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.
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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
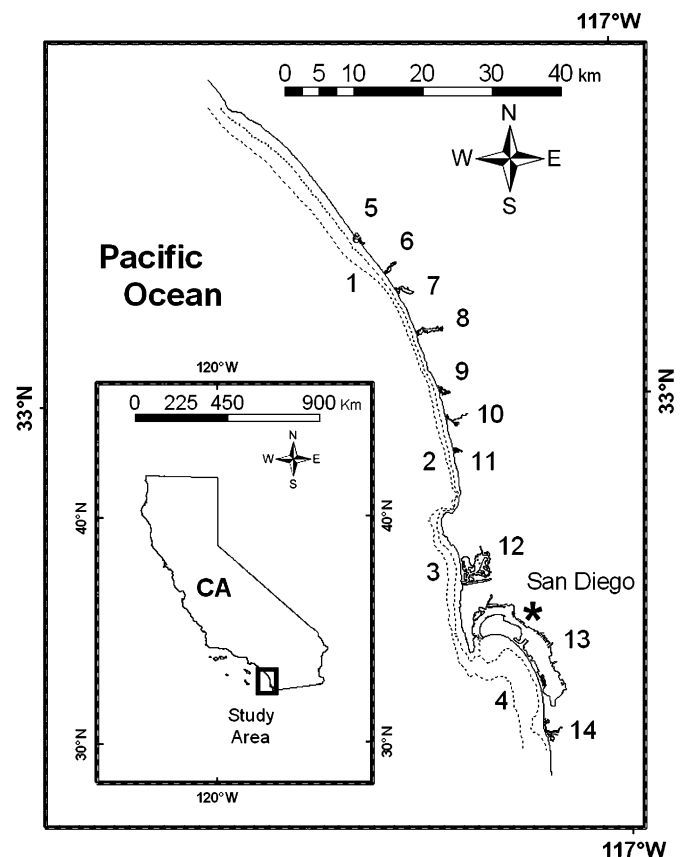

Fig. 1. San Diego County coastline study region highlighting the 14 sectors sampled to generate halibut distribution data. Sectors are: 1. Oceanside (EX), 2. La Jolla (EX), 3. Pacific Beach (EX), 4. Imperial Beach (EX), 5. Oceanside Harbor (B), 6. Buena Vista (L), 7. Agua Hedionda (L), 8. Batiquitos (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:

$$J_i = A_i D_i \tag{1}$$

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:

$$J_t = \sum_{i=1}^{H} J_i \tag{2}$$

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

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

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
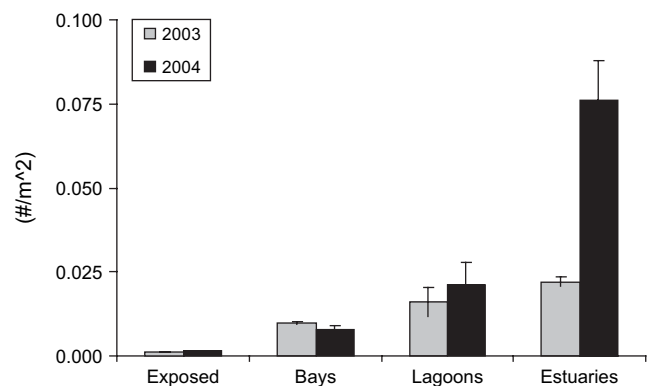

Fig. 2. Mean 0-group halibut densities (± 1 SE) from each of the four nursery habitat types in San Diego County, CA, in 2003 (gray bars) and 2004 (black bars). Means are based on density surfaces interpolated in ArcMap 8.3 from field surveys in each of the 14 study sectors. Coast 0—20 m habitat = North 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/m² between depths of 4.5–5 m (Fig. 3A), while within protected embayments, highest juvenile halibut densities (~0.9 indiv/m²) 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/m²) recorded where surface temperature exceeded 21.5 °C and lowest average densities (0.001 indiv/m²) 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/m²). 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/m² (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/m²) occurred at depths > 5.2 m, while highest average densities (0.005 indiv/m²) 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/m² (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/m² compared to 0.013 indiv/m²). 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/m²) 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 ~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 ~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)	2004 (n 277)			
	0.021 (0.003)	0.033 (0.006)			0.1504
Site exposure	Exposed (n 163)	Protected (n 297)			
	0.003 (0.0003)	0.043 (0.006)			<0.0001
Nursery type	Exposed (n 163)	Bay (n 190)	Lagoon (n 27)	Estuary (n 80)	
	0.003 (0.0003)*	0.016 (0.002)*	0.073 (0.016)**	0.094 (0.018)**	<0.0001
Bottom structure	Vegetated (n 33)	Unvegetated (n 184)			
	0.003 (0.001)	0.027 (0.003)			<0.0001
Sediment grain size	Coarse sand (n 22)	Fine sand (n 262)	Very fine sand (n 128)	Coarse silt (n 12)	Medium silt (n 2)
	0.019 (0.007)	0.028 (0.006)	0.031 (0.005)	0.04 (0.027)	0.012 (0.012)	0.9545
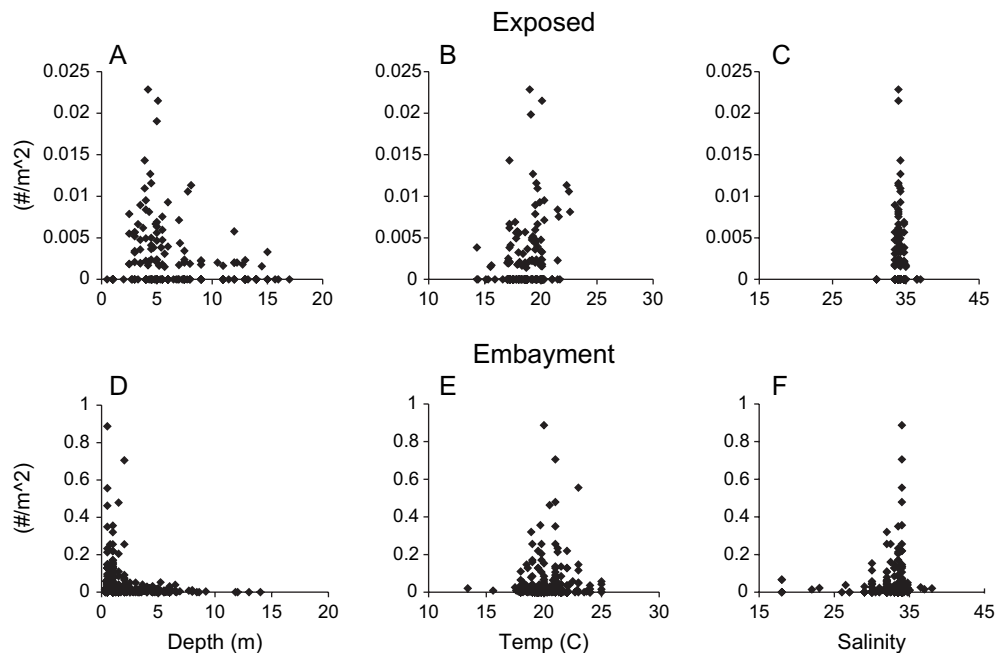
Fig. 3. Scatterplots of 0-group halibut density in relation to depth, temperature and salinity gradients. Data (pooled from 2003 and 2004) represent halibut densities estimated from trawls and block-net seining obtained concurrently with environmental data. Panels A–C show trends along exposed habitats ($N = 163$), 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
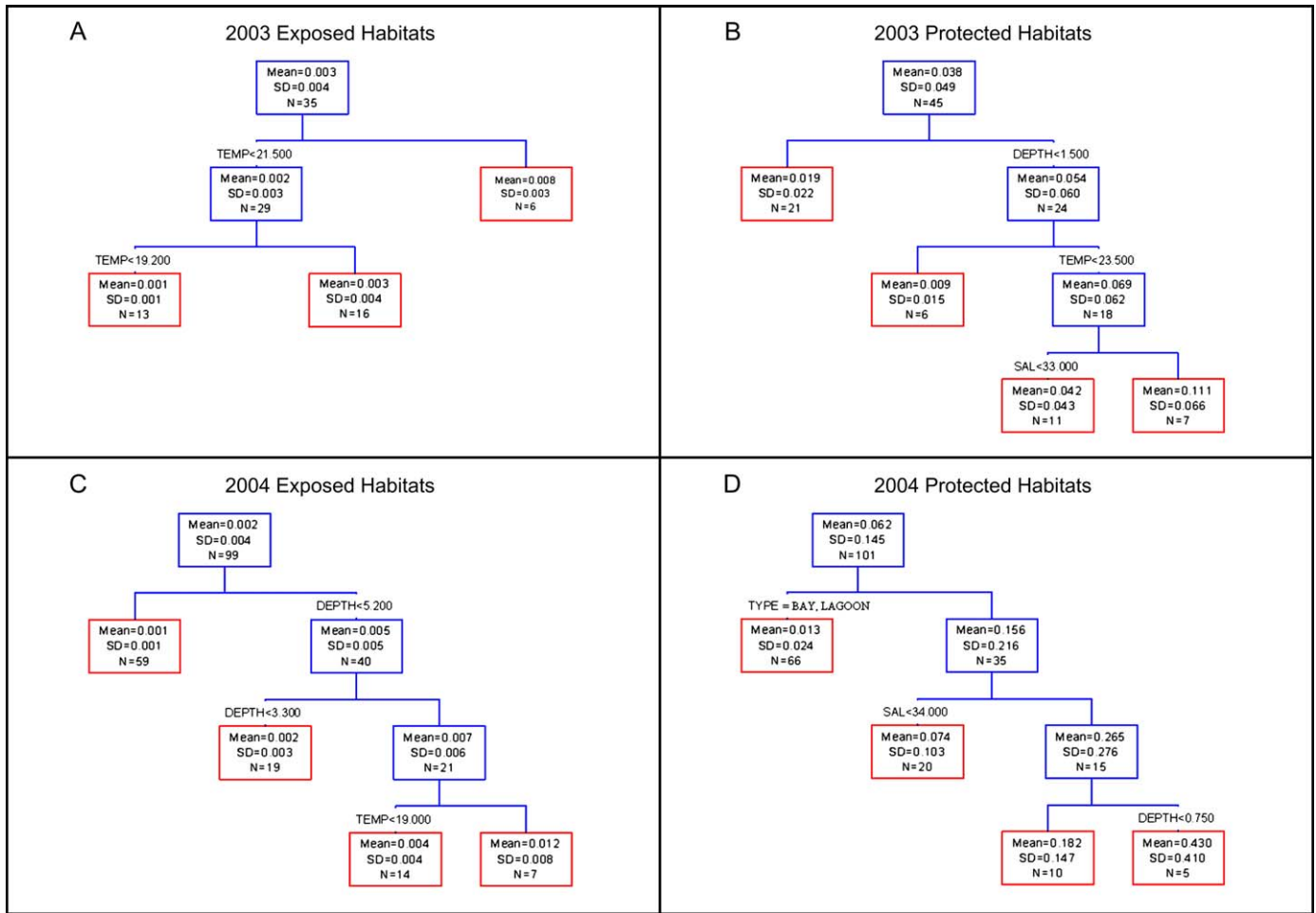
Fig. 4. Regression tree analysis for 0-group halibut density in 2003 (A&B) and 2004 (C&D) in Exposed (A&C) and Protected (B&D) habitats. Data represent halibut densities estimated from trawls and block-net seining obtained concurrently with environmental data. Potential explanatory variables used in 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
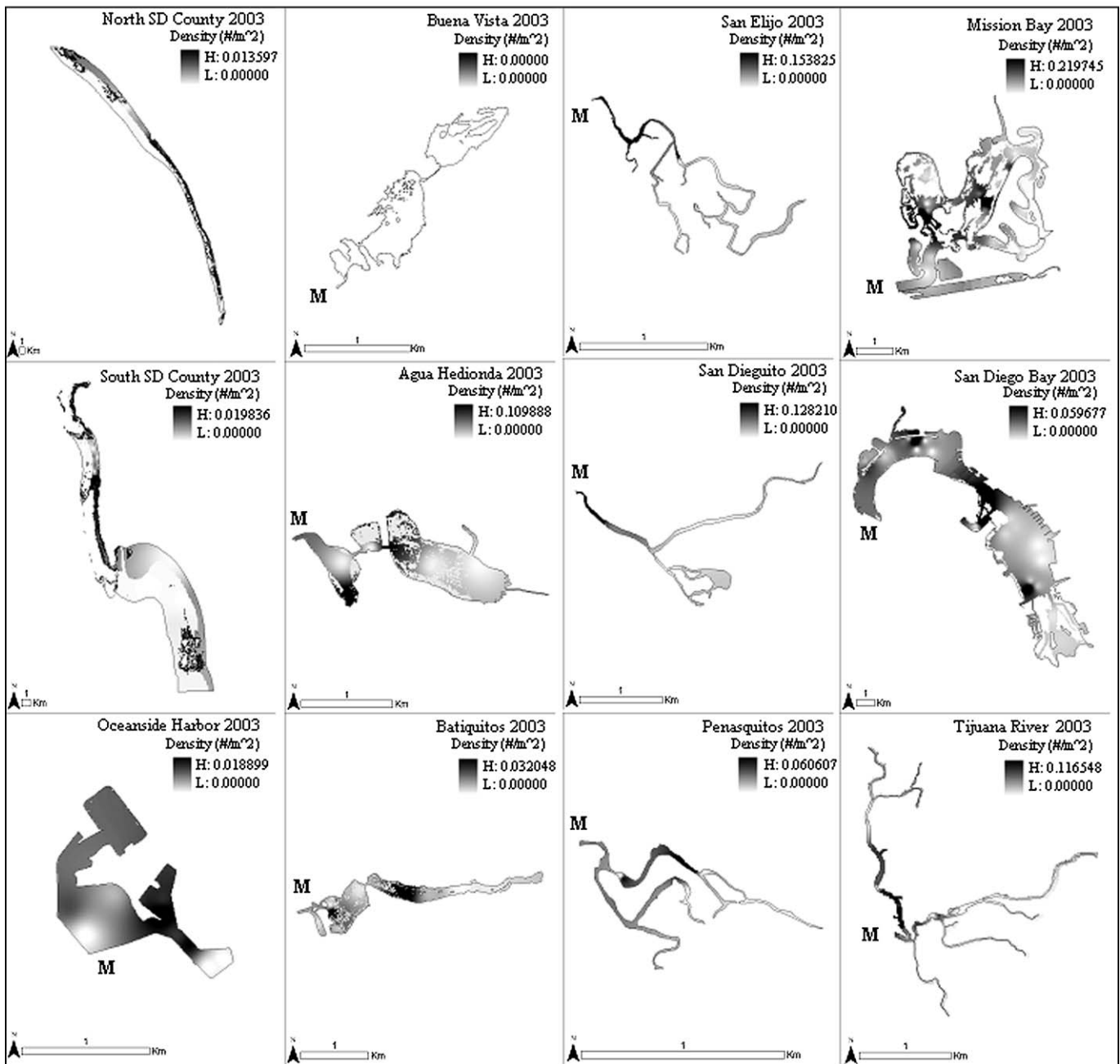
Fig. 5. The 2003 (A) and 2004 (B) distribution of 0-group halibut in the nearshore habitats of San Diego County, CA. Maps are interpolations of 234 (2003) and 293 (2004) data observations taken during fall 2003 and 2004. Density grids were generated using the Inverse Distance Weighting (IDW) spatial 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
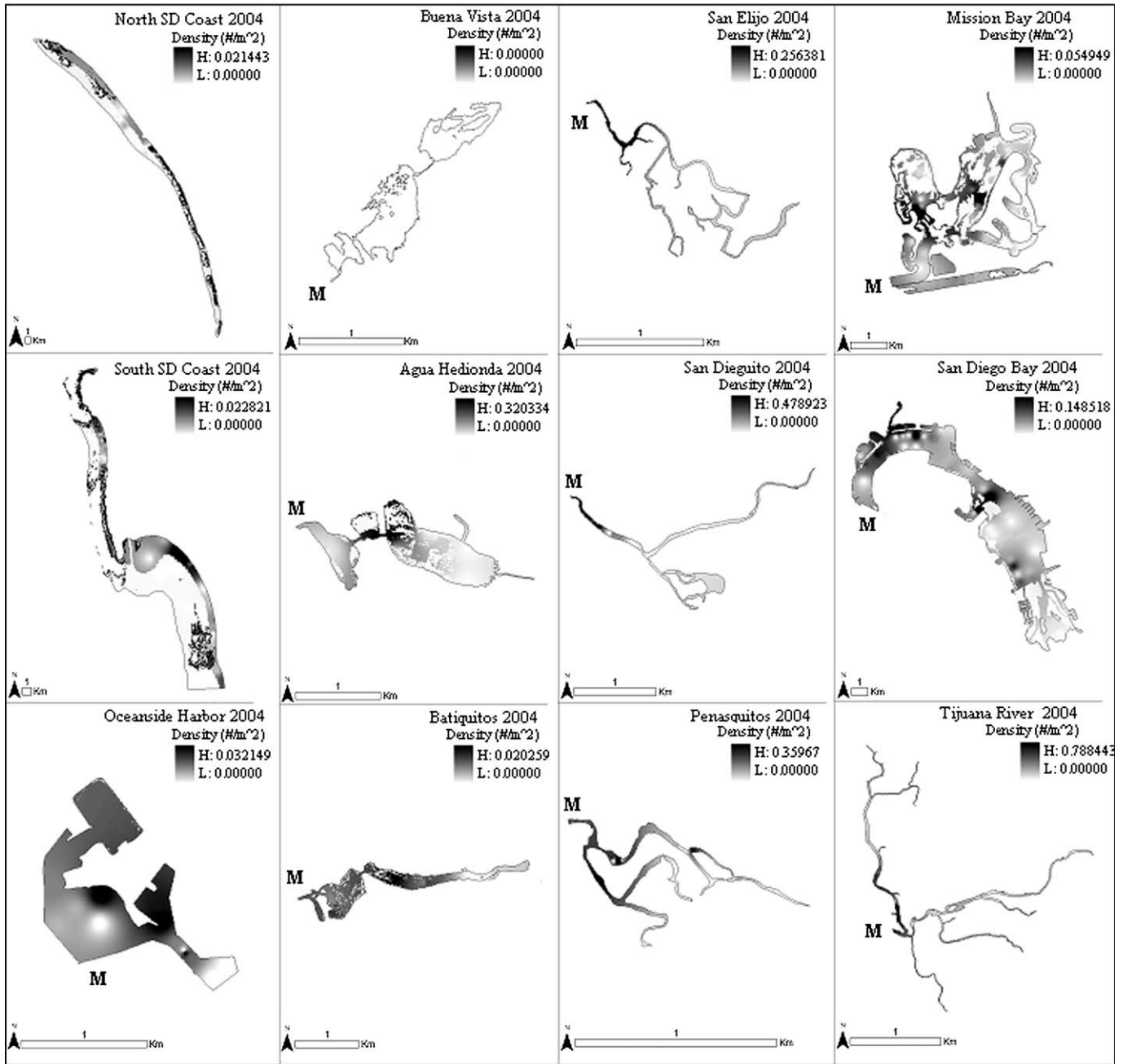
Fig. 5 (*continued*).

(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
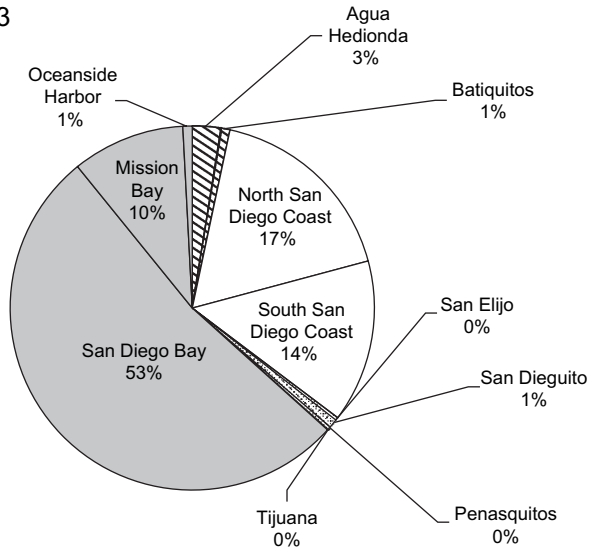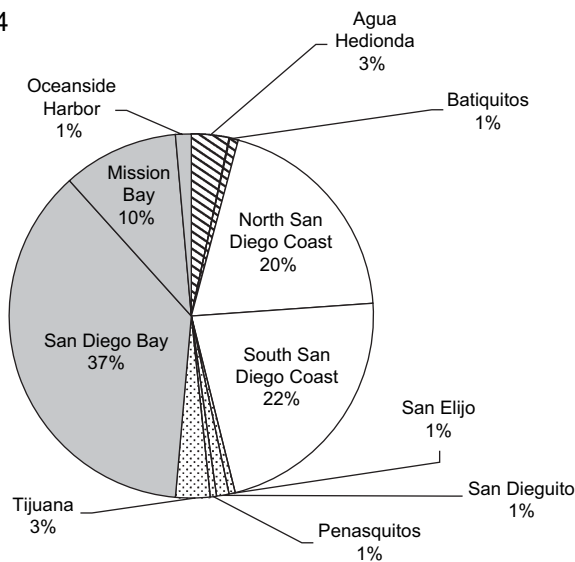
Fig. 6. Resident 0-group halibut in each of the potential nursery habitat types in San Diego County, CA, in 2003 (A) and 2004 (B). Percentages represent expected contribution (EC) from each habitat type based upon fish occupying each nursery site at time of study available to recruit to older age classes. 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.

Acknowledgements

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