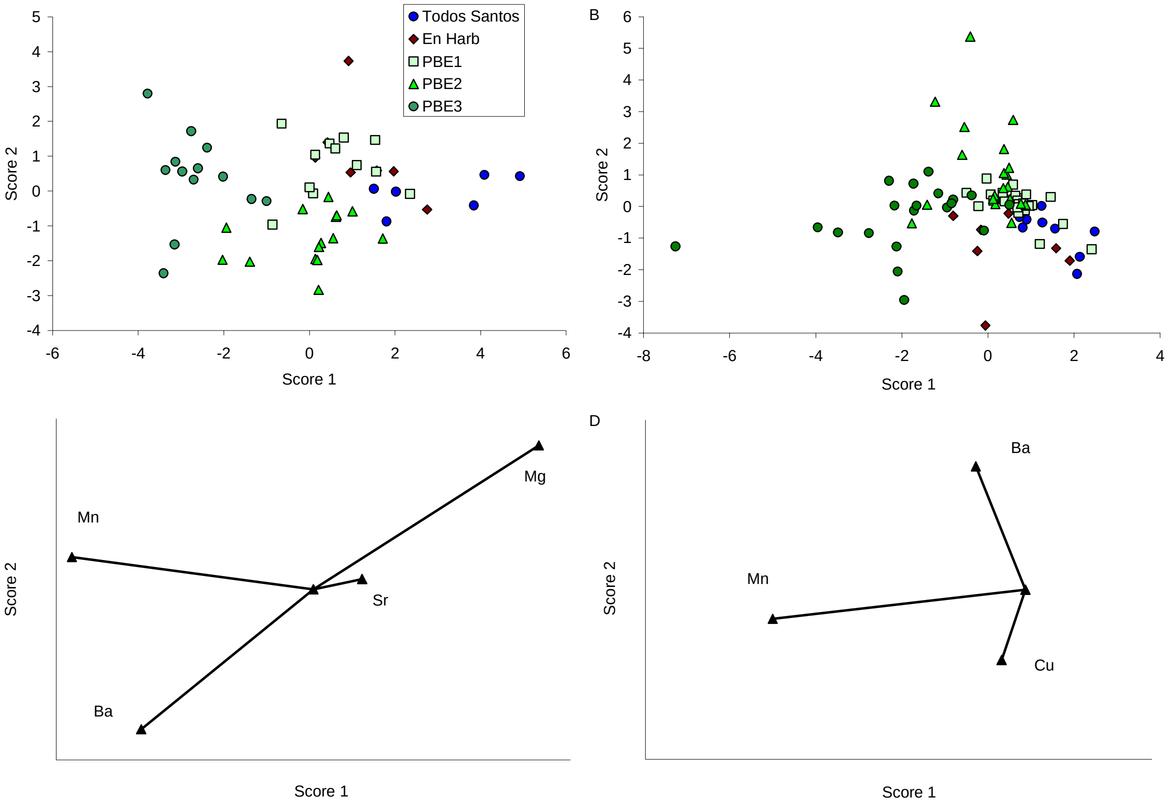

Figure 3.2. Discriminant scores of isotope ratios to Ca in otoliths of juvenile halibut collected during the fall of 2002 (Mg, Mn, Sr and Ba) and 2003 (Mn, Cu and Ba) within putative nursery habitats in Todos Santos Bay. Sites are grouped as Todos Santos, Ensenada Harbor (En Harb), outer Punta Banda Estuary (PBE 1), middle Punta Banda Estuary (PBE 2) and inner Punta Banda Estuary (PBE 3). Scatterplots of 2002 (A) and 2003 (B) DFA scores are presented. Also shown are 2002 (C) and 2003 (D) discriminant functions, standardized by within variances, for the isotope ratios used to create algorithms. Vectors represent the relative contribution of each isotope ratio to the resulting scores for each group.

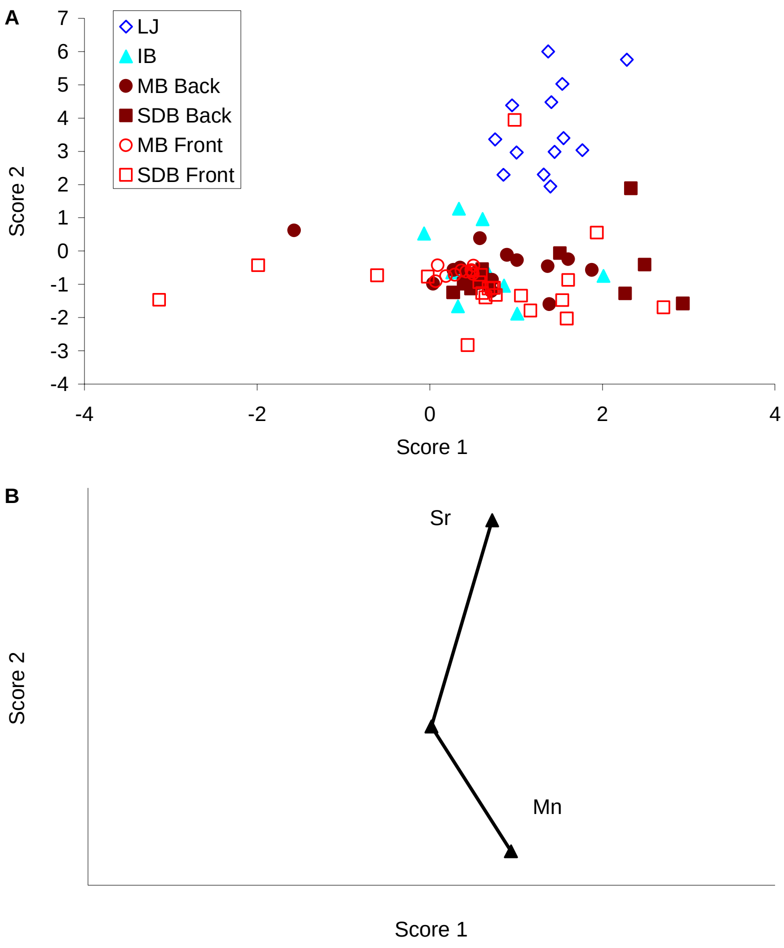

Figure 3.3. Discriminant scores of isotope (Mn & Sr) ratios to Ca in otoliths of juvenile halibut collected during the fall of 2001 at sites in southern Diego County, grouped between exposed sites: La Jolla (LJ) and Imperial Beach (IB); and bay sites: inner Mission Bay (MB Inner), outer Mission Bay (MB Outer), inner San Diego Bay (SDB Inner), and outer San Diego Bay (SDB Outer). (A) Scatterplot of DFA scores; (B) Discriminant functions, standardized by within variances, for the isotope ratios used to create algorithms. Vectors represent the relative contribution of each isotope ratio to the resulting scores for each group.

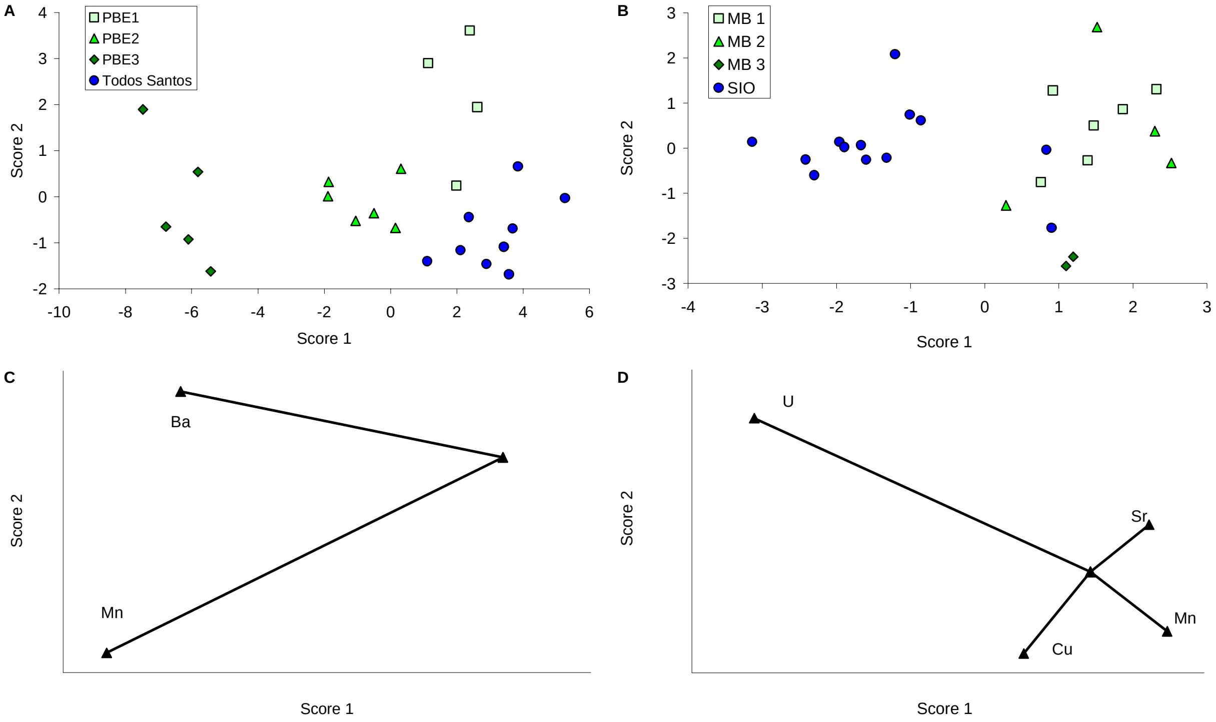

Figure 3.4. Discriminant scores of isotope ratios (X:^{48}Ca) from the post rostrum margin of otoliths of outplanted juvenile halibut incubated in Punta Banda Estuary and Mission Bay. Punta Banda (A) and Mission Bay (B) results presented as scatterplots of DFA scores. Punta Banda (C) and Mission Bay (D) discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores. Sites in (A) are grouped as: outer Punta Banda Estuary (PBE 1), middle Punta Banda Estuary (PBE 2) and inner Punta Banda Estuary (PBE 3), and Todos Santos = embayment "outlier". Sites in (B) are grouped as: outer Mission Bay (MB 1), middle Mission Bay (MB 2), inner Mission Bay (MB 3) and SIO = embayment "outlier".

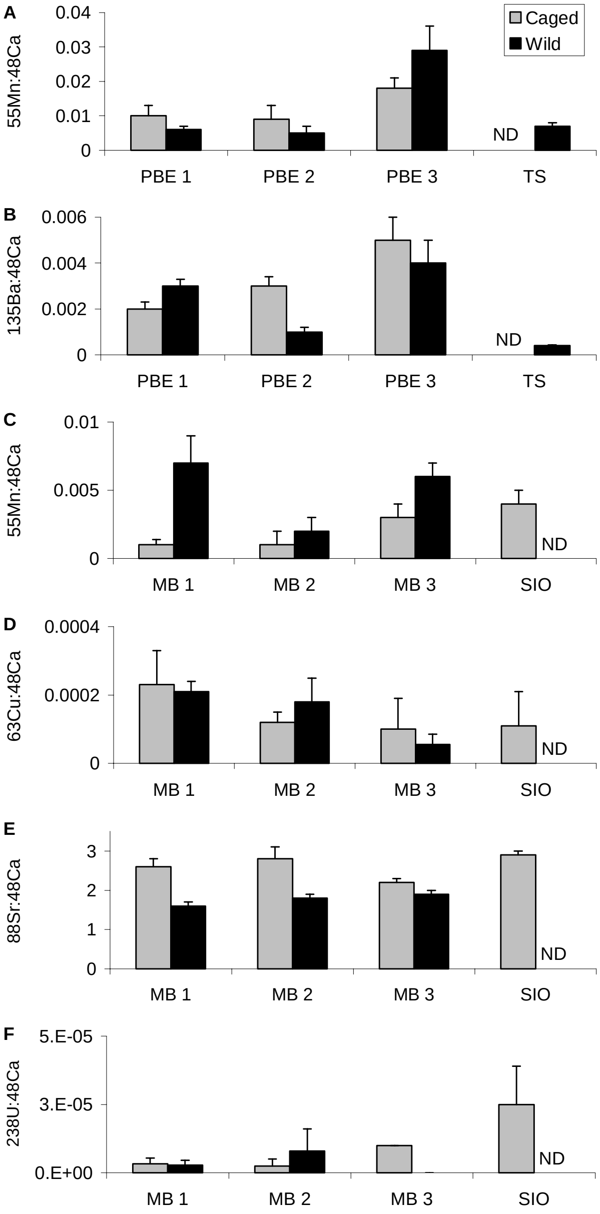

Figure 3.5. Isotopic ratios (X:^{48}Ca) in otoliths of outplanted and wild-caught juvenile halibut collected within embayment zones during the Punta Banda (A-B) and Mission Bay (C-F) caging experiments. Error bars represent +1 standard error. (A, C) ^{55}Mn, (B) ^{135}Ba, (D) ^{63}Cu, (E) ^{88}Sr, (F) ^{238}U and. Results of otolith microchemistry group comparisons (ANOVA) are included in Table 3.5.

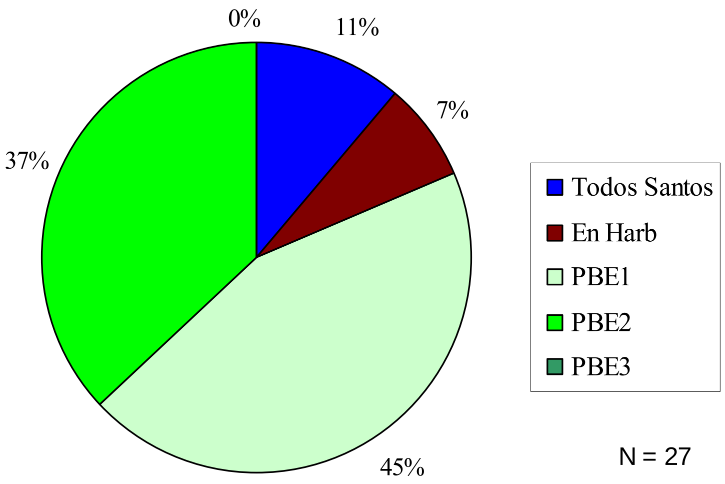

Figure 3.6. Relative contribution (0-group fish advancing to older age classes) of putative nursery habitats within Todos Santos Bay. Contribution was determined retroactively via elemental fingerprinting of juvenile and sub-adult halibut otoliths. Contribution from specific zones within Punta Banda Estuary are presented.

Table 3.1. Number of juvenile (80-120 mm SL) halibut collected from cages deployed during the spring (S) and fall (F) of 2003 and 2004. Cages (N = 2, except for SIO where N = 3) were outplanted and allowed to incubate for 2 months within a number of zones inside Punta Banda Estuary (PBE) and Mission Bay (MB). Each cage contained 4 halibut at t = 0. Each lost cage is denoted with *. See Figure 3.1 for caging locations.

Region	Zone	S 2003	F 2003	S 2004	F 2004
PBE					
	PBE1	0 **	0 **	4	0 **
	PBE2	8	4	8	6
	PBE3	0 **	2 *	5	0 **
	CICESE	0 **	0	0	0 **
MB					
	MB 1	0 **	5	0 *	8
	MB 2	4	5	4	2
	MB 3	4 *	4	8	2 *
	SIO	0 ***	11	10	6

Table 3.2. Classification matrix of assignments for otolith signals from juvenile halibut collected from putative nursery habitats within the Todos Santos Bay system. Discriminant Function Analysis (DFA) was used to generate assignment algorithms. Rows list actual collection sites and columns list the predicted site of collection using DFA algorithms, with replacement. Success rates are presented for individual sites (A): Todos Santos Bay, Port of Ensenada (Port En), outer Punta Banda Estuary (PBE1), middle Punta Banda Estuary (PBE2) and inner Punta Banda Estuary (PBE3), as well as by sites grouped by habitat type (B): semi-exposed coast, port and estuary.

A

	Predicted						Habitat
	Todos Santos	Port En	PBE1	PBE2	PBE3	% Correct	% Correct
Actual							
Todos Santos	5	1	0	0	0	83	83
Port En	2	3	2	0	0	43	43
PBE1	1	3	7	1	0	58	90
PBE2	0	0	2	12	1	80	
PBE3	0	0	0	1	12	92	
Totals	8	7	11	14	13	74	83

B

	Predicted						Habitat
	Todos Santos	Port En	PBE1	PBE2	PBE3	% Correct	% Correct
Actual							
Todos Santos	7	0	3	0	0	70	70
Port En	2	6	1	0	1	60	60
PBE1	0	1	23	3	0	85	93
PBE2	1	0	6	11	2	55	
PBE3	2	1	0	2	15	75	
Totals	12	8	33	16	18	70	86

Table 3.3. Classification matrix of assignments for otolith signals from juvenile halibut collected along San Diego County. Discriminant Function Analysis (DFA) was used to generate assignment algorithms. Rows list actual collection sites and columns list the predicted site of collection using DFA algorithms, with replacement. Success rates are presented for individual sites (% correct site),individual bays (bay % correct) and zones within bays (zone % correct). Sites include La Jolla (LJ), Imperial Beach (IB), inner Mission Bay (MB Inner), inner San Diego Bay (SDB Inner), outer Mission Bay (MB Outer), and outer San Diego Bay (SDB Outer).

	Predicted						Site	Bay	Zone
	LJ	IB	MB Inner	SBD Inner	MB Outer	SDB Outer	% Correct	% Correct	% Correct
Actual									
LJ	13	0	0	0	0	0	100	100	100
IB	0	1	5	2	1	1	10	10	10
MB Inner	0	0	11	0	0	0	100	(MB) 83	(Inner) 91
SBD Inner	1	1	6	3	0	0	27	(SDB) 44	
MB Outer	0	0	8	2	5	3	28		(Outer) 44
SDB Outer	1	0	7	4	1	8	38		
Total	15	2	37	11	7	12	49	63	61

Table 3.4. Classification matrix of assignments of otolith signals from outplanted juvenile halibut outplanted in and near (A) Punta Banda Estuary during the spring of 2004 and (B) Mission Bay during the fall of 2003. Discriminant Function Analysis (DFA) was used to generate assignment algorithms. Rows list actual collection sites and columns list the predicted site of collection using DFA algorithms, with replacement. PBE1, PBE2 and PBE3 represent the outer, middle and inner sections of the Punta Banda Estuary, and Todos Santos Bay (TSB) is an embayment "outlier". MB1, MB2 and MB3 correspond to the outer, middle and inner areas of Mission Bay and SIO is an embayment "outlier".

A

	Predicted				
	PBE1	PBE2	PBE3	TSB	% Correct
Actual					
PBE1	3	0	0	1	75
PBE2	0	6	0	0	100
PBE3	0	0	5	0	100
TSB	0	0	0	9	100
Total	3	6	5	10	96

B

	Predicted				
	MB 1	MB 2	MB 3	SIO	% Correct
Actual					
MB 1	3	3	0	0	50
MB 2	0	3	1	0	75
MB 3	0	0	2	0	100
SIO	1	0	1	11	85
Total	4	6	4	11	76

Table 3.5. Summary of 2-way ANOVA results on untransformed data testing for significance of "embayment zone" and "caging" on the isotope to Ca ratios recorded from the post rostrum margin of juvenile halibut otoliths. Fisher's post-hoc test results are included for between-group comparisons of embayment zones. Mean ratios are shown in Figure 3.5.

						Between Group		
	SS	df	MS	F-value	p-value	Zone 1,2	Zone 1,3	Zone 2,3
PBE								
55MN								
Zone	0.002	2	0.001	6.904	0.003	0.934	<0.001	<0.001
Cage	<0.001	1	<0.001	0.092	0.763			
Zone*Cage	<0.001	2	<0.001	1.337	0.276			
Error	0.005	35	<0.001					
138BA								
Zone	<0.001	2	<0.001	5.456	0.009	0.307	0.038	0.004
Cage	<0.001	1	<0.001	0.675	0.417			
Zone*Cage	<0.001	2	<0.001	0.739	0.488			
Error	<0.001	35	<0.001					
MB								
55MN								
Zone	<0.001	2	<0.001	2.219	0.131	0.058	0.447	0.020
Cage	<0.001	1	<0.001	8.459	0.008			
Zone*Cage	<0.001	2	<0.001	2.267	0.125			
Error	<0.001	24	<0.001					
65CU								
Zone	<0.001	2	<0.001	1.745	0.195	0.350	0.040	0.258
Cage	<0.001	1	<0.001	<0.001	0.993			
Zone*Cage	<0.001	2	<0.001	0.217	0.806			
Error	<0.001	24	<0.001					
88SR								
Zone	0.276	2	0.138	0.854	0.438	0.281	0.865	0.264
Cage	3.7	1	3.7	22.895	<0.001			
Zone*Cage	0.772	2	0.386	2.388	0.113			
Error	3.878	24	0.162					
238U								
Zone	<0.001	2	<0.001	0.216	0.808	0.495	0.878	0.453
Cage	<0.001	1	<0.001	0.255	0.618			
Zone*Cage	<0.001	2	<0.001	1.584	0.226			
Error	<0.001	24	<0.001					

Table 3.6. Classification matrix of assignments of otolith signals from wild-caught juvenile halibut collected from multiple zones within Punta Banda Estuary, using signals from otoliths of outplanted juvenile halibut in Discriminant Function Analysis (DFA) to generate the assignment model. Because no fish from cages outplanted along the exposed coast were recovered, we used wild-caught fish collected in exposed habitats (Todos Santos) to generate otolith-signal algorithms. Rows list the actual collection site (of wild-caught fish), and columns list the predicted site of origin using DFA algorithms (from outplanted fish), with replacement. Data were generated from otoliths rings 80-90 µm off the post rostrum margin, representing environmental conditions at the time of cage deployment (2 months prior). Outplanting zones include Todos Santos = embayment "outlier", outer estuary (PBE1), middle estuary (PBE2) and inner estuary (PBE3).

	Todos Santos	PBE1 Caged	PBE2 Caged	PBE3 Caged
PBE1 Wild	1	4	3	0
PBE2 Wild	0	1	2	0
PBE3 Wild	0	2	1	0

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Chapter 3 of this dissertation, in full, is being submitted to the journal Marine Ecology Progress Series (Fodrie, F.J. and S. Herzka. Tracking juvenile fish movement and nursery contribution within arid coastal embayments via otolith microchemistry.) The dissertation author was the primary investigator and author of this paper.

IV.

Linking habitat utilization to population dynamics of a coastal finfish: nursery contribution, connectivity and concentration

Abstract

Quantifying nursery habitat value is essential for effective management of coastal ecosystems and finfish populations. We investigated the nursery role of four coastal ecosystem types for the California halibut (*Paralichthys californicus*) using the following metrics: (1) nursery contribution, (2) connectivity of subpopulations migrating from juvenile to sub-adult habitats, and (3) impact of nursery habitat availability and usage on sub-adult population size. Potential nurseries in San Diego County, California, were grouped using a novel classification scheme that delineated exposed, bay, lagoon and estuarine environments. Assignment of nursery origins for individual fish via elemental fingerprinting indicated that exposed coasted, bays, lagoons and estuaries contributed 42%, 45%, 11% and 2% of advancing juvenile California halibut during 2003-2004, respectively. These results were remarkably similar to the expected contribution from nursery habitats based on field surveys, indicating that in this system juvenile distributions are a good indicator of unit-area productivity of nurseries. Elemental fingerprinting also demonstrated that individuals egressing from bays did not migrate far

from their nursery origin (<10 km), resulting in reduced connectivity between the northern and southern halves of the 110-km study region over the timescale of ~ 1 generation. Low connectivity interacted with patchiness of embayment availability along the coastline to generate a gradient in nursery habitat limitation for halibut populations, with larger sub-adult populations observed along the southern half of the study region, in closer proximity to large bays. We conclude that the placement and abundance of nursery habitat alternatives along the coastal seascape of southern California has significant impacts on the population size and metapopulation dynamics of halibut populations. Also, mingling orthogonal approaches (detailed field surveys and elemental fingerprinting) strengthened our ability to determine the functional role of nursery habitat alternatives for the California halibut.

Introduction

For many 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., Checkly et al. 1998), at settlement (e.g., Allen et al. 1990; Peterson and Summerson 1992), or during advancement to older age classes (e.g., Modin and Pihl 1994;). For many species, settled juveniles must pass through nursery habitat 'filters' that can impact productivity of adult populations through habitat- or site-specific growth or mortality (e.g. Sogard 1992). Because many finfish species are habitat generalists, juvenile fish may occupy habitats characterized by differences in recruitment contribution for stock size or demography (Beck et al. 2001). 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. Key aids 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 impacts of nursery availability and usage on stock size (Nash and Geffen 2000). While these issues have received considerable attention over the last 25 years, few studies have evaluated them collectively (Mumby 2005). We address these three components of nursery "value" along the southern California coastline for the California halibut (*Paralichthys californicus*).

Coastal habitats such as estuaries and semi-enclosed bays have historically been considered essential nursery habitat for many economically and ecologically important fish and crustacean species (Gunter 1967, Chambers 1992). Distribution data are commonly utilized by scientists, managers and user groups as verification of finfish reliance upon specific coastal habitats as nurseries (e.g., Krygier and Pearcy 1986, Kramer 1990). 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 (Van Horne 1983). 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). Over finer scales, examinations of food resources (Burke 1995), growth rates (Phelan et al. 2000, Sogard et al. 2001), ecophysiology (Yamashita et al. 2000, Madon 2002) and survival (Heck and Crowder 1991) can be vital indicators of habitat quality (Able 1999). However, translating these data into estimates of overall productivity of fish populations and species fitness remains difficult without knowing the nursery origin of adults.

Understanding the strength of linkages between nursery and adult habitats is greatly aided by the ability to track individuals through space and time. This is especially true for finfish with spatially-separated juvenile and adult populations such as red drum, speckled sea trout, bluefish, summer flounder, southern flounder, English sole and California halibut (Beck et al. 2001; Gillanders et al. 2003). In recent years, trace element analyses have been employed to determine the trajectory of marine fishes egressing from putative nurseries (Yamashita et al. 2000; Gillanders 2002; Brown 2006). This is possible because trace elements are incorporated into the hard parts of organisms (otoliths in the case of teleosts) during growth in a manner that reflects the surrounding environment experienced by individuals (Campana 1999). 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. Thus, provided that site differences exist in environmental trace element concentrations, otoliths can carry a permanent record, or fingerprint, that allows researchers to retroactively track fish though time and space (e.g. Gillanders and Kingsford 2000). This method represents an alternative to tracking fish by ID tags, radio telemetry and physical modeling, and is particularly advantageous because it reduces the dilution problems and artifacts associated with tagging that are so familiar to marine scientists (Herzka unpublished).

Our primary goal was to assess the value of nursery habitats for a model species along the southern California coastline. To evaluate nursery value, we incorporate the following concepts: (1) Contribution - do all nursery habitats contribute equally to the adult population, and how does the realized contribution (assessed via elemental fingerprinting) relate to the expected contribution (derived from juvenile distributions and habitat availability)? (2) Connectivity – over what spatial scales do halibut move during the migration from juvenile to adult habitats, and over what length of coastline are the impacts of habitat-specific nursery contribution integrated? (3) Concentration – does adult population size appear to be regulated by nursery contribution either through (a) juvenile density-dependent interactions (Iles and Beverton 2000), or (b) nursery habitat limitation (Schmitt and Holbrook 2000)?

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 advanced (elemental fingerprinting; stable isotopes; genetics; demographic or metapopulation modeling) methodologies (see Gillanders et al. 2003). Forrester and Swearer (2002) used otolith microchemistry along a 300 km stretch of California coastline and estimated that ~58% of adult California halibut utilized protected habitats, while the remaining fish utilized exposed habitats. We advance their foundation work in a number of ways, including increased spatial resolution in fingerprints, and combining juvenile distribution surveys and retroactive tracking via elemental fingerprinting to assess nursery value. We demonstrate that incorporation of both traditional and advanced methods provide a more complete evaluation of nursery utilization and productivity for nearshore habitat conservation and management.

Methods

Study species. The California halibut, *Paralichthys californicus*, is an ecologically and economically important flatfish found in coastal waters of western North America (Kramer and Sunada 1992). Following settlement from the plankton, juveniles occupy shallow exposed shorelines, coastal bays, lagoons and estuaries as putative nurseries (e.g., Allen 1988; Allen et al. 1990; Kramer 1990). During this time, the environmental conditions of nearby sediments and the water column are recorded within their otoliths (Campana 1999; Forrester and Swearer 2002). After a 1-year residency, halibut migrate to adult habitats generally characterized by deeper water (Kramer 1991). This nursery-generalist life-history strategy, in concert with the spatial fragmentation of habitat types along the California coastline, makes the California halibut ideal for the application of elemental fingerprinting to address questions of: (1) nursery habitat productivity, (2) ontogenetic migratory connectivity of fish egressing from nursery grounds, and (3) influence of nursery ground processes in the determination of population size.

Study region. San Diego County is located in the southwestern-most corner of the continental United States, bounded by the Pacific Ocean along 112 km of coastline (N 33.39, W 117.61 – N 32.54, W 117.13). The coast is bordered by a narrow shelf, and punctuated by a series of relatively small (< 25 hectares) or highly modified embayments. In order to sample all possible nursery habitats utilized by juvenile halibut (Campana et al. 2000), the county was divided into 14 sites for surveying and collecting fish (Figure 4.1). 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 (Figure 4.1). Exposed habitats included the narrow ribbon of coastline from 0-20-m depth bracketed by sandy beaches or rocky cliffs on one side and the Pacific Ocean on the other. Embayment (bay, lagoon and estuary) classification was supported by geomorphologic characteristics such as surface area, average depth and surface area to perimeter (A/P) ratios, as well as 0-age halibut densities (a proxy of habitat-specific carrying capacity) (Fodrie and Mendoza 2006). Bays were characterized by surface areas >84 hectares, average depths >4 m, and A/P ratios >10. In San Diego County, bays are kept open and relatively deep to serve as harbors for shipping and recreational boating. Lagoons were distinguished by low-tide surface areas of 35-84 hectares, average depths ~ 3 m, and A/P ratios between 2.4-8.4. Estuaries were defined by low-tide surface areas <25 hectares and average depth <2.5 m. Estuaries were also characterized by high wetland (salt marsh) cover that resulted in A/P ratios <2 (Table 4.1).

Expected contribution of nurseries. To assess potential contribution from each putative nursery, we estimated the population sizes of 0-age halibut (fish <1 year old, <225-mm standard length, SL) within each of the 14 sites. These results provided null hypotheses for the expected contribution of each nursery habitat to adult halibut populations. It was against these contribution projections that elemental fingerprinting assessments of realized contribution (below) were evaluated to more fully define relative productivity of individual nurseries. The methods for estimating 0-age population sizes to calculate expected contribution were detailed in Fodrie and Mendoza (2006), and are summarized briefly here. In 2003 and 2004, 234 and 293 point-collections were made, respectively, within San Diego County, canvassing each of our 14 study sites. 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). All surveys occurred during October and November using a combination of otter trawls and block-net seining. These catch-rate data were corrected to estimate local density using gear efficiencies derived from mark-recapture experiments for both of the sampling gears we employed (Fodrie and Mendoza 2006; Herzka unpublished). Georeferenced juvenile densities were entered into a Geographic Information System database and a density surface was mapped over each site. By integrating the density surface over each potential nursery, we were able to produce an estimate of total 0-age halibut occupying each of the 14 sites during 2003 and 2004. From these data we predicted a contribution from each site and habitat type (exposed, bay, lagoon and estuary) to adult populations assuming no growth or survivorship differences.

Realized contribution of nurseries. Elemental fingerprinting was employed to determine the nursery habitat origin of +1-age halibut, and estimate the realized contribution from putative nurseries in producing the fish that recruited to older classes. We used otolith signatures of 0-age halibut collected during the fall surveys in 2003 and 2004 from each site in San Diego County to generate a library of elemental fingerprints. For large embayments such as Mission and San Diego bays, there are distinct chemical signals recorded in the otoliths of fish occupying different zones along the long-axes of the bays (Chapter 3). 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 2002). California halibut settle at approximately 10 mm SL and spend some period migrating among habitats (Allen 1988; Kramer 1991); therefore we only included fish 50-200 mm SL to generate fingerprints. We assumed fish at this size had been residents long enough to record local conditions in their otoliths (e.g., Gillanders and Kingsford 2000; Chapter 3).

During the spring of 2005, we collected the fish that would have occupied local nurseries during 2003 (2-year-olds) and 2004 (1-year-olds) by means of 10-minute otter trawls and timed hook-and-line fishing. We collected +1-age fish in all habitat sites in San Diego County during 2005, except from Batiquitos and Penasquitos. To avoid uneven spatial-sampling of +1-age fish that could bias our contribution results, we divided effort proportionally with habitat availability. For example, because 15% of coastal habitat for 1- and 2-year-old halibut in San Diego County is in San Diego Bay, 15% of our sampling effort occurred within the Bay during the spring of 2005.

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 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 samples using a Milli-Q wetted microcloth. Otoliths were sanded and polished in the saggital plane to expose rings following the general methods of Secor et al. (1991). 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 to dry and await analysis. 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. Because halibut are flatfish, one gill opening samples water directly at the sediment interface and the other does not. We only examined otoliths from the blind side of fish to ensure that all otoliths were recording from the same environment (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 50% intensity, 15-μm s^{-1} scan speed, and 20-μm spot size. Post-run inspection revealed that ablations could range between 20-35 μm in width, and 8-14 μm in depth (n = 10). Therefore, we sampled roughly 1-2 weeks of growth in each line (Kramer 1990). For the 0-age 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 margin (PRM), 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 PRM was 1300 μm for the 0-age fish we analyzed in 2003 and 2004.

For the 1- and 2-year-old 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 nursery origin. On these fish, we ablated material at 1300 $\pm$ 300 μm outside the otolith nucleus in the direction of the PRM. This range allowed us to target what appeared to be fall growth using the otolin-hyaline banding for reference (Beckman and Wilson 1995). Successive rings appeared to have "elbows" indicating the approximate location of the PRM 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 (ICPMS). We sampled for the following isotopes: ^{26}Mg, ^{48}Ca, ^{55}Mn, ^{63}Cu, ^{88}Sr, ^{65}Cd, ^{135}Ba, ^{208}Pb, and ^{238}U (hereafter referred to by elemental abbreviation) to maximize our power to discriminate among habitats (Becker et al. 2005). To determine isotope intensities, a chromatogram was generated for each isotope in each sample, and resulting peaks were analyzed individually. A “peak” was defined as having a maximum value greater than three standard deviations above the mean of the background, and background levels were subtracted from peaks using linear regression of non-peak values. We calculated the raw count per second (cps, area under the peak) for each isotope in each sample. The background-corrected cps values were then multiplied by a correction factor generated from standards (below), using recorded run numbers and linear estimations of machine drift. The sample cps values were then divided by the counts of ^{48}Ca, a rare isotope of Ca, which was used as an internal standard in order to account for the amount of otolith ablated. These ratios were used for all subsequent analyses.

Glass standards spiked with trace elements (National Institute of Standards and Technology Standard Reference Material 612, 614, and 616; NIST 612: Pearce et al 1997; NIST 614 and 616: Horn et. al. 1997) were analyzed at the beginning and end of each analysis day to account for machine drift. NIST standards were analyzed using a 300-µm line sampled at 50% intensity, 10-µm s^{-1} line speed, and 50-µm spot size. Unfortunately, no calcium carbonate matrix-matched standards were available at the time we conducted these analyses, but NIST does provide good precision and allows for intra-study consistency between samples (Putten et al. 1999).

Data analyses. Element ratios (X:^{48}Ca) recorded from the otoliths of 0-age 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), (3) and habitat (exposed, bay, lagoon and estuary) fingerprints. We ran DFAs with 2003 and 2004 juvenile signatures considered separately as well as combined. DFA is a data reduction approach that utilizes multivariate datasets to generate a series of orthogonal algorithms (scores) that maximize variance among data groups. All DFAs were conducted in a stepwise manner, by running the analysis on all element ratios, and dropping the least significant variable as determined by the F-to-remove statistic. This 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. Using (1) the collection sites of sub-adults as an analog for recapture locations, and (2) the nursery origins 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 adult populations.

We combined our survey and elemental fingerprinting results to test mechanisms of population regulation related to nursery habitat use. The first mechanism we evaluated was the concentration hypothesis (Iles and Beverton 2000), which states that density-dependent growth or mortality caps nursery production during the juvenile phase limits adult population sizes when high densities of juvenile fish concentrate into spatially limited nurseries (by). To assess this hypothesis, we used model II regression (Sokal and Rohlf 2000) to examine the relationship between: (1) the change between realized and expected contribution, and (2) 0-age halibut densities recorded during 2003 and 2004 in each nursery habitat type (reported by Fodrie and Mendoza, 2006). Essentially, this is a means for evaluating habitat-specific survivorship against local density. To decompose the relative impacts of habitat size versus habitat usage (local density) on survivorship, we also regressed the change in realized/expected contribution against nursery habitat availability.

The second regulating mechanism we considered was habitat limitation. The habitat limitation concept suggests that adult population size can be regulated through the quantity of habitat available to settling organisms by restricting the supply of new recruits to adult populations if settling (in this case, nursery) habitat is constrained (Gibson 1994; Schmitt and Holbrook, 2000). This doesn't 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. To examine if this occurs in local halibut populations, we regressed the catch rate (CPUE) of 1- and 2-year fish during 10 minute 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 should have similar carrying capacities for +1-age fish. All regression analyses were completed in StatView 5.0.1 (SAS Institute Inc.).

Results

Nursery habitat contribution. Intensive field surveys and GIS simulation produced estimates of approximately 789, 000 0-age halibut occupying nearshore habitats in San Diego County during the fall of 2003, and approximately 826, 000 0-age individuals during the following fall (for more detail see Fodrie and Mendoza 2006). Based on the distribution of 0-age 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 (Figure 4.2A, B).

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 4.2A,B, Figure 4.3A, D). 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 4.2A,B). Therefore, nursery origins of California halibut were determined at the resolution of habitat 'type' (exposed, bay, lagoon and estuary) (DFA results generated with individual sites and from regional groupings are included in Appendix 2, but not used hereafter). At least 15 fish were analyzed from each habitat type (exposed, bay, lagoon and estuary) 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). In Chapter 3, we found that northern and southern exposed habitats of San Diego County could be distinguished from one another in 2001, but this did not appear to be the case in 2003 or 2004 when all specimens from exposed habitats clustered together. 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 4.2A). 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 4.2B). 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 4.2A,B). In both years, exposed and estuarine habitats were characterized by higher Ba concentrations than were recorded in lagoons and bays (Table 4.3, Figure 4.3C). Bay signals were separated from other habitats by low Mg and Ba, and by higher Pb (2003) and Cu (2004) in the otoliths of 0-age fish (Table 4.3, Figure 4.3E). 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, but was not elevated in 2004 and not included in the final DFA (Table 4.3).

Combining 2003 and 2004 data to generate DFA scores resulted in lower (48 %) overall correct classifications for habitat signals (Table 4.2C). These “smudged” fingerprints indicated that there is important 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 4.3). Another example was that Cu concentrations were higher in all habitats during 2003 than in 2004 (Table 4.3). 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 1- and 2-year old halibut was assigned to a nursery origin using the DFA fingerprints generated from 0-age 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 (Figure 4.2C). From the 129 one-year-old fish we analyzed, contributions were 49 %, 42 %, 16 % and 2 %, respectively, from the same four habitats during 2004 (Figure 4.2D).

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 +1-age 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 in the northern one-third of the County. Three of the four estuaries occur centrally within the study region, although Tijuana River is the southernmost embayment we included. Of the 1- and 2-year-old fish we collected in the southern one-half of the County, there was nearly equal contribution from exposed and bay habitats (Figure 4.4). Lagoons and estuaries accounted for less than 6 % of the nursery contribution in this half of the county. The sub-adult fish we collected in San Diego Bay during 2005 were predominated by fish with bay (nursery) origins, while +1-age fish in Mission Bay, Pacific Beach and Imperial Beach had apparently utilized bay and exposed nurseries in about equal numbers. We collected one fish from Tijuana River that was also determined to have a bay origin. In the northern half of the County, the most common nursery origin was exposed habitat (Figure 4.4). 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. This suggests that fish egressing from bays in the southern half of the County are not moving farther than 10 km while migrating to +1-age habitats (Figure 4.4). Unlike bays, fish egressing from lagoons migrated all over the study system and were collected in equal numbers from as far north as Oceanside Harbor and as far south as San Diego Bay (Figure 4.5).

The concentration hypothesis and population regulation. Realized contribution of nursery habitats in San Diego County, in terms of producing the individual 0-age fish that successfully recruit to older age classes, were markedly similar to the expected contribution we calculated from distribution results ($r^2 = 0.900$, $p < 0.001$; Figure 4.6A). The agreement between expected and realized contribution was especially strong in 2003, while in 2004 exposed and lagoon habitats produced more recruits than expected, and bays and estuaries produced fewer than expected (Figure 4.6A). There was no relationship ($r^2 = 0.012$, $p = 0.789$) between local 0-age halibut density and the offset between realized and expected contribution from nursery habitats (Figure 4.6B). If high density capped nursery production through growth or mortality costs, we would have expected a decrease in realized contribution, relative to expectations, as local abundances within putative nurseries increased. This analysis was conducted with data from 4 habitat types that are characterized by an order-of-magnitude difference in local 0-age halibut densities, but also potentially different carry capacities (Fodrie and Mendoza 2006). Within a habitat type, only estuaries showed a notable drop in realized contribution as density increased. However, this was also the habitat where highest local densities were observed (Figure 4.6B). There was also no relationship between the offset in realized versus expected contribution and nursery habitat availability (area) ($r^2 = 0.047$, $p = 0.604$;

Figure 4.6C). We did observe an important, but non-significant relationship ($r^2 = 0.792$, $p = 0.150$) between CPUE of +1-age 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 (Figure 4.7). There was also an inverse relationship between latitude and CPUE of exposed sites, 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 indicate that all coastal habitat types contribute to older age classes of California halibut. Although only 15% of the potential nursery habitat area occurred within embayments (bays, lagoons and estuaries; Fodrie and Mendoza 2006), approximately 58% of 0-age halibut were determined to have embayment origins in 2003 and 2004 (n = 204; Figure 4.2). The majority of these fish utilized Mission and San Diego bays as nurseries. Our findings parallel the results of Forrester and Swearer (2002), who concluded that approximately 57% of adult halibut had utilized protected embayments as nursery habitats, while the remainder spent their juvenile period in the shallows of the exposed coastline (n = 19).

By generating data for both expected (field surveys) and realized (elemental fingerprinting) nursery habitat contribution, we were able to explore variation in survivorship among nursery types. For example, the realized contribution (as a proportion of total contribution) from lagoon habitats greatly exceeded expectations during 2004, but was below expectations during 2003. Meanwhile, the reverse was observed for estuarine habitats. It was beyond the scope of this project to test for mechanisms of differential growth or survivorship between years in these habitats, but we have now identified these habitats as sites of interest for future work. Fodrie and Mendoza (2006) reported that local densities were higher during 2004 over 2003 in all 13 putative nursery sites, except for San Diego Bay. Their survey results also indicated that the exposed habitat adjacent to the mouth of San Diego Bay became a high-density zone in 2004, having been density-depressed during the previous fall. Our realized contribution results demonstrated that bays contributed less than predicted during 2004 based on surveys of habitat availability and use. We hypothesize that survey results between years identified a response (emigration during 2004) of juvenile halibut within San Diego Bay to unfavorable environmental conditions in the second year, which was also observed in this study as a decreased contribution from bays relative to expectations (Figure 4.2).

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 species exiting coastal nurseries along the southeast coast of Australia remained within several kilometers of their nursery origin (Gillanders 2003). In tropical systems, fishery production has decreased on coral reefs where adjacent mangrove stands have been removed (Mumby et al. 2004). Some species, such as juvenile sole, simply remain in nursery sites for extended periods (Rogers 1993). Even for species with life histories that include a large seasonal migration, elemental fingerprinting has indicated that fish have an ability to return to their natal habitats and regions (Thorrold et al. 2001). Tracking California 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 resulted in dampened connectivity between ontogenetically migrating halibut from the northern and southern halves of the study region over the timescale of ~ 1 generation (Figure 4.8). Mark-recapture studies of California halibut have indicated that the majority of halibut remain with several km 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 that there is little connectivity of populations across latitude once fish have settled. Because we sampled at a single location (single growth period in time) on the otoliths of 1- and 2-year old halibut, we are unable to say if these fish made only one migration from nursery to sub-adult (collection) habitats, or made repeated migrations between habitats (annually) in order to exploit feeding, reproductive and wintering grounds (Gibson 2005).

Limited connectivity among ontogenetically migrating halibut populations should result in highly variable patterns of nursery habitat contribution along the coastline that are tightly linked to local nursery habitat availability and usage. For instance, in Chapter 3 we reported that within Todos Santos Bay, Baja California, Mexico, embayments (Ensendada Harbor and Punta Banda Estuary) produced 89 % of successful recruits that advanced to the +1-age classes during 2002 and 2003. Semi-exposed beaches were responsible for only 11 % of recruits. These results are very different that what has been reported for central and southern California, possibly because Todos Santos has relatively more (undisturbed) embayment habitat as compared with southern California.

The migratory potential of fish egressing from lagoons was far greater than that observed for fish that originated in the large bays along San Diego County (Figure 4.4, 4.6, 4.9). While the exact reasons for this are unclear, one possible explanation is that fish attempt to remain in, or return to, similar habitats as those occupied during the juvenile phase. Fish that have left lagoons may have a harder time relocating these relatively small habitats that are defined by small, periodically closed, mouths. Fish residing in bays can move over much larger distances without ever moving into another habitat type. If these fish do exit bays, relocating them might be easier given the larger mouths and semi-diurnal plume of bay water that is repeatedly flushed into and out of the mouth (Chadwick and Largier 1999). Given this scenario, a random-walk search pattern of lagoon-derived fish seeking preferred habitat could result in higher dispersion.

Concentration 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 is largely the result of difficulties related to tracking fish from juvenile to adult habitats (Gillanders et al. 2003), and scaling individual growth or survivorship rates, that vary between habitats, up to population-level fitness (Able 1999). Iles and Beverton (2000) have stated that for species whose juveniles concentrate into spatially limited nurseries, local populations can approach carrying capacity and this limits the amount of contribution possible from individual habitats. Several studies have reported that growth or mortality can vary among successive year classes characterized by an order-of-magnitude difference in settlement (Modin and Pihl 1994). Iles and Beverton (2000) termed this the "concentration hypothesis" and tested for compensatory dynamics by analyzing the variability in the population-recruitment relationship for species that concentrate into nurseries and those whose juveniles remain scattered. Iles and Beverton (2000) reported that for species that do concentrate in nurseries the scatter of recruitment around the population-recruitment relationships tended to be less variable; predictable from theory.

The variable patches of habitat types and embayment sizes along the southern California coastline are an ideal system for testing the concentration hypothesis for a flatfish population. Our results indicate that 0-age halibut did not experience density-dependent growth or mortality costs that were related to local juvenile density (Figure 4.6). Instead, realized contribution was tightly correlated to expected contribution regardless of local density. Thus, local density did not appear to cap the contribution of nursery habitat types along the southern California coastline. Although there was a decrease in productivity within estuaries related to density, relative to what could have been expected from 0-age population size, small-scale distributions add further support for this conclusion. Among the 4 estuarine habitats we included in our study, densities increased in 2004 over 2003 ranging from 50 % (San Dieguito) to 800 % (Tijuana River). Despite these increases, the distribution of fish within these habitat sites indicated that fish were not spreading out into “marginal” habitat as densities increased. Rather, a slight trend towards shoaling of juveniles could be observed in 2004 in each of the sites (Fodrie and Mendoza 2006). We conclude that either halibut did not approach local carrying capacity at the densities we observed in 2003 and 2004, or that the inclusion of 4 unique habitat types made it difficult to observe compensatory mechanisms given that we only recorded data from two consecutive years and did not have site-specific contributions. Although habitat selection could be a non-adaptive trait, juvenile halibut likely select nursery habitats to maximize fitness (sensu foraging theory: MacArthur and Pianka 1966). The availability of 4 unique habitat types and a generalist life-history strategy may provide juvenile halibut with more options for locating suitable habitat that is utilized below carry-capacity, and could result in diminished density-dependent regulation for this species.

Although juvenile density-dependent mortality was not observed to regulate recruitment pulses to +1-age 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 strongly linked to the relative contribution from embayment habitats (bays, lagoons and estuaries) (Figure 4.7). The term habitat limitation was originally applied to the spatial resources required during settlement (Schmitt and Holbrook 2000), but is equally suitable for nursery habitat availability. Moreover, 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 be occupied and 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 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 adults 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). Following inshore spawning, larvae spend 3-4 weeks in surface waters distributed across the continental shelf (Moser and Watson 1990) before transport shoreward and settlement in shallow coastal environments at 7-9 mm SL (Allen 1988). At this point, pre- or post settlement halibut may move along the coastline looking for suitable nursery habitat and away from regions with relatively little embayment habitat.

A key result was that CPUE from exposed habitats were considerably lower (less than half) in the northern half of the study region than in the southern half (Figure 4.7). These are similar +1-age habitats separated by only 10s of km. This suggests that habitat availability interacted with dampened connectivity of ontogenetically migrating populations (Figure 4.4, 4.6, 4.9) to generate the observed gradient in habitat limitation. Our results suggest that if embayment habitat were more available along the northern half of San Diego County, either through habitat conservation or large-scale restoration, CPUE for sub-adult halibut along this stretch of coastline would be elevated (Appy 1997, Fodrie and Mendoza 2006), and that recruitment subsidies will not come from neighboring stretches of coastline at generational timescales. Although fishing effort confounds any direct conclusion, there appears to be clear “hotspots” of commercial take along the Alto and Baja California coastlines that are in close proximity to large tracks of nursery habitat such as Humboldt Bay, Half-Moon Bay (adjacent to San Francisco Bay), the Santa Barbara Flats (J. Hunter personal communications) and Bahia Magdalena (Kramer and Sunada 1992).

A similar result has been documented in tropical systems where mangroves are utilized by juvenile fishes. Although many coastal finfish species are able to utilize multiple nursery habitat types (sandflat, seagrass, mangrove), the abundance of many ecologically and commercially important fishes was observed to double when adult habitat (coral reef) was located in close proximity to mangrove stands (Mumby et al. 2004). Moreover, the largest herbivorous species in the Atlantic, *Scarus guacamaia*, has suffered local extinction at sites where mangrove nurseries have been removed (Mumby et al. 2004). Despite the variable effects of larval supply and fishing pressure, nursery habitat availability has clear impacts on the population dynamics of finfish species both in southern California (this study) and the Caribbean (Mumby et al. 2004), even for species whose juveniles can inhabit a number of nursery types.

Determining habitat value to improve conservation. 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 has provided a needed 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 adults. In our study system, bay habitats contributed the largest number of recruits, but exhibited low unit-area production relative to lagoons and estuaries. 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 (Figure 4.2). Conversely, habitats with highest unit-area production (lagoons and estuaries) were distinguished by producing few fewer successful recruits on an absolute scale because of their limited size (Figure 4.2). Using Beck et al.'s nursery-role concept, only lagoons and estuaries would achieve nursery status even though they comprised 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 (sensu Gibson 1994) results in an almost complete reversal of trends for San Diego County (Table 6.1). Selection between these alternative ranking schemes could have significant impacts on the priorities for nearshore habitat conservation along southern California.

The current epistemology of elemental fingerprinting studies largely neglects inclusion of traditional approaches that could place tracking results in a broader ecological context. Ideally, experiments incorporating modeling, artificial tags or natural tags would be used in concert with distribution analyses or caging experiments that tease apart habitat-specific feeding growth or mortality rates. For instance, detailed distribution analyses, when feasible, can help to ensure that all possible nursery sources are included in the catalogue of habitat tags generated via elemental fingerprinting (sensu Campana et al. 2000). Surveys of habitat availability and use should also provide null hypotheses for the expected value of nursery habitats types for halibut populations, against which tracking studies to assess marine connectivity, or demographic modeling of population fitness can be weighed to more meaningfully evaluate habitat productivity.

Figures and Tables

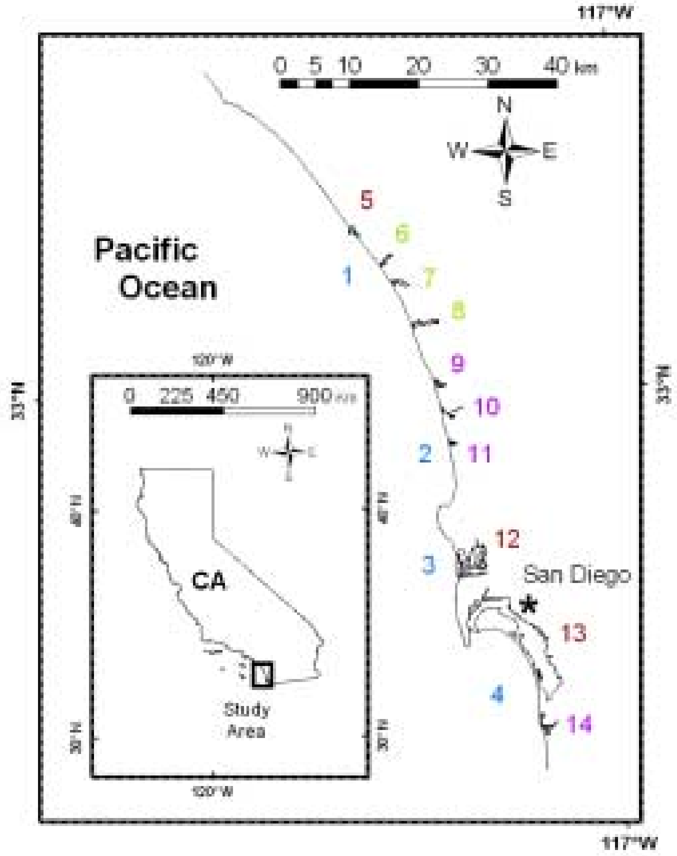

Figure 4.1. San Diego County Coastline study region highlighting the 14 blocks sampled to generate halibut distribution data and provide samples for trace element fingerprinting. Sectors are: 1. Oceanside (EX), 2. La Jolla (EX), 3. Pacific Beach (EX), 4. Imperial Beach (EX), 5. Oceanside Harbor (B), 6. Buena Vista (L), 7. Agua Hedionda (L), 8. Batiquitos (L), 9. San Elijo (E), 10. San Dieguito (E), 11. Penasquitos (E), 12. Mission Bay (B), 13. San Diego Bay (B), and 14. Tijuana River (E). Letters following each site indicate: exposed (EX), bay (B), lagoon (L) and estuary (E) habitats. Coastline and 10 m, 20 m bathymetry contours are shown with solid and dashed lines, respectively.

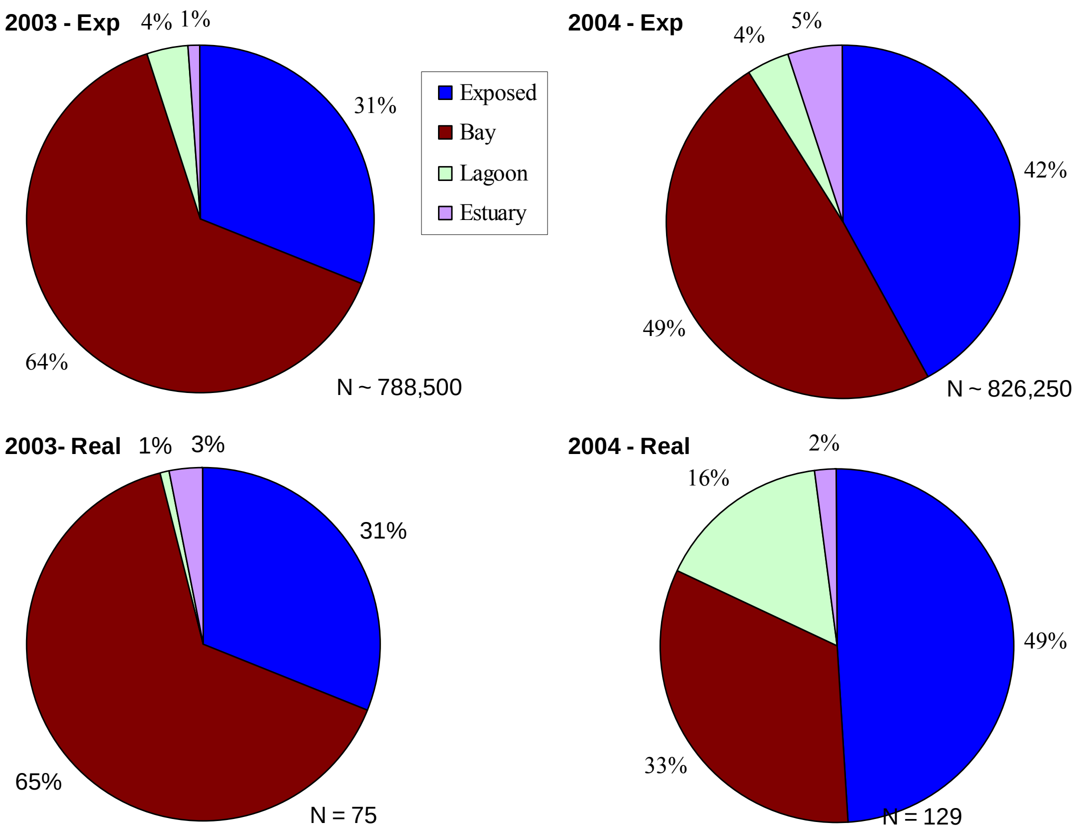

Figure 4.2. Expected (A & B) and realized (C & D) contribution (expressed as a percentage) of nursery habitats along San Diego County from 2003 (A & C) and 2004 (B & D) in producing the individual 0-age halibut that successfully advanced to the +1-age and adult population sampled in 2005. Expected contributions are based on 2003 and 2004 field surveys of 0-age halibut distributions and nursery habitat availability. Realized contributions are based on elemental fingerprinting results. 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.

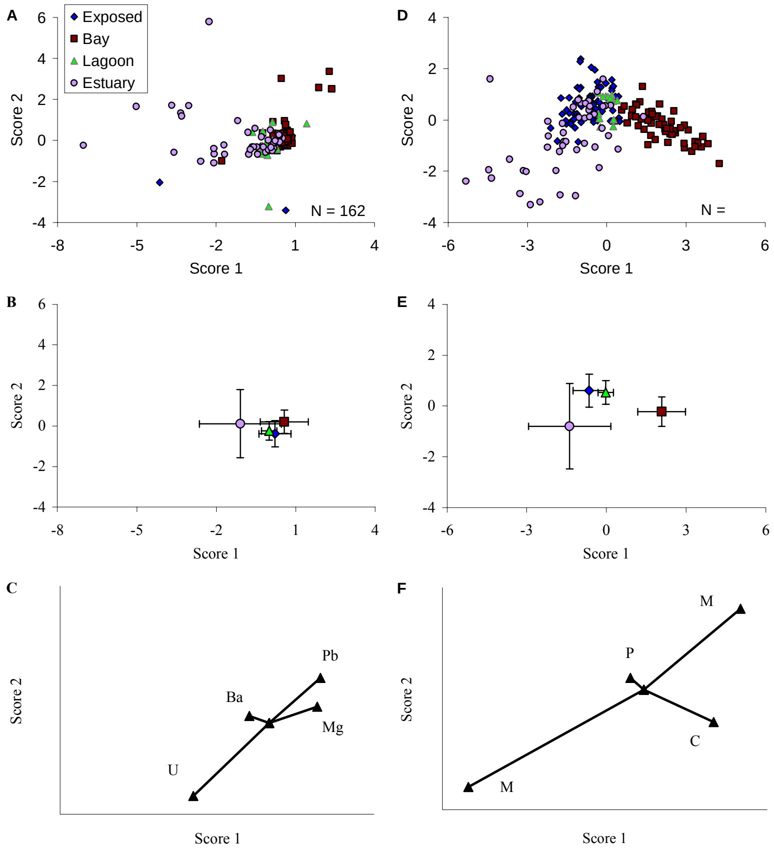

Figure 4.3. Discriminant scores of isotope ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2003 from all putative nursery sites in San Diego County during (A-C) 2003 (A-C; Mg, Ba, Pb & U) and (D-F; Mg, Cu, Ba & Pb). Data are grouped as: Exposed = Oceanside, La Jolla, Pacific 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, D) Scatterplot of DFA scores; (B, E) Same data as A plotted as averages with ± 1 standard deviation; and (C, F) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

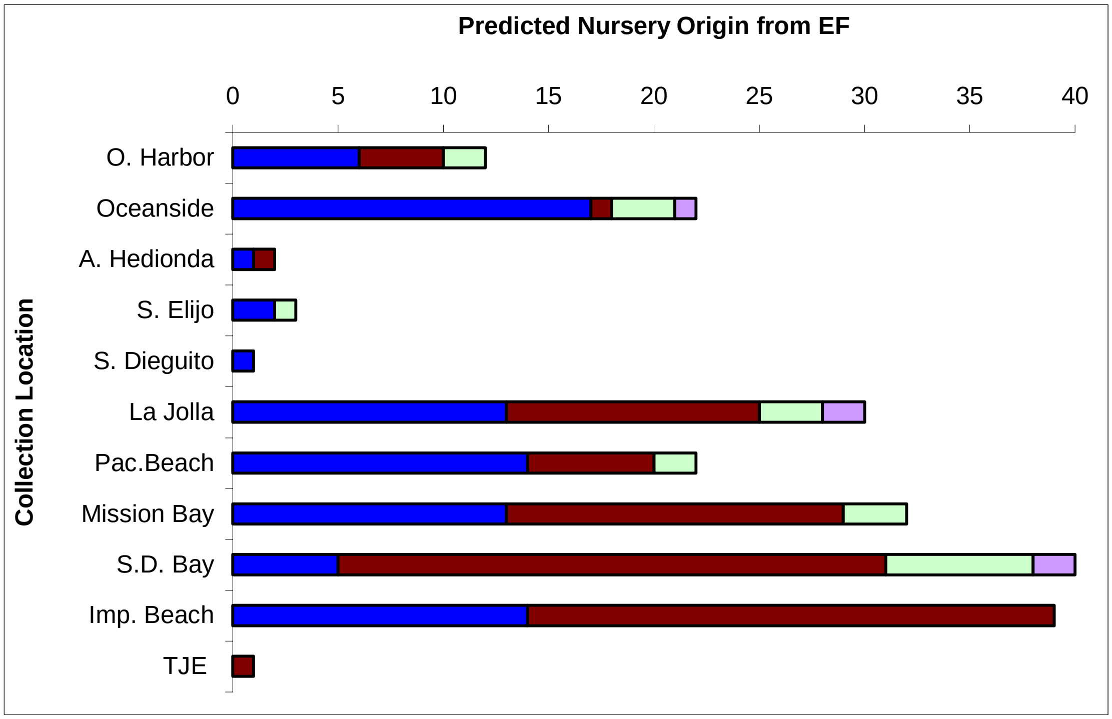

Figure 4.4. Determination of nursery origin of 1- and 2-year-old halibut collected in 2005 within San Diego County with respect to eventual collection sites. Nursery origin was determined via elemental fingerprinting of California halibut otoliths. Sites positioned along the left margin represent locations where 1-and 2-year-old fish were collected and the pattern of the bars indicate the nursery origin of individual fish.

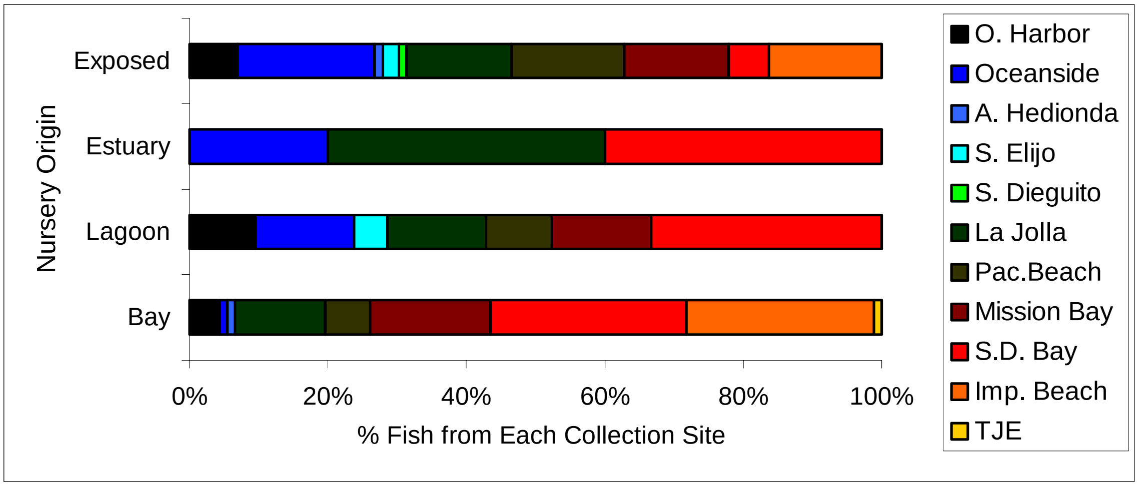

Figure 4.5. Recipient sites for advancing juveniles egressing from each of the 4 potential nursery types (Exposed, Bay, Lagoon and Estuary) considered in this study. Nursery habitats are positioned along the left margin and eventual collection sites of 1-and 2-year-old fish are represented by unique bar patterns.

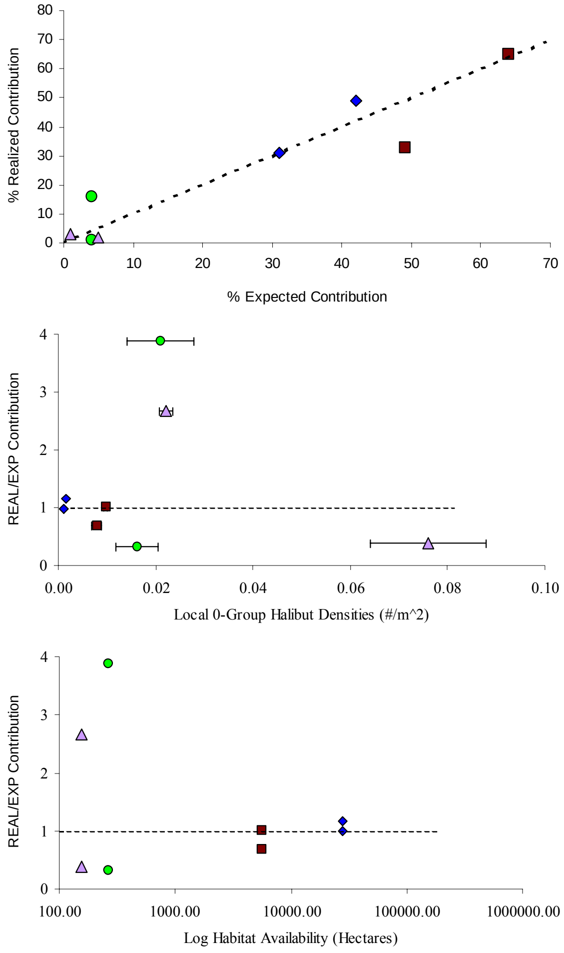

Figure 4.6. (A) The relationship between expected and realized contribution from putative nursery habitats along San Diego County. Dashed line represents the one-to-one line. (B) The relative change in expected contribution (from field surveys of juvenile halibut distributions and habitat availability) and realized contribution (determined via elemental fingerprinting) plotted in relation to local 0-age halibut density observed in San Diego County (± 1 standard error). (C) Same as (B) but plotted against (log) habitat area. Local 0-age 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.

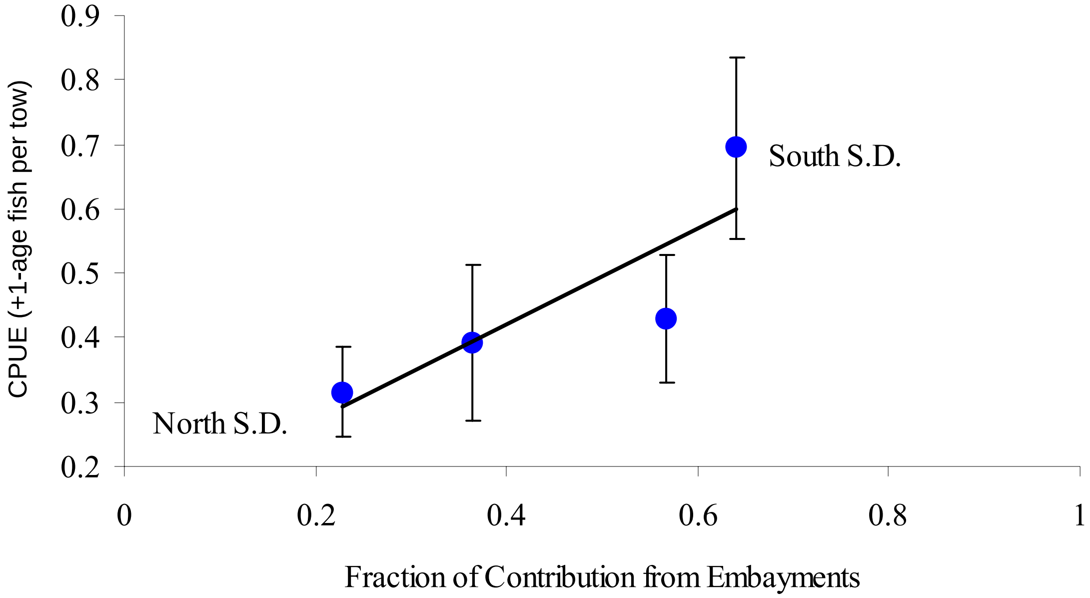

Figure 4.7. Catch-Per-Unit-Effort (fish collected per 5 min tow ± 1 standard error) of 1- and 2-year-old halibut along the 4 exposed study sites (Oceanside, La Jolla, Pacific Beach and Imperial Beach) during 2005 plotted against the fraction of fish collected from each exposed site retroactively determined via elemental fingerprinting to have utilized embayment habitat (bay, lagoon or estuary) as a nursery in 2003 or 2004.

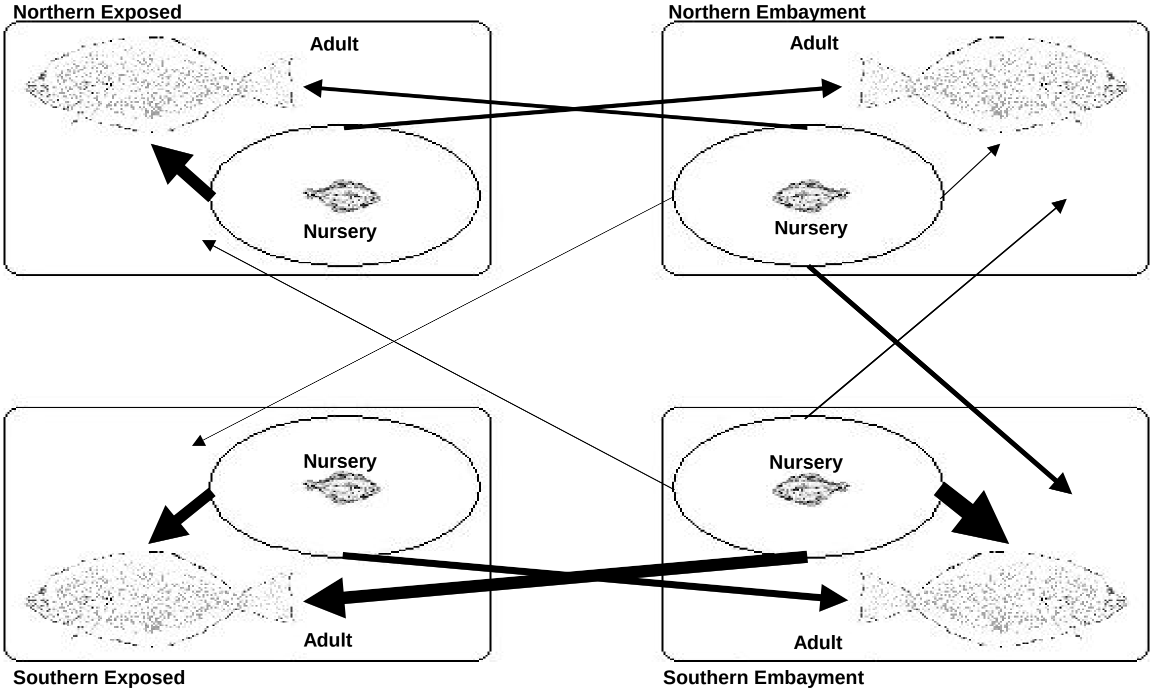

Figure 4.8. Connectivity diagram for populations of ontogenetically migrating halibut egressing from nursery habitats within the study region. The model is divided spatially in to 4 regions: Northern Exposed, Southern Exposed, Northern Embayments and Southern Embayments. Line weighting represents the number of fish that were observed with each migration route.

Table 4.1. Summary table of geomorphologic characteristics and juvenile halibut distributions putative nursery habitats in San Diego County. Nursery habitat types indicated with EX (Exposed), B (Bay), L (Lagoon) and E (Estuary). Data summarized from Fodrie and Mendoza (2006).

	North San Diego Coast	South San Diego Coast	Oceanside Harbor	Buena Vista	Agua Hedionda	Batiquitos	San Elijo	San Dieguito	Penasquitos	Mission Bay	San Diego Bay	Tijuana Estuary	Total
Habitat Classification	EX	EX	B	L	L	L	E	E	E	B	B	E	-
Low-Tide Bottom Area (hectares)	14535.4	13266.1	84.5	35.5	83.9	73.9	10.3	24.3	5.7	851.9	4174.0	16.9	33162.4
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 (#)	137654	112408	6516	0	20502	6783	2468	6092	730	78876	413137	3355	788522
2004 Resident Halibut (#)	162314	182134	11489	0	28022	7528	5369	9213	4382	85901	305397	24497	826247

Table 4.2. 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 Bataquitos; and Estuary = San Elijo, San Dieguito, Penasquitos and Tijuana River. Comparisons to randomized data sets are provided. Classification matrices are presented for (A) 2003, (B) 2004 and (C) 2003 and 2004 data combined.

A 2003

	Predicted Site					
	Exposed	Bay	Lagoon	Estuary	% Correct	RAND
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

B 2004

	Predicted Site					
	Exposed	Bay	Lagoon	Estuary	% Correct	RAND
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

C 2003 & 2004

	Predicted Site					
	Exposed	Bay	Lagoon	Estuary	% Correct	RAND
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 4.3. Means (with 1 standard error) of isotope 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. Estuary = San Elijo, San Dieguito, Penasquitos and Tijuana River.

	Samples (N)	24Mg/ 48Ca	55Mn55/ 48Ca	63Cu/ 48Ca	88Sr/ 48Ca	112Cd/ 48Ca	135Ba/ 48Ca	206Pb/ 48Ca	238U/ 48Ca
2003									
Exposed	30	0.046 (0.044)	0.006 (0.001)	0.0005 (0.0002)	2.765 (0.357)	0.00005 (0.00002)	0.010 (0.008)	0.0003 (0.0002)	0.00002 (<0.00001)
Bay	72	.002 (<0.001)	0.011 (0.001)	0.0050 (0.002)	2.636 (0.229)	0.00004 (<0.00001)	0.002 (0.001)	0.0050 (0.0020)	0.00001 (<0.00001)
Lagoon	17	.006 (0.004)	0.014 (0.003)	0.0004 (0.0002)	3.259 (0.213)	0.19500 (0.190)	0.003 (<0.001)	0.0010 (0.0003)	<0.00001 (<0.00001)
Estuary	43	0.087 (0.072)	0.035 (0.011)	0.023 (0.012)	5.312 (0.613)	0.00100 (0.00037)	0.140 (0.066)	0.0250 (0.0120)	0.00030 (0.00020)
2004									
Exposed	71	0.089 (0.069)	0.017 (0.012)	0.00032 (0.00021)	2.341 (0.043)	0.00003 (<0.00001)	0.019 (0.011)	0.00036 (0.00027)	0.000048 (0.000030)
Bay	55	0.002 (0.001)	0.004 (<0.001)	0.00041 (<0.00003)	2.213 (0.049)	0.00002 (<0.00001)	0.002 (<0.001)	0.00002 (<0.00001)	0.000001 (<0.000001)
Lagoon	15	0.002 (<0.001)	0.006 (0.001)	0.00005 (<0.00001)	2.235 (0.087)	0.00002 (<0.00001)	0.002 (<0.001)	0.00002 (<0.00001)	0.000001 (<0.000001)
Estuary	49	0.003 (0.001)	0.009 (0.001)	0.00022 (0.00010)	2.695 (0.189)	0.00800 (0.00500)	0.008 (0.001)	0.00200 (0.00100)	0.000004 (0.000002)

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Chapter 4 of this dissertation, in full, is being submitted to the journal Limnology and Oceanography (Fodrie, F.J. and L. Levin. Linking habitat utilization to population dynamics of a coastal finfish: nursery contribution, connectivity and compensation.) The dissertation author was the primary investigator and author of this paper.

V.

Consequences of nursery habitat selection for the demography of California halibut populations

Abstract

Many fish and invertebrate species partition habitat use spatially or temporally based on mortality, growth or fecundity tradeoffs among environments. We used cohort analyses and stage-based population projection matrix models of California halibut, *Paralichthys californicus*, in southern California coastal waters to explore the population-level impacts of habitat selection by juvenile fish, and evaluate the functional role of putative nurseries in determining population growth rate (λ). Twelve nursery- and year-specific models suggested a growing population, but with important differences for sub-populations whose juveniles utilized exposed coastline (declining population) or protected embayment (growing population) habitats. While a habitat may contribute a significant number of recruits for replenishing older populations, it can nevertheless contribute negatively to population growth rate. Although elasticity analyses demonstrated that λ is theoretically most sensitive to changes in adult, sub-adult and juvenile survival, contribution analyses revealed that juvenile growth, juvenile survivorship and sub-adult growth actually drove differences in λ observed among

nurseries and years. Findings were relatively insensitive to measurement error in larval mortality or adult fecundity, for which uncertainties in vital rate estimates were greatest. Goals for coastal habitat conservation required to promote positive population growth for California halibut were generated by weighting overall mortality and stage durations in accordance with the percentage of fish from the population that utilized exposed verses embayment habitats. Based on this simulation that incorporated 1987-1988 and 2002-2003 data, at least 37.5% of recruits to the adult stage must originate from embayment nurseries to produce stable or positive population growth ($\lambda \geq 1$).

Introduction

Habitat heterogeneity has important implications for metapopulation dynamics, predator-prey interactions, genetics and population demography (Dias 1996). For many of the mobile marine fish and invertebrate species that occupy nearshore waters, environmental gradients are especially evident and dictate the distribution of individuals based upon mortality, growth or fecundity tradeoffs among locations (e.g., Labonne and Gaudin 2006). A key aid for preserving coastal ecosystems essential for nearshore species is the ability to link habitat-specific differences in vital rates with overall population health. This allows targeted conservation of those habitats that act as productivity “hotspots” (e.g., Crowder et al. 2000).

One of the most common and potentially important forms of habitat partitioning in coastal marine environments is the use of nursery habitats by juvenile fish and crustaceans. Nurseries represent fundamentally different settings, or only a portion of the environments occupied by older life-history stages (Gunter 1967; Gillanders et al. 2003). Chambers (1992) estimated that 75 % of biomass in the commercial fishery landings in the United States is comprised of species that are dependent on coastal habitats and estuaries, often during the juvenile phase. Because juvenile fish are relatively mobile and are destined to undergo ontogenetic migrations, specialized habitat associations for these fish may be lacking (Able and Fahay 1998). Still, juvenile fish may be better adapted for a subset of the habitats they occupy and relatively maladapted for others (Dias 1996; sensu Beck et al. 2001). As a result, considerable effort has been dedicated to documenting habitat-specific differences in growth and survivorship experienced by juvenile fish and invertebrates within alternative putative nurseries (e.g., Sogard 1992; Modin and Pihl 1994; Perkins-Visser et al. 1996; Phelan et al. 2000; Sogard et al. 2001). An important next step is to translate these nursery- and site-specific differences in vital rates to estimates of overall population growth rates (λ), corrected for the relative usage of each nursery type.

Ecologists are widely interested in the comparative importance of early or late life-history stages in determining population dynamics (Underwood and Denley 1984; Gaines and Roughgarden 1985; Rijnsdorp 1994), as well as targeted management strategies that influence juvenile or adult mortality and growth in order to enhance population size (e.g., Crouse et al. 1987, Gerber et al. 2005). Because juvenile growth or mortality can vary among nursery habitat alternatives, we consider whether those differences have consequences for the overall health of marine populations. Our research addresses the influence of individual life-history stages and vital rates on the demography and population growth rate of the California halibut, *Paralichthys californicus*, highlighting the variation in λ that results from utilization of nursery habitat alternatives. We consider the following questions: (1) Can vital rates such as juvenile mortality and stage duration vary significantly among nursery habitat alternatives? Moreover, does there appear to be density-dependent mortality during the juvenile phase that dampens transfer of recruitment pulses from specific habitat types to older age classes (Gunter 1956)? (2) To which vital rates (growth, survivorship and fertility) is λ most sensitive, and how sensitive is λ to these rates during the juvenile phase? Do sensitivities reflect the rates that actually contribute to observed variation in λ? And, (3) How does selection of alternative nursery habitats by juvenile halibut affect overall λ for the population?

Stage-structured matrix models were combined with nursery-specific cohort analyses of mortality and growth for the California halibut to generate estimates of λ as a metric for habitat value (Lefkovitch 1965). The eigenvalue structure of matrices integrates life-history information and was exploited to translate individual growth or mortality costs into estimates of overall population growth rate (Caswell 2001). Additionally, prospective and retrospective analyses of models were used to evaluate the population-level consequences of variation in life-history parameters (Caswell 2000).

Methods

Study species and sites. Populations of California halibut, *Paralichthys californicus*, were studied within several habitats along the coastline of San Diego County, California. The California halibut is a key member of the regional icthyofauna community within coastal embayments and along the exposed coastline over soft sediments (Allen 1990). Broadcast spawning by adult halibut occurs throughout the spring, summer and fall (Ginsburg 1952; Allen et al. 1990), and halibut larvae remain in surface waters over the continental shelf (Moser and Pommeranz 1999) before settling in shallow-water habitats (Allen et al. 1990). Following settlement, juvenile halibut can occupy several habitat types characterized as exposed or embayment (bays, lagoons or estuaries), with higher juvenile densities observed in embayments (Fodrie and Mendoza 2006). At approximately 1 year of age, juvenile halibut egress from nurseries and join the sub-adult, then adult population (Kramer 1991). Individual halibut can live up to 30 years, but the vast majority of fish found in San Diego County waters are less than half that age (MacNair et al. 2001). Based on juvenile distribution data (e.g., Allen 1988; Kramer 1991), the California halibut is considered to be estuarine-dependent. However, the nursery-generalist strategy exhibited by the California halibut makes it an ideal species for investigating the demographic consequences of nursery habitat selection in a heterogeneous coastal environment.

We surveyed juvenile halibut populations in every month during 2002 and 2003 from three putative nursery habitat types in order to determine habitat-specific mortality and growth. We sampled along 1 exposed habitat (Scripps Beach, adjacent to the Scripps Institution of Oceanography; 32.93˚ N, -117.26˚ W) and inside 2 embayment habitats

(Mission Bay; 32.76° N, -117.25° W; and Tijuana River; 32.56° N, -117.13° W). Mission Bay and Tijuana River were classified as bay and estuarine habitat, respectively, by Fodrie and Mendoza (2006). These embayment types potentially function very differently as fish habitat due to differences in total size, average depth, wetland cover, hydrologic modification and juvenile halibut carrying capacity (Fodrie and Mendoza 2006). Additionally, monthly juvenile halibut density data were extracted from Kramer (1990) to provide additional estimates of mortality and growth at Scripps and in Mission Bay during 1987 and 1988, and from one additional embayment habitat, Agua Hedionda (33.15° N, -117.34° W), which was classified as a lagoon by Fodrie and Mendoza (2006).

In 1994, sub-adult and adult halibut were collected along the entire San Diego County coastline during the Southern California Bight Biomass Survey (SCBBS) conducted by the California Department of Fish and Game (S. Wertz, personal communication). These data were used to calculate mortality and growth for post-juvenile stages.

Model parameterization. We divided the halibut life cycle into four biologically relevant stages. Stages were based on fish length, and included: larvae (L: hydrated egg to ~10 mm SL); juvenile (J: ~10 to 220 mm SL); sub adult (SA: ~220 to 475 mm SL); and adult (A: >475 mm SL) (Figure 5.1). The division between L and J stages was based on settlement from the water column by larvae ready to begin life in the demersal stage (Allen et al. 1990). J and SA stages were distinguishable from one another based on the timing of juvenile egression from primary nursery habitats (Kramer 1991), as well as

50% male maturity (Love and Brooks 1990). The division between SA and A stages was defined by the timing of 50% female maturity (Love and Brooks 1990).

Monthly censuses for juvenile fish were completed in each nursery habitat during 2002 and 2003 using an otter trawl (Scripps and Mission Bay) or block-net seining (Tijuana River). Each census consisted of 3 ten-minute tows of the otter trawl or three sets of block-net seining Juvenile halibut collected during each month were sized into 20 mm bins ranging from 40 to 220 mm SL (Figure 5.2). Bin size was chosen to match the format used by Kramer (1990), who reported juvenile halibut hectare^{-1}. For each year, the number of fish collected each month from individual habitats were imported into cohort life tables and from these tables monthly mortality rates (z_m) were calculated as (e.g., Law 1975):

(1) $$z_m = 1 - (n_{(t+1)} / n_{(t)})$$

where $n_{(t)}$ is the number of fish in the cohort at time t and $n_{(t+1)}$ is the number of fish remaining at the next time step, $t+1$ (one month later). Only individuals 60-120 mm SL were used to calculate habitat-specific mortality in order to minimize biases that could have resulted from: (1) migration of individuals following settlement or early egression of juveniles to sub-adult habitats, and (2) differences in size selectivity between the gears used in the 1987-1988 and 2002-2003 surveys (Figure 5.3). We assumed that mortality of individuals 10-40 mm and 120-220 mm could be approximated by the 60-120 mm individuals and not dramatically impact the nursery habitat comparisons we were interested in.

The number of sub-adult and adult halibut >2 years old (based on size-at-age divisions of MacNair et al. 2001) collected during the SCBBS were entered into a static life table (e.g. Lowe 1969), and from this table annual (then monthly) mortality rates were calculated using Eq. (1) for sub-adult (2 to 4 years old) and adult ($\geq$4 years old) fish. We only considered the females collected during the SCBBS for calculating adult mortality. Although sub-adults are not confined to the primary nursery habitats we were most interested in for this study, we were able to tune the sub-adult survival rates in relation to the differences in survivorship experienced by sub-adult fish that were retroactively assigned to a nursery origin in 2003 and 2004 via an elemental fingerprinting approach (Chapter 4).

We assumed that 99.9% of all hydrated eggs failed to reach the size at which halibut larvae settle since there are no available estimates of larval mortality for California halibut (sensu Timko 1975). This is reasonable for highly fecund broadcast spawners with intermediate pelagic larval durations and minimal parental investment (Thorson 1966). Assuming that 99.9% of all hydrated eggs failed to reach settlement produced models that were tuned for $\lambda \sim 1$.

To determine nursery- and year-specific juvenile stage durations, we tracked the center of distribution (mean size) of cohorts in each nursery habitat in order to estimate the time needed for individuals entering our surveys at 40 mm to exit at 220 mm (both in our surveys and the data extracted from Kramer (1990)). To account for the individuals

10-40 mm that we were not able to include in our analyses, we uniformly added 1 month to each of our estimates of juvenile stage duration (Kramer 1991).

Stage durations for larvae (L), sub-adults (SA) and adults (A) were complied from previously published reports. Gadomski and Caddell (1991) reported that the typical duration of the larval stage for California halibut was 41 days (1.3 months) at temperatures between 16 and 20 ˚C. The time between 50% male and 50% female maturity is roughly 3 ¼ years (39 months) and defines the stage duration for sub-adult halibut (Love and Brooks 1990). In our models, halibut could live to the age of 20 (240 months) regardless of nursery habitat utilization. Duration of the adult stage was determined by subtracting the stage durations of L, J and SA from a total of 240 months. Since juvenile stage duration was variable between habitat types and years, so was the adult stage duration.

Due to the stage structure we considered, only individuals in the adult stage at time *t* contributed to the pool of new larvae at time *t*+1. California halibut are relatively long-lived, highly fecund, iteroparous, and spawn over about 6-8 months of the year. Caddell et al. (1990) conducted a series of laboratory examinations with individuals 350-775 mm TL (1-8 Kg; ~2-11 years old; MacNair et al. 2001) and estimated average fecundity to be 407,833 hydrated eggs month^{-1}, although they did not report on size-specific fecundity. Lavenberg (1987) reported that females experience a mean interval of 7.14 days between spawning during a reproductive season marked by 12-20 events, and that average batch fecundity of female halibut was ~ 350,000 (588,333 hydrated eggs month^{-1} over 12 months). Female reproductive effort should limit the amount of contribution to the larval pool based on the 2.3:1 M:F sex ratio observed along San Diego County during the 1994 SCBBS. All vital rate data collected from life tables or the literature are included in Table 5.1.

Matrix population models. Population growth rates were calculated from 12 stage-based matrix models generated for 4 nursery habitats throughout 4 years (Scripps, Mission Bay and Agua Hedionda in 1987-1988; Scripps, Mission Bay and Tijuana River in 2002-2003) following Caswell (2001). Each model was analyzed using one-month time steps in order to match the approximate duration of the shortest stage (larvae) and frequency of juvenile surveys. Using entries for each nursery habitat and year (Table 5.2), the 12 matrices were constructed as:

(2) $$n_{t+1} = Mn_t$$ or:

(3) $$\begin{bmatrix} L_{t+1} \\ J_{t+1} \\ SA_{t+1} \\ A_{t+1} \end{bmatrix} = \begin{bmatrix} P_1 & 0 & 0 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{bmatrix} \times \begin{bmatrix} L_t \\ J_t \\ SA_t \\ A_t \end{bmatrix}$$ such that:

(4) $$L_{t+1} = (P_1 \times L_t) + (F_4 \times A_t)$$

(5) $$J_{t+1} = (G_1 \times L_t) + (P_2 \times J_t)$$

(6) $$SA_{t+1} = (G_2 \times J_t) + (P_3 \times SA_t)$$ and

(7) $$A_{t+1} = (G_3 \times SA_t) + (P_4 \times A_t)$$

where G_i is the probability of surviving and advancing from stage *i* to stage *i*+1 during a one-month time interval; P_i is the probability of surviving and remaining in the same stage during a one-month time interval; and F_4 is the contribution of individuals in stage A to stage L during a one-month interval (*i* = 1,2,3 or 4).

Survivorship and growth entries for the L, J, SA and A stages were calculated from the field and literature surveys described above. Both P_i and G_i are dependent on survival (p_i) and growth (γ_i) probabilities (Caswell 2001):

(8) $$P_i = p_i(1-\gamma_i)$$ and

(9) $$G_i = p_i\gamma_i$$ where

(10) $$p_i = e^{-z_m}$$ and

(11) $$\gamma_i = [(1-p_i)p_i^{d_i-1}]/[1-p_i^{d_i}]$$

where z_m is the monthly mortality rate and d_i is the duration of the i^{th} stage (Crouse et al. 1987).

We calculated average individual fertility (F_4) in the adult stage as:

(12) $$F_4 = (0.18)[(1+P_4)f_4]$$

where f is average monthly fecundity of adults and P_4 is calculated from Eq. (8). Eq. (12) is adapted from Caswell (2001) assuming $G_4 = 0$ since halibut cannot grow out of the adult stage.

λ, prospective and retrospective analyses. Using MATLAB (Appendix 3), the population growth rate (λ) (dominant eigenvalue), stable-age distribution (right dominant eigenvector, standardized to sum to 1), and reproductive value of individuals in stage *i* (left dominant eigenvector), as well as overall eigenvector structure was determined for each of the 12 matrices.

For each matrix, changes in λ resulting from changes in any one matrix entry can be evaluated using the sensitivity index (S_{ij}), defined as:

(13) $$S_{ij} = (v_i w_j)/\langle \mathbf{w},\mathbf{v} \rangle$$

where **w** is the first right eigenvector of the matrix, **v** is the first left eigenvector of the matrix, w_j is the j^{th} element of the first right eigenvector, v_i is the i^{th} element of the first left eigenvector, and <**w**,**v**> is the scalar product of those vectors (Caswell 2001) (Table 5.3). Because matrix entries can differ greatly in magnitude, it is useful to consider what impact a 1% change in P_i, G_i and F_4 would have on λ. Elasticities (E_{ij}) sum to 1 and indicate the rank importance of matrix entries in determining population growth and maintenance (de Kroon et al. 2000). This proportional sensitivity of individual matrix entries (a_{ij}) can be calculated as:

(14) $$E_{ij} = (a_{ij} / \lambda) \times S_{ij}$$

Elasticities demonstrate how much impact a potential change in a matrix entry can have on λ, and is considered a prospective analysis. Another measure is needed to quantify the impact of observed spatial and temporal differences of vital rates in generating variation in λ (Caswell 2000). Therefore, retrospective decomposition analyses were employed to determine the contribution of individual matrix entries in producing observed growth rates. These life table response experiments (LTREs) were used to examine the sources of variation in λ among habitats and years. Contribution (C_{ij}) values for each matrix entry were calculated as:

(15)

$$C_{ij} = (a_{ij}^{(k)} - a_{ij}^{(\bullet)}) \times S_{ij} \big| (M^{(k)} + M^{(\bullet)}) / 2$$

where $a_{ij}^{(k)}$ is the value of matrix entry a_{ij} in the k^{th} matrix, and $a_{ij}^{(\cdot)}$ is the average value of matrix entry a_{ij} from the 12 separate matrices. S_{ij} is the sensitivity of λ to matrix entry a_{ij} evaluated using the average of the k^{th} and overall average matrix (Caswell 2001). To generate these LTREs, average matrices were constructed for each year (comparing habitats) and putative nursery type (comparing years).

Matrix entries weighted by nursery habitat contribution. To fully understand the consequences of nursery habitat utilization for overall population demography, one must consider both the differences in habitat-specific vital rates and the relative degrees to which alternative nursery habitats are utilized. We generated “composite” population growth rates from a series of simulation models in which the vital rates used to populate matrix entries were derived from weighted averages of exposed and embayment nursery habitat mortalities and stage durations. Weighted averages were based on the proportion of juvenile fish that utilized exposed versus embayment (bay, lagoon or estuary) habitats as nurseries, and were simulated to range between 0 and 100% (Table 5.1). Weighted vital rates were entered into Eq. 8-12 to populate matrix entries. This was done separately for each of the four years in which we had juvenile cohort data, and produced projections of λ for the overall California halibut population along San Diego County. Prior to averaging exposed and embayment habitat rates, we first had to calculate the relative weighting for Mission Bay, Agua Hedionda and Tijuana River vital rates to generate an embayment "composite" during each year. Fodrie and Mendoza (2006) extensively surveyed the San Diego County coastline in 2003-2004 and found that 78% of all California halibut juveniles that utilized embayment habitats were located in bays. Therefore, we weighted the Mission Bay rates by 78%, and the Agua Hedionda (1987-1988) and Tijuana River (2002-2003) rates by 22% in order to produce mortality and stage duration composites for embayment habitats.

Statistics. For each of the vital rates that were allowed to vary among models (juvenile mortality, juvenile stage duration, sub-adult mortality, adult stage duration), in addition to population growth rate (λ), we tested for differences among habitats (years pooled) and years (habitats pooled) using one-way ANOVAs. The absence of data from Agua Hedionda in 2002-2003 and Tijuana River in 1987-1988 precluded the use of two-way tests. For each variable we considered, data passed the assumptions of normality (Chi^2-test) and equal variance (F-max test) among groups. Fisher's (LSD) post-hoc test was used for pairwise comparisons. Additionally, the evidence for density-dependent juvenile mortality at Scripps, Mission Bay, Agua Hedionda and Tijuana River was evaluated using model II regressions of habitat-specific monthly mortality versus local juvenile densities (1987-1988) or catch rates (2002-2003). All statistics were conducted using StatView (© SAS Institute Inc.).

Results

Nursery-driven variation in mortality and growth. Based on cohort analyses, monthly juvenile mortality (z_m) averaged 0.73, 0.38, 0.55 and 0.35 at Scripps Beach, Mission Bay, Agua Hedionda Lagoon and Tijuana River Estuary, respectively, across four years of collections. The difference in rates was statistically significant (ANOVA; $F_{3,4} = 6.921$; $p = 0.013$). However, there was considerable interannual variation in mortality rate among years within individual habitat types. For instance, SIO and MB were characterized by notably higher juvenile mortality during 1987 (0.97 and 0.41, respectively) than in 1988 (0.56 and 0.30, respectively), with "intermediate" mortality rates during the more recent surveys in 2002 and 2003. Conversely, juvenile mortality in Agua Hedionda was 50% higher in 1988 over 1987. Because of this interannual variability, Fisher's post-hoc only found that Scripps > Mission Bay and Tijuana River, while all other pair-wise comparisons indicated no difference in mortality among sites ($\alpha = 0.05$).

Juvenile mortality rates appeared to be density independent during 1-month intervals. There was a positive, nearly linear relationship between the density (1987-1987) or catch rate (2002-2003) of juvenile California halibut collected each month (time = t) within a habitat and density or catch rate of juveniles collected in the same habitat one month later (time = t+1) (Figure 5.4A-B). Also, there was no strong or statistically significant (non-zero slope) relationship between mortality and local density (1987-1988) or catch rates (2002-2003) in any of the habitats for which we collected cohort information ($r^2 < 0.2$; $p > 0.05$ in all 6 cases) (Figure 5.4C-D).

The monthly mortality rate (z_m) of sub-adult California halibut (SA; 1- to 4-year-olds) captured during the 1994 SCBBS averaged 0.195 based on our static life-table analysis (Figure 5.5). This system-wide SA mortality was adjusted to represent nursery-specific rates. Adjustments were made using the results of an elemental fingerprinting study that retroactively assigned 1- and 2-year-old California halibut to a nursery origin during 2003 and 2004 (Chapter 4). Following nursery origin assignments, relative survivorship rates from age 1 to age 2 could be calculated for sub-populations of fish egressing from each nursery type. After corrections, SA mortality was highest for fish that utilized exposed nurseries (0.198), and lowest for fish that utilized estuarine nurseries (0.190) (Table 5.1; ANOVA; $F_{3,4} = 8.000$; $p = 0.009$). Mature females (A; <4 years old) collected during the 1994 SCBBS experienced an average monthly mortality of 0.071 (Figure 5.5).

Juvenile and adult stage durations were not significantly different among nursery alternatives (ANOVA; $F_{3,4} = 1.222$; $p = 0.363$ for both since $A_d = 240 - L_d - J_d - SA_d$, and L_d and SA_d were constants). Of the 4 vital rates (juvenile mortality, juvenile stage duration, sub-adult mortality, adult stage duration) that we tested, none were shown to be statistically different among years for the population along San Diego County ($p > 0.05$). This was mostly due to the variability among habitats we observed.

Nursery-driven variation in λ. Population growth rates (λ month^{-1}) averaged over the four years we collected juvenile vital-rate data were 0.97, 1.14, 1.03 and 1.17 for sub-populations of fish that utilized Scripps Beach (Exposed), Mission Bay (Bay), Agua

Hedionda (Lagoon) and Tijuana River (Estuary) as juvenile habitat, respectively (Figure 5.6A). Differences among λ for the subpopulations that utilized alternative juvenile habitat types were significant (ANOVA; $F_{3,4} = 13.814$; $p = 0.002$). Post-hoc analyses revealed that Scripps = Agua Hedionda < Mission Bay = Tijuana River ($\alpha = 0.05$). The sub-populations that utilized MB and TJE were characterized by $\lambda > 1$ in every year, although only Tijuana River was characterized by a λ clearly different than 1 (equilibrium) based on 95% confidence intervals (2 standard deviations) of habitat-specific population growth estimates observed over multiple years. Juvenile populations that utilized SIO were characterized by $\lambda < 1$ in all years except 1988 ($\lambda = 1.01$), while the juvenile halibut that utilized AH were characterized by population growth rates of 1.08 and 0.98 in 1987 and 1988, respectively. Average population growth rates pooled for all nursery types was not significantly different among years (ANOVA; $F_{3,4} = 0.095$; $p = 0.960$) (Figure 5.6B). Overall, λ ranged from a low of 0.93 (Scripps, 1987) to a high of 1.20 (Mission Bay, 1988).

Sensitivity of λ to stage-specific vital rates. Population growth was hypothetically most sensitive to changes in adult survival (P_4), and to a lesser extent, sub-adult (P_3) and juvenile (P_2) survival of fish that did not grow out of these stages (Figure 5.7). This trend was most pronounced at SIO, but held true for all habitats and years. Survival and growth from one stage to the next (G_1, G_2 and G_3) and fertility (F_4) would be expected to have only modest, surprisingly equal, impacts on λ. For all 12 matrices, λ appeared most insensitive to changes in (P_1), larval survival without advancement to the juvenile stage.

Retrospective decomposition analysis revealed that the life-history elements to which λ was most sensitive were not always the same ones that drove observed differences in population growth among habitats and years. For instance, λ was theoretically most sensitive to adult survival (P_4); however, P_4 varied only slightly among models (via stage duration, Eq. 8, 10-11) and did not contribute significantly to the differences we observed in λ (Figure 5.8, 5.9). Rather, survival and advancement of juvenile fish from the juvenile to sub-adult stage (G_2) had the largest contribution to the variation we observed both among habitats (Figure 5.8) and years (Figure 5.9). Among habitats, the G_2 matrix entry contributed to below average population growth at SIO during all years, and above average population growth at Mission Bay (although barely in 2003) and TJE (Figure 5.8). At Agua Hedionda, G_2 helped produce elevated population growth in 1987 relative to other nursery habitat alternatives, but not during the following year. There were also import differences in the contribution of G_2 on λ among years within each of the habitats we considered. While G_2 contributed to anomalously high population growth during 1988 for the sub-populations utilizing SIO and MB as nurseries, the reverse was observed in Agua Hedionda (Figure 5.9). Within TJE, juvenile survival and growth were higher in 2003 than 2002, although the overall impact on λ was modest compared with other habitats. Other matrix entries that contributed to observed differences in λ among habitats and years included juvenile survival without advancement (P_2) and, in some instances, sub-adult survival and growth (G_3).

Incorporating nursery habitat contribution into estimates of λ. Population growth rates weighted for nursery habitat contribution were positively, though non-linearly, related to the percentage of juvenile fish that utilized embayment (bay, lagoon or estuary) habitats as nurseries during each year we collected vital-rate data (1987-1988, 2002-2003) (Figure 5.10). Estimated population growth rate was highest in 1987 and most negative in 1988, but the percentage of embayment contribution in both years would have to be determined (by elemental fingerprinting or other approach) before an exact λ could be resolved. Our simulations indicated that in order to reach a stable or growing population ($\lambda \geq 1$), embayment contribution of juveniles that advance to the adult stock needed to be at least 0%, 70%, 38%, and 40% of all nursery contribution during 1987, 1988, 2002 and 2003, respectively. Based on the four years we included in our analyses, at least ~38% of nursery contribution must originate from within embayments for long-term California halibut population persistence, assuming equal larval production in all years.

Discussion

Population growth rate as a measure of nursery value. A nursery habitat may generate positive, stable or negative population growth independent of the number of recruits it contributes for replenishing older populations. This is an under appreciated dynamic of nursery habitat utilization but has clear relevance for conservation strategies. In Chapter 4, we utilized an elemental fingerprinting approach to demonstrate that 42% of recruits that advanced from primary nurseries around San Diego utilized exposed habitats during 2003-2004. This raw contribution of recruits with an exposed nursery origin was much larger than had been previously acknowledged, and raised doubts about estuarine-dependence for California halibut. Our demographic data suggests that the production of recruits from exposed habitats came at the cost of high juvenile mortality. As a result, sub-populations utilizing exposed habitats experienced negative population growth in 3 of the 4 years we considered, and, over the long-term, must be subsidized by migrants from embayment habitats through adult movements or larval transport in order to persist (Morris 1991). Measuring population growth is not definitionally equivalent to understanding source/sink dynamics (Watkinson and Sutherland 1995), but there is considerable overlap with regards to management implications in a heterogeneous environment. Specifically, our simulation models indicate that approximately 37.5% of recruits must have an embayment nursery origin in order for California halibut population to be stable or increasing (Figure 5.10). Ecosystem management programs are typically resource limited, and these data could promote stock success for this species by guiding habitat conservation to the nurseries that generate maximum population growth.

Two popular frameworks for measuring nursery habitat value for fishery production include: (1) total contribution of new recruits to the adult stock, determined by both habitat quality and quantity (Gibson 1994), and (2) the nursery-role concept, which stresses per unit area production to the adult stock (Beck et al. 2001). However, under either of these schemes it would seem possible to have a high total or unit-area contribution from a nursery site that generates dampened population growth. For instance, Fodrie (Chapters 2, 4, 5) employed multiple approaches to rank the nursery value of exposed, bay, lagoon and estuarine habitats for the California halibut under these three frameworks (total contribution, unit-area contribution and population growth). The result was three separate rankings of nursery value for juvenile halibut among these four habitat types (Table 6.1). For managers, selecting among these metrics of habitat value could have a strong influence on the sites or life stages that are targeted for protection in order to enhance ecosystems, and understanding the conservation goals may dictate which framework is most desirable (e.g. Minton 1999; Crowder et al. 2000). Including population demography as a metric of nursery value, that allows sensitivity analyses of individual life-history stages, seems particularly advantageous for the many coastal finfish species in which the relative impacts of perturbations to both early (via habitat degradation) and late life-history stages (via harvest) of a declining population confound one another. Levin and Stunz (2005) utilized simulations of stage-structured models for red drum, *Sciaenops ocellatus*, to demonstrate that wetlands restoration (utilized by juvenile fish) could lead to a 2% increase in λ for the population they considered even without changes in fishing practices. This change resulted in a shift from negative to positive population growth for red drum, and along with our data highlight the advantages of considering population demography in identifying Essential Fish Habitats.

Influence of mortality and growth on juvenile distributions. Our monthly surveys demonstrated that juvenile halibut densities could vary by an order of magnitude among habitats Three potential mechanisms for disparities in juvenile habitat usage include nursery-related inequalities in predation pressure (top-down forcing), growth (bottom-up forcing) and hydrodynamic decoupling of habitat quality and utilization (via larval transport) (Heck et al. 2003; Lipcius et al. 1997). Our data support top-down control of juvenile halibut distributions, with larval supply potentially playing a role.

Based on the mortality rates we observed among habitats, coastal embayments appear to provide a refuge from high predation on juvenile halibut. The lack of growth differences between nurseries suggests that variation in mortality was likely driven by predation, not starvation (Table 5.1). There are a number of potential predators along the exposed coastline that are known to eat flatfish, including larger California halibut, speckled sand dabs, thornback rays, round sting rays, barred sand bass, and probably California sea lions and harbor seals (Allen et al. 1990). Although several of these species are also found within embayments, average sizes of these species in embayments are generally much smaller than along the exposed coast (Allen et al. 2002). Differences in substrate types and water clarity may also make juvenile halibut more susceptible to predation along the exposed coastline (Drawbridge 1991).

Juvenile stage durations were not different ($p > 0.05$) among habitats, suggesting that growth advantages were not provided by specific nursery types. Kramer (1991) also presented data that indicated there were no growth differences between individual juveniles collected from along the exposed coastline and from within protected embayments. This is somewhat surprising, given the difference in temperatures between exposed and embayment habitats and the number of studies that have documented growth differences for juvenile fish among habitats and estuaries (e.g., Sogard 1992; Perkins-Visser et al. 1996; Phelan et al. 2000). Heck et al. (2003) argue that growth advantages for juvenile fish are tied to the utilization of structure habitats more than any other factor. Juvenile halibut are distinguished by selection of unstructured benthic habitats in both exposed and embayment habitats (Fodrie and Mendoza 2006). This, in part, may explain our observations.

Given the disparity we observed in mortality, an obvious question is why don't all juvenile halibut migrate into coastal embayments to maximize fitness? Over large spatial scales (>10 km) nursery selection may necessarily be a non-adaptive trait due to the constraints experienced by individuals according to where they settle (Allen 1988). While halibut are indeed capable of some migration following settlement (Chapter 3), individuals that settle along the exposed coast several km from embayment mouths might not be able locate prefered habitats. Selection pressure to locate embayment habitats may also be mitigated by the temporal variability we observed in monthly mortality along the exposed coastline during the four years we collected data, ranging from 56%-97%. Alternatively, utilizing multiple nursery habitat types may serve as a bet hedging strategy that buffers halibut populations against environmental ebbs and flows (Kramer 1991; sensu Dias 1996).

Stock regulation. The "concentration hypothesis" as defined by Iles and Beverton (2000) poses that juveniles can concentrate into spatially-limited nurseries far beyond carrying capacity, at which point depensation will limit the amount of contribution possible from those sites. This is a variation of "supply-side ecology" applied to nursery habitat utilization (sensu Gaines and Roughgarden 1985), and has received substantial attention in flatfish recruitment studies attempting to understand the relationship between temporal or spatial variation in juvenile growth or mortality and adult population size (e.g. Modin and Pihl 1994, Nash and Geffen 2000). We observed no relationship between mortality rates and density (Figure 5.4C-D), and a positive relationship between the number of fish in a juvenile cohort during a given month and one month later (Figure 5.4A-B).

These data contribute to the debate over the regulating mechanisms of flatfish 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 juvenile fish were observed to be a good predictor of unit-area contribution from individual nurseries for up to two years based on elemental fingerprinting results to retroactively track the nursery origins of fish (Chapter 4). We recognize that our design would not have detected density-dependent mortality for fish less than 60 mm, a period when larval and juvenile California halibut may be especially vulnerable to mortality (Kramer 1991). Consequently, either larval supply or very early post-settlement processes may still control population structure. Although mortality appeared to be density-independent and non-seasonal (Figure 5.2), there were strong differences among habitats and years (Table 5.1). Therefore, juvenile mortality would seem to have the potential to amplify recruitment variability for the California halibut rather than reduce it (Bailey 1994).

Sensitivity of λ to stage-specific vital rates and model performance. Elasticity analyses of matrix models demonstrated that regardless of juvenile habitat selection or year, λ was most sensitive to changes in adult survival (P_4) (Figure 5.7). Because adults: (1) represent an extremely small fraction of all California halibut (>0.001%) in a stable population (Figure 5.11A), (2) are the only contributor (given our model structure) to reproductive output (Figure 5.11B), and (3) are highly fecund; they are extremely valuable individuals for population maintenance and therefore λ is particularly sensitive to their survival rate. Sensitivity to P_4 was elevated at Scripps because local juvenile mortality was higher, and as a result the value of keeping fish alive once they reach maturity was accentuated. However, pre-recruitment life-history events (juvenile growth, juvenile survivorship) dominated the actual contribution to observed differences in λ (Figure 5.8, 5.9). This represents both the natural variability resulting from the nursery generalist strategy of the California halibut, but also the lack of data to explore the variability of larval and adult vital rates (see Heppell et al. 2000). Although larval- and adult-stage vital rates may not vary as a function of nursery habitat utilization, there is little doubt they vary in time. The magnitude of variation in larval survival, as well as adult fecundity, and their contribution to interannual variation in population growth remain uncertain, and represent high priorities for future research. Pfister (1988) has hypothesized that λ should be least sensitive to the life-history entries that experience greatest variability. In the models we constructed, λ was most insensitive to larval survival without growth (P_1) by a wide margin (Figure 5.7), and may indicate an elevated coefficient of variation of larval mortality relative to other rates, predictable given the species' intermediate longevity, iteropartiy and high fecundity (e.g., Lasker 1981).

The difference in population growth for California halibut during the El Nino and La Nina years of 1987 and 1988 is especially interesting for the population structure of California halibut populations. Settlement (i.e. larval supply or survival) appeared to be highest during cool years, but within "cool" years is highest in areas with warmer water temperatures (Figure 5.2) (Kramer 1991). Simultaneously, juvenile growth and survival (G_2) contributed to elevated population growth during 1988, when cool, La Nina conditions were beginning (Figure 5.9). Previously, population projection matrix models have demonstrated that El Nino cycles have strong impacts on other southern California ichtyofauna (Davis and Levin 2002). The increases in settlement and juvenile advancement could have meant that 1988 was a boom year for the halibut and that the 1988 cohort was a dominant year class until very recently (Hjort 1926). This should have been especially evident in regions with large amounts of exposed or semi-exposed coastline such as the Santa Barbara Flats, which supports a large commercial fishery for California halibut (J. Hunter, personal communication). Data from a 1994 survey do not support this hypothesis (MacNair et al. 2001).

The overall weighted average of $\lambda_{monthly}$ for the four years we obtained juvenile cohort data was 1.03. This is equivalent to 42% population growth year^{-1}, and is likely an overestimation of population fitness. The most likely source for this error was the mortality we were unable to include for juvenile halibut 10mm-60mm SL due to gear biases between the 1987-1988 (Kramer 1990) and 2002-2003 surveys (Figure 5.3). Estimates in larval mortality of adult fecundity, especially size-specific fecundity, must also be viewed as potential sources of error in overall population growth. Regardless of these uncertainties, the data demonstrate that habitat-specific differences in growth and survivorship experienced by juvenile fish and invertebrates within alternative putative nurseries have the potential to generate significant variation in $\lambda_{monthly}$ ($0.93 < \lambda < 1.21$). The model results should be viewed as qualitative estimates of population demography, and instructive for considering habitat value.

Figures and tables

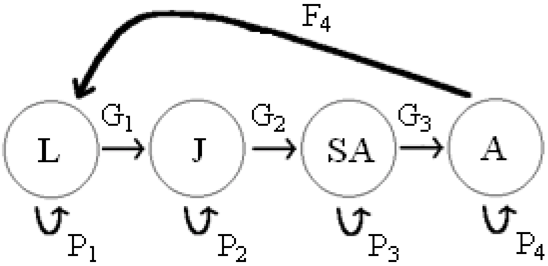

Figure 5.1. Life-cycle diagram used to construct stage-based population projection matrix models for the California halibut. L = larvae; J = juvenile; SA = sub adult; and A = adult. P_i is the probability of surviving to remain in the same stage during one time step. G_i is the probability of surviving and advancing to the next life-history stage during one time step. F_4 is the contribution of offspring by individual adults to the larval pool during one time step. i = 1,2,3 or 4.

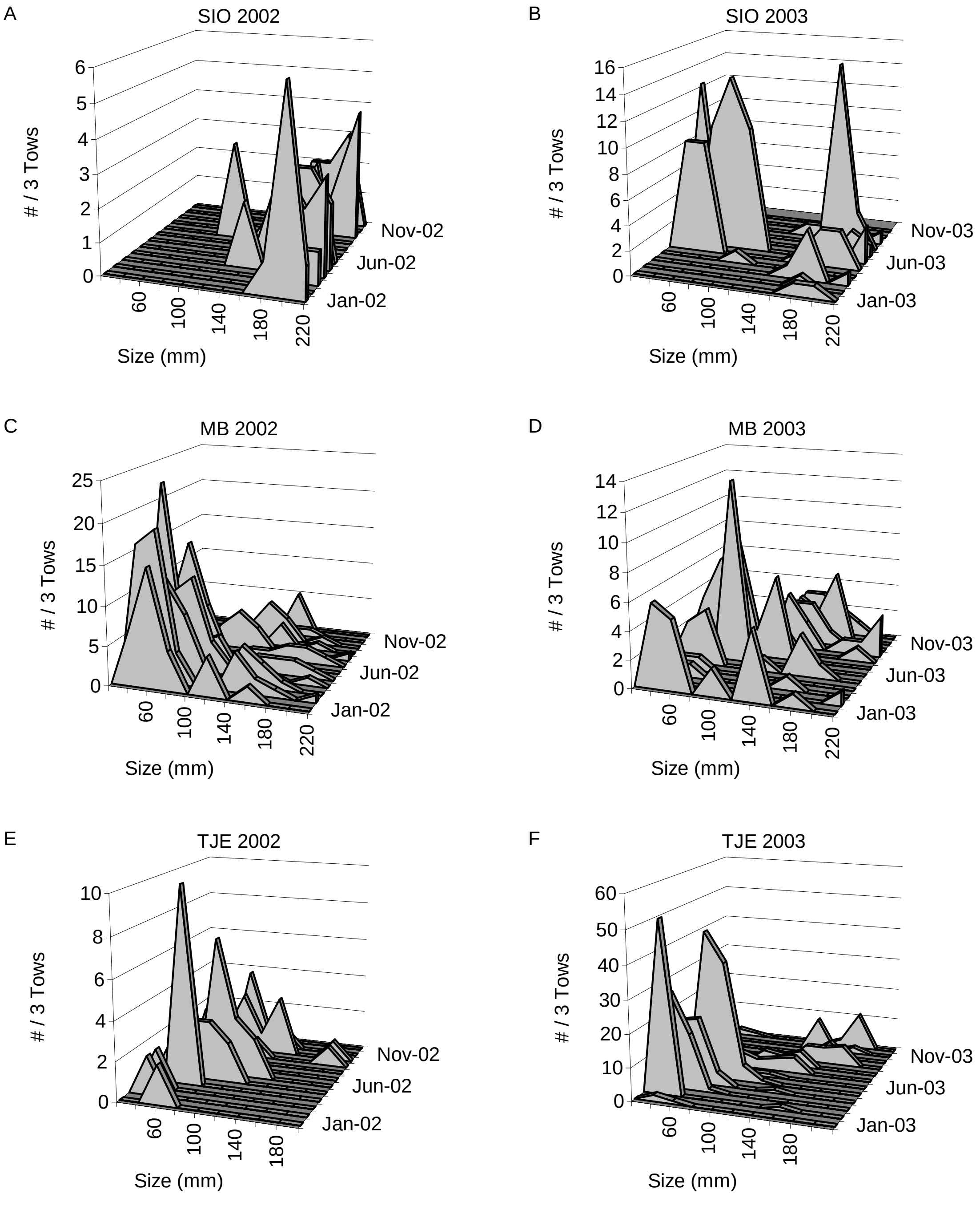

Figure 5.2. Number of juvenile California halibut (in 20-mm SL divisions) caught every month in 3 ten-minute tows at SIO (A-B), Mission (C-D) and Tijuana River (E-F) during 2002 (A, C and E) and 2003 (B, D and F). The data were used to calculate habitat-specific mortality rates and juvenile stage durations during 2002 and 2003.

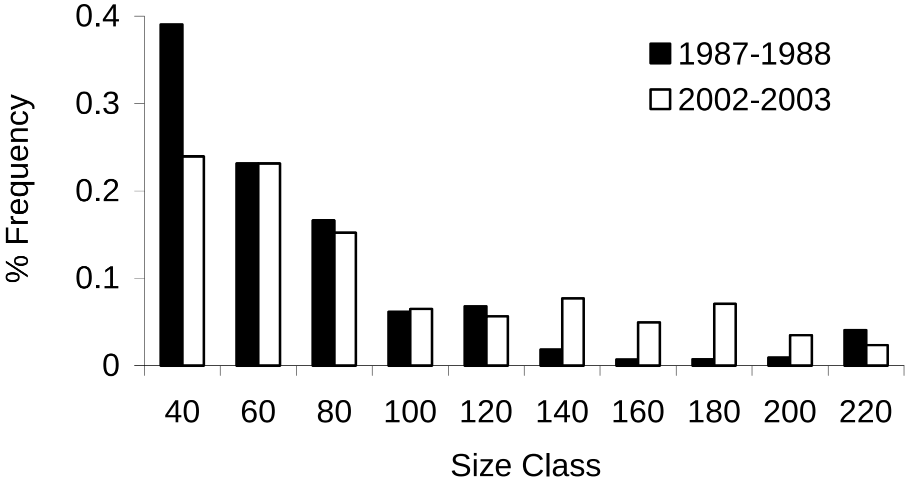

Figure 5.3. Size frequencies of juvenile California halibut collected during 1987-1988 and 2002-2003 in putative nursery habitats.

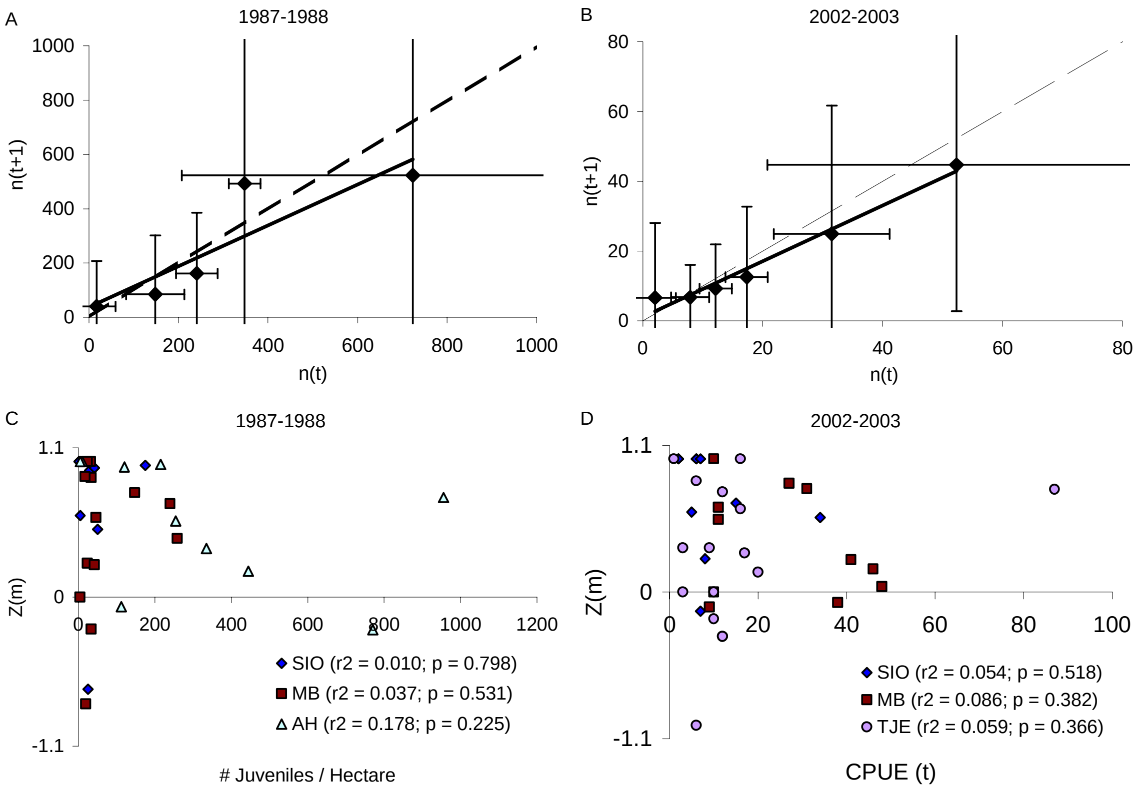

Figure 5.4. (A-B) Relationship between the numbers of juvenile California halibut collected each month (time = t) within a habitat and numbers of juveniles collected at in the same habitat one month later (time = t+1) during the (A) 1987-1988 surveys, and (B) 2002-2003 surveys. Data from individual study sites are pooled in both A and B, and individual data points represent the $n_{(t)}$ and $n_{(t+1)}$ averages ($\underline{+}$95% confidence intervals) for all data dived into 5 (A) or 6 (B) bins. (C-D) Density independence of mortality rates (z_m) based upon cohort tables generated from (C) juvenile densities during 1987-1988, and (D) juvenile catch rates during 2002-2003.

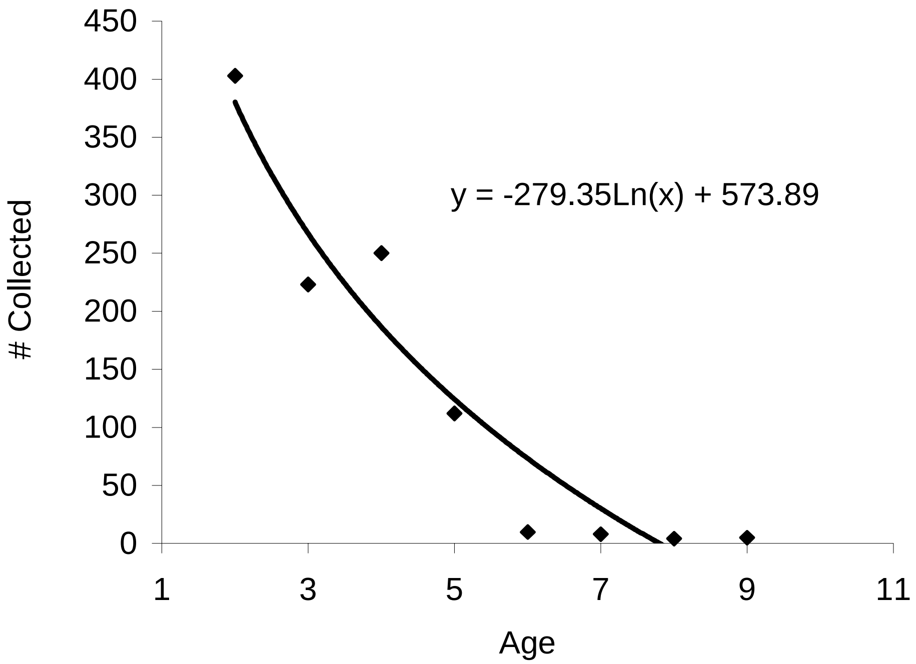

Figure 5.5. Number of California halibut age 2 and greater collected during the 1994 Southern California Bight Biomass Survey along San Diego County (courtesy of S. Wertz, California Department of Fish and Game).

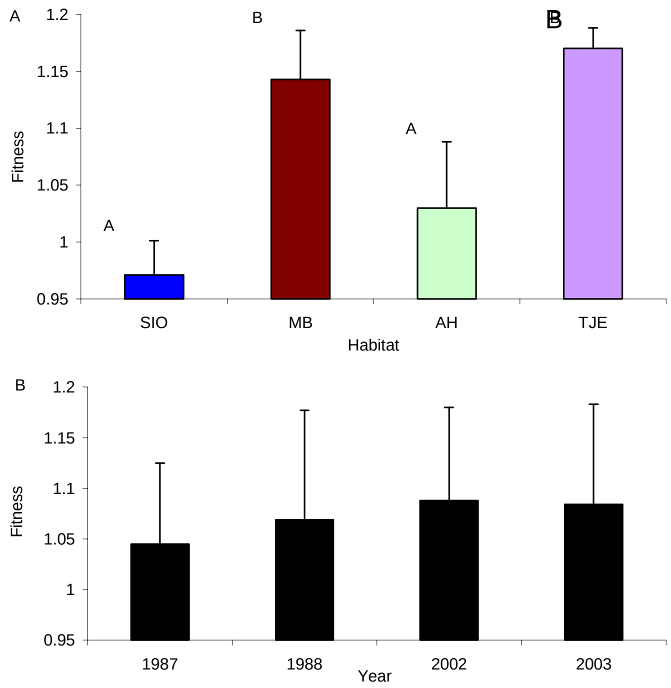

Figure 5.6. Average fitness (λ) generated from the 12 separate matrices grouped by (A) nursery habitats, and (B) years. Different letters in (A) indicate statistically significant (α = 0.05) differences among groups. Data are presented with +1 SD.

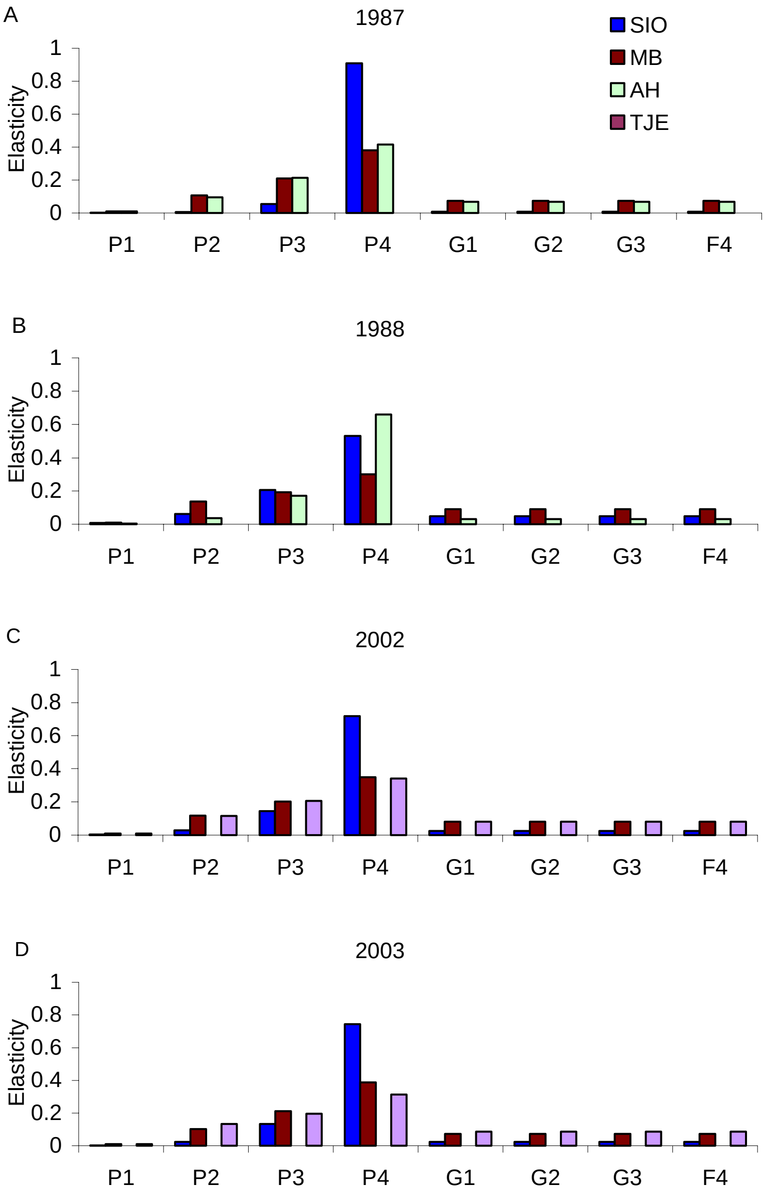

Figure 5.7. Elasticity of each matrix element to changes in fitness (λ) during (A) 1987, (B) 1988, (C) 2002, and (D) 2003 for the populations utilizing Scripps (SIO), Mission Bay (MB), Agua Hedionda (AH) and Tijuana River (TJE) as nursery habitat.

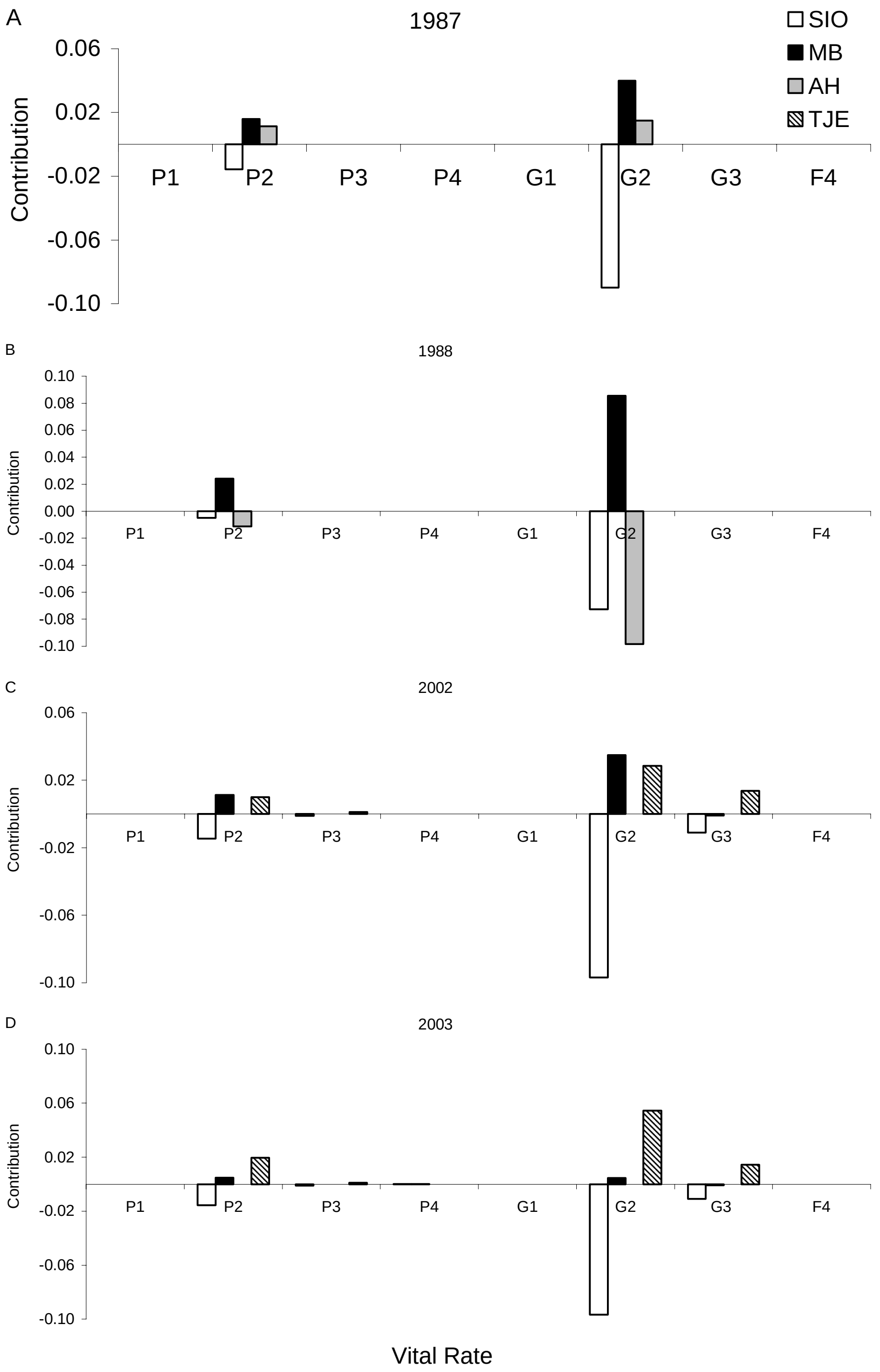

Figure 5.8. Contribution of each matrix element for deviations in fitness (λ) during (A) 1987, (B) 1988, (C) 2002, and (D) 2003 for the populations utilizing Scripps (SIO), Mission Bay (MB), Agua Hedionda (AH) and Tijuana River (TJE) as nursery habitat.

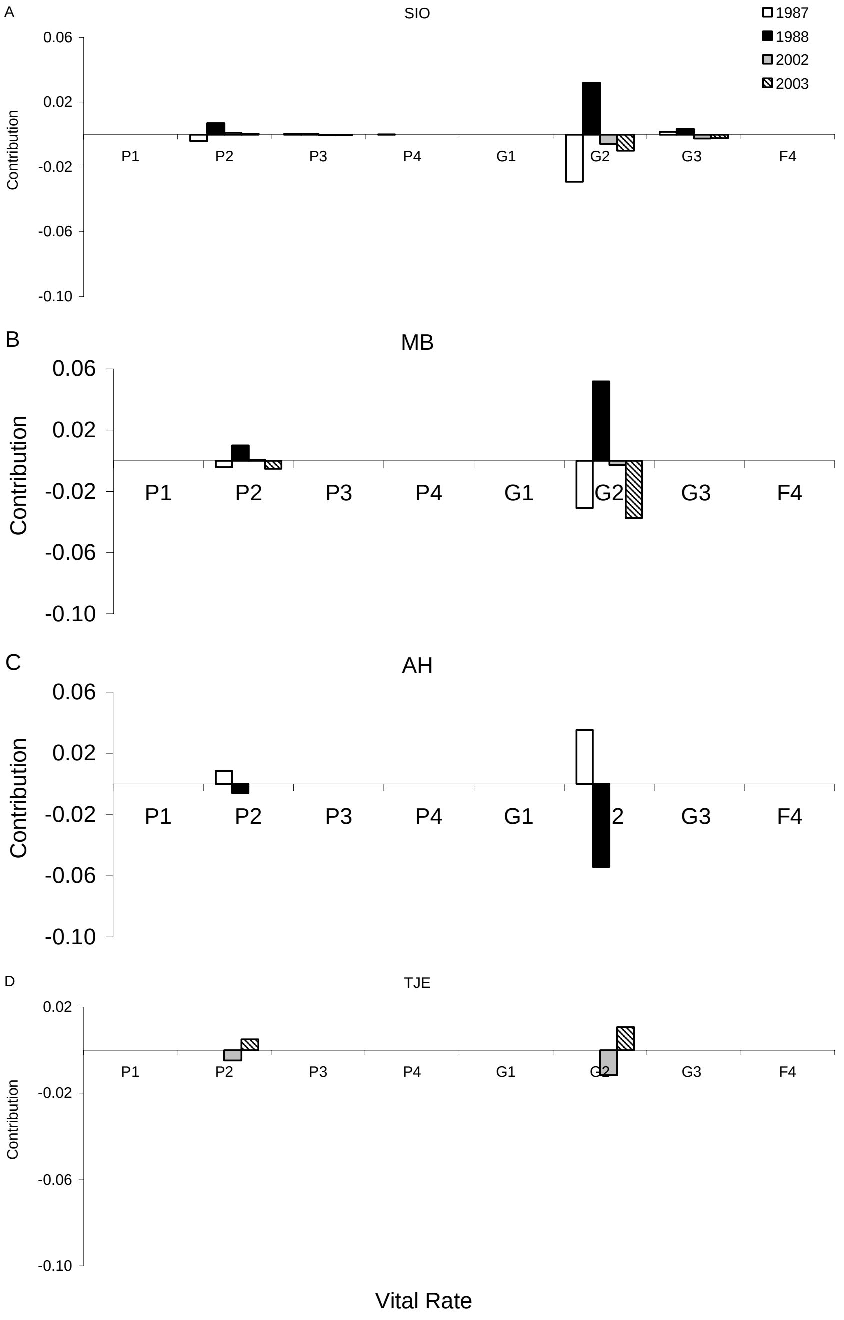

Figure 5.9. Contribution of each matrix element for deviations in fitness (λ) during four years of juvenile cohort analyses for the populations utilizing (A) Scripps (SIO), (B) Mission Bay (MB), (C) Agua Hedionda (AH) and (D) Tijuana River (TJE) as nursery habitat.

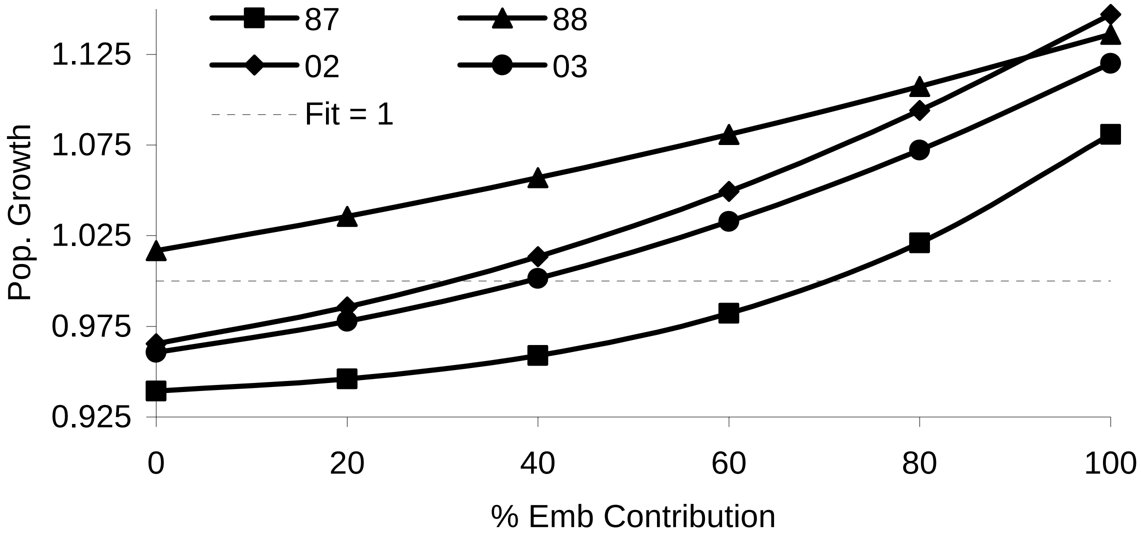

Figure 5.10. Overall population fitness (λ) resulting from the percentage of fish that utilized exposed (Scripps) versus embayment (Mission Bay, Agua Hedionda or Tijuana River) habitat as nurseries during 1987, 1988, 2002 and 2003.

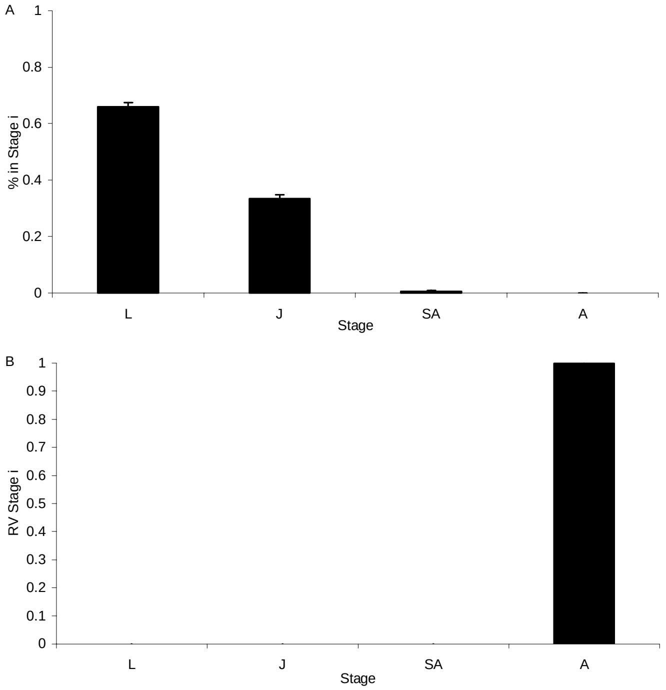

Figure 5.11. Average (A) stable-stage distributions and (B) reproductive values of stage *i* from the 12 separate matrices that were generated. Data are presented with +1 SD.

Table 5.1. Stage-specific vital rates for California halibut utilizing three alternative nursery types in 1987-1988 and 2002-2003 (F, fecundity; z, mortality; and d, stage durations). Rates are based on a one-month time step. SIO = Scripps; MB = Mission Bay; AH = Agua Hedionda; and TJE = Tijuana River.

Stage	**Larvae (L)** (0-40 mm)			**Juvenile (J)** (40-220 mm)			**Sub Adult (SA)** (220-475 mm)			**Adult (A)** (>475 mm)		
Vital Rate	F	z	d (mo)	F	z	d	F	z	d	F	z	d
1987-1988												
SIO 87	0	0.999	1.30	0	0.970	9.00	0	0.195	39.00	566422	0.071	190.70
SIO 88	0	0.999	1.30	0	0.560	10.00	0	0.195	39.00	566422	0.071	189.70
MB 87	0	0.999	1.30	0	0.410	11.00	0	0.195	39.00	566422	0.071	188.70
MB 88	0	0.999	1.30	0	0.300	10.00	0	0.195	39.00	566422	0.071	189.70
AH 87	0	0.999	1.30	0	0.450	10.00	0	0.195	39.00	566422	0.071	189.70
AH 88	0	0.999	1.30	0	0.660	10.00	0	0.195	39.00	566422	0.071	189.70
2002-2003												
SIO 02	0	0.999	1.30	0	0.680	10.00	0	0.200	39.00	566422	0.071	189.70
SIO 03	0	0.999	1.30	0	0.700	10.00	0	0.200	39.00	566422	0.071	189.70
MB 02	0	0.999	1.30	0	0.370	10.00	0	0.195	39.00	566422	0.071	189.70
MB 03	0	0.999	1.30	0	0.420	10.00	0	0.195	39.00	566422	0.071	189.70
TJE 02	0	0.999	1.30	0	0.380	10.00	0	0.190	39.00	566422	0.071	189.70
TJE 03	0	0.999	1.30	0	0.310	11.00	0	0.190	39.00	566422	0.071	188.70
Rates Weighted by Embayment Contribution												
1987												
%												
0	0	0.999	1.30	0	0.970	9.00	0	0.195	39.00	566422	0.071	190.70
20	0	0.999	1.30	0	0.860	9.36	0	0.195	39.00	566422	0.071	190.34
40	0	0.999	1.30	0	0.750	9.71	0	0.195	39.00	566422	0.071	189.99
60	0	0.999	1.30	0	0.639	10.07	0	0.195	39.00	566422	0.071	189.63
80	0	0.999	1.30	0	0.529	10.42	0	0.195	39.00	566422	0.071	189.28
100	0	0.999	1.30	0	0.419	10.78	0	0.195	39.00	566422	0.071	188.92
1988												
%												
0	0	0.999	1.30	0	0.560	10.00	0	0.195	39.00	566422	0.071	189.70
20	0	0.999	1.30	0	0.524	10.00	0	0.195	39.00	566422	0.071	189.70
40	0	0.999	1.30	0	0.488	10.00	0	0.195	39.00	566422	0.071	189.70
60	0	0.999	1.30	0	0.452	10.00	0	0.195	39.00	566422	0.071	189.70
80	0	0.999	1.30	0	0.417	10.00	0	0.195	39.00	566422	0.071	189.70
100	0	0.999	1.30	0	0.381	10.00	0	0.195	39.00	566422	0.071	189.70
2002												
%												
0	0	0.999	1.30	0	0.680	10.00	0	0.200	39.00	566422	0.071	189.70
20	0	0.999	1.30	0	0.618	10.00	0	0.199	39.00	566422	0.071	189.70
40	0	0.999	1.30	0	0.557	10.00	0	0.198	39.00	566422	0.071	189.70
60	0	0.999	1.30	0	0.495	10.00	0	0.196	39.00	566422	0.071	189.70
80	0	0.999	1.30	0	0.434	10.00	0	0.195	39.00	566422	0.071	189.70
100	0	0.999	1.30	0	0.372	10.00	0	0.194	39.00	566422	0.071	189.70
2003												
%												
0	0	0.999	1.30	0	0.700	10.00	0	0.200	39.00	566422	0.071	189.70
20	0	0.999	1.30	0	0.639	10.04	0	0.199	39.00	566422	0.071	189.66
40	0	0.999	1.30	0	0.578	10.09	0	0.198	39.00	566422	0.071	189.61
60	0	0.999	1.30	0	0.517	10.13	0	0.196	39.00	566422	0.071	189.57
80	0	0.999	1.30	0	0.456	10.18	0	0.195	39.00	566422	0.071	189.52
100	0	0.999	1.30	0	0.395	10.22	0	0.194	39.00	566422	0.071	189.48

Table 5.2. Stage-based population matrix entries for California halibut. Twelve separate matrices were generated that summarize life-history rates from 1987-1988 (SIO, MB and AH) and 2002-2003 (SIO, MB, TJE). SIO = Scripps; MB = Mission Bay; AH = Agua Hedionda; and TJE = Tijuana River. Matrix entries are abbreviated as in Figure 5.1.

	P1	**P2**	**P3**	**P4**	**G1**	**G2**	**G3**	**F4**
1987-1988								
SIO 87	0.1312	0.3790	0.8227	0.9315	0.2371	0.0001	0.0001	196928
SIO 88	0.1312	0.5696	0.8227	0.9315	0.2371	0.0016	0.0001	196928
MB 87	0.1312	0.6580	0.8227	0.9315	0.2371	0.0057	0.0001	196928
MB 88	0.1312	0.7272	0.8227	0.9315	0.2371	0.0136	0.0001	196928
AH 87	0.1312	0.6336	0.8227	0.9315	0.2371	0.0041	0.0001	196928
AH 88	0.1312	0.5162	0.8227	0.9315	0.2371	0.0007	0.0001	196928
2002-2003								
SIO 02	0.1312	0.5061	0.8187	0.9315	0.2371	0.0006	0.0001	196928
SIO 03	0.1312	0.4961	0.8187	0.9315	0.2371	0.0005	0.0001	196928
MB 02	0.1312	0.6829	0.8227	0.9315	0.2371	0.0078	0.0001	196928
MB 03	0.1312	0.6518	0.8227	0.9315	0.2371	0.0052	0.0001	196928
TJE 02	0.1312	0.6766	0.8269	0.9315	0.2371	0.0072	0.0001	196928
TJE 03	0.1312	0.7243	0.8269	0.9315	0.2371	0.0091	0.0001	196928

Table 5.3. Sensitivities of the 8 matrix entries for each annual and habitat-specific, stage-based population matrix. Twelve separate matrices were generated that summarize life-histories from 1987-1988 (SIO, MB and AH) and 2002-2003 (SIO, MB, TJE). SIO = Scripps; MB = Mission Bay; AH = Agua Hedionda; and TJE = Tijuana River. Matrix entries are abbreviated as in Figure 5.1.

	P1	P2	P3	P4	G1	G2	G3	F4
1987-1988								
SIO 87	0.01	0.01	0.06	0.92	0.03	71.57	81.41	3.60E-08
SIO 88	0.06	0.11	0.25	0.58	0.21	31.05	559.86	2.51E-07
MB 87	0.08	0.18	0.28	0.45	0.35	14.46	928.61	4.16E-07
MB 88	0.10	0.23	0.28	0.39	0.46	8.02	1234.02	5.53E-07
AH 87	0.08	0.16	0.28	0.48	0.31	17.87	824.36	3.70E-07
AH 88	0.04	0.07	0.20	0.69	0.13	47.55	354.58	1.59E-07
2002-2003								
SIO 02	0.03	0.05	0.17	0.74	0.11	45.84	339.40	1.28E-07
SIO 03	0.03	0.05	0.16	0.77	0.09	48.68	301.00	1.14E-07
MB 02	0.09	0.20	0.28	0.43	0.39	11.67	1036.65	4.65E-07
MB 03	0.08	0.18	0.28	0.46	0.34	15.25	902.19	4.04E-07
TJE 02	0.09	0.20	0.29	0.42	0.40	13.00	897.18	4.77E-07
TJE 03	0.10	0.22	0.28	0.40	0.43	11.18	971.42	5.17E-07

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Chapter 5 of this dissertation, in full, is being submitted to the Canadian Journal of Fisheries and Aquantic Sciences (Fodrie, F.J., L. Levin and A. Lucas. Consequences of nursery habitat selection for the demography of California halibut populations.) The dissertation author was the primary investigator and author of this paper.

VI.

CONCLUSIONS

Metrics of nursery habitat value

Halting the decline or facilitating the restoration of nearshore habitats designed to enhance nursery function will require an improved method of prioritizing where to spend limited time, money, and effort. One problem in setting priorities, however, is that the concept of nursery habitat has rarely been defined clearly, even in research studies that purport to test it. Most studies of the nursery-role concept have focused on seagrasses or wetlands and examined the effects of these habitats on one of three factors: the density, survival, or growth of juveniles.

Throughout the thesis, two alternative frameworks were considered for evaluating nursery habitat value. The nursery-role concept of Beck et al. (2001) states that nurseries are best ranked using unit-area contribution of juveniles to and adult population, while Gilbson (1994) felt it necessary to consider both habitat quality and quantity. As a result, Gibson (1994) focused attention on total recruitment potential that a potential nursery provided.

For the California halibut, data revealed that management priorities will be dramatically influenced by deciding between these two criteria for evaluating nursery value (Table 6.1). Highest unit-area contribution came from estuaries during both 2003 and 2004, but overall only contributed 2 % of all the individuals that successfully recruited to the older age classes during that same period (Chapter 2,4). Conversely, exposed habitats contributed approximately 40 % of all fish that advanced to the sub-adult population during the study, but were defined by only 1/15 to 1/30 of the unit-area contribution that was observed from estuaries and lagoon system (and 1/5 – 1/10 that of bay habitats).

By considering the demographic consequences of nursery habitat utilization, it was also possible to generate an additional metric of nursery value for the California halibut- population grow rate (Chapter 5). While a habitat may contribute a significant number of recruits for replenishing older populations, and potentially even contribute at a high unit-area rate, it can nevertheless contribute negatively to population growth rate (or vice versa). Going further, demographic simulations indicated that there is a minimum threshold of relative contribution needed from embayment habitats (~38% of total recruitment to the adult stock during 1987-1988, 2002-2003) for population maintenance. Potentially, the northern range limit of this species by a lack of embayment habitat along the northern California and Oregon coastline, which results in the inability of the species to achieve this threshold of embayment contribution (the California halibut is ecologically extinct north of Humboldt Bay, CA).

Table 6.1. Ranking of nursery habitat value based on 3 distinct metrics of habitat productivity. Scale is: 1 = most production, 4 = least production. Data used to evaluate unit-area contribution (Beck et al. 2001) and total contribution (Gibson 1994) are taken from Chapter 2,4. Data used to rank population growth (Caswell 2001) are from Chapter V.

Ranked Nursery-Role Value			
Nursery Type	Unit-area Contribution	Total Contribution	Population Growth
Exposed	4	2	4
Bay	3	1	2
Lagoon	2	3	3
Estuary	1	4	1

Evidence for a novel embayment classification scheme for describing fish habitat

Coastal embayments of Alto and Baja California have a diversity of forms and may function as unique ecosystems. Despite this, there is no classification scheme for distinguishing among these embayments as fish habitat. Currently, the best classification framework includes several marine hydrogeomorphic units such as lagoons, deltas, ports and exposed bays (Ferren et al. 1996). The data presented here support a classification scheme that divides embayments into bays, lagoons and estuaries. Hydrologically, all operate as reverse estuaries during the majority of the year (Zedler 1982). Bays are qualitatively different from other embayments in that they are kept open and relatively deep to serve as harbors for shipping and recreational boating. Estuaries are unique due to high wetland (salt marsh) cover.

This classification scheme accurately discriminated among embayments using: (1) basic geomorphologic characters such as average depth, spatial coverage and area-to-perimeter ratios (Chapter 2), (2) distribution of seagrass confined to bays and lagoons (Chapter 2), (3) 0-age halibut densities, which were shown to be highest within estuarine habitats (especially in 2004), elevated in lagoons, and lowest within bays. These differences may represent alternate carrying capacities in each of the embayment related to resource (space, food, shelter) availability (Chapter 2), (4) unit-area contribution tracked local density and was highest for estuaries, followed by lagoons and then bays. Alternatively, total contribution was highest in bay systems, and lowest among embayments within coastal estuaries (Chapter 4), (5) densities of other recreation important species such as barred sand bas, spotted sand bass, diamond turbot (Fodrie unpublished), (6) community diversity operating as a function of embayment size (Horn and Allen 1976), (7) elemental fingerprints (Chapter 3,4). The ability to identify and exploit signal variation over appropriate spatial and temporal scales will ultimately determine the resolution of studies tracking the movements of fish between juvenile and adult habitats. We compared three grouping schemes for classifying putative nurseries via DFA, and concluded that the highest classification success was achieved by grouping blocks into 4 nursery types: exposed, bay, lagoon and estuary (Chapter 4 and Appendix 2), and (8) population growth rates (Chapter 5). This novel approach for distinguishing nurseries may be applicable outside southern California along arid coastlines such as southern Africa and southwestern Australia that are characterized by small, patchily distributed embayments. Delineating these habitats using this scheme in management and conservation efforts could help to ensure “no net loss” of habitat productivity (Minns 1997), which is particularly important as coastal systems continue to experience significant change (Brown and McLachlan 2002, Kennish 2002).

Applied conservation

There are very few studies on movement patterns of individuals from potential nurseries to adult habitats, and this is a vital missing link in our understanding of nursery function. Movement of individuals is one of the most difficult variables to measure in ecology. Fortunately, vast improvements in technology -- archival data loggers, stable isotopes, genetic markers, and otolith microchemistry -- now enable researchers to track and infer movements. Throughout this study, regional managers have been intrigued by the potential of the elemental fingerprinting approach to determine if southern California halibut stocks are augmented by fish migrating northward from more “pristine” nursery habitats in Mexico. The elemental fingerprinting results presented in Chapter 4 indicate that this likely doesn’t occur. Very few sub-adult fish identified as having utilized bays as nursery habitat were collected more that 10 km away from the two large bays systems along the San Diego County coast. Thus, it appears as though many fish remain near their nursery origin and there is little connectivity resulting from the ontogenetic migration of fish from juvenile to adult habitats. As a result, there is probably little enhancement of the U. S. fishery resulting from the migration of juvenile fish along Baja California, Mexico, to sub-adult habitats. More broadly, the tendency of juveniles to remain near large, bay nurseries, interacting with the high recruitment potential supported by bays, may explain the "hot spots" of fishery production that occurs along the coastline generally in close proximity to large embayments.

Another application for these data include evaluation of recent and future changes to the southern California coastline. In 1996, Batiquitos was dredged and the mouth jettied as part of a large-scale enhancement project. As a result, the area available to 0-group halibut has greatly increased. Subsequently, halibut utilization of this site has risen from zero (Appy 1999) to roughly 10,000 juvenile halibut each year (Chapter 2). Moreover, as much as 8% of realized contribution to the adult stock may have from Bataquitos during 2004 (Chapter 4). Because halibut productivity was identified as a key goal behind the restoration, these data should be extremely relevant for assessing the ecological success of the enhancement program.

Several complementary tools were integrated to understand how nursery habitat usage affects the population dynamics of California halibut. Distribution, elemental fingerprinting and demographic approaches were used in concert to fill gaps in our knowledge on the role of coastal ecosystems as fish habitat. Table 6.2 provides a summary of the information gained from these approaches

Table 6.2. Ecological information gained about nursery habitat value from orthogonal approaches utilized during the development of the thesis.

Habitat and distribution mapping	**Growth & Survivorship**	**Tracking (Elemental Fingerprinting or Acoustics)**	**Molecular Analysis**	**Demographic Modeling**
Quantification of habitat types over large scales that can serve as a reference against which future conditions or studies can be compared	Small-scale habitat benefits, measures of habitat value	Retroactive tracking of environmental conditions or habitats utilized by individual fish	Spaital extent of finfish stocks relying on particular habitats or sites Role of fragmented, essential fish habitats in structuring populations	Identification of fitness benefits and key vital rates associated with habitats or sites Projection of population fitness as the spatial extent of habitats or sites varies

Future directions

Collecting juvenile halibut over four years from as many as 14 potential nursery sites provided new details about the spatial and temporal dynamics of chemical signatures in the otoliths of fish from southern California (Appendix 2). Interannual variability of chemical signals proved to be a significant obstacle, and precluded the use of habitat fingerprints generated from juvenile fish collected across multiple years. One of the remaining difficulties in applying elemental fingerprinting to a broad suite of conservation, metapopulation dynamic and evolutionary questions is that chemical signatures have to be evaluated during each experiment. This condition is exacerbated by the minimal predictive power we have in understanding how environmental gradients will be recorded in otoliths.

Population growth rate offers an important new metric of habitat value, and the data extracted from cohort analyses and demographic modeling in Chapter 5 indicate that nursery habitat selection can have significant impacts on the maintenance of California halibut populations. An important next step will be to develop models that can compare the variability in juvenile vital rates that result from nursery selection, with the variability in vital rates in all other life-history stages that result from environmental fluctuations not related to nursery usage (climate shift, fishing pressure).

The data presented here were collected with a macroscopic view of habitat use by the California halibut, and answered question of habitat utilization mostly at the population level. Important differences among habitats were identified for the first time (such as realized versus expected contribution as a measure of relative survivorship among habitats) and opened the door for more targeted research to explore the mechanisms responsible for differences among habitats. For instance, in 2004 lagoon habitats were shown to actually contribute (via elemental fingerprinting; Chapter IV) far more than would have been expected based upon the distribution of halibut and nursery habitat (Chapter II). Possible explanations involve decreased predation, seasonality of habitat use and migration paths of ontogentically migrating fish, but these remain untested and await further research.

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APPENDIX 1

Biology and ecology of the California halibut, *Paralichthys californicus*

Introduction

The California halibut, *Paralichthys californicus*, is one of the ~ 570 flatfishes (Order: Pleuronectiformes) found throughout the world's oceans and brackish water environments (Figure A1.1). It ranges from Washington State, USA, to the southern tip of Baja California (Miller and Lea 1972) in waters shallower than 100 m. This species is considered by scientists, managers and fishermen to be of both great ecological and economical value. Below is a summary of what was known about the biology and ecology of the halibut at the time this thesis was begun.

Species taxonomy and identification

The California halibut is one of twenty-four species in the genus *Paralichthys*, which itself is in the family Paralichthyidae. Members of this family have recently been reclassified, separated out of the family Bothidae. Other species of *Paralichthys* (including Summer, *P.dentatus*, Southern, *P. lethostigma*, and Gulf, *P. albigutta*, flounders) occur in coastal areas of the western Atlantic Ocean from Maine to Mexico and eastern Pacific Ocean from Washington to the southern tip of South America (as well as at least one species in the western Pacific). It is assumed that the Pacific species were separated from their Atlantic cogeners during the closing of the Isthmus of Panama, but the more detailed phylogenetic relationships of members within the genus remains unknown.

The first principle in classing flatfish is to determine the side of the body to which the eyes have migrated following the larval phase. However, the California halibut is anomalous in that for any given specimen, the eyes can be on the right or left side. In fact, about 65% of California halibut are “left” eyed (as are all other bothids and Paralichthyids), and 35% are “right” eyed. The mechanism responsible for this plasticity of phenotype is not known. Other, coarse scale identifying features of this species are sharp teeth, a maxillary that extends posteriorly behind the rear edge of the lower eye, an elliptical body, a high arch of the of the lateral line dorsal to the pectoral fin and a doubly indented caudal fin. Kucas and Hassler (1986) report 66-76 dorsal, 49-59 anal and 10-13 pectoral fin rays, as well as ~ 100 lateral line scales, 7-11+18-23 gill rakers and 34-36 vertebrae. However, identifying juvenile and adult flatfish is relatively easy and this level of examination is generally not required.

Spawning and larval biology and ecology

Major spawning sites, if any, remain unknown for the California halibut, and there have been few studies of the spawning behavior of this fish. Caddell et al. (1990) presented data that indicate spawning is primarily nocturnal, while Lavenberg (1987) reports that most spawning commences around noon and is completed well before midnight. Lavenberg (1987) also reports that females experience a mean interval of 7.14

days between spawning events during the spawning season, and that batch fecundity, or the number of eggs produced per spawning period, of a 5-year old female halibut is ~ 305,000. It is known that halibut migrate from deeper waters to more shallow, nearshore waters following winter (Young 1961), and spawning is most concentrated from February to May (Ginsburg 1952) in waters 5 to 15 meters deep (Young 1961). However, settlement data indicates that spawning continues throughout the summer and fall (Allen et al. 1990). It is during this period that adult halibut are most accessible with hook and line fishing.

The eggs of California halibut were incorrectly reported by Schott (1971) to be demersal, but have since been determined to be pelagic (positively buoyant), although there position in the water column is still not well documented. The mean egg diameter has been described by Gadomski and Caddell (1996) and Oda (1991), and is broken down into chorion (0.75 mm), yolk (0.58 mm) and a single oil globule (0.12 mm). Oda (1991) contains a thorough description of the developmental stages of a typical halibut egg. The time of hatching for halibut eggs appears to be, on average, around 48 hours (Gadomski and Caddell 1996), but the hatching age is extremely temperature dependent similarly to many other fish species. California halibut eggs survive well only in waters between 12-20 °C (Gadomski and Caddell 1991), and this may have important implications for the timing and location of halibut spawning.

Once hatched, halibut larvae remain in the water column for approximately three weeks (J. Hunter, personal communications) to over one month (Gadomski and Caddell 1991) before settling in the shallows of nearshore habitats. During this period, the vast majority of halibut larvae are found within 10 km of shore (Moser and Pommeranz 1999) all larvae collected from off the coast are found between San Francisco Bay, Ca, and Magdalena Bay, Mexico, with maximum densities reaching 0.17 per m^2 between Point Conception, Ca, and Sebastian Viscaino Bay, Mexico (Moser and Pommeranz 1999). Moser and Pommeranz (1999) reported that all halibut larvae were collected in tows shallower than 30 m, with the highest concentration at 10 m depth, although some diel vertical migration is suspected. Halibut larvae require higher temperatures (24 °C) than do halibut eggs for maximum survival, and this may preclude larvae from occurring at deeper levels in the water column. Alternatively, halibut larvae may simply be tracking the food resources they depend upon during this period. Oda (1991) contains a thorough description of the developmental stages of a typical halibut egg.

It is not known if larvae are actively or passively carried towards shore (where they settle) but it is thought that storms play an important role in transporting larvae into slope and/or eddy circulations offshore, where they can then be dispersed to other regions (Mullen et al. 1985). Assuming a post-flexion swimming speed of 10-20 mm s^{-1}, halibut larvae are capable of actively migrating across the continental shelf over the course of a 20-40 d larval phase.

Settlement

The distribution of small, settled halibut is probably the most well studied aspect of the biology and ecology of the California halibut (Haaker 1975, Plummer et al. 1983, Allen 1988, Allen et al. 1990, Kramer 1990, Kramer 1991). Settlement of California halibut occurs from April until September, with peak settlement occurring from June until August depending upon the site (Allen 1992). Interestingly, settlement appears to be highest during cool years, but within these years settlement is highest in areas with warmer water temperatures (Kramer 1991). The oceanographic and biological mechanisms for this observed pattern are not known.

At settlement, in waters < 10 m deep (Kramer 1991), halibut are approximately 7-9 mm in length and are fully metamorphosed (Allen et al. 1990). Density of settled fish in enclosed bays has been reported to be up to five times higher than that along the coast, and settlement density in semiprotected coastlines one and one-half times higher than along fully exposed coastlines (Allen et al. 1990). Still, total settlement along exposed coastlines may be greater than in protected areas due to sheer size. Juveniles are concentrated in waters < 4 m deep (Kramer 1991). There is debate regarding the movements of juvenile halibut. Schott (1971) and Haaker (1975) indicate that juvenile halibut do not move extensively once settled. Alternatively, size class data from along the coast and within bays led Kramer (1991) to hypothesize that halibut migrate into bays following settlement. Still, there remains considerable uncertainly about the dependence of halibut on different nearshore habitats as nursery grounds.

Habitat requirements, substrate preferences, and feeding ecology

As noted above, halibut are thought to be estuarine-dependent as a result of their utilization of coastal bays, lagoons and estuaries as nursery grounds by small individuals (evidenced by the high densities of halibut within these habitats, e.g., Kramer 1991). The perceived advantages of using bays, lagoons and estuaries are increased growth (increased food resources) and decreased levels of predation (Kramer 1990). However, Kramer (1991) presented data that indicated there were no growth differences between individual juveniles collected from along the exposed coastline and from within protected embayments.

Young halibut are known to prefer unvegetated substrates when very small, but migrate towards the edges of grass beds when older (Valle et al. 1998). This may represent a shifting balance between predation risk from species (mainly from barred and spotted sand bass) within the beds on small halibut and food resources obtained by slightly larger halibut that ambush prey items entering and exiting seagrass beds. Adult halibut are known to prefer sandy or soft sediments where they can bury themselves and ambush passing prey. Smaller halibut prefer silt/clay sediments covered with shell fragments while larger halibut prefer sandy sediments covered with rock fragments (Drawbridge 1990). This spatial segregation of size classes may benefit the halibut stock by reducing interspecific competition as well as cannibalism.

California halibut are typical, raptorial predators that ambush prey from underneath. Even though they have rather small eyes, halibut are highly visual predators that are cued by such factors as shape, visibility, locomotor activity, and body size of prey (Townsend and Windfield 1985). The most critical cue for the halibut appears to be the length to width ratio of possible prey items (Drawbridge 1990). Halibut strike when prey items come within 1.5 head-lengths of the halibut, and will pursue prey items off the bottom for some distance (personal observations). Feeding activity appears to be greatest in the late afternoon and during nights with full moons (Drawbridge 1990). This is not surprising for a visual predator. Like most ambush predators, a large number of halibut stomach that are examined are found to be empty (Wertz and Domeier 1997). Laboratory experiments indicate that juvenile halibut prefer turbid waters (Drawbridge 1990). This may be due to the importance of remaining well hidden, while small, outweighing the importance of feeding (i.e., the risk of being preyed upon in clear water > reward of feeding in clear water).

Prey, predators, and competitors

The relative importance of prey items changes during the lifetime of the California halibut. Most generally, there is a shift from demersal crustaceans earlier in life towards pelagic fishes as halibut age and grow. The most important prey item of small halibut has, on several occasions, been documented to be mysids (two species) and other benthic crustaceans such as harpacticoid and calanoid copepods as well as various amphipods (e.g. Wertz and Domeier 1997, Drawbridge 1990). As halibut reach a length of 30 mm, gobies appear more in the stomach of captured halibut (personal observations). Stomachs of large halibut contain mostly Pacific sardine, northern anchovy, white croaker and seasonally, California market squid (Wertz and Domeier 1997).

Predation on small halibut comes from a number of species including barred sand bass, spotted sand bass, and larger halibut (Ford 1965, Allen 1990, Valle et al. 1999). Adult halibut are preyed upon by California sea lions, harbor seals, several species of elasmobranchs and humans (Kramer and Sunada 1992).

Species likely to compete with the halibut are those that share similar feeding tactics and habitat associations. This includes other large-mouthed flatfish and bottomdwelling fish predators such as lingcod and lizardfish (Allen 1990). During the juvenile phase, many of the species that prey upon the halibut, in addition to diamond turbot and sculpins, are likely to compete with smaller halibut for food items. Certainly, the California halibut plays an important role as both prey and predator for many species along the southern California and Baja California coastline during its lifetime. Although not competators per se, parasites are thought to have a significant impact on halibut growth and individual fitness. Trematodes, cestodes and nematodes infected, as a group, greater than 50% of halibut intestines in specimens taken from Anaheim Bay, Ca (Bane and Bane 1971). Additionally, copepods and isopods are ectoparasites on the halibut (Bane and Bane 1971).

Movement of California halibut along the coast

The movement of the halibut along the coast is of interest to researchers for several reasons, but is especially important for proper management of harvest rates. There have been three major tagging studies of the California halibut. Tupen (1990) tagged 1052 halibut off the coast of central California during 1987-1988. The California Department of Fish and Game tagged 16,827 fish over forty years from Tomales Bay, Ca, to Sebastian Viscaino Bay, Baja California (Domeier and Chun 1995). Most recently, Posner and Lavenberg (1999) reported on 26, 827 halibut that were tagged by volunteers from Morro Bay, Ca, to the US-Mexico border. All three studies demonstrate similar results. Of the halibut recaptured, the majority of fish remained within a very few kilometers of the original tagging site. Distance moved during tagging and recapture was not significantly related to length of fish or time at liberty. All three studies reported that a few, large halibut did migrate as much as 300 km. Of these studies, almost all fish were > 35 cm in length. As a result, little is known about the potential for ontogenetically migrating halibut moving between juvenile and adult habitats to connect halibut stocks separated by latitude.

Divergences in allelic frequencies at two loci, Est-5 and Xdh, from specimen pools of halibut collected at Los Angeles and San Diego, Ca, further support the contention that halibut stocks are not heavily connected along the coast of California (Hedgecock and Bartley 1988). Other possible explanations for the observed divergence include a) historical factors, with halibut stocks not yet returned to equilibrium, b) diversifying selection, and c) the result of sampling different stages (adults from Los Angeles and juveniles from San Diego).

Growth, mortality and maturation

Schott (1971) reported that halibut grow 120 mm TL during their first six months, 250 mm by the end of their first year and then 100 mm every subsequent year until about age 10 when growth begins to slow. MacNair et al. (2001) reported that females grew faster and on average were bigger than their male contemporaries. Sagittal otoliths have often been used to age fish, and this includes the halibut. There exists a nearly linear relationship between length of otolith and length of fish, as well as between the number of growth increments observed within an otolith and the known age of halibut (Figure A1.2).

Halibut demonstrate a Type III survivorship curve. This is typical of species that are highly fecund, with planktotrophic reproductive strategies. For adult halibut, estimated annual mortality rate are on average 0.60 for males and 0.49 for females (MacNair et al. 2001). Males > 25 years old and females as old as 40 have been reported, although now the oldest fish collected are often 12-15 years old at most. Notably, females outnumber males along the southern California coastline 4.3 to 1, as reflected by catch data (Clark 1931; MacNair et al. 2001).

According to Love and Brooks (1990), 50% of males from the southern California Bight mature at an age of 1.3 years and length of 22.7 cm, while nearly all males are mature by 2.5 years and 32.0 cm. Females from the bight reached 50 % maturity at 4.3 years and 47.1 cm length, and most were mature by the age of 6.0 years and at a length of 60.0 cm. These sizes- and lengths-at-maturity are less than those reported by others (Clark 1930, 1931) nearly 70 years prior to the data accrued by Love and Brooks (1990). Potentially, these trends are the result of selective fishing.

Fishery

Since the late 19th century, the California halibut has been a prized commercial and recreational species. Notably, it remains the single most important commercially important species in California waters that is considered to be facultatively estuarine-dependent, and this may have important consequences for the manner in which the halibut is managed (J. Hunter personal communication). Kramer and Sunada (1992) report that the largest commercial catch of halibut occurred in 1919 at 4.7 million pounds, and since 1932 has averaged a little less than 1 million pounds annually. Over the last thirty years, the number of halibut caught each year by recreational fishermen has averaged around 15,000. Catch data indicate that halibut populations cycle between high and low stock sizes approximately every twenty years (Barsky 1990). Historically, trawl nets, gill and trammel nets, and hook and line methods have been employed to catch halibut. Since 1994, gill and trammel nets have been prohibited within 3 miles of the California coastline and it is thought that this management decision will increase the yield-per-recruit of the California halibut, decrease the catch of commercial fishermen and increase the catch of recreational fishermen. The size limit for the commercial and recreational fishery is 22 inches. Based on this, males will mature 4-5 years, and females 1-2 years prior to reaching legal take size (Love and Brooks 1990).

Figure A1.1. The California halibut, *Paralichthys californicus*, and its sagittal otoliths. Individual images include juvenile and mature halibut.

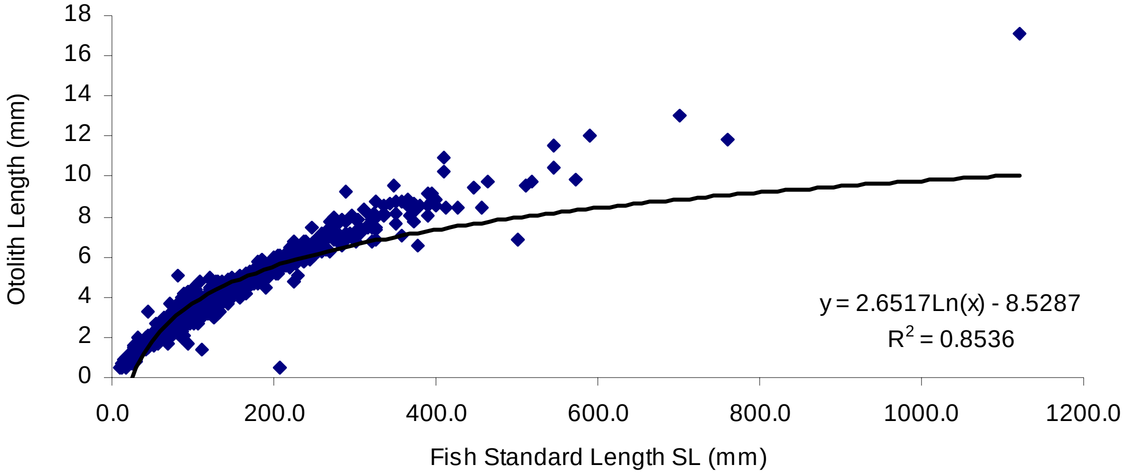

Figure A1.2. Relationship between halibut standard length (SL) and sagittal otolith length.

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APPENDIX 2

Supplementary analyses of otolith microchemistry from juvenile California halibut collected within San Diego County during 2001-2004

In Chapter 4, a habitat classification scheme that included exposed coasts, bays, lagoons and estuaries was used to generate a library of habitat-specific fingerprints that could be used to characterize nursery signals via Discriminant Function Analysis (DFA). In addition to the "habitat-scale" of defining nursery fingerprints, DFAs were also conducted with the 14 putative nursery sites considered: (1) individually, and (2) broken down into regions (northern exposed, northern embayment, southern exposed and southern embayment). Table A2.1 and Figures A2.1-3 demonstrate the ability to distinguish individual putative nursery sites during 2003 and 2004 using Discriminant Function Analysis. Table A2.2 and Figures A2.4-6 consider the same years and data, but with sites grouped at the regional scale for generating DFA algorithms.

Along the southern half of San Diego County, juvenile collections were made for two additional years (2001 and 2002), and were combined with the data from 2003 and 2004 to further explore the spatial and temporal variability of otolith signals. Table A2.3 and Figures A2.7-11 present the signal variability at the individual site level, while Table A2.4 and Figures A2.12-16 consider the same data but with the sites grouped into the same four habitat types considered in depth in Chapter 4.

Table A2.1. Classification matrix of assignments for otolith signals from juvenile halibut collected within 14 putative nursery sites 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. Data are generated for (A) 2003, (B) 2004, and (C) 2003-2004 combined. The success rates are presented for individual sites, including (from North to South): Oceanside Harbor (O Harb); Oceanside, Agua Hedionda (AH); Bataquitos (Bat); San Elijo (S Elijo); Penasquitos (Penas); La Jolla (LJ); Pacific Beach-Ocean Beach (PB-OB); Mission Bay (MB); San Diego Bay (SDB); Imperial Beach (IB) and Tijuana River (TJE).

							Predicted							
A. 2003	O Harb	Oceanside	AH	Bat	S Elijo		Penas	LJ	PB-OB	MB	SDB	IB	TJE	% Correct
Actual														
O Harb	5	1	0	0	0		0	0	0	2	1	0	0	56
Oceanside	0	8	0	0	0		0	0	0	0	2	0	0	80
AH	0	1	1	0	3		0	1	0	2	0	0	0	13
Bat	0	1	0	4	2		1	0	0	1	0	0	0	44
S Elijo	2	3	0	1	7		0	6	0	1	0	0	0	35
Penas	0	0	0	2	2		3	1	0	2	2	0	1	23
LJ	0	4	0	0	1		0	0	0	0	2	0	0	0
PB-OB	0	6	0	0	1		0	0	1	0	0	0	0	13
MB	2	9	0	3	0		0	0	0	9	5	0	0	32
SDB	5	6	0	0	1		0	0	0	8	14	0	0	41
IB	1	4	0	0	0		0	0	0	0	0	0	0	0
TJE	0	0	0	0	2		0	1	0	2	0	0	6	55
Total	15	43	1	10	19		4	9	1	27	26	0	7	36

B. 2004	O Harb	Oceanside	AH	Bat	S Elijo	S Dieg		LJ	PB-OB	MB	SDB	IB	TJE	% Correct
Actual														
O Harb	10	0	0	0	0	0		0	0	1	5	0	0	63
Oceanside	1	7	2	0	2	0		0	0	0	0	7	0	37
AH	2	0	6	4	0	0		0	0	0	0	1	0	46
Bat	1	0	0	1	0	0		0	0	0	0	0	0	50
S Elijo	2	0	1	0	7	1		0	0	0	0	1	0	58
S Dieg	0	1	1	0	2	11		0	0	0	0	2	0	65
LJ	2	2	2	0	7	0		0	1	0	0	4	0	0
PB-OB	0	2	1	2	1	0		0	1	1	0	6	0	7
MB	1	0	3	2	0	0		0	0	0	5	1	0	0
SDB	1	0	1	0	0	0		0	1	4	19	1	0	70
IB	0	4	3	4	1	0		0	1	0	0	7	0	35
TJE	1	2	3	0	4	0		0	1	0	0	6	3	15
Total	21	18	23	13	24	12		0	5	6	29	36	3	38

C. 2003-2004	O Harb	Oceanside	AH	Bat	S Elijo	S Dieg	Penas	LJ	PB-OB	MB	SDB	IB	TJE	% Correct
Actual														
O Harb	21	0	0	0	0	0	0	0	0	0	0	4	0	84
Oceanside	2	13	0	1	0	0	0	0	3	0	3	7	0	45
AH	3	3	1	3	3	0	0	0	3	0	0	5	0	5
Bat	2	1	0	5	3	0	0	0	0	0	0	0	0	45
S Elijo	9	3	0	5	11	0	0	0	3	0	0	1	0	34
S Dieg	2	4	0	2	3	0	0	0	1	1	0	4	0	0
Penas	0	0	1	2	5	1	1	0	0	0	2	0	0	8
LJ	3	4	2	1	1	1	0	0	0	0	0	13	0	0
PB-OB	0	6	1	0	1	0	0	0	3	0	2	9	0	14
MB	9	3	1	4	1	0	1	0	2	3	9	8	0	7
SDB	16	7	0	0	1	1	0	0	4	6	11	15	0	18
IB	5	6	0	0	0	0	0	0	3	0	0	11	0	44
TJE	5	5	4	0	2	0	2	0	2	0	2	6	3	10
Total	77	55	10	23	31	3	4	0	24	10	29	83	3	24

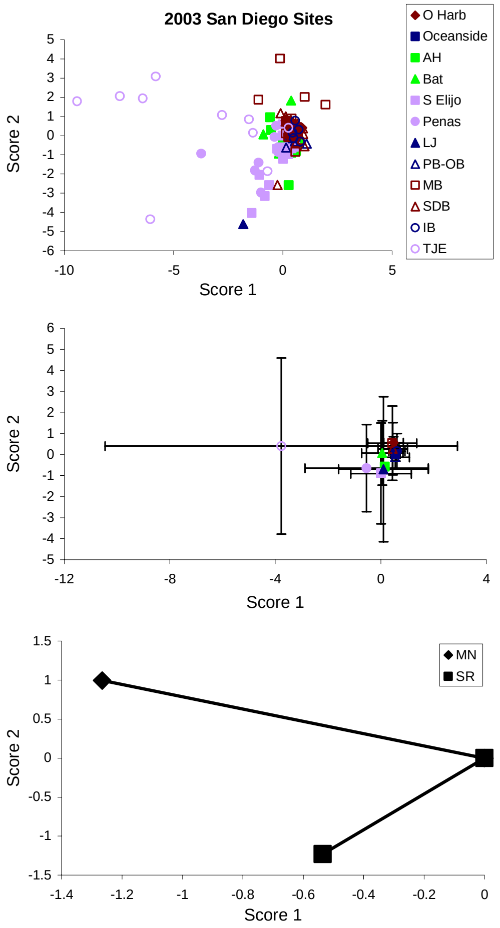

Figure A2.1. Discriminant scores of isotope (Mn & Sr) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2003 from all putative nursery sites in San Diego County. Nursery sites include (from North to South): Oceanside Harbor (O Harb); Oceanside, Agua Hedionda (AH); Bataquitos (Bat); San Elijo (S Elijo); Penasquitos (Penas); La Jolla (LJ); Pacific Beach-Ocean Beach (PB-OB); Mission Bay (MB); San Diego Bay (SDB); Imperial Beach (IB) and Tijuana River (TJE). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

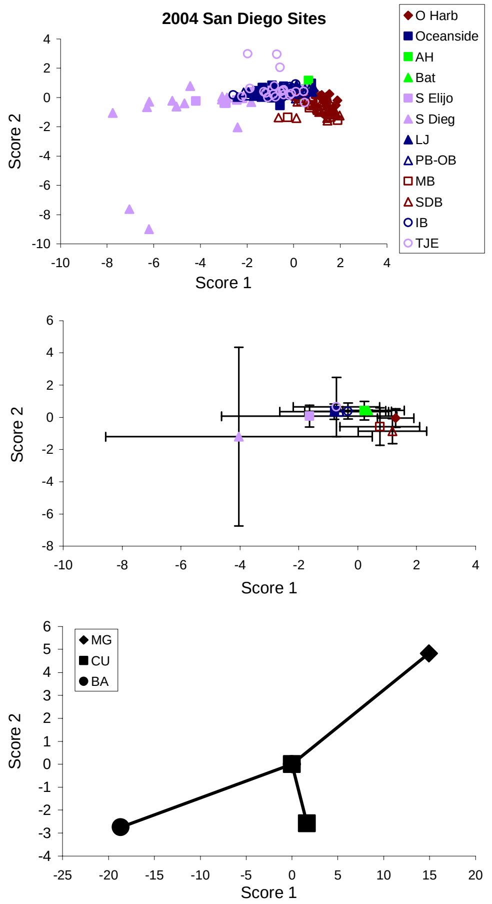

Figure A2.2. Discriminant scores of isotope (Mg, Cu & Ba) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2004 from all putative nursery sites in San Diego County. Nursery sites include (from North to South): Oceanside Harbor (O Harb); Oceanside, Agua Hedionda (AH); Bataquitos (Bat); San Elijo (S Elijo); San Dieguito (S Dieg); La Jolla (LJ); Pacific Beach-Ocean Beach (PB-OB); Mission Bay (MB); San Diego Bay (SDB); Imperial Beach (IB) and Tijuana River (TJE). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

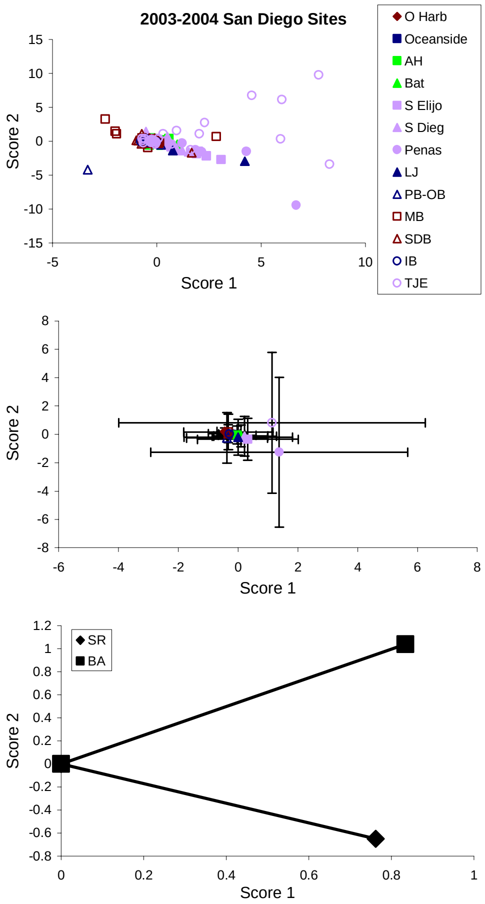

Figure A2.3. Discriminant scores of isotope (Sr & Ba) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2003 and 2004 from all putative nursery sites in San Diego County. Nursery sites include (from North to South): Oceanside Harbor (O Harb); Oceanside, Agua Hedionda (AH); Bataquitos (Bat); San Elijo (S Elijo); San Dieguito (S Dieg); Penasquitos (Penas); La Jolla (LJ); Pacific Beach-Ocean Beach (PB-OB); Mission Bay (MB); San Diego Bay (SDB); Imperial Beach (IB) and Tijuana River (TJE). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

Table A2.2. Classification matrix of assignments for otolith signals from juvenile halibut collected within 14 putative nursery sites 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. Data are generated for (A) 2003, (B) 2004, and (C) 2003-2004 combined. The success rates are presented for the following groups: North Exposed (Oceanside and La Jolla); North Embayment (Oceanside Harbor, Agua Hedionda, Bataquitos, San Elijo, San Dieguito and Penasquitos); South Exposed (Pacific Beach-Ocean Beach and Imperial Beach); and South Embayment (Mission Bay, San Diego Bay and Tijuana River).

A. 2003

	Predicted				
	North		South		
	Exposed	Embayment	Exposed	Embayment	% Correct
Actual					
North Exposed	15	2	0	0	88
North Embayment	25	17	0	16	29
South Exposed	11	1	0	1	0
South Embayment	28	6	0	40	54
Total	79	26	0	57	44

B. 2004

	North		South		
	Exposed	Embayment	Exposed	Embayment	% Correct
Actual					
North Exposed	15	7	14	1	41
North Embayment	6	24	16	14	40
South Exposed	7	7	20	0	59
South Embayment	2	5	9	43	73
Total	30	43	59	58	54

C. 2003-2004

	North		South		
	Exposed	Embayment	Exposed	Embayment	% Correct
Actual					
North Exposed	14	8	30	2	26
North Embayment	12	45	33	28	38
South Exposed	5	5	34	3	72
South Embayment	14	14	60	45	34
Total	45	72	157	78	39

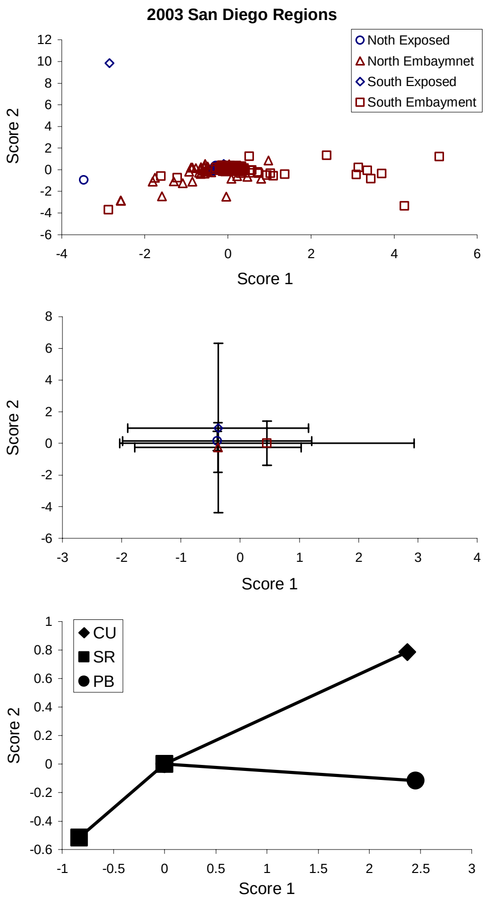

Figure A2.4. Discriminant scores of isotope (Cu, Sr & Pb) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2003 from all putative nursery sites in San Diego County. Sites are grouped as: North Exposed (Oceanside and La Jolla); North Embayment (Oceanside Harbor, Agua Hedionda, Bataquitos, San Elijo, San Dieguito and Penasquitos); South Exposed (Pacific Beach-Ocean Beach and Imperial Beach); and South Embayment (Mission Bay, San Diego Bay and Tijuana River). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

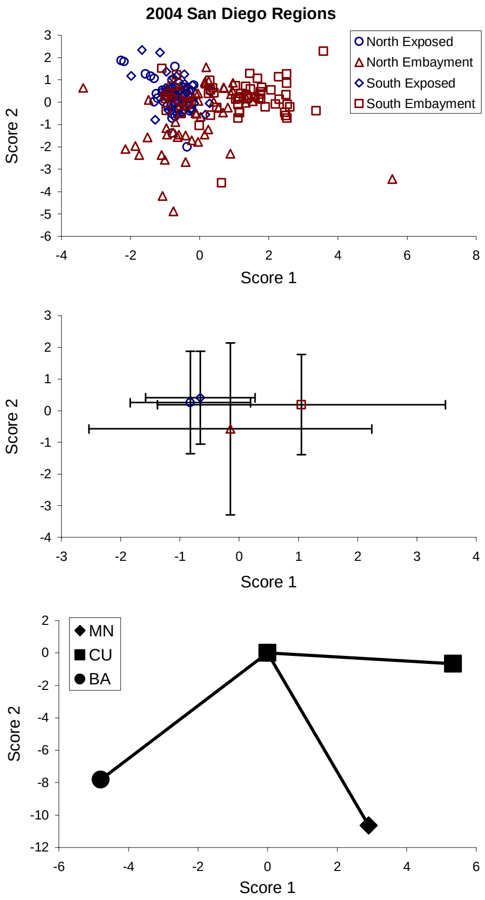

Figure A2.5. Discriminant scores of isotope (Mn, Cu & Pb) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2003 from all putative nursery sites in San Diego County. Sites are grouped as: North Exposed (Oceanside and La Jolla); North Embayment (Oceanside Harbor, Agua Hedionda, Bataquitos, San Elijo, San Dieguito and Penasquitos); South Exposed (Pacific Beach-Ocean Beach and Imperial Beach); and South Embayment (Mission Bay, San Diego Bay and Tijuana River). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

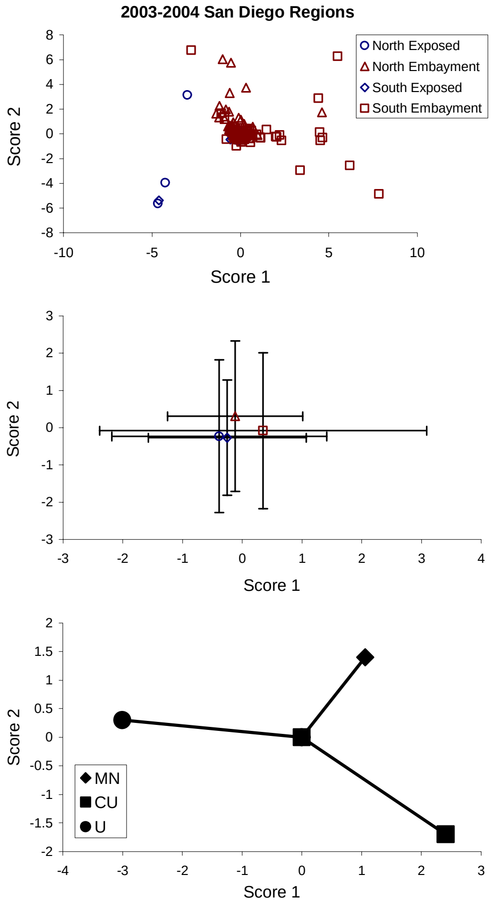

Figure A2.6. Discriminant scores of isotope (Mn, Cu & U) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2003 and 2004 from all putative nursery sites in San Diego County. Sites are grouped as: North Exposed (Oceanside and La Jolla); North Embayment (Oceanside Harbor, Agua Hedionda, Bataquitos, San Elijo, San Dieguito and Penasquitos); South Exposed (Pacific Beach-Ocean Beach and Imperial Beach); and South Embayment (Mission Bay, San Diego Bay and Tijuana River). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

Table A2.3. Classification matrix of assignments for otolith signals from juvenile halibut collected within all putative nursery sites along southern half of 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. Data are generated for (A) 2001, (B) 2002, (C) 2003, (D) 2004 and (E) 2001-2004 combined. The success rates are presented the following nursery sites: La Jolla (LJ); Imperial Beach (IB); Mission Bay (MB); San Diego Bay (SDB); and Tijuana River (TJE).

			Predicted			
A. 2001	LJ	IB	MB	SDB	TJE	% Correct
Actual						
LJ	13	0	0	0	0	100
IB	0	5	3	2	0	50
MB	0	2	13	3	0	72
SDB	1	1	8	11	0	52
TJE	0	0	0	0	2	100
Total	14	8	24	16	2	69

B. 2002	LJ	IB	MB	SDB	TJE	% Correct
Actual						
LJ	8	1	5	8	1	35
IB	6	12	2	9	2	39
MB	0	0	5	6	0	45
SDB	1	0	1	4	0	67
TJE	0	0	1	0	4	80
Total	15	13	14	27	7	43

C. 2003	LJ	IB	MB	SDB	TJE	% Correct
Actual						
LJ	4	3	0	0	0	57
IB	1	3	0	3	0	43
MB	3	11	8	7	0	28
SDB	2	6	8	18	0	53
TJE	3	0	2	0	6	55
Total	13	23	18	28	6	44

D. 2004	LJ	IB	MB	SDB	TJE	% Correct
Actual						
LJ	3	13	5	4	1	12
IB	2	10	0	0	0	83
MB	1	2	9	0	0	75
SDB	3	1	8	15	0	56
TJE	12	0	3	0	5	25
Total	21	26	25	19	6	43

E. 2001-2004	LJ	IB	MB	SDB	TJE	% Correct
Actual						
LJ	1	7	4	46	0	2
IB	6	26	1	38	0	37
MB	4	3	15	47	1	21
SDB	6	4	8	69	1	78
TJE	5	7	4	18	4	11
Total	22	47	32	218	6	35

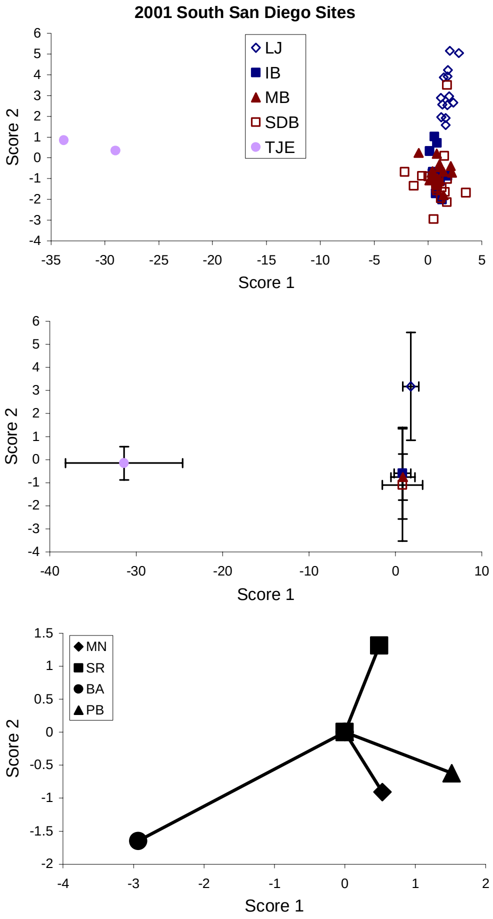

Figure A2.7. Discriminant scores of isotope (Mn, Sr, Ba & Pb) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2001 from all putative nursery sites along the southern half of San Diego County. Nursery sites include: La Jolla (LJ); Imperial Beach (IB); Mission Bay (MB); San Diego Bay (SDB); and Tijuana River (TJE). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

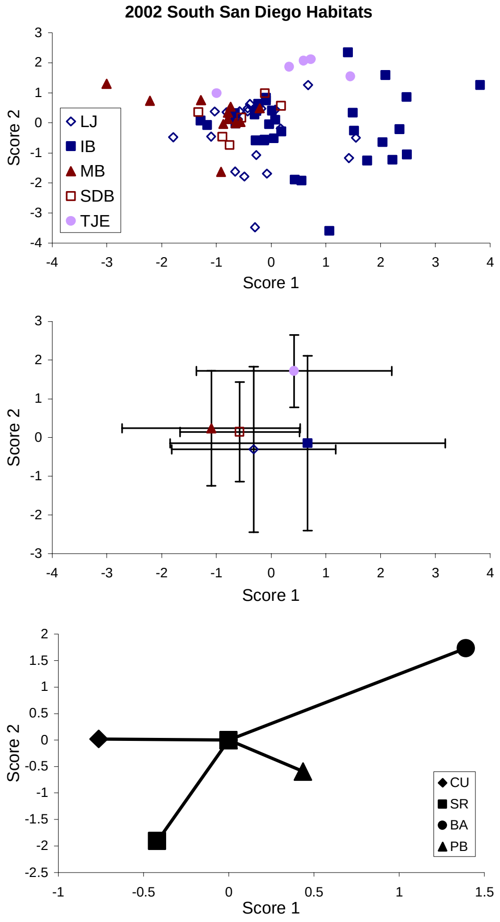

Figure A2.8. Discriminant scores of isotope (Cu, Sr, Ba & Pb) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2002 from all putative nursery sites along the southern half of San Diego County. Nursery sites include: La Jolla (LJ); Imperial Beach (IB); Mission Bay (MB); San Diego Bay (SDB); and Tijuana River (TJE). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

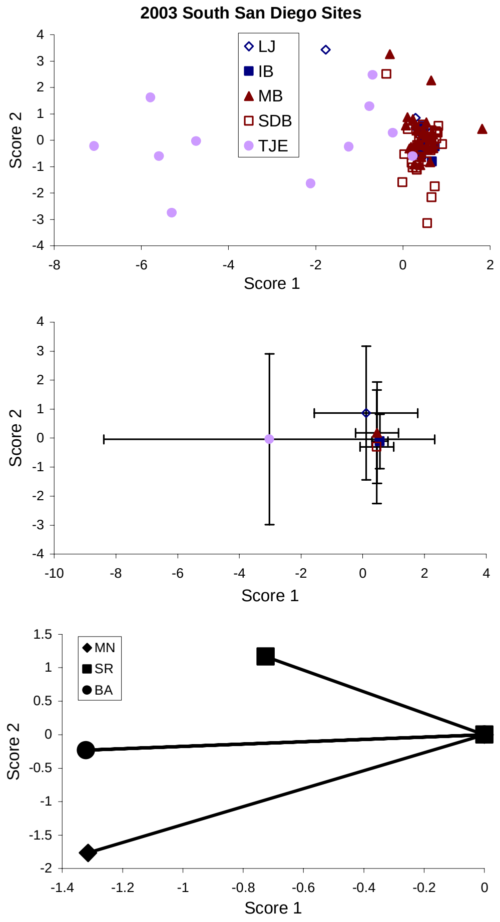

Figure A2.9. Discriminant scores of isotope (Mn, Sr & Ba) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2003 from all putative nursery sites along the southern half of San Diego County. Nursery sites include: La Jolla (LJ); Imperial Beach (IB); Mission Bay (MB); San Diego Bay (SDB); and Tijuana River (TJE). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

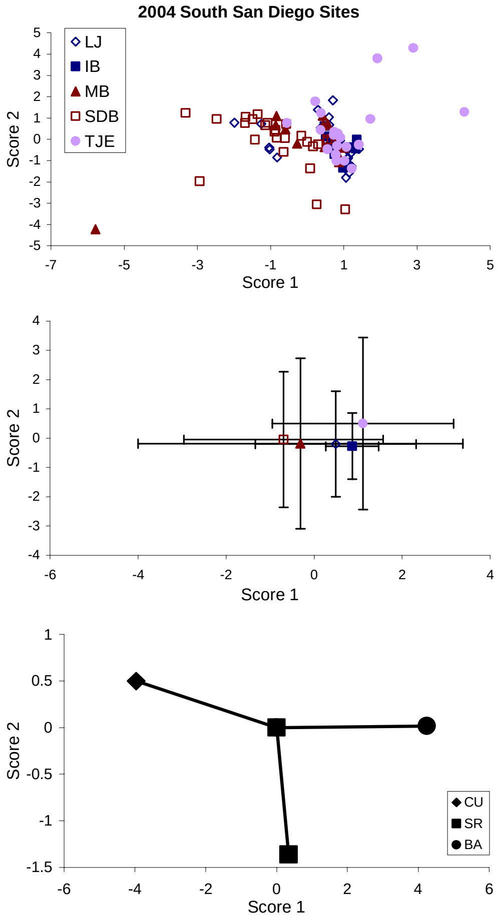

Figure A2.10. Discriminant scores of isotope (Cu, Sr & Ba) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2004 from all putative nursery sites along the southern half of San Diego County. Nursery sites include: La Jolla (LJ); Imperial Beach (IB); Mission Bay (MB); San Diego Bay (SDB); and Tijuana River (TJE). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

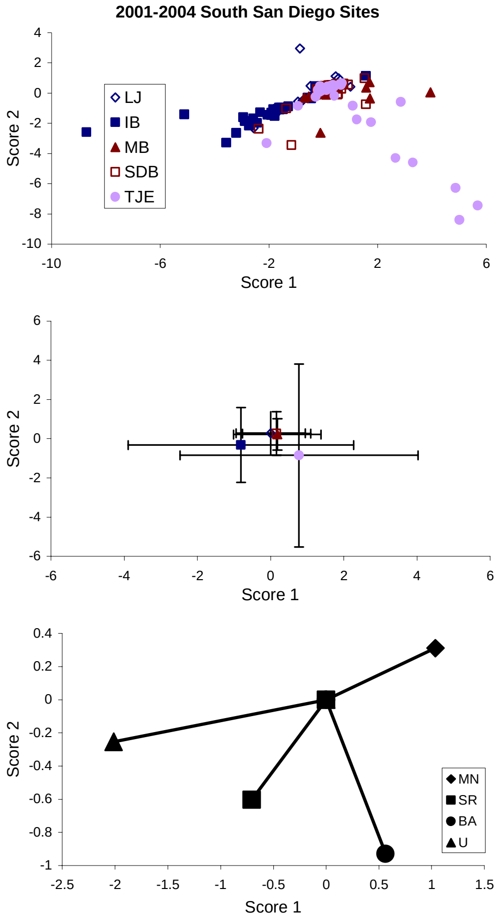

Figure A2.11. Discriminant scores of isotope (Mn, Sr, Ba & U) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2001-2004 from all putative nursery sites along the southern half of San Diego County. Nursery sites include: La Jolla (LJ); Imperial Beach (IB); Mission Bay (MB); San Diego Bay (SDB); and Tijuana River (TJE). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

Table A2.4. Classification matrix of assignments for otolith signals from juvenile halibut collected within all putative nursery sites along southern half of 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. Data are generated for (A) 2001, (B) 2002, (C) 2003, (D) 2004 and (E) 2001-2004 combined. The success rates are presented for nursery habitat groupings, including: Exposed (La Jolla and Imperial Beach); Bay (Mission Bay and San Diego Bay); and Estuary (Tijuana River).

A. 2001

	Predicted			
	Exposed	Bay	Estuary	% Correct
Actual				
Exposed	17	6	0	74
Bay	2	37	0	95
Estuary	0	0	2	100
Total	19	43	2	88

B. 2002

	Exposed	Bay	Estuary	% Correct
Actual				
Exposed	31	18	5	57
Bay	1	15	1	88
Estuary	0	1	4	80
Total	32	34	10	66

C. 2003

	Exposed	Bay	Estuary	% Correct
Actual				
Exposed	11	3	0	79
Bay	16	47	0	75
Estuary	3	2	6	55
Total	30	52	6	73

D. 2004

	Exposed	Bay	Estuary	% Correct
Actual				
Exposed	35	0	3	92
Bay	1	38	0	97
Estuary	13	0	7	35
Total	49	38	10	82

E. 2001-2004

	Exposed	Bay	Estuary	% Correct
Actual				
Exposed	33	96	0	26
Bay	16	138	4	87
Estuary	5	28	5	13
Total	54	262	9	54

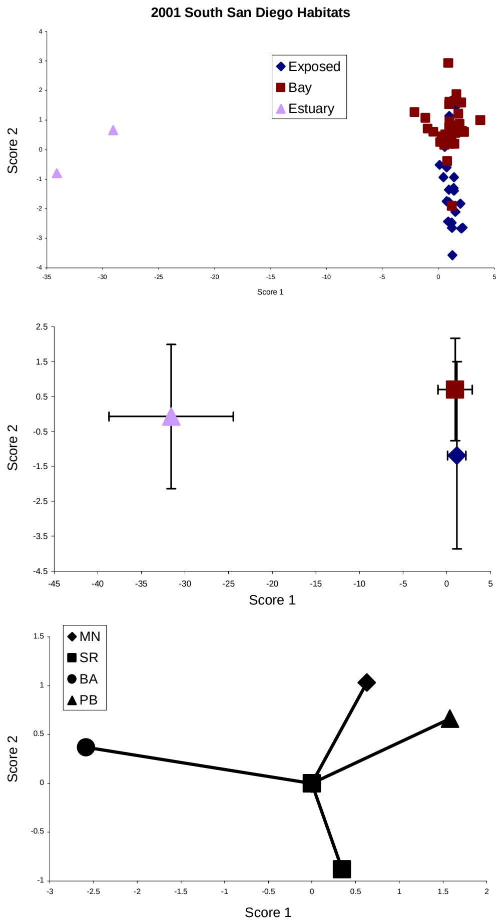

Figure A2.12. Discriminant scores of isotope (Mn, Sr, Ba & Pb) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2001 from all putative nursery sites along the southern half of San Diego County. Sites are grouped according to nursery habitat type, including: Exposed (La Jolla and Imperial Beach); Bay (Mission Bay and San Diego Bay); and Estuary (Tijuana River). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

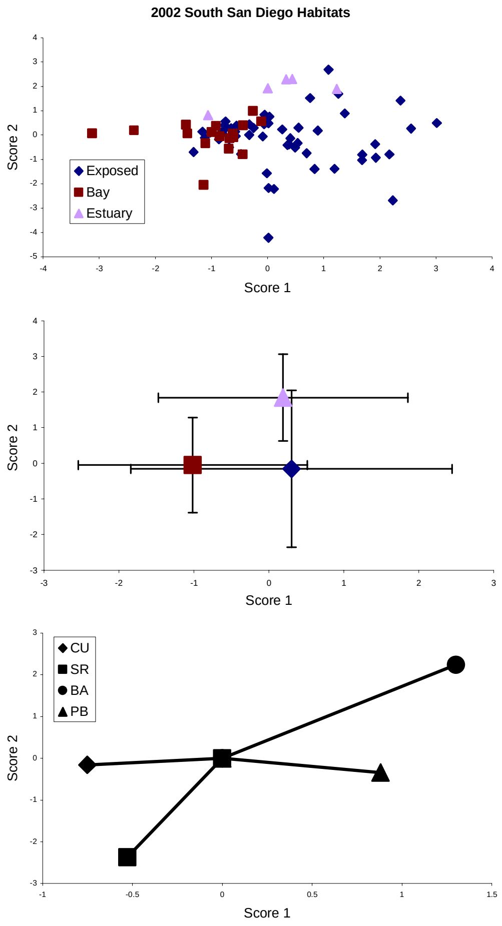

Figure A2.13. Discriminant scores of isotope (Cu, Sr, Ba & Pb) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2002 from all putative nursery sites along the southern half of San Diego County. Sites are grouped according to nursery habitat type, including: Exposed (La Jolla and Imperial Beach); Bay (Mission Bay and San Diego Bay); and Estuary (Tijuana River). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

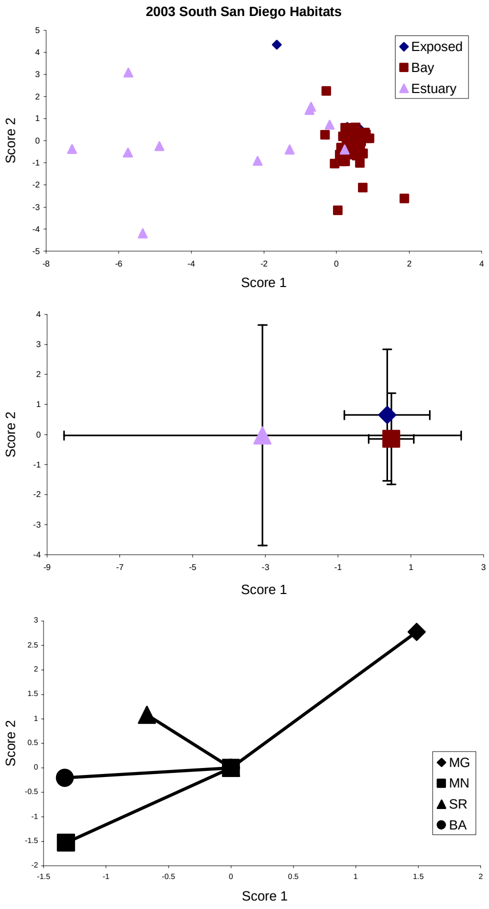

Figure A2.14. Discriminant scores of isotope (Mg, Mn, Sr, & Ba) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2003 from all putative nursery sites along the southern half of San Diego County. Sites are grouped according to nursery habitat type, including: Exposed (La Jolla and Imperial Beach); Bay (Mission Bay and San Diego Bay); and Estuary (Tijuana River). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

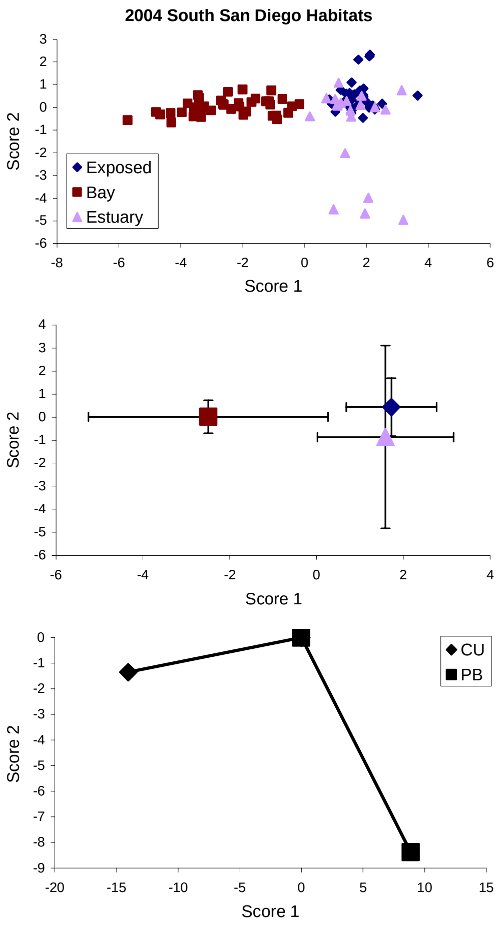

Figure A2.15. Discriminant scores of isotope (Cu & Pb) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2004 from all putative nursery sites along the southern half of San Diego County. Sites are grouped according to nursery habitat type, including: Exposed (La Jolla and Imperial Beach); Bay (Mission Bay and San Diego Bay); and Estuary (Tijuana River). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

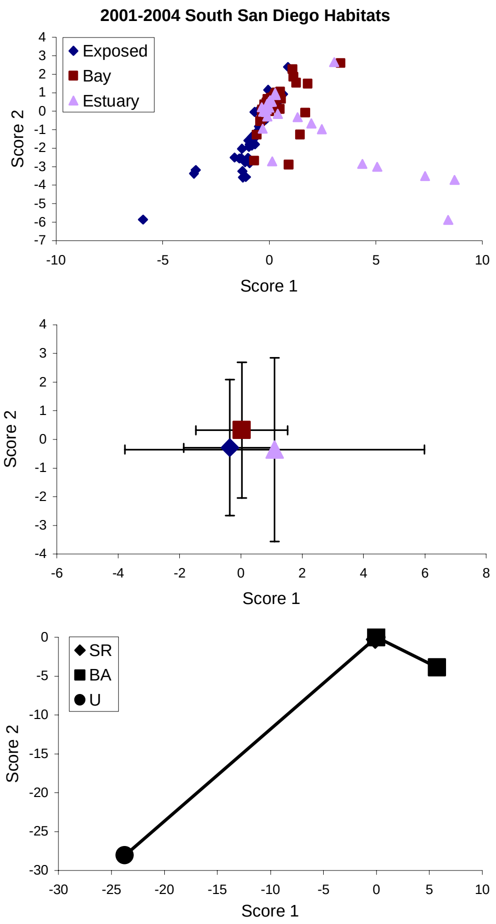

Figure A2.16. Discriminant scores of isotope (Sr, Ba & U) ratios to ^{48}Ca in otoliths of 0-age halibut collected during the fall of 2001-2004 from all putative nursery sites along the southern half of San Diego County. Sites are grouped according to nursery habitat type, including: Exposed (La Jolla and Imperial Beach); Bay (Mission Bay and San Diego Bay); and Estuary (Tijuana River). (A) Scatterplot of DFA scores; (B) Same data as A plotted as averages with 95% confidence intervals; and (C) Discriminant functions, standardized by within variances, for the isotope ratios used to create the DFA. Vectors represent the relative contribution of each isotope ratio to the resulting scores.

APPENDIX 3

MatLab M-file text code for generating population matricies, lambdas, sensitivities and elasticies for exploring the demographic consequences of utilization of nursery habitat alternatives for the California halibut

```
% Notes, indicated by "%"


larv = [F1 z1 d1];
juv1 = [F2 z2 d2];
juv2 = [F3 z3 d3];
adult1 = [F4 z4 d4];
adult2 = [F5 z5 d5];  %individual F (fecundity), z (mortality rate) and d (stage duration)
                        parameters using a standard Lefkovitch model

matx = [larv; juv; subadult; adult];  %life history matrix (number of rows controls size of
matrix A!)

[m,n]=size(matx);

for i=1:m;
   p(i)=exp(-matx(i,2));
   gamma(i)=((1-p(i))*p(i)^(matx(i,3)-1))/(1-p(i)^matx(i,3));
   P(i)=p(i)*(1-gamma(i));
   G(i)=p(i)*gamma(i);
   F(i)=(.25)*((1+P(i))*(matx(i,1))+G(i)*(matx(i,1)));
end

A=zeros(m,m);

for i=1:m
   j=i;
   A(i,j)=P(i);  %populates diagonal with P vector entries
end

for i=2:m
   j=i-1;
   A(i,j)=G(j); %populates off diagonal with G vector entries (1:n-1)
```

```
end

for j=2:m
   i=1;
   A(i,j)=F(j);  %populates first row with F vector entries (2:n)
end

A
[r_eigvec, eigval] =eig(A)
[lambda,Ir]=max(diag(eigval))   %right eigvalues, vectors... these are lambda and
dominant eigvector is stable age dist.

[l_eigvec,l_eigval]=eig(A.')

[xxx,Il]=max(diag(l_eigval))
l_eigvec=conj(l_eigvec)

r_vec=r_eigvec(:,Ir)
l_vec=l_eigvec(:,Il)


for i=1:m
   for j=1:m
      S(i,j)=(r_vec(j)*l_vec(i))/dot(r_vec,l_vec);
   end
end

S

for i=1:m
   for j=1:m
      E(i,j)=(A(i,j)/lambda)*S(i,j);
   end
end

E
```