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Huntington Beach Wetlands Restoration (CA) Final Report

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Summary

- After restoration of tidal connection, fish abundance, species richness, and diversity within Brookhurst Marsh were generally equivalent to levels in the Talbert Marsh reference site within one year;
- However, community composition (species identity and relative abundances) remained different between the two marshes after one year with Brookhurst having higher percent composition of topsmelt, jacksmelt and anchovy and a lower percentage of killifish, diamond turbot, and sculpin than Talbert Marsh;
- After two years, observed differences in community composition have been reduced (although some of this convergence could be due to less frequent sampling);
- Caging experiment and laboratory rearing methods were successfully tested, indicating that California halibut can grow in laboratory and field cage conditions. In addition, we learned that closed bottom cages (allowed to equilibrate for several months with sediment at the bottom) were more effective than open bottom cages (which allowed escape);
- Based on caging experiments, diet and growth rates of California halibut within Brookhurst Marsh are not significantly different than Talbert, indicating potentially rapid development of trophic support for at least some functional groups of fish in this system.

Project Narrative

Coastal wetlands provide a variety of key ecosystem functions that include food web support, nutrient cycling, and nursery habitat for many ecological and economically important fish species (Mitsch and Gosselink 1993; Minello et al. 2003). Loss of coastal wetlands and their associated services during the past century has been extensive; in California, less than 10% of historical distributions remain intact (Dahl 1990; MacDonald et al. 1990). To offset such habitat loss, wetland managers and conservation groups have increasingly turned to restoration and mitigation as potential solutions. Post-restoration monitoring and assessments for these projects typically focus on structural attributes of the restored habitats (Zedler and Langis 1991; Talley and Levin 1999), but recent research has emphasized the importance of evaluations that include ecosystem function (Zedler 2001). Nevertheless, in-depth function-based assessments of restoration effectiveness in California wetlands remain rare. Our overall project objective was to determine how and to what degree fish, especially juvenile California halibut, *Paralichthys californicus*, utilize the newly-restored Huntington Beach Wetlands. The California halibut, *Paralichthys californicus*, is generally considered to be facultatively dependent on coastal wetlands for nursery habitat (Kramer 1991; Fodrie and Levin 2008). As a consequence, halibut are a model organism for investigating the functional recovery of a newly restored coastal wetland, particularly with respect to provision of habitat and trophic support for fish. We monitored overall fish community structure and the fine-scale distribution, movement patterns, long-term site fidelity, and diet of halibut within Brookhurst Marsh (restored in 2009) and nearby Talbert Marsh (restored in 1989) for two years after the completion of the Brookhurst Marsh restoration project, from July 2009 through June 2011.

The Huntington Beach Wetlands (HBW) complex is an approximately 200-acre remnant of a 2900-acre wetland area which historically existed at the mouth of the Santa Ana River in Huntington Beach, Orange County, California (33˚ 39' N, 117˚ 59' W; Fig. 1). This area consists of restored salt marsh and coastal dune habitat, and is bisected by roadways into four distinct sections, including the Talbert, Brookhurst, Magnolia, and Newland marshes. These marshes are

hydraulically linked to each other and to the Pacific Ocean by a flood control channel running along the northeastern border of the site. Historically, this site was subject to diking and filling of natural creeks for the purpose of oil and gas exploration, which isolated the area from surface tidal exchange for over 70 years (Dage and Reardon, 2004). In 1984 the land was designated as open space and industrial energy production by the City of Huntington Beach's Land Use Plan. The dike separating Talbert Marsh (25 acres) from the flood control channel was breached in 1989, restoring full tidal influence to this section. Additional projects restored tidal flow to Brookhurst Marsh (67 acres) in 2009 and Magnolia Marsh (41 acres) in 2010; tidal flow has not yet been restored to Newland Marsh. Since its restoration in 1989, Talbert Marsh has grown to support many species and habitats characteristic of southern California salt marshes. Pickleweed, *Sarcocornia pacifica,* dominates most of the intertidal areas, while patches of cordgrass, *Spartina foliosa*, are found in the low marsh. Small areas of saltgrass, *Distichlis spicata*, saltwort, *Batis maritima*, and alkali-heath, *Frankenia salina*, occur in the middle marsh (Merkel and Woodfield, 2004). Although itself a restoration, Talbert Marsh provides a realistic standard against which to judge newer restorations in the Huntington Beach Wetlands due to its relative similarity to less disturbed marshes in the region and proximity to the other marshes, enabling comparisons to be made within a similar environmental context (Bell et al., 1997).

The restoration of the Huntington Beach Wetlands offers a unique opportunity to obtain detailed information on the temporal and spatial processes of functional recovery of an important coastal ecosystem. We were able to take to take advantage of an existing collaboration among numerous parties that include federal agencies (NOAA), private companies and utilities (AES, Southern California Edison), NGO's (Huntington Beach Consortium), and local government (Orange County, City of Huntington Beach). As a consequence, our data will benefit not just those individuals responsible for the restoration and management of these specific wetlands (i.e., the Huntington Beach Wetlands Conservancy), but also agencies charged with oversight of other local areas (e.g., Bolsa Chica Ecological Reserve, Colorado Lagoon). Here we report on the status of the Brookhurst Marsh fish community for the first two years after the restoration of full tidal influence relative to the Talbert Marsh reference site, with specific emphasis on California halibut.

Our primary objectives were to: (1) characterize post-restoration variation in overall fish community structure between Brookhurst and Talbert Marshes through time; (2) quantify population structure and movement behavior of juvenile halibut in the HBW complex, as related to underlying environmental variables; and (3) evaluate the degree to which the two marshes are providing trophic support to resident halibut.

Methodology

Objective 1: Fish Community Structure

Fish Abundance Surveys

To make post-restoration comparisons of fish species assemblages, Brookhurst and Talbert Marshes were sampled over a two year period; due to logistical constraints, sampling effort varied between years. Marshes were sampled monthly from July 2009 to June 2010 (Year 1) and quarterly (September, December, March, June) from July 2010 to June 2011 (Year 2). Each sampling period, a total of six sites selected randomly using GPS coordinates were surveyed on a single day in each marsh. Sampling in the two marshes was typically done on

consecutive days. Sites were selected so that both "inner" (landward) and "outer" (seaward) channels of each marsh were sampled, resulting in 3 inner and 3 outer sites per marsh per sampling date. Surveys were performed between mid and high tides during daylight hours and were conducted using a 31.1 m × 1.2 m beach seine net (0.64 cm stretch mesh). The net was deployed using a kayak and was set parallel to shore in a semi-circle pattern before being hauled to shore by hand. All fish collected were identified, counted, and the first ten individuals of each species in each seine were measured to the nearest mm. Fork length was recorded for species with forked tails (FL), and standard (SL) and total length (TL) for all other species. Individuals of the family *Gobiidae* could not be definitively identified to species during field collections, so all specimens from that family were designated as a single "species group". After processing, all fish were released at the site of capture, with the exception of those used for tracking or stable isotope and diet analyses (see Objectives 2 and 3 for details).

Data Analyses

Fish abundance data were analyzed separately by year due to the differences in sampling effort. For each marsh and date combination, data were summed across the three replicate seines within the inner and outer locations, resulting in two abundance samples for each marsh per sampling date (n = 12 dates in Year 1 and 4 dates in Year 2). To facilitate inter-year comparisons, monthly samples in Year 1 were pooled into different seasons for analyses (Summer = July, August, September; Fall = October, November, December; Winter = January, February, March; Spring = April, May, June).

Univariate measures of community structure were calculated for each sample, including species richness (S), the Shannon-Wiener diversity index (H'), and species evenness (J'). We also used multivariate approaches to assess differences in fish assemblage structure between marshes through time. Abundance data were log(x+1)-transformed prior to analysis to equalize variances among groups (univariate analyses) and increase the relative contributions to Bray-Curtis similarity coefficients (multivariate analyses; Clarke 1993). Both unconstrained (non-metric multidimensional scaling, MDS) and constrained (canonical analysis of principal coordinates, CAP) ordinations were used to visualize differences in fish communities between marshes and seasons. MDS plots represent multidimensional relationships as faithfully as possible in low-dimensional space (Field et al. 1982). In this case, each circle in the two-dimensional plot represents the multivariate species assemblage (i.e., fish community) at a unique sampling time and location. The relative distance between any two symbols indicates the degree of community similarity/dissimilarity between those samples, based on species identities and abundances and calculated using the Bray-Curtis coefficient (Bray and Curtis 1957). Symbols that are close together represent locations that have more similar communities than do those represented by symbols that are far apart.

In contrast to rank-based unconstrained ordinations like MDS plots, constrained ordinations provide quantitative (distance-based) information on differences in multivariate location between groups by reference to a specific a priori hypothesis, such that the data are displayed to specifically highlight whatever differences might exist (Anderson and Willis 2003). To test statistically for differences in assemblages between groups, rank-based two-way Analyses of Similarity (ANOSIMs) were paired with MDS plots and distance-based Permutational Multivariate Analyses of Variance (PERMANOVAs) were paired with CAP plots, in both cases with marsh and season as the main factors. Although these tests often give similar answers, a primary advantage of PERMANOVA relative to the purely non-parametric ANOSIM

approach is that PERMANOVA allows for the partitioning of multivariate variation into complex experimental designs (e.g., including nesting and interaction terms) (Anderson 2001a). Location within marsh (i.e., inner vs. outer) could not be incorporated as a separate factor into the ANOSIM analyses as they are limited to simple two-way designs. Although we were able to test for location effects with PERMANOVA, the differences in fish community structure across locations within a marsh were not statistically significant so we dropped that term from subsequent models. The test statistic of PERMANOVA (*pseudo-F*) is a multivariate analogue of Fisher's *F* ratio (Anderson 2001a and 2001b). Pair-wise comparisons among levels of a given factor following a significant overall PERMANOVA test were done as direct multivariate analogues to the univariate two-tailed *t*-test (Anderson et al. 2008). No corrections for multiple comparisons were made as most *ad hoc* corrections (e.g., Bonferroni) are inexact and overly conservative (Day and Quinn 1989). Instead, we limited the number of tests we did to the factor of greatest interest to us: differences between marshes within a given season.

Species responsible for observed variation in community structure were identified using a similarity percentages analysis (SIMPER) that calculates the percentage contribution of each species to the average Bray-Curtis dissimilarities between groups (Clarke 1993). Individual species contributing 5% or more to the dissimilarity between marshes were analyzed separately with univariate two-way PERMANOVAs. PERMANOVA can be used to analyze univariate data when the resemblance matrix is based on Euclidean distance, offering a more robust alternative to traditional parametric ANOVA tests, particular when data are characterized by many zeros and extreme non-normality (hallmarks of species abundance data). Univariate measures of community structure were also analyzed with PERMANOVAs. All permutational tests, multivariate ordinations, and SIMPER analyses were done with PRIMER v6 software with the PERMANOVA+ add on (PRIMER-E, Ltd., Plymouth, UK).

To identify possible differences in the functional traits of key fish species found in each marsh, the species identified as most important in the SIMPER analysis were assigned to one of three functional groups based on their feeding strategy, habitat association, and degree of mobility: Marsh Channel, Marsh Surface, and Cosmopolitan (found throughout the marsh system). Average abundances and standard lengths of individuals from each functional group were compared between marshes with separate two-sample *t*-tests on $\log(x+1)$ transformed data; data were pooled across years. Assumptions of normality and equal variances were tested with normal probability plots and Levene's tests, respectively; tests were done with Minitab 16 statistical analysis software.

Objective 2: Halibut Population Structure and Movement Behavior

Environmental Data

A map of the HBW was generated in ArcMap (ESRI, Redlands, CA) using waypoints of water level at mean high tide to delineate Brookhurst Marsh, Talbert Marsh, and the tidal flood control channel connecting them (hereafter, "Tidal Channel"; Fig. 2). Benthic habitats (sediment type and vegetation) within the wetland complex were mapped during June of 2010 (Fig. 3). Eelgrass (*Zostera marina*) beds in the tidal channel outside Brookhurst and Talbert Marshes were located at low tide on foot or from a kayak and GPS waypoints established at each flection points along the edge of the bed. The tidal creeks in Talbert Marsh empty almost completely at tides lower than 0.4 m which enabled waypoints of eelgrass beds to be taken entirely on foot. Brookhurst Marsh, being newly dredged and opened to tidal influence at the start of this study, contained no eelgrass in summer 2010. Some areas of the main tidal channel were difficult to

map using this technique and aerial photographs (taken by B. Perry, CSULB Geology) were overlaid onto the site map of the HBW and used to create polygons of any identifiable eelgrass beds.

The creeks in Brookhurst Marsh were restored by removing large quantities of sediment with heavy machinery, leaving a benthos comprised of fine-sediment bare of vegetation in 2009. Coupled with random spot checks of the benthos, the subtidal creeks of Brookhurst Marsh were assumed to be characterized solely by mud substratum immediately following the restoration. The southeastern portion of the Tidal Channel had also been recently dredged to improve the flow of flood water to the ocean. Haphazard benthic sampling in this area indicated a primarily sandy substratum with patches of eelgrass along portions of the edges and corners of the Tidal Channel. When a distinct benthic type was encountered during the habitat survey, waypoints were taken of its perimeter to illustrate the change. Benthic water temperature was monitored using six HOBO Pendant 8K-UA-002-64 underwater temperature data logging devices (Onset Computer Corporation, Pocassett, MA) deployed at inner and outer locations for both marshes and the Tidal Channel (Fig. 2) from November 2009 to November 2010. As described above, monthly samples were grouped into seasons (three months per season) for subsequent analyses.

Relative water flow was estimated using Plaster of Paris clod cards (Thompson and Glenn 1994). This method uses the dissolution of clod cards (final weight/initial weight) to estimate relative differences in water flow among locations (Jokiel and Morrissey 1993; Meroz-Fine et al. 2005). A mixture of one part DI water to two parts Plaster of Paris was poured into ice cube trays, producing rectangular blocks with a water displacement of ~28 mL. Clod cards were mounted to circular pins and suspended from floats at eight locations corresponding to inner and outer locations for the sites throughout the HBW (Fig. 2). Four replicates were used in each location, spaced approximately 1 m from each other in the middle of the water column. Four control clod cards were placed in a dish of seawater for 24 hrs to test the integrity of the mix and to calibrate the test to the dissolution rate of clod cards in zero flow. Clod card weight was standardized by sanding excess material once the plaster had cured for three days (Mean ± SD: 30.46 ± 1.439 g). The cards were allowed to cure for three additional days after sanding. The cards were deployed in the field on a near full-moon lunar cycle during the summer of 2011 (26 June 2011 – 27 June 2011). After 24 h exposure to a 3.9 m change in tide height, the cards were collected, dried for three days, and reweighed.

Halibut Population Surveys

Due to differences in benthic habitat types among areas of the HBW, three methods of halibut population sampling were employed in the monthly surveys from July 2009 – July 2010. Although each sampling method showed some degree of size selectivity or habitat bias, using all three ensured a more accurate representation of the halibut population.

i. Beach Seines

The protocol for seining in Brookhurst and Talbert Marshes was described in the previous section, however, this method was not effective in the Tidal Channel due to the large amount of eelgrass and debris in the channel that fouled the nets.

ii. Beam Trawls

A trawl net (1 m beam trawl, 0.5 cm delta netting, and 0.1 cm heavy delta chafing netting on cod end) was towed for approximately 100 m at 2-3 knots from a 4.3 m skiff within the Tidal

Channel and was estimated to cover approximately 100 m^2 per tow. The Channel is bisected by a roadway bridge (Brookhurst Street) between Talbert and Brookhurst Marshes which made continuous trawling through the area impractical; therefore three trawls were done at haphazardly selected locations south of the bridge and three done north of the bridge. This method could not be effectively used in the marsh creeks as the restricted waterways did not provide adequate space to maneuver the skiff for continuous trawl paths and speeds.

iii. Hook and Line Surveys

Two teams of two fishers sampled six haphazardly selected locations within each site (Brookhurst Marsh, Talbert Marsh, Tidal Channel) using artificial lures (pink plastic grubtails with a 1-0 lead head hook size); each team sampled three locations. Fishers were stationed approximately 10 m from each other and casted consistently for 20 min at a rate of approximately two casts min^{-1}. Although the size-selectivity of hook and line surveys may be geared toward larger individuals, this method allowed equal sampling effort within the three sites of the HBW without the complications experienced by either the beach seines or beam trawls. Halibut caught during population surveys were weighed (g), measured (total length TL, cm), and tagged. Individuals > 18 cm TL received a small T-bar anchor tag (FLOY Tag, Seattle, WA) inserted in the post-cranial muscle tissue with a Fine Fabric pistol grip needle gun. T-bar anchor tags contained a unique ID code and a phone number in case of recovery. Halibut < 17.9 cm TL received sub-dermal injections of colored latex on their blind side near the pectoral fin. These marks were administered as a color-dot system to identify individuals (Thedinga et al. 1997).

Short-Term Movement Behavior

Fine-scale movements of 13 halibut (> 25 cm TL) were quantified using externally mounted acoustic transmitters (V9-1L, 29mm long, 2.9g in water, 63, 75, 78, 81, and 84 kHz, fixed pulse interval; VEMCO Ltd, Nova Scotia) attached to the post-cranial musculature using chromic gut. The use of chromic gut ensured that the transmitter would fall free from the fish after a few weeks. Six of the 13 fish were released at their site of capture (referred to as the "non-transplant" group in future between-group analyses) and were tracked for multiple, non-consecutive 24-hr periods. One additional fish (Fish #1) was caught near Talbert Marsh but released at the mouth of Brookhurst Marsh, shortly after the restoration was completed, and this fish was monitored for three 24–hour periods. The first 24-hr tracking period for Fish #1 was not used in any comparisons because it was unclear whether the translocation of this fish to the entrance of Brookhurst Marsh may have altered the fish's behavior during this period. All subsequent tracks of Fish #1 were used in analyses of activity space, home range, and habitat association and for comparisons among fish.

No tagged halibut were observed to enter within-marsh creek habitat, therefore, in summers 2010 and 2011, seven fish caught from the Tidal Channel were tagged and translocated to the innermost creek of Brookhurst Marsh, a displacement distance of ~ 1 km, to determine whether and how larger halibut would use marsh creek habitat. These seven fish were referred to as the "transplant" group in subsequent analyses. Three individuals were tracked for > 24 hrs in 2010, and four additional individuals were tracked in 2011 for varying time periods (9 – 18 hrs). All fish were tracked from a 4.3 m skiff using a directional hydrophone (Vemco model VH110) and a VR100 receiver. Waypoints were taken every 15 min with a handheld GPS with a positional accuracy of ~ 2 m. Preliminary range tests indicated that relocation positioning accuracy was within the positional accuracy of the handheld GPS (~2 m). Occasionally,

conditions allowed for direct visual observation of a tagged individual, providing additional confirmation of habitat utilization and behavior. Visual confirmation of transmitter retention was performed by free-diving on individuals who did not exhibit movement during the first three hours of an active tracking event.

Long-Term Movement Behavior

Eighteen halibut (22.7-53.7 cm TL) were obtained through hook and line fishing from March – June 2010; individuals were affixed with coded transmitters (V9-2L-R64K, 9 mm x 21 mm, 69 kHz, pulse interval: 60-90 sec, approx. 290 day battery life; VEMCO Ltd, Nova Scotia). These fish were monitored using six VR2W acoustic receivers deployed as a linear array: one in the entrance of Brookhurst Marsh, four in the Tidal Channel, and one at the ocean Inlet (Fig. 2). Receivers were suspended within 1 m of the benthos on a rope and buoyed by a subsurface float to ensure they remained upright in all tide cycles. Range tests were conducted to determine the detection range of the receiver array by suspending a coded acoustic transmitter (5-s pulse interval) above the benthos and towing it through the HBW by kayak. The average (± SD) detection range of receivers in the array was 160 ± 107 m, though ranges were largely dependent on local channel morphology and the amount of eelgrass near each station.

Due to restricted detection range, high degree of ambient noise, and effects of tidally induced water flow across receivers, we used a conservative measure of halibut presence – detection of a tagged individual three or more times within an hour at one receiver. Duration of stay was defined as the number of days an individual was detected post-tagging before leaving the HBW. The Ocean Inlet station was deployed in July 2010 to more accurately capture exit behavior, therefore individuals were presumed to have left the HBW when their final detections were at the Talbert Outer or Ocean Inlet stations. Time spent in various regions of the HBW was approximated using the proportion of total detections per acoustic receiver station.

Data Analyses

To determine within-season thermal heterogeneity of the HBW, average daily water temperatures were calculated for each monitoring station and compared with Kruskal-Wallis tests. When tests were significant, pairwise Mann-Whitney U-tests were used to identify which sites were significantly different from each other, using a sequential Bonferonni approach to correct for multiple comparisons (Holm 1979). Spline interpolation maps were created to illustrate differences in average seasonal temperature among monitoring locations in ArcGIS using data from the 2010 observation period. Average daily water temperatures of the entire HBW were compared graphically to ocean surface temperatures measured at Newport Beach, CA (NOAA buoy 46230). A one-way ANOVA with Tukey's post hoc test was used to test for differences in the mean dissolution rate of clod cards among sites.

Catch per unit effort (CPUE) was calculated for each sampling method (beach seines: halibut seine^{-1}, beam trawls: halibut tow^{-1}, hook and line surveys: halibut fisher hour^{-1}) and ANOVAs done for each method to identify seasonal CPUE differences among sites. Measurements (TL) of halibut caught during abundance surveys could not be normalized, so a Kruskal-Wallis test was used to test for differences in mean TL of halibut caught among sites in the HBW.

To evaluate short-term movement behavior, GPS waypoints of halibut locations were used to quantify activity space (AS), defined in this study as the area occupied by a halibut in one 24-hr period. Individuals were tracked for multiple periods over the approximate 10-d

battery life of the transmitter, and all relocation positions were combined for each individual to calculate home range. Home range (HR) is defined in this study as the total area used by tagged halibut over the entire 10-d tracking period. Minimum Convex Polygons (MCP) were created for both activity space and home range using the Hawth's Tools extension of ArcMap 9.2 (Beyer 2004), which creates a polygon encompassing all observed locations for the specified time period. Over-estimation of area use by tagged individuals was potentially problematic for this species based on the largely sedentary behavior that was observed in most individuals, yet probabilistic methods of calculating core area use were inappropriate considering the narrow waterways in the HBW. Core area was therefore determined by manually stripping the five furthest points from the geometric mean center of activity until the change in area was reduced by less than 5% in subsequent peels (Worton 1995; Hatchwell et al. 2001; Bath et al. 2006). A correlation analysis was performed to test for a relationship between TL and core activity space. The same analysis was performed between TL and home range size. A General Linear Model (GLM) was used to test the effect of season (Spring, Summer, Fall, Winter), average daily water temperature (13-25º C), day length (number of daylight hours), tidal swing (the summation of tide height change during the observation period), and interactions between these variables on size of activity space (m^2).

To determine the potential for habitat selection by halibut, GPS position data from each track was layered over the habitat map of the HBW. Euclidean Distance Analysis (EDA, the shortest straight line distance) ratios were calculated for each habitat type by dividing the mean distance from observed halibut locations to each habitat type, by the mean distance from a randomly generated set of waypoints to each habitat type. This produces a ratio where values = 1 indicate that habitat use is proportional to a habitat's availability, values < 1 show higher association to a habitat than expected based on its availability, and values > 1 indicate low association to a particular habitat in relation to its availability. Multivariate analysis of variance (MANOVA) was used to test whether mean EDA ratios were significantly different from one (where habitat use is equal to availability) (Conner and Plowman 2001; Bellquist et al. 2008; Mason and Lowe 2010). If habitat use in general was non-random, an ANOVA was used to test whether the mean EDA ratio for a specific habitat differed from unity.

Differences in movement behavior between transplanted and non-transplanted fish were compared by dividing the observation periods into two distinct time blocks: Time 1 for the transplant group was defined as the time spent within marsh habitat (Brookhurst Marsh) and Time 2 was defined as the time spent within the Tidal Channel. Times 1 and 2 for the non-transplant group corresponded to the first and second halves of the first 24-hr observation period (all in the Tidal Channel). This partitioning allowed for formal analysis of movement behavior associated with habitat type and also treatment. Average Rate of Movement (ROM) was calculated for each individual by dividing the distance traveled between successive positions by the time elapsed between them (~15 min). Mixed model GLM analyses were used to compare average distance traveled while active and average ROM between groups and time periods. This mixed model is based on least squares means rather than expected mean squares, and does not produce a sums of squares table. This method was used because it allowed the random, nested terms (fish within treatment) to be properly incorporated from the outset of the test (SAS v.9.1 SAS software, Cary, NC).

Objective 3: Trophic Support for Halibut

Stomach Content and Stable Isotope Analyses

We used stomach contents and stable isotope analyses to compare halibut diets across habitats within the Huntington Beach Wetlands. In addition to the point occurrence or frequency of prey items found in the stomachs of fish, stable isotope ratios provide a "time-integrated" description of trophic relationships and sources of prey (Witting et al. 2004). Diet composition of each halibut sampled (see below for details) was determined using analysis of stomach contents. The digestive tract was removed, stomach contents were emptied into a Petri dish, and all items sorted and identified to the lowest possible taxonomic level (Allen 1988); unidentifiable diet items were classified as "unknown". White muscle samples for stable isotope analysis were dissected from the dorsal musculature of each halibut. Stable isotope analysis was performed on both fish muscle tissue and individual diet items found in each stomach. Samples were washed in Milli-Q water (Millipore, Billerica, Massachusetts, USA), placed in combusted vials (500˚C for 4 h), and dried to a constant weight in a 50°C oven for 24 h (Whitcraft and Levin 2007). Dried samples were then placed in pre-weighed tin boats and sent to the Stable Isotope Facility at University of California, Davis for analysis. Isotopic composition of the samples was analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 mass spectrometer (Sercon Ltd., Cheshire, UK). Stable isotope ratios are reported in standard δ notation as a ratio of heavy to light isotope content (15N:14N or 13C:12C). Values are expressed as parts per thousand (‰) and are relative to international standards Vienna Pee Dee Belemnite and air for carbon and nitrogen, respectively.

Wild-Caught Fish

A subset of the halibut collected in the fish abundance surveys described above (seine, trawl, or hook-and-line from Brookhurst Marsh, Talbert Marsh, and the Tidal Channel) was retained for diet analysis. All individuals were weighed (g), measured (cm), and then immediately euthanized in seawater ice slurry in the field. After approximately 30 min, halibut were placed in labeled bags and kept on ice until completion of sampling activities. Samples were then returned to the laboratory and stored at -20°C until later dissection.

Laboratory Experiment

To build upon our study of wild-caught juvenile halibut diets in the Huntington Beach Wetlands, we did a caging study to compare the diet and growth of halibut restricted to feeding in specific habitats. When a consumer moves to a new habitat where available foods differ in their isotopic composition from those in the previous habitat, the change will be gradually reflected in the consumer's body tissues (so-called "isotopic turnover"; Herzka 2005). If the isotopic composition of a consumer is to be used as an indication of its current diet (e.g., as an indication of an individual's diet during the caging experiment), the amount of time required for isotopic turnover to occur first needs to be determined (Bosley et al. 2002). For this reason, we first did a preliminary experiment under controlled conditions in the laboratory to determine the minimum amount of time that juvenile halibut should remain in cages.

The lab experiment was conducted between July and October 2010. A total of 43 halibut (range 4.0 cm to 7.7 cm SL) were collected from Seaplane Lagoon, Port of Los Angeles, California (33˚44'51.46 N, 118˚15'07.94 W). The collection method was the same as described for beach seines performed in the Huntington Beach Wetlands, however, we sampled from a different location to reduce our impact in the new restoration. Sampling occurred over several days until an appropriate number of fish had been collected. After capture, halibut were placed in aerated coolers and brought to the Cabrillo Marine Aquarium, San Pedro, California. Halibut

were measured, weighed, and 30 individuals retained for treatment in the lab experiment. The remaining 13 individuals were euthanized by immersion in seawater ice slurry for 30 minutes, serving as a control group to represent the initial variability in isotopic signatures. Experimental individuals were randomly assigned to one of three experimental diets: krill, clam, or smelt (n = 10 halibut per treatment). These food types were chosen from available food sources at the aquarium and were determined to be isotopically distinct prior to the experiment. Within each diet treatment, fish were distributed into 20-gal tanks of filtered seawater (n = 2 tanks per treatment; 5 fish per tank). Before placement in tanks, halibut were tagged using a subcutaneous latex dye injection below the dorsal fin on the ventral side (Thedinga et al. 1997). Tanks were maintained at 16˚C, and fish were fed their assigned diets twice daily, with excess food cleared after 15 min.

To determine the timeline of isotopic turnover, one fish from each tank was removed and euthanized at intervals of 4, 6, 8, 10, and 12 weeks after treatment began, resulting in 2 halibut samples per time period per diet. A final length and weight measurement was recorded, and fish were stored at -20˚C until later dissected. All halibut were dissected for muscle tissue samples that were prepared and analyzed for stable isotopes as described for wild caught halibut. Relative growth rates were calculated for each halibut by dividing the total change in length or mass by the initial value and number of weeks spent in treatment.

Caging Experiment

We did an initial caging experiment between October and December 2010. Four cages were deployed in subtidal areas of Talbert and Magnolia Marshes and eight cages in Brookhurst Marsh. Although not part of our initial sampling design, we decided to include Magnolia Marsh as it had only recently been opened to tidal influence (in summer 2010) and might therefore provide an interesting contrast with Brookhurst Marsh (open for more than a year at that point). The additional cages in Brookhurst Marsh were necessary due to its larger size; cages were divided between inner and outer areas of that marsh. Each cage consisted of a PVC frame (0.5 x 0.5 x 0.5 m) covered on 5 sides with 6-mm Vexar mesh. Bottoms of the cages were left without mesh covering to enhance the feeding ability of enclosed fish. The corner of each cage had a 0.25 m PVC extension that allowed the mesh sides to extend into the sediments. Sand bags filled with sediment from the caging sites were tied to each corner for stabilization. Cages were allowed to settle in each marsh for at least eight weeks before halibut were added.

A total of 69 halibut (3.4-9.8 cm SL) were collected from Alamitos Bay, Long Beach, California (33˚44'52.06 N, 118˚07'08.83 W). The collection method was the same as described for beach seines performed in the Huntington Beach Wetlands; sampling occurred over several weeks until an appropriate number of halibut had been collected. As halibut were collected, they were measured, weighed, tagged, and 64 individuals randomly assigned to one of 3 treatment groups (marshes). The remaining 5 halibut were euthanized by immersion in seawater ice slurry for 30 minutes to serve as a control group. As fish were collected, they were transported in aerated coolers to the Huntington Beach Wetlands and placed in pre-constructed cages in either Brookhurst, Talbert, or Magnolia marshes. Following methods outlined in Fodrie and Herzka (2008), four halibut were placed in each cage of the 16 cages. Cages were regularly checked for debris and positioning, but otherwise were left undisturbed for eight to nine weeks. At the end of the experiment, the halibut were measured, weighed, and euthanized in a seawater ice slurry for 30 min before being returned to the lab and stored at -20˚C until further processing. Halibut were

dissected for muscle isotope samples and stomach contents as described previously. Relative growth (length and mass) was also calculated for each halibut.

Unfortunately, only nine halibut were recovered at the end of the experiment, all from Magnolia cages (see Results for details). The Talbert cages were physically removed from the channels at one point by persons unknown and several of the Brookhurst cages had evidence of burrowing activity by large crabs that created opens through which a small fish could escape. As a consequence, we attempted the caging experiment a second time between April and July 2011. In order to decrease the amount of fish loss, cages from the first experiment were redesigned to include a mesh covering on the bottom surface. Cages were redeployed in similar sites, although due to difficulties in collecting a sufficient number of halibut, only Brookhurst and Talbert marshes were included in the second caging attempt (n = 12 cages total). Halibut were sampled from the same site with the same methods as the first caging experiment, although only 49 individuals (3.3-11.1 cm SL) were collected. Seven halibut were used as a control group, 28 halibut were placed in cages in Brookhurst Marsh (six cages with four fish each and two cages with two fish each), and 14 halibut were placed in cages in Talbert Marsh (one cage with two fish and three cages with four fish each). Cages were again left for eight weeks, and at the end of the experiment, halibut were processed as above.

Data Analysis

Data collected from stomach content and stable isotope analyses were generally multivariate in nature. Stomach content data was recorded as presence/absence of each food type per fish. Stable isotope data included δ15N and δ13C values for each halibut muscle sample or prey item, and these isotopes were analyzed in combination to allow the overall differences in isotopic composition between samples to be tested. Differences in isotopic signatures between types of prey items found in stomach contents were tested using analysis of similarity (ANOSIM) on a resemblance matrix based on Euclidean distances. Once isotopic differences between known prey types were confirmed, a canonical analysis of principal coordinates (CAP) ordination was created from isotopic signatures of identified prey items and the "Add New Samples" procedure used to classify "unknown" prey items based on their isotopic content. This procedure places each new observation into the CAP ordination and determines which group centroid is closest to it in canonical space (Anderson and Willis 2003). Thus each "unknown" sample was reclassified as one of the previously identified prey types based on its isotopic values. These new classifications were then used in subsequent analyses of diet composition. Due to known ontogenetic shifts in diet found in California halibut (Allen 1988; Kramer 1991), fish were separated into different size classes (extra-small (newly settled): < 2.6 cm; small: 2.7-7.9 cm; medium: 8-22.9 cm; and large: > 23 cm SL). Differences in diet composition and isotopic signatures of halibut were compared among size classes and habitats within each size class with ANOSIM.

Relative growth was compared between diet treatments in the laboratory experiment with univariate ANOVAs. A resemblance matrix of Euclidean distances was created from δ15N and δ13C values from each sample, and sample isotopic signatures were added to the analysis in order of increasing time interval (i.e., time spent in treatment) to determine the length of time necessary for halibut muscle isotope composition to reflect differences in diet. ANOSIM tests were used to compare the isotopic signatures of halibut between treatments for each time interval.

Due to the low numbers of fish recovered from cages and the difference in timing between caging experiments within each marsh, no formal statistical analyses were performed to compare growth, stomach contents, or isotopic composition between marshes. We instead describe general patterns for each metric within each marsh and discuss the isotopic composition of experimental fish only in relation to the respective control groups from each experiment (Magnolia in 2010; Brookhurst and Talbert in 2011). Multivariate differences in halibut muscle isotopic composition between fish held in each marsh and their respective control group were tested with ANOSIM.

Although the general utility of stable isotope analyses is well established, we also tested the relationship between what a halibut eats and its resulting isotopic signature by measuring the correlation between the isotopic ratios of muscle tissue and stomach contents collected from the same fish. Halibut muscle isotopic signatures were examined using a similarity profile (SIMPROF) permutation test. This analysis tests for significant clusters of samples within a given dataset. The cluster labels for fish muscle samples were then applied to stomach content data from the same fish. If an individual halibut had multiple isotope samples for its stomach contents, those values were averaged to create a single value. We then tested for similarities in multivariate patterns between diet composition and halibut muscle isotopic signatures with the RELATE routine in PRIMER, calculating a rank correlation coefficient between the respective resemblance matrices.

Results

Objective 1: Fish Community Structure

Year 1

Fish were absent from Brookhurst Marsh prior to restoration due to the lack of marsh channels, however, fish abundance increased dramatically immediately water flow was restored such that 5217 fish were collected in Brookhurst Marsh during the first year. By comparison, 3878 fish were collected in Talbert Marsh. A total of twenty species were collected over the course of the first year, fifteen of which occurred in both marshes (Table 1). California killifish, *Fundulus parvipinnis*, was the most abundant species in Talbert Marsh, comprising 36.5% of the total abundance; topsmelt, *Atherinops affinis*, was the most abundant species in Brookhurst Marsh, with a relative abundance of 39.6%.

None of the univariate measures of diversity differed significantly between marshes, although there were seasonal effects for each index in both marshes (Table 2). Average species richness and Shannon-Wiener diversity index were significantly greater in the spring than any other season. Species evenness was greater in the spring than in the summer or fall, but not significantly different from winter (PERMANOVA, pairwise t-test, $p < 0.05$) (Fig. 4).

Multivariate analyses showed different trends than the univariate diversity measures, with marsh and season both having significant effects on fish community structure. Fish assemblages were significantly different in each season (ANOSIM, $R = 0.486$, $p < 0.001$; Fig. 5A) and significant differences between the two marshes occurred within all seasons, except for winter (ANOSIM, $R = 0.33$, $p < 0.001$; Fig. 5B). Distance-based PERMANOVA analyses gave similar results (Table 3). The CAP ordination produced two axes to distinguish samples among the eight marsh-by-season groups, with the first canonical axis separating the fish assemblages into seasonal groups, and the second canonical axis separating samples by marsh (Fig. 6). The sizes of each of these first two canonical correlations, indicating the strength of association between

the multivariate data cloud and the hypothesis of group differences, were large ($\delta_1 = 0.89$ and $\delta_2 = 0.80$).

Nine fish species were identified in the SIMPER analysis as contributing at least 5% to the dissimilarity between marshes. These species included California killifish, Pacific staghorn sculpin *(Leptocottus armatus)*, diamond turbot *(Hypsopsetta guttulata),* goby *(Gobiidae),* bay pipefish *(Syngnathus leptorhynchus),* California halibut *(Paralichthys californicus),* topsmelt, jacksmelt (*Atherinopsis californiensis),* and deepbody anchovy *(Anchoa compressa)*.

California killifish abundance was significantly greater in Talbert Marsh during fall and spring, although no overall seasonal differences in abundance occurred (PERMANOVA, pairwise t-test, $p < 0.05$) (Table 4; Fig. 7). The abundance of Pacific staghorn sculpin varied among seasons, but not between marshes. The average number of sculpin peaked during the winter and spring, declined during summer, and was lowest in fall (PERMANOVA, pairwise t-test, $p < 0.05$) (Table 4; Fig. 7). Diamond turbot abundance also varied among seasons and not between marshes, with the average abundance highest during winter, intermediate during spring, and lowest during summer and fall (PERMANOVA, pairwise t-test, $p < 0.05$) (Table 4; Fig. 7). These three species were classified into one functional group based on their demersal nature and association with the marsh surface for food (Armstrong et al. 1995; West et al. 2003; Madon 2008).

Deepbody anchovy abundance varied between marshes and among seasons, with a significant interaction between both factors. Significantly more anchovy occurred in Brookhurst Marsh during spring and summer, and no difference between marshes occurred during fall and winter. Overall, most anchovy occurred in summer, were less abundant in the spring, and during fall and winter abundances were at or near zero (PERMANOVA, pairwise t-test, $p < 0.05$) (Table 4; Fig. 7). There were also differences between marsh and season for topsmelt. The average number of topsmelt was greatest in the fall, intermediate during the summer and winter, and lowest in the spring. During spring there were significantly more topsmelt in Brookhurst than Talbert (PERMANOVA, pairwise t-test, $p < 0.05$) (Table 4; Fig. 7). Jacksmelt abundance varied between seasons, only occurring during summer in both marshes (Table 4; Fig. 7). These three species were classified into one functional group based on their association with the marsh channel and their pelagic, schooling nature (Madon 2008).

The abundance of California halibut and the species group goby did not differ between seasons or between marshes within any season (Table 4; Fig. 7). Bay pipefish abundance varied with season, having the lowest average in the summer compared to all other seasons (PERMANOVA, pairwise t-test, $p < 0.05$) (Table 4; Fig. 7). These three species were grouped into the "Cosmopolitan" functional group due to their use of both shallow marsh surface and seagrass areas in addition to deeper subtidal channel areas (West et al. 2003; Madon 2008; López-Rasgado and Herzka 2009).

Year 2

Due to the reduced sampling effort during Year 2, fewer fish were collected in each marsh. A total of 1564 fish were collected in Brookhurst Marsh and 1670 fish were collected in Talbert Marsh. Thirteen species were collected over the course of the second year, ten of which occurred in both marshes (Table 1). Topsmelt dominated the catch in both marshes, with a relative abundance of 80.2% in Brookhurst Marsh and 42.9% in Talbert Marsh.

The univariate measures of diversity showed different patterns from the first year, with both marsh and season interacting to have significant effects on the Shannon-Wiener diversity

index and species evenness (Table 2). The average Shannon-Wiener diversity index was lowest during summer, increased through the fall and winter, and peaked in the spring. The only significant difference between marshes occurred during summer, when diversity in Talbert was more than six times that in Brookhurst (PERMANOVA, pairwise t-test, $p < 0.05$) (Fig. 4). Average species evenness was significantly greater during winter and spring than in the summer or fall. Evenness was greater in Talbert Marsh during summer and greater in Brookhurst Marsh during fall (PERMANOVA, pairwise t-test, $p < 0.05$) (Fig. 4). No significant differences between marshes or seasons occurred for species richness in Year 2 (Table 2).

Rank-based multivariate analyses found a significant effect of season (ANOSIM, $R = 0.542$, $p = 0.003$; Fig. 8), but there were too few permutable units to allow for a strong test for the effect of marsh within season. Distance-based multivariate analyses also showed that fish community structure was significantly affected by season during the second year, with differences occurring between summer and winter, summer and spring, and between fall and winter (Table 4). Fish assemblages were significantly different between the two marshes only during winter (PERMANOVA, pairwise t-test, $p < 0.05$). The CAP ordination showed a similar result, with the first canonical axis separating the fish assemblages into seasonal groups, and the second canonical axis showing the difference between marshes during winter (Fig. 9). The sizes of each of these first two canonical correlations for the second year were large ($\delta_1 = 0.97$ and $\delta_2 = 0.82$).

The abundance patterns of individual fish species identified in the Simper analysis from Year 1 differed slightly in Year 2. California killifish abundance did not vary between marshes or seasons (Table 4). The abundance of Pacific staghorn sculpin varied among seasons, but not between marshes. The average number of sculpin peaked during the winter and spring, was intermediate during fall, and was lowest in summer (PERMANOVA, pairwise t-test, $p < 0.05$) (Table 4; Fig. 10). Season and marsh interacted to have significant effects on diamond turbot abundance. The average abundance was highest during winter, intermediate during spring and fall, and lowest during summer. A significant difference between marshes occurred during winter, with Talbert Marsh having more diamond turbot than Brookhurst Marsh (PERMANOVA, pairwise t-test, $p < 0.05$) (Table 4; Fig. 10).

Deepbody anchovy abundance was not significantly different between marshes or seasons (Table 4). There were significant differences between marshes and seasons for topsmelt (Table 4). The average number of topsmelt was greatest in the summer, intermediate during the fall, and lowest in winter and spring. During winter there were significantly more topsmelt in Brookhurst than Talbert (PERMANOVA, pairwise t-test, $p < 0.05$) (Fig. 10). Jacksmelt were not collected during Year 2.

The abundance of California halibut and bay pipefish did not differ between seasons or between marshes within any season (Table 4). The abundance of the species group goby varied with season, having the lowest average in the fall, intermediate abundance in the winter, and the highest average during spring and summer (PERMANOVA, pairwise t-test, $p < 0.05$) (Fig. 10).

Functional Group Analyses

When combining data from both sampling years, the overall difference in abundance of each functional group differed significantly between marshes. On average, more “Marsh Surface” fish (California killifish, Pacific staghorn sculpin, and diamond turbot) occurred in Talbert Marsh, more “Marsh Channel” fish (topsmelt, deepbody anchovy, and jacksmelt) occurred in Brookhurst Marsh, and no significant difference occurred between marshes for the

abundance of "Cosmopolitan" fish (goby, California halibut, and bay pipefish) (Table 5). The length data of each group followed the same pattern, with "Marsh Surface" fish being significantly longer in Talbert Marsh, "Marsh Channel" fish being longer in Brookhurst Marsh, and no difference in length occurring for "Cosmopolitan" fish (Table 5). Most length data for the individual species followed the same pattern as the corresponding functional group, except for two of the species. The average length of diamond turbot was not significantly different between marshes, and the average length of gobies was longer in Talbert Marsh (Table 6).

Objective 2: Halibut Population Structure and Movement Behavior

Environmental Data

The benthos of the HBW in June 2010 was characterized as mud (53%), sand (46%), and shell hash (1%) with scattered beds of eelgrass (Zostera marina) covering 16% of the available subtidal area (Fig. 3). Sand and shell hash substrata (~95% sand, ~5% silt/clay) are predominantly found within the Tidal while the marsh habitats consist almost entirely of mud (~35% sand, ~65% silt/clay; C. Whitcraft, unpubl. data). There were significant differences in seasonal water temperatures among monitoring stations of the HBW (all $p < 0.001$), with the inner portions of Brookhurst and Talbert marshes the warmest during Spring and Summer (Fig. 11). Average daily marsh water temperatures were warmer than average daily ocean surface temperatures for most of the year. Additionally, absolute maximum and minimum daily water temperatures were recorded for the HBW (Fig. 12). Relative water flow based on clod card dissolution was significantly different among all sites in the HBW ($F_{7, 24} = 1842.1$, $p < 0.001$). Water flow in the Tidal Channel between the two marsh habitats was nearly four times as high as that found in the innermost creeks of the marshes (Fig. 13).

Halibut Population Surveys

A total of 144 beach seines, 42 beam trawls, and 60 fisher hours were completed during the study period (July 2009 – July 2010). There was no significant difference in catch per unit effort (CPUE) for beach seine surveys between Brookhurst (average ± SD; 0.236 ± 0.166 fish seine^{-1}) and Talbert marshes (0.209 ± 0.172 fish seine^{-1}) ($t_{21} = -0.22$, $p = 0.83$). Though hook and line surveys were conducted throughout the HBW, halibut were only caught within the Tidal Channel (Fig. 14). There was no significant seasonal change in CPUE for any sampling method (Table 7). Overall, 77 halibut were caught during population surveys (Fig. 15) and there was no significant difference in mean TL of halibut caught among the three sites in the HBW ($H = 1.16$, df = 2, $p = 0.56$; Figs 16-17).

Short-Term Movement Behavior

Ten halibut were caught in the Tidal Channel and actively tracked from August 2009 – June 2010. None of the halibut left the HBW at any point during the 10-day observation period, nor were they observed to enter either marsh habitat. Average home range size for actively tracked individuals represented only 9% of the total available habitat (range: 1.3 - 22%). There was no correlation between daily activity space (range: 279 – 6,426 m^2) and total length ($r = 0.41$, $p = 0.06$), nor was there a correlation between home range size (range: 1,712 – 28,667 m^2) and total length ($r = 0.42$, $p = 0.26$). Activity space size did not vary significantly according to season, average daily water temperature, day length, tidal swing, and there were no significant interactions between these variables ($F_{10, 12} = 0.39$, $p = 0.3$). Home range size was also unaffected by these variables ($F_{7, 1} = 3.26$, $p = 0.4$).

There was significant habitat selection detected for actively tracked halibut (MANOVA: Wilk's $\lambda = 0.005$, $F_{4, 6} = 327.31$, $p < 0.0001$). Halibut (>20 cm TL) were associated with shell hash, eelgrass, and sandy substratum disproportionately to the overall habitat availability (Table 8, Fig. 18). Fifty-four percent of all observed fish positions occurred within 2 m of the eelgrass edge even though eelgrass beds comprised only 16% of the total available benthic habitat.

Translocations

Because no large halibut (>20 cm TL) were caught in either marsh habitat and none of the seven individuals caught and tracked in the Tidal Channel entered either marsh, seven fish were transplanted to the back of Brookhurst Marsh to observe their movement behavior in the newly restored environment. Of the seven transplanted fish, one died in the days following the first 24-hr track, although a cause of death was not determined. Data collected for this particular fish were not utilized in any analyses. All remaining fish returned to the Tidal Channel within 16 h. Distance traveled while active was not affected by group or time period; however, there was a significant interaction effect ($F_{1, 20} = 5.49$, $p = 0.041$; Fig. 19A). The same was true for ROM ($F_{1, 20} = 11.79$, $p = 0.006$; Fig. 19B). Individuals within the transplant group exhibited significantly higher average ROM (all $p < 0.003$) and average distance traveled while active (all $p < 0.04$) during Time 1, while within Brookhurst Marsh (Fig. 19).

Long-Term Movement Behavior

Due to a defect in the epoxy used to cement transmitters to the external mount, usable data was only collected for six of the 18 tagged individuals. Passively tracked halibut showed associations to the same general regions within the HBW as those which were actively tracked (Fig. 20). Four of these halibut were tagged in May 2010, one in June 2010 (which exhibited the longest residency time), and an additional halibut in December 2010 (which had the shortest residency time). Four of these six fish retained their transmitters until exiting the HBW (range of duration of detection: 3 – 114 d). Two individuals that were tagged in May (#29677, #29678) left during a rapid rise in average water temperature from mid – June 2010 to late – July when average water temperatures in the Tidal Channel reached 21.5ºC (average before rise: 17.5ºC, after rise: 18.4ºC). Fish #29663, tagged 19 December 2010, left three days later during a major rain event (7.5 cm over 4 d, average monthly rainfall: ~6.6 cm). Halibut #29671, tagged in May 2010, remained in the HBW for 114 days before its final detections at the ocean Inlet station, even though other halibut tagged on the same day emigrated from the HBW likely in response to rising water temperature in June. No individual was detected re-entering the receiver array during the study period (Fig. 21; receivers removed June 2011). Capture and release sites, locations of all observed locations, and calculated home ranges of non-transplanted and transplanted halibut are presented in Figs. 22 and 23, respectively.

Objective 3: Trophic Support for Halibut

Wild-Caught Fish

A total of 59 wild-caught halibut were collected for diet analysis. Beach seines were used to collect 17 fish from the restored Brookhurst Marsh and 11 fish from the reference Talbert Marsh. Halibut from Brookhurst had an average standard length (SL) of 9.8 cm (range 2.5 cm to 16.9 cm), and in Talbert the average standard length was also 9.8 cm (range 4.5 cm to 19.0 cm). In the Channel, 28 halibut were collected using beam trawls (average SL = 7.08 cm, range 2.0 cm to 40.0 cm) and 3 halibut were collected using hook-and-line (average SL = 30.9 cm, range 23.5 cm to 44.2 cm). No halibut were collected in the marshes using hook-and-line. The stomach

contents of 54 halibut were examined, of which 43 (80%) contained prey. A majority of prey items found were partially digested, and therefore items were placed in one of four general categories, including "copepods", "shrimp", "fish", and "unknown". Copepods were generally identified as being of the order Harpacticoida, and fish prey as being of the family Gobiidae, although definitive identifications to the species level were not possible. A large proportion of prey items were categorized as "unknown"; the Channel habitat had the highest frequency of items in this category (56%; Fig. 24). Most prey items were analyzed for stable isotope content, although the minimum weight required for isotope samples prevented some prey items from isotopic analysis.

The isotopic composition of prey items followed the expected pattern of trophic enrichment, with copepods having depleted δ15N values relative to fish (Fig. 25). When the isotopic signatures of prey items were compared between categories of known tissue types, a significant difference was found between copepods and fish (ANOSIM, $R = 0.665$, $p = 0.001$), and also between copepods and shrimp (ANOSIM, $R = 0.623$, $p = 0.028$). The "unknown" prey items had isotopic signatures which spanned a similar range of δ15N and δ13C values as the other three categories (Fig. 25), and these signatures were used to classify each sample as one of the three prey types using the "add new samples" procedure in the CAP analysis. Of the 23 "unknown" samples, 11 were classified as copepods, 7 were classified as fish, and 5 were classified as shrimp (Fig. 26). After adding the "unknown" samples to their respective categories, a test for the difference in prey types was re-run, and a significant difference was found between all three categories (ANOSIM, $R = 0.704$, $p < 0.001$). These new classifications were used in subsequent analyses to compare the diet composition of halibut in each habitat (Fig. 27).

The isotopic signatures of fish collected from the Inlet were significantly different from all other habitats, which were not different from one another (ANOSIM, $R = 0.428$, $p < 0.001$; Fig. 28). This pattern, however, is likely driven primarily by a strong association between habitat and fish size. When isotopic signatures of fish were compared by size class, all groups were significantly different from one another (ANOSIM, $R = 0.696$, $p < 0.001$; Fig. 29). Of the different size classes to which individual halibut were assigned, "extra small" occurred almost exclusively in the Inlet while "large" halibut (> 23 cm SL) only occurred in the Channel. No comparisons between habitats were performed for these size classes. Diet composition of "small" halibut varied between habitats with fish caught in the Channel generally having a higher proportion of copepods in their stomachs, however, small sample size limits the conclusions that can be drawn from these data (Fig. 30). Significant differences in halibut muscle isotopes were found between Brookhurst and Talbert Marshes, but none between either marsh and the Tidal Channel (ANOSIM, R = 0.25, $p = 0.034$; Fig. 31). "Medium" halibut exhibited no obvious differences in either diet composition (Fig. 32) or muscle isotopes (ANOSIM, $R = 0.037$, $p = 0.272$; Fig. 33) among habitats.

Laboratory Experiment

Juvenile halibut in the "smelt" treatment group grew twice as fast as fish in the other two treatment groups (Fig. 34), however, this difference was not statistically significant due to the small sample sizes ($n = 2$ tanks per diet) and correspondingly low statistical power. Nevertheless, the controlled laboratory conditions resulted in clear changes in isotopic composition of juvenile halibut (Fig. 35), with each treatment group having significantly different isotopic signatures from all other treatment groups and the control after 8 weeks (ANOSIM, $R = 0.749$, $p < 0.001$).

Caging Experiment

Halibut caged in Brookhurst or Talbert Marshes in 2011 grew at a similar rate, more that five times faster than halibut caged in Magnolia Marsh in 2010 (Fig. 36). During the 2010 caging experiment, 9 halibut were recovered from cages in Magnolia Marsh, but none from the other marshes (see Methods for details). The stomach contents of those fish were examined, of which 6 (67%) contained prey. Items were placed in one of three general categories, including "isopods", "shrimp", or "fish". Fish prey items were generally identified as being of the genus Syngnathus (pipefish), although definitive identifications to the species level were not possible (Fig. 37). During the 2011 caging experiment, 14 halibut were recovered from cages in Brookhurst Marsh, of which 13 (93%) contained prey. Only 2 halibut were recovered from cages in Talbert Marsh, and both contained prey items in their stomachs. No fish prey items were found in the stomachs of halibut caged in Brookhurst or Talbert marshes (Fig. 37).

The isotopic signatures of halibut caged in Magnolia Marsh were not significantly different from the control group for 2010 after 8 weeks, although they were starting to diverge by that point (ANOSIM, $R = 0.216$, $p = 0.075$; Fig. 38). In contrast, the isotopic signatures of halibut caged in Brookhurst Marsh (but not Talbert Marsh, possibly due to small sample size) were significantly different from the control group in 2011 (ANOSIM, $R = 0.205$, $p = 0.028$; Fig. 39). The average change in δ15N values for caged fish relative to controls was similar in absolute value for all three marshes, although fish caged in Magnolia Marsh had enriched values while fish caged in Brookhurst and Talbert marshes had depleted values relative to controls (Fig. 40A). A similar pattern was observed for δ13C values, with absolute values being similar among marshes but the direction of change being positive in Magnolia Marsh but negative for Brookhurst and Talbert marshes (Fig. 40B).

Efficacy of Stable Isotope Analyses

The SIMPROF test identified eight clusters of halibut muscle isotope samples that differed significantly at the 0.05 level (Fig. 41). The pattern observed for halibut muscle isotope signatures was highly correlated with that of the stomach content isotope signatures from those same fish (RELATE, $r_s = 0.55$, $p < 0.001$; Fig. 42), confirming the utility of stable isotope analyses as a tool for assessing recent diet composition.

Discussion

Fish Community Structure

Overall, it is fairly clear that the restoration of full tidal influence in Brookhurst Marsh resulted in a rapid increase in the quantity of viable fish habitat in the Huntington Beach Wetlands. Similar to other studies of fish community responses to the restoration of coastal wetlands, we saw an immediate response to the opening of Brookhurst Marsh to tidal flow, and the abundance of fish increased dramatically over the first few months of sampling. Because fish are capable of rapidly colonizing new habitat, abundance alone may not indicate habitat value (La Peyre et al. 2007). During the first year of sampling, classic univariate assessments (S, H', and J') indicated that the species richness, diversity, and evenness of fish in the restored Brookhurst Marsh was similar to that in the reference Talbert Marsh within months after tidal influence was restored. Seasonal differences were significant for all indices in both marshes, with each index reaching a maximum in the spring both years. These patterns are consistent with seasonal differences in fish communities that have been documented in other bays and estuaries

throughout California, with temperature and salinity usually identified as key environmental drivers (Allen et al. 2006). In contrast to univariate measures, more sensitive multivariate metrics suggested that in addition to overall seasonal differences, Brookhurst Marsh was not necessarily equivalent to Talbert Marsh as fish assemblages were significantly different between the two marshes in all seasons except winter. Although Brookhurst Marsh served as habitat to a similar number of species as Talbert Marsh the relative abundance of each species differed, indicating possible differences in the functioning of each habitat.

For example, while California killifish was the most abundant species in Talbert Marsh during the first year, comprising 36.5% of the total catch within this marsh, this species made up only 3.4% of the total catch in Brookhurst Marsh. Killifish access marsh surfaces at high tide to feed on benthic macroinvertebrates, detritus, and insect larvae (West et al. 2003), and studies have shown that they can increase their capacity for growth with the addition of these surfaces to their subtidal feeding areas (Madon 2008). The greater abundance of this species in Talbert Marsh could be a reflection of higher abundances and availability of benthic prey items which may yet be lacking in Brookhurst Marsh due to the short time span since its opening to tidal flow. The deeper channels found in Brookhurst Marsh did, however, provide fitting habitat for the more pelagic, schooling species present in the study area. Two species (topsmelt and jacksmelt) made up 77.6% percent of the total catch in Brookhurst Marsh during the first year of sampling. Williams and Zedler (1999) found similar results in a southern California salt marsh, where topsmelt abundance was closely related to sites with greater depths and lower temperatures. Because constructed channels in restored wetlands will most likely differ from natural channels in both depth and slope (Visintainer et al. 2006), these results indicate the importance of channel design in the restoration of coastal salt marshes.

Multivariate analyses of fish community composition found little evidence of significant differences between marshes in Year 2. The lack of any detectable difference between marshes could be interpreted in several ways. Fish species are known to rapidly colonize newly available habitat (La Peyre et al. 2007), and it is possible that Brookhurst Marsh gained a similar fish assemblage to Talbert Marsh during the monitoring period. However, other processes linking primary production to higher trophic levels, and thus influencing food chain support for fish and other vertebrates, develop at much slower timescales. Studies have shown that restored marshes can take 3-5 years to regain similar biomass of *Spartina alterniflora,* 10-15 years to develop similar benthic invertebrate communities, and as much as 30 years for soil properties like organic carbon and nitrogen to reach similar levels as reference sites (Craft et al. 2003). In some cases, constructed or restored wetlands will never match natural or reference wetlands for certain properties (Zedler and Callaway 1999). For these reasons, and in combination with the differences in the relative abundances of certain marsh species that were found in our study, it is unlikely that the two fish communities are functionally equivalent at this point. The more likely reason that our multivariate analyses did not detect significant differences between marshes during most of the second year was the reduction in sampling effort that year. In support of this idea, the average abundance and length of functional groups were consistently different between marshes. Fish species designated as channel associated (topsmelt, jacksmelt, and anchovy) were more abundant and larger in Brookhurst Marsh. Species more associated with benthic habitat and the marsh surface (killifish, staghorn sculpin, and diamond turbot) were more abundant and larger in Talbert Marsh.

Halibut Population Structure and Movement Behavior

The population structure of halibut in the HBW was largely comprised of juveniles and a small proportion of reproductively mature individuals (7% - 36%, based on the average size of maturity of female and male halibut), a trend seen in similar studies in other southern California estuaries (Barry and Cailliet 1981; Allen 1988; Allen et al. 2002; Fodrie and Mendoza 2006). The intent of population surveys was to sample all sites within the HBW and across the size range of halibut. Although the three sampling methods used for population surveys allowed us to catch a wider size range of halibut, larger fish were likely underrepresented by standardized sampling. Intensive, targeted fishing to obtain halibut used in telemetry studies consistently caught significantly larger halibut within the Tidal Channel (40 ± 10.4 cm TL) than those caught in population surveys (13.9 ± 9.7 cm TL).

Although the HBW exhibited a wider range of annual water temperatures during this study (low: 11.1º C in winter and high: 30.2º C in summer) than annual temperatures recorded within San Diego Bay, CA (15-27º C) (Allen et al. 2002), there was no difference in seasonal distribution of halibut within the HBW. It is possible that the topography and hydrology of the HBW is influencing halibut distribution. The hydrology of the restored estuary varies from that found within natural systems because of the influence of the artificially created flood control channel. The HBW is a highly channelized estuary with lots of restricted marsh creeks, which may cause temperatures to cool faster in the winter or heat up faster in the summer. Additionally, water flow is not equal throughout the system, creating pockets of slow-moving water throughout the estuary which may affect water quality and the distribution of prey or habitat. While this is not uncommon in natural systems, the flood control channel likely promotes greater water flow than natural estuarine creeks, which are capable of natural erosion.

Another factor that influences the distribution of flatfishes is sediment. Many flatfishes are ambush predators that bury themselves in the sediment to camouflage their presence. Sediment grain size can play an important role in structuring halibut distribution throughout the estuary (Powell and Schwartz 1977; Burke 1991; Reichert and Van Der Veer 1991) where smaller individuals are generally associated with finer sediments (mud) and larger individuals tend to be found in more coarse sediments (sand) (Drawbridge 1990; Moles and Norcross 1995). Accumulation and distribution of these sediment types are often generated by runoff and tidal transport. All of the larger halibut tracked in this study were most frequently associated with coarse shell hash and sand in the Tidal Channel, whereas smaller halibut were most often found in marsh creeks and areas in the Tidal Channel containing mud. The occurrence of small halibut within the Tidal Channel was likely facilitated by the presence of eelgrass beds, which provide shelter and protection from larger halibut and other predators. The eelgrass beds within the Tidal Channel have created small pockets of low flow, enabling the settlement of finer-grain sediments that juvenile halibut < 20 cm TL are known to associate with (Ginsburg and Lowenstam 1958; Fonseca et al. 1982; Heiss et al. 2000). Sediment samples taken near vegetated areas of the HBW had higher silt/clay content (~85% sand, ~15% silt/clay) than unvegetated areas (~95% sand, ~5% silt/clay). These eelgrass beds may also supply a potential source of prey for larger individuals. Eelgrass beds support higher species diversity, species richness, and abundances of fishes and invertebrates compared to unvegetated areas (Briggs and O'Connor 1971; Adams 1976; Onuf and Quammen 1983; Heck et al. 1989), providing a concentrated food source for larger predators. While the habitat found within the Tidal Channel may support more larger halibut than the marsh creeks, the prevalence of eelgrass beds within the Tidal Channel may be

providing adequate habitat for smaller halibut as well, which may reduce size segregation among the sites of the HBW.

While population surveys indicate that there is a wide range of sizes of California halibut (2.6 – 60.5 cm TL) within the HBW, and that their distribution may be affected by the presence of eelgrass beds, static survey methods are restricted to describing general habitat use. This study is the first to use acoustic telemetry to characterize the fine-scale movement behavior of this species, a method better suited to understanding habitat use of a key species than what can be assumed based on presence-absence data. The goal of this project was to catch and track halibut in Brookhurst and Talbert Marshes; however, larger halibut were not as routinely caught in these locations as in the Tidal Channel. Active tracking shows that halibut movement behavior is characterized by prolonged periods of inactivity punctuated by abbreviated periods of movement while remaining in a relatively small area. Size of area used was not dependent on body size as may be predicted based on traditional bioenergetic assumptions that larger organisms occupy larger areas in order to satisfy their greater metabolic needs (McNab 1963; Harestad and Bunnell 1979; Girrleman and Harvey 1982; Lowe and Bray 2006). However, California halibut are ambush predators which spend large amounts of time at rest and halibut tracked within the HBW may be utilizing tidal water flow as a prey-delivery system which may negate the need to expand area resulting from localized resource depletion.

Despite evidence that tidal cycle, temperature, and season can affect the movement behavior of flatfishes (Walsh and Peters 1999; Rooper et al. 2003; Madon 2008), these variables did not have a significant effect on the activity space or home ranges sizes of actively tracked California halibut regardless of the wide range of annual temperatures observed throughout the HBW during this study. While the lack of a pattern may be a result of the relatively short time scale of the active tracks, it may also be due to the unique combination of coarse sediment, dense eelgrass beds, and relatively high water flow found year-round within the Tidal Channel. Though dissolved oxygen was not measured for the purpose of this study, a number of other studies have linked low levels of dissolved oxygen to higher water temperatures and low relative water flow (Boicourt 1992; Balls et al. 1996) which can have an effect on dispersal and survival of fish (Coble 1961; Burton et al. 1980; Bejda et al. 1992). Salinity may also affect the distribution or movement behavior of halibut within the HBW as it does with other species of flatfishes (Ottesen and Bolla 1998; Jonassen et al. 1999; Yamashita et al. 2001), though the only behavioral modification which could be attributed to changes in salinity in this study were observed in the emigration behavior of one halibut in the long-term tracking study. Utilization of sand substratum within the HBW, found exclusively within the Tidal Channel, was greater than expected based on the availability of this sediment type. Though eelgrass began to grow into the entrance of Brookhurst Marsh by Fall 2010, eelgrass was only found within Talbert Marsh and the Tidal Channel during the active tracking study, and over half of all observed halibut positions occurred within 2 m of eelgrass beds. The difference in sediment type, water flow, and eelgrass coverage between the sites of the HBW may explain why halibut utilized the Tidal Channel most often. Previous studies have found that predation pressure for fishes transitioning from one habitat to another is generally higher at eelgrass ecotone edges and the areas immediately surrounding them (Kark and van Rensburg 2006; Hammerschlag et al. 2010; Tuya et al. 2010). The Tidal Channel is relatively narrow (~40 m wide), which forces pelagic, tidally transported prey to funnel through this habitat, transporting potential prey items past eelgrass ecotones where halibut lie and wait, taking advantage of the eelgrass and the tidal flow delivery.

The presence of halibut >25 cm within Brookhurst Marsh at different times of year suggests that conditions are suitable for larger halibut to be present in the marsh creeks; however, the six halibut caught in the Tidal Channel and then transplanted to the innermost creeks of Brookhurst Marsh all quickly returned to the Tidal Channel. Transplanted individuals within Brookhurst Marsh traveled faster and farther than non-transplanted individuals during either time period. The rapid emigration, high ROM, and large distances traveled observed among all transplanted individuals suggests that environmental conditions in Brookhurst Marsh may be unfavorable, or at least not preferred. While it seems plausible that differences in water temperature may have driven this type of behavior, there was no significant difference in hourly water temperature between these two sites during the translocation experiments. It is more likely that transplanted halibut were exhibiting simple homing behavior to the general vicinity of their site of capture as has been seen in telemetry studies in both terrestrial and marine systems. This homing behavior may be associated with habitat suitability, innate propensity, or a simple response to stimuli (Rawson and Hartline 1964; Able et al. 1984; Matthews 1990; Dittman and Quinn 1996). Most transplanted halibut made forays into the branches of the marsh creeks before eventually reaching the Tidal Channel. This may indicate that they were unfamiliar with this new area and had to navigate to the Tidal Channel by trial and error, only exhibiting behavior similar to non-transplanted individuals once they reached familiar or more favorable conditions. The mean center of activity (time 1 and 2 combined) for non-transplanted individuals was on average 111 m (± 95.8 m) from their site of capture, while transplanted individuals returned to within 282 m (± 154 m) of their location of capture within the Tidal Channel. This suggests that, while halibut may be exhibiting homing behavior, they are homing to a general area or habitat type rather than a specific location within the Tidal Channel. During the majority of this study, Brookhurst Marsh contained no eelgrass beds. As eelgrass beds are generally assumed to support higher abundances of small fish and epibenthic invertebrates, the lack of eelgrass within Brookhurst Marsh may limit the prey density in this site. Additionally, Brookhurst Marsh is characterized by significantly lower water flow than what is found in the Tidal Channel where transplanted individuals were caught. Though dissolved oxygen was not measured during my study, a number of other studies have linked low levels of dissolved oxygen to low relative water flow which can have an effect on dispersal and survival of fish (Coble 1961; Burton et al. 1980; Bejda et al. 1992). Although average distance traveled and ROM for the transplant group during time 1 became indistinguishable from the non-transplant group upon reaching the Tidal Channel, it is still unclear whether individuals are returning to the Tidal Channel to take advantage of the higher water flow and eelgrass-sand ecotone habitat, or simply homing to their general location of capture.

Although fish were actively tracked over different times of the year, none of those individuals were observed to emigrate from the HBW; however, longer term passive tracking indicates prolonged site fidelity and periods of emigration that may be associated with season. Though active tracking provides detailed information on fine-scale habitat use and movement behavior, it is limited by the short battery life (~10 d) of the transmitters and observations are typically on one fish at a time. Passively tracked individuals may be observed simultaneously over longer periods of time which allow for observations of bulk movement in response to stimulus. Halibut passively tracked via stationary acoustic receivers were of comparable size to those used in active tracking events. Passively tracked halibut showed associations to the same locations (Tidal Channel) and utilized similar amounts of space as those which were actively tracked. While actively tracked individuals did not leave the estuary in response to changes in

environmental conditions (e.g. water temperature, tidal cycle, etc), departures of passively tracked halibut appear to coincide with dramatic environmental events such as spikes in water temperature and major storm events. Though prolonged exposure to changes in temperature and salinity may be deleterious, other flatfishes have shown the ability to acclimate to changes in temperature and salinity during short-term exposure (Munro et al. 1994; Arjona et al. 2007; Lou et al. 2011). It is possible that California halibut are moderately tolerant to short-term changes in environmental conditions, such as those seen during active tracking, but cannot physiologically tolerate exposure to extreme conditions for protracted periods. Halibut were not observed to re-enter the HBW once they had emigrated, possibly because these individuals may have located suitable adjacent coastal habitats. However, tagged individuals may have transitioned to offshore adult habitat as California halibut are assumed to emigrate from coastal habitats to deeper water after reaching approximately 25 cm TL (Haaker 1975; MacNair et al. 2001). Though halibut may periodically return to their estuary of origin on a seasonal or annual basis, we had no way to measure this as the transmitters used for this study expired after 8 months.

While no eelgrass was present in Brookhurst Marsh when halibut were tracked in 2010, eelgrass has moved into Brookhurst marsh. If halibut prefer eelgrass ecotone habitat, one would expect halibut to spend more time in the marsh as eelgrass invades Brookhurst Marsh. Eelgrass beds may reduce water flow in this site even further, and if water flow is an important factor influencing use of Brookhurst marsh by larger halibut, this site may never provide suitable habitat for this size class. However, the presence of smaller halibut in Brookhurst Marsh indicates that this restoration may be providing adequate habitat and food resources for halibut in other life history stages.

Trophic Support for Halibut

The diet of juvenile California halibut collected in the Huntington Beach Wetlands included prey types typical for this species in the southern California region (Allen 1988), and the restored Brookhurst Marsh appeared to provide similar trophic support to that found in the reference Talbert Marsh and subtidal flood control channel during the first two years following restoration.

We used several methods to analyze the diet of halibut. The analysis of stomach contents allows daily feeding habits of fish to be established, while stable isotopes are indicative of feeding patterns incorporated into body tissues over a longer timeframe (McMahon et al. 2005). The combination of these methods allowed us to not only describe a complete picture of juvenile halibut diets in a restoration setting, but it also allowed prey items that were partially digested and unidentifiable to be categorized along with known prey types. The significant difference in isotopic content between prey types aided in this classification, which increased the power of our analyses. Also, the significant correlation between halibut muscle isotopic content and diet composition confirmed the validity of isotopic analysis as a tool for assessing diet differences among habitats.

Previous studies of California halibut have shown a marked ontogenetic shift in diet, with benthic oriented invertebrates important to smaller individuals and teleosts becoming more important to diets in larger individuals (Allen 1988; Kramer 1991). Our results followed this pattern, with different size classes having significantly different isotopic signatures. In addition, larger halibut had enriched $\delta 15N$ values relative to smaller individuals, which indicates larger halibut were feeding at a higher trophic level (i.e., teleosts versus invertebrates). In general, fish within a given size class had similar isotopic signatures, suggesting that (at least for halibut)

Brookhurst Marsh is already providing food resources comparable to the more established reference marsh. This conclusion is bolstered by the observation that growth rates and isotopic turnover of juveniles caged in each habitat were robust and similar between marshes.

The presence of newly settled juveniles within the Huntington Beach Wetlands demonstrates the connectivity of this habitat with nearby coastal ocean areas, which is important not only for providing access to the newly restored Brookhurst Marsh as potential nursery habitat, but also allows primary production in marsh areas to contribute to the secondary production in deeper waters (Weinstein et al. 2000). The selection of specific habitats by juvenile fish within a wetland system may be based on availability, physical transport processes, local environmental conditions, structural complexity, or prey and predator interactions (Herzka 2005). Abundance, growth, and mortality of juvenile fish may vary considerably between these habitats, and thus specific regions within wetland areas may contribute more to the production of recruits to the adult population (López-Rasgado and Herzka 2009). Because increased food resources and growth are factors used to distinguish coastal salt marsh areas as nursery habitat for juvenile fish (Kramer 1991; Minello et al. 2003), these metrics can be used in the assessment of nursery function in restored habitats. The use of feeding habits and growth of juvenile fish to assess habitat quality and function is based on the assumption that individuals are not moving between specific habitats with potentially different conditions during the period that diet or growth is measured (López-Rasgado and Herzka 2009). Because fish may encounter spatially and temporally variable environmental conditions as they move through a wetland system (Herzka 2005), caging experiments guarantee that a fish has remained in a given area of interest and has only been exposed to the local conditions of that specific habitat ((López-Rasgado and Herzka 2009).

The results of this study suggest that the restoration of Brookhurst Marsh has already had significant positive effects on the local fish community. Although the abundances and biomass of some marsh-specific species are not yet comparable between the newly-restored marsh and a nearby reference site, the abundances, diet, and growth rates of a transient, facultative user of estuarine habitats were not significantly different, suggesting the rapid development of trophic support for some functional groups in this system. The observed connectivity of the HBW with the nearby coastal ocean (as evidenced by the recruitment of small fish into the wetlands and the export of larger tagged individuals) is also encouraging, as it suggests that this new habitat has already become part of the wider array of coastal wetland habitats in southern California.

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Table 1. Total abundance of each species collected in each marsh per sampling year. Numbers in parentheses are relative abundances. Sample size in each marsh: Year 1, $n = 24$ (2 events per month); Year 2, $n = 8$ (2 events per quarter)

Common Name	Scientific Name	Year 1		Year 2	
		Talbert	Brookhurst	Talbert	Brookhurst
Topsmelt	*Atherinops affinis*	848 (0.219)	2067 (0.396)	716 (0.429)	1254 (0.802)
California Killifish	*Fundulus parvipinnis*	1416 (0.365)	177 (0.034)	547 (0.328)	95 (0.061)
Jacksmelt	*Atherinopsis californiensis*	321 (0.083)	1869 (0.380)		
Staghorn Sculpin	*Leptocottus armatus*	538 (0.139)	376 (0.072)	248 (0.149)	54 (0.035)
Goby	*Gobiidae*	110 (0.028)	79 (0.015)	61 (0.037)	10 (0.006)
Deepbody Anchovy	*Anchoa compressa*	13 (0.003)	310 (0.059)		55 (0.035)
Grunion	*Leuresthes tenuis*	223 (0.058)	92 (0.018)	10 (0.006)	14 (0.009)
Diamond Turbot	*Hypsopsetta guttulata*	174 (0.045)	64 (0.012)	10 (0.006)	3 (0.002)
Bay Pipefish	*Syngnathus leptorhynchus*	64 (0.017)	79 (0.015)	33 (0.020)	36 (0.023)
Striped Mullet	*Mugil cephalus*	85 (0.022)	69 (0.013)	2 (0.001)	8 (0.005)
Shiner Surfperch	*Cymatogaster aggregata*	36 (0.009)	3 (< 0.001)	42 (0.025)	31 (0.02)
California Halibut	*Paralichthys californicus*	29 (0.007)	16 (0.003)	1 (< 0.001)	2 (0.001)
Bay Blenny	*Hypsoblennius gentilis*	9 (0.002)	4 (< 0.001)		
Gray Smoothhound	*Mustelus californicus*	3 (0.0008)	9 (0.002)		
Round Ray	*Urobatis halleri*	4 (0.001)	1 (< 0.001)		1 (< 0.001)
California Tonguefish	*Symphurus atricauda*	3 (< 0.001)			
California Corbina	*Menticirrhus undulates*	1 (< 0.001)			
Giant Kelpfish	*Heterostichus rostratus*		1 (< 0.001)		
Spotted Bay Bass	*Paralabrax maculofasciatus*		1 (< 0.001)		
Barred Sand Bass	*Paralabrax nebulifer*	1 (< 0.001)			
Threadfin Shad	*Dorosoma petenense*				1 (< 0.001)
	Total	3878	5217	1670	1564

Table 2. Results by year of separate two-factor PERMANOVAs of three diversity indices, with marsh and season as main effects. Significant *p*-values (< 0.05) are in bold. Sample size in each marsh: Year 1, $n = 24$; Year 2, $n = 8$.

Diversity Index	Source	Year 1					Year 2				
		DF	***SS***	***MS***	***Pseudo -F***	***P***	***DF***	***SS***	***MS***	***Pseudo -F***	***P***
Shannon-Wiener (H')	Marsh	1	0.049	0.049	1.79	0.181	1	0.0006	0.0006	0.09	0.769
	Season	3	0.593	0.198	7.26	**0.001**	3	0.250	0.083	12.33	0.003
	M x S	3	0.023	0.008	0.28	0.845	3	0.208	0.069	10.24	**0.006**
	Residual	40	1.09	0.027			8	0.054	0.007		
Species Richness (S)	Marsh	1	0.083	0.083	0.03	0.833	1	3.063	3.063	1.26	0.294
	Season	3	54.000	18.000	6.57	**0.001**	3	30.688	10.229	4.20	0.055
	M x S	3	18.917	6.306	2.30	0.092	3	2.188	0.729	0.30	0.812
	Residual	40	109.67	2.742			8	19.5	2.438		
Species Evenness (J')	Marsh	1	0.095	0.095	2.45	0.137	1	0.007	0.007	1.79	0.219
	Season	3	0.423	0.141	3.63	**0.023**	3	0.184	0.061	16.48	0.004
	M x S	3	0.006	0.002	0.05	0.984	3	0.409	0.136	36.57	**0.001**
	Residual	40	1.552	0.039			8	0.030	0.004		

Table 3. Results from the two-factor PERMANOVA for fish community structure in each year, with marsh and season as factors. Data were log (x+1) transformed prior to analysis. Significant

Source	Year 1					Year 2				
	DF	***SS***	***MS***	***Pseudo -F***	***P***	***DF***	***SS***	***MS***	***Pseudo -F***	***P***
Marsh	1, 40	7249.2	7249.2	7.84	**< 0.001**	1, 8	1284.8	1284.8	2.36	0.052
Season	3, 40	26410	8803.2	9.52	**< 0.001**	3, 8	5759.6	1919.9	3.52	**< 0.001**
M x S	3, 40	3859.2	1286.4	1.40	0.145	3, 8	3079.2	1026.4	1.88	0.053
Residual	40	36994	924.8			8	4364.2	545.5		

p-values (< 0.05) are in bold. Sample size in each marsh: Year 1, n = 24; Year 2, n = 8.

Table 4. Results by year of separate two-factor univariate PERMANOVAs of abundances of nine fish species, with marsh and season as factors. Data were log (x+1) transformed prior to analysis. Significant p-values (< 0.05) are in bold. Sample size in each marsh: Year 1, n = 24; Year 2, n = 8.

Species	Source	Year 1					Year 2				
		DF	***SS***	***MS***	***Pseudo -F***	***P***	***DF***	***SS***	***MS***	***Pseudo -F***	***P***
Deepbody Anchovy	Marsh	1, 40	14.71	14.71	31.07	< 0.001	1, 8	1.62	1.62	1.51	0.253
	Season	3, 40	24.52	8.17	17.27	< 0.001	3, 8	2.66	0.89	0.83	0.510
	M x S	3, 40	22.60	7.53	15.91	**< 0.001**	3, 8	2.66	0.89	0.83	0.517
	Residual	40	18.94	0.47			8	8.56	1.07		
Jacksmelt	Marsh	1, 40	1.91	1.91	1.50	0.231					
	Season	3, 40	114.88	38.29	30.04	**< 0.001**					
	M x S	3, 40	5.72	1.91	1.50	0.234					
	Residual	40	50.99	1.27							
Topsmelt	Marsh	1, 40	26.38	26.38	14.14	**< 0.001**	1, 8	3.32	3.32	10.80	**0.011**
	Season	3, 40	26.95	8.98	4.81	**0.005**	3, 8	10.76	3.59	11.68	**0.002**
	M x S	3, 40	6.47	2.16	1.16	0.344	3, 8	3.19	1.06	3.46	0.071
	Residual	40	74.66	1.87			8	2.46	0.31		
California Killifish	Marsh	1, 40	34.12	34.12	16.18	**< 0.001**	1, 8	3.88	3.88	1.84	0.213
	Season	3, 40	6.03	2.01	0.95	0.420	3, 8	5.90	1.97	0.93	0.473
	M x S	3, 40	12.39	4.13	1.96	0.137	3, 8	10.11	3.37	1.59	0.267
	Residual	40	84.34	2.11			8	16.91	2.11		
Staghorn Sculpin	Marsh	1, 40	3.18	3.18	3.45	0.073	1, 8	0.96	0.96	1.23	0.294
	Season	3, 40	73.64	24.55	26.64	**< 0.001**	3, 8	32.63	10.88	13.96	**0.003**
	M x S	3, 40	0.74	0.25	0.27	0.843	3, 8	3.90	1.30	1.67	0.256
	Residual	40	36.86	0.92			8	6.23	0.78		
Diamond Turbot	Marsh	1, 40	3.65	3.65	4.43	**0.046**	1, 8	0.33	0.33	2.41	0.185
	Season	3, 40	7.68	2.56	3.11	**0.037**	3, 8	1.51	0.50	3.66	0.097
	M x S	3, 40	3.78	1.26	1.53	0.226	3, 8	2.86	0.95	6.94	**0.028**
	Residual	40	32.97	0.82			8	1.10	0.14		
Goby	Marsh	1, 40	0.05	0.05	0.06	0.814	1, 8	1.26	1.26	2.46	0.153
	Season	3, 40	5.94	1.98	2.08	0.123	3, 8	4.82	1.61	3.15	0.070
	M x S	3, 40	0.93	0.31	0.32	0.804	3, 8	6.22	2.07	4.06	**0.038**
	Residual	40	38.09	0.95			8	4.09	0.51		
California Halibut	Marsh	1, 40	0.19	0.19	0.53	0.469	1, 8	0.03	0.03	0.33	0.578
	Season	3, 40	0.19	0.06	0.17	0.916	3, 8	0.33	0.11	1.22	0.374
	M x S	3, 40	2.28	0.76	2.10	0.120	3, 8	0.09	0.03	0.33	0.807
	Residual	40	14.52	0.36			8	0.72	0.09		
Bay Pipefish	Marsh	1, 40	0.0003	0.0003	0.0004	0.982	1, 8	0.57	0.57	0.91	0.367
	Season	3, 40	7.25	2.42	2.89	0.050	3, 8	0.37	0.12	0.20	0.900
	M x S	3, 40	0.47	0.16	0.19	0.903	3, 8	2.89	0.96	1.55	0.279
	Residual	40	33.42	0.84			8	4.97	0.62		

Table 5. Results of two-sample T-tests for differences in average abundance and length between marshes for three functional groups of fish species. Data from the two years of sampling were combined and log (x+1) transformed prior to analysis. Numbers in parentheses are ± 1 SE. Significantly larger values ($p < 0.05$) are in bold. Sample size for abundance in each marsh per group: n = 96 events. Sample sizes for length are specified below.

Species Group	Abundance				Length (cm)					
	T	***P***	**Talbert**	**Brookhurst**	***T***	***P***	**Talbert**	***n***	**Brookhurst**	***n***
Marsh Channel	3.17	0.001	19.77 (5.32)	**57.90 (15.30)**	12.51	< 0.001	8.07 (0.13)	529	**9.95 (0.09)**	949
Marsh Surface	-3.87	< 0.001	**30.55 (5.68)**	8.01 (1.44)	-2.09	0.018	**6.33 (0.07)**	909	6.15 (0.11)	505
Cosmopolitan	-0.45	0.656	3.10 (0.70)	2.31 (0.39)	-0.37	0.715	10.44 (0.35)	227	10.70 (0.43)	215

Table 6. Results from two-sample T-tests for differences between marshes in average length of nine fish species in three functional groups. Data from the two years of sampling were combined and log (x+1) transformed prior to analysis. Numbers in parentheses are ± 1 SE. Significantly larger values ($p < 0.05$) are in bold.

Species	*T*	*P*	Length (cm)			
			Talbert	*n*	Brookhurst	*n*
Marsh Channel Fishes						
Deepbody Anchovy	2.36	0.010	9.23 (0.68)	13	**10.72 (0.18)**	154
Jacksmelt	2.12	0.018	10.05 (0.34)	82	**11.22 (0.34)**	111
Topsmelt	11.92	< 0.001	7.66 (0.13)	434	**9.57 (0.10)**	684
Marsh Surface Fishes						
California Killifish	-2.75	0.003	**6.44 (0.06)**	405	6.15 (0.10)	181
Staghorn Sculpin	-3.62	< 0.001	**6.82 (0.11)**	348	6.26 (0.13)	257
Diamond Turbot	1.16	0.249	4.95 (0.22)	156	5.75 (0.58)	67
Cosmopolitan Fishes						
Goby	-3.62	< 0.001	**7.34 (0.31)**	116	5.87 (0.30)	86
California Halibut	-0.66	0.513	11.10 (1.10)	25	11.70 (2.40)	18
Bay Pipefish	-0.33	0.741	14.44 (0.49)	86	14.28 (0.46)	111

Table 7. CPUE of each sampling method by season. *F* (ANOVA) and *H* (Kruskal-Wallis) test statistics and associated *p*-values indicate non-significance at the $\alpha = 0.05$ confidence level.

Method	Test Statistic	P-value
Beach Seine (all sites, $n = 144$)	$F_{4, 7} = 1.14$	$p = 0.413$
Beam Trawl (Tidal Channel, $n = 42$)	$H_4 = 3.26$	$p = 0.515$
Hook and Line (Tidal Channel, $n = 60$ fisher hours)	$H_4 = 5.54$	$p = 0.236$

Table 8. Euclidean distance analysis (EDA, shortest straight line distance) ratios calculated for each habitat type. EDA ratios = 1 indicate that habitat use is proportional to a habitat's availability, values < 1 show higher association to a habitat than expected based on its availability, and values > 1 indicate low association to a particular habitat in relation to its availability. Numbers are *t*-statistics (*p*-values) from pairwise comparisons of the distance between observed fish positions and randomly generated positions to each benthic habitat type found within the HBW.

Habitat Type	Eelgrass	Shell Hash	Sand	Mud
Eelgrass	-----			
Shell Hash	-1.99 (0.080)	-----		
Sand	4.29 (0.002)	2.43 (0.040)	-----	
Mud	-10.93 (< 0.001)	-4.93 (< 0.001)	-13.07 (< 0.001)	-----

Figure 1. Brookhurst and Talbert Marshes and the tidal flood channel connecting them in the Huntington Beach Wetlands, Huntington Beach, CA, before and after the 2009 restoration of Brookhurst Marsh. A reference site for this study, Talbert Marsh was restored in 1989. Image source: Google Earth.

Figure 2. Map of the Huntington Beach Wetlands Complex (HBW). Stippled area indicates marsh habitat. Dark grey indicates available aquatic habitat (creeks, channels, and inlets) within the study site at mean high tide. Circles indicate clod card stations (26 June 2011 – 27 June 2011), stars indicate temperature data logger stations, in place from 1 December 2009 – 31 December 2010. Hashed area indicates the approximate detection range of stationary VR2W acoustic receivers (triangles) used for long-term monitoring (May 2010 – June 2011).

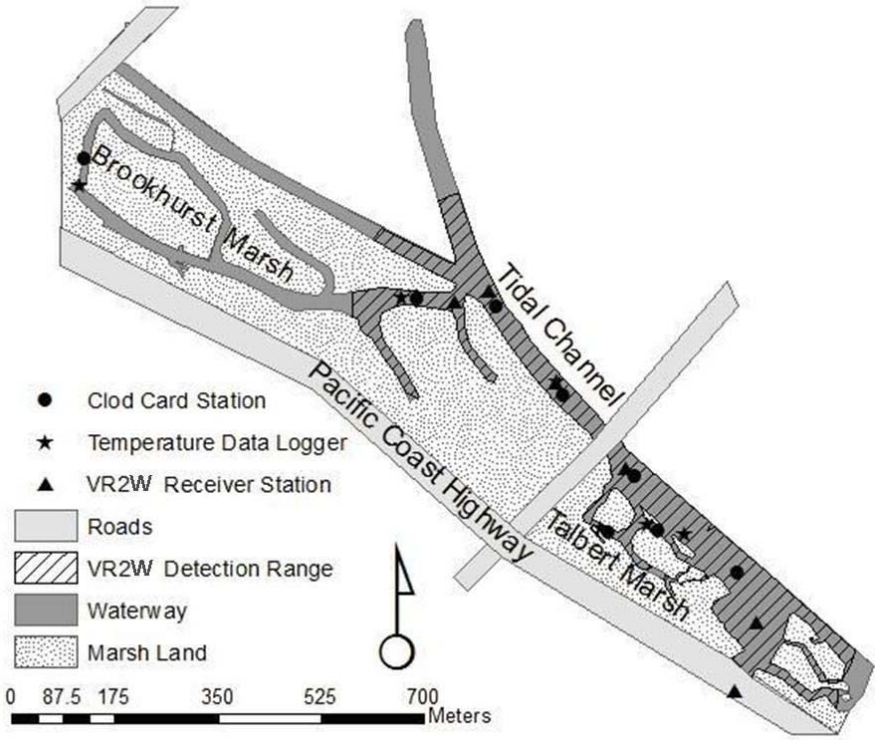


Figure 3. Major habitat types (sediment and vegetation) within the HBW during summer 2010. Colors correspond to benthic habitat types.

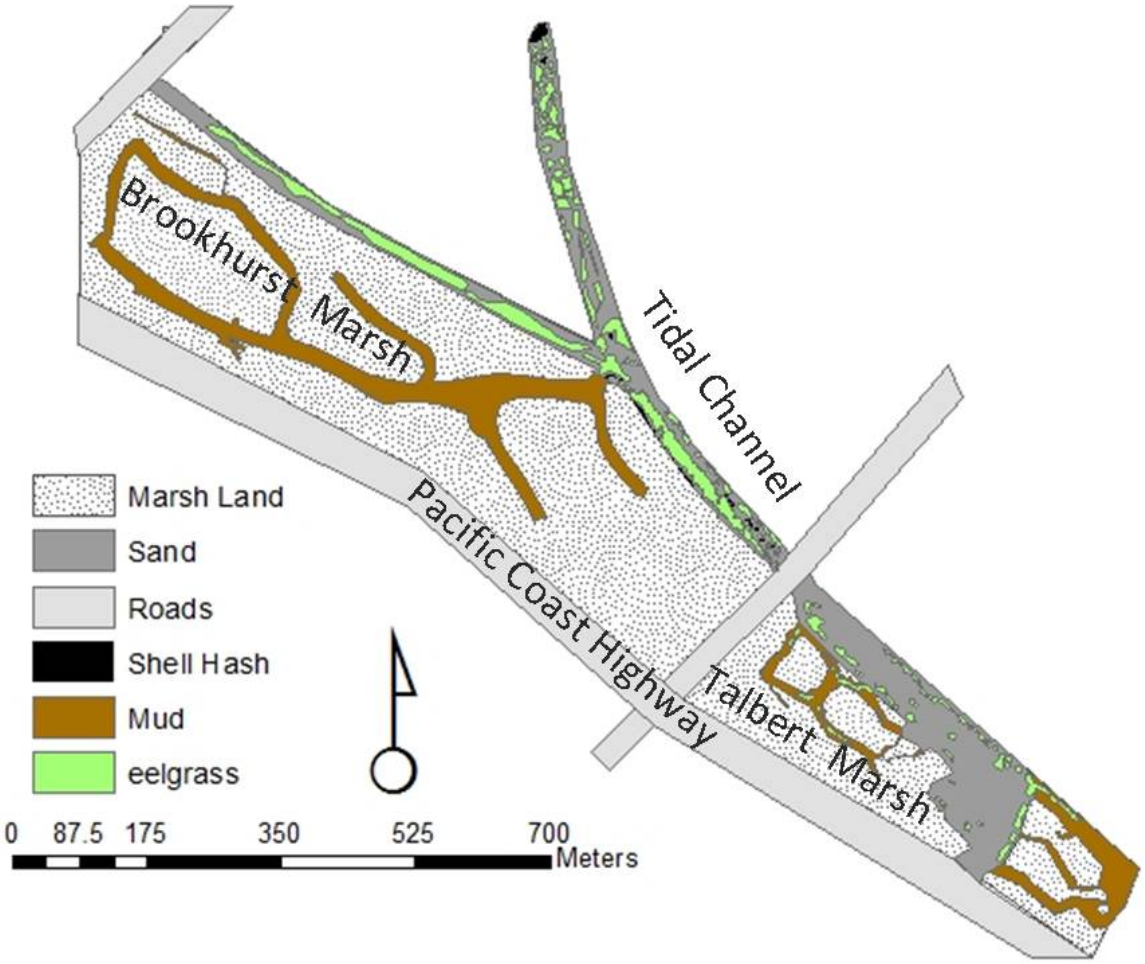


Figure 4. Average (± 1 SE) species richness, Shannon-Wiener diversity index, and species evenness between marshes by season and year. Different letters indicate statistically significant differences among seasons while asterisks indicate significant differences between marshes within season (PERMANOVA, $p < 0.05$). Gray bars = Brookhurst Marsh; White bars = Talbert Marsh. (Sample size in each marsh: Year 1, $n = 24$; Year 2, $n = 8$).

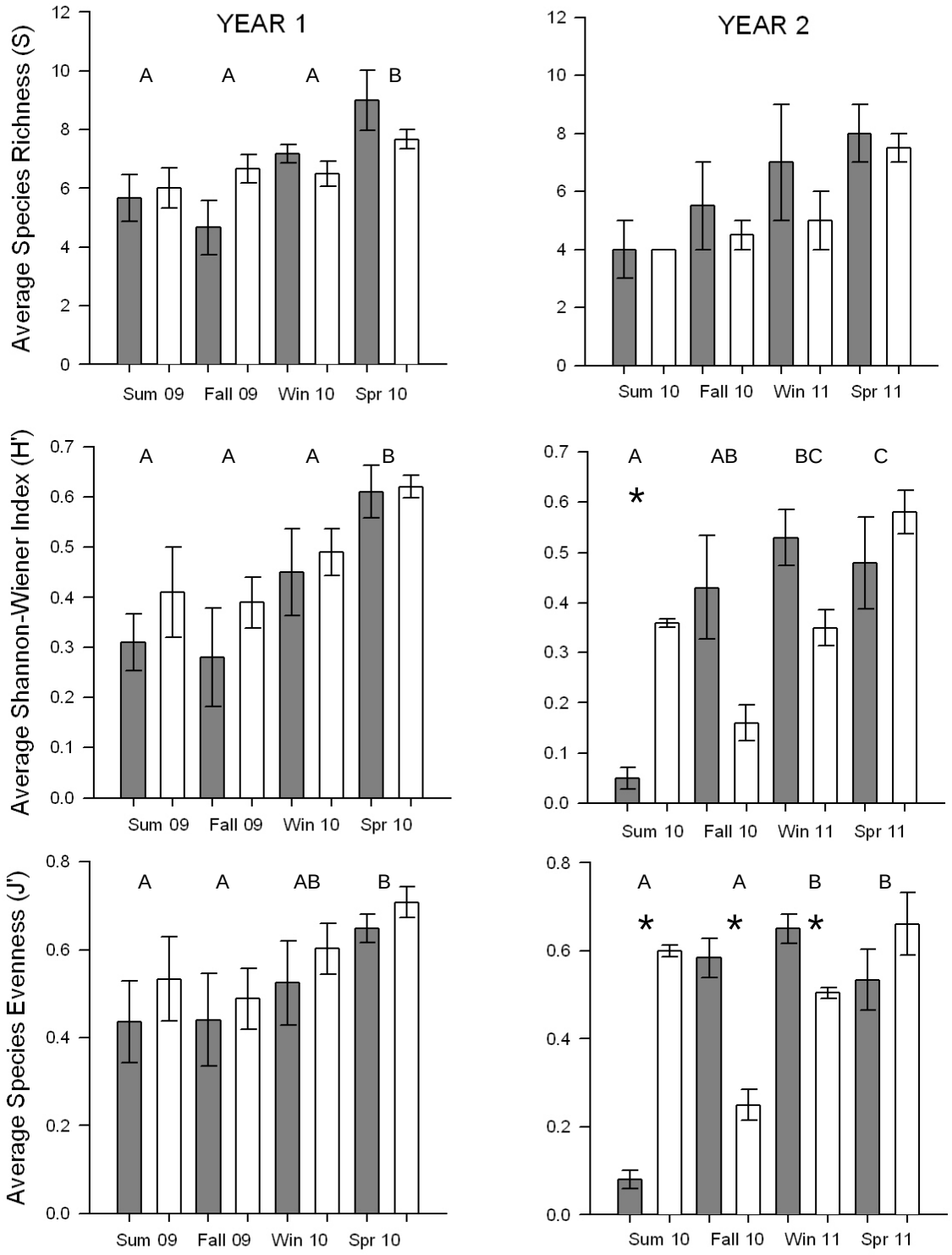


Figure 5. Non-metric multidimensional scaling (MDS) ordinations of fish assemblages, based on log(x+1) transformed abundances from the 48 samples collected in Year 1 by season (A) marsh within season (B). Ellipses drawn on graphs illustrate seasons that were statistically significantly different from one another (ANOSIM). Marshes were significantly different in all seasons but winter (details in text).

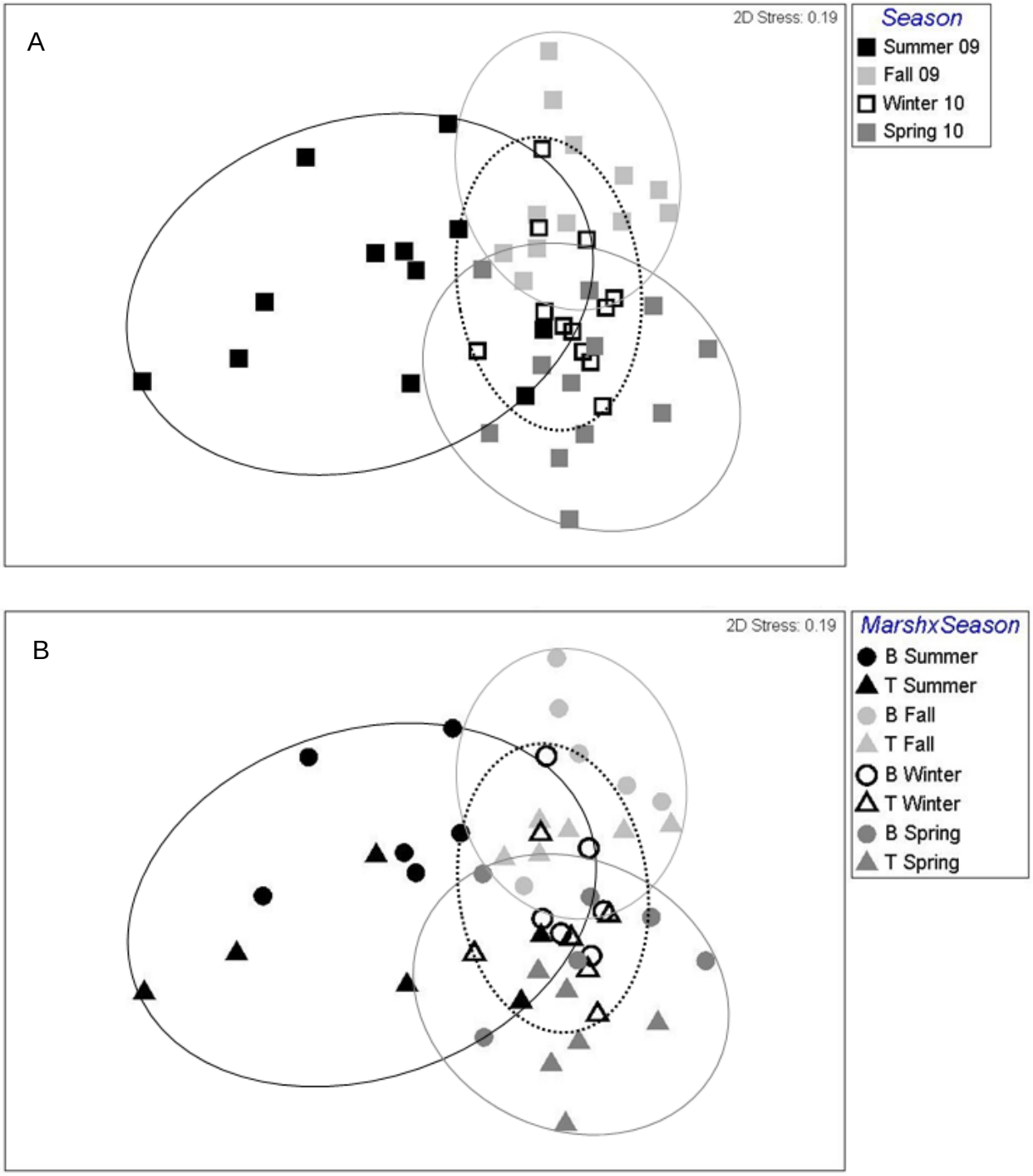


Figure 6. Canonical analysis of principal coordinates (CAP) ordination of fish assemblages, based on log(x+1) transformed abundances from the 48 samples collected in Year 1. Species identified in the SIMPER analysis as contributing at least 5% to the dissimilarity between marshes are indicated, with vector length representing the strength of correlations of each species with the CAP axes (unit circle corresponds to r = 1).

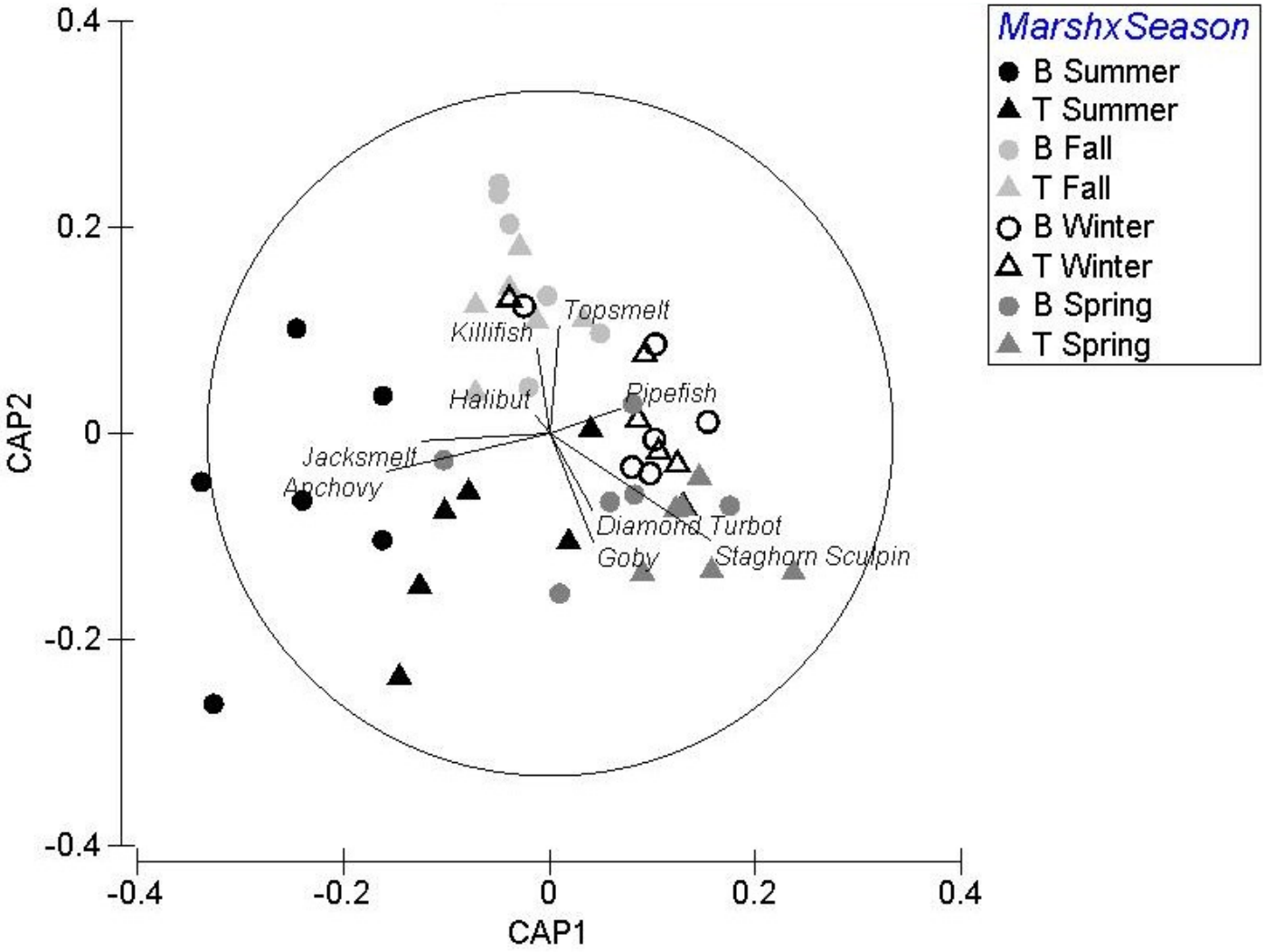


Figure 7. Average (± 1 SE) abundances for nine fish species identified in the SIMPER analysis of Year 1 between marshes by season. Different letters indicate statistically significant differences among seasons while asterisks indicate significant differences between marshes within season (PERMANOVA, $p < 0.05$). Gray bars = Brookhurst Marsh; White bars = Talbert Marsh. (Sample size in each marsh: $n = 24$).

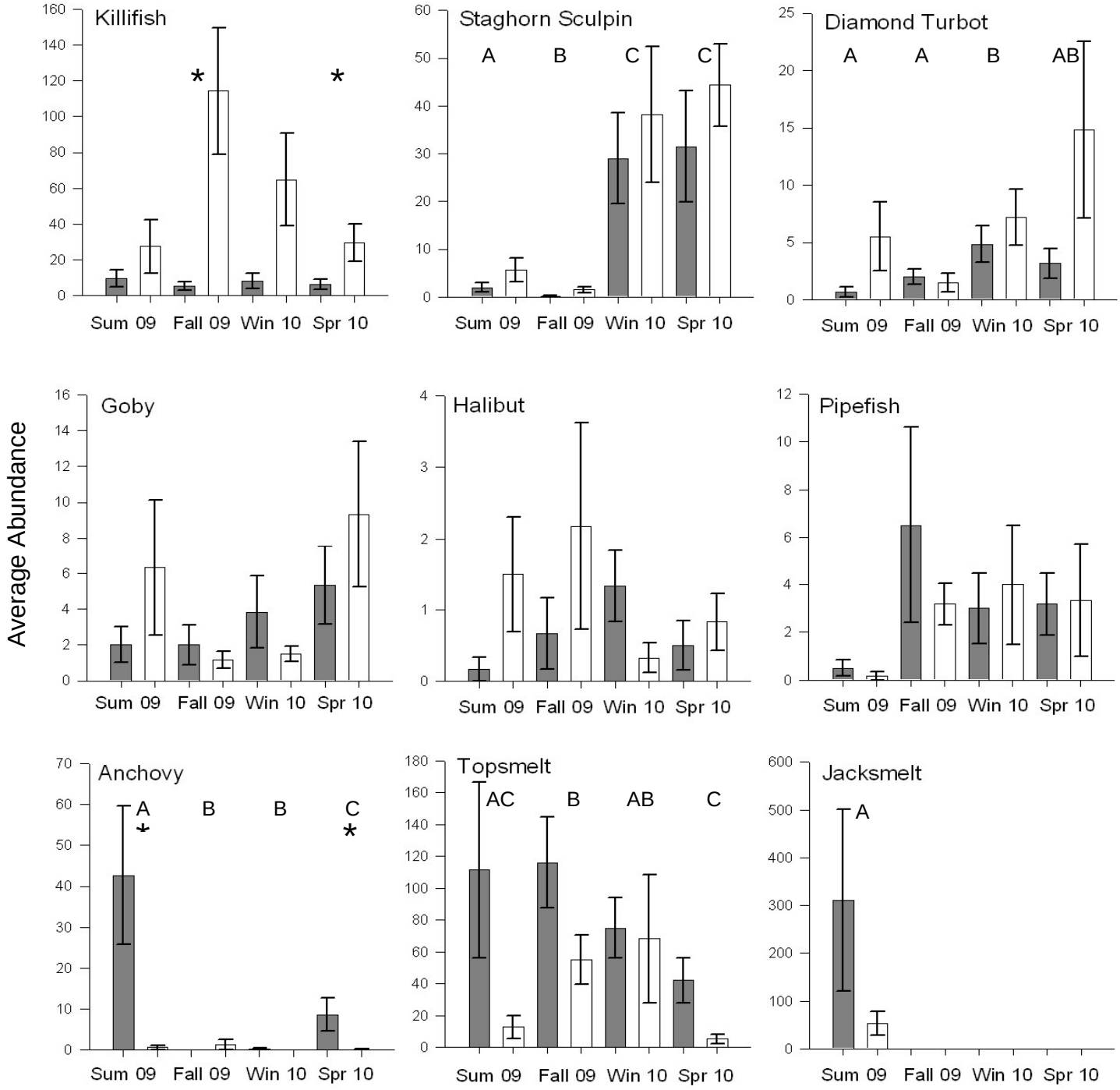
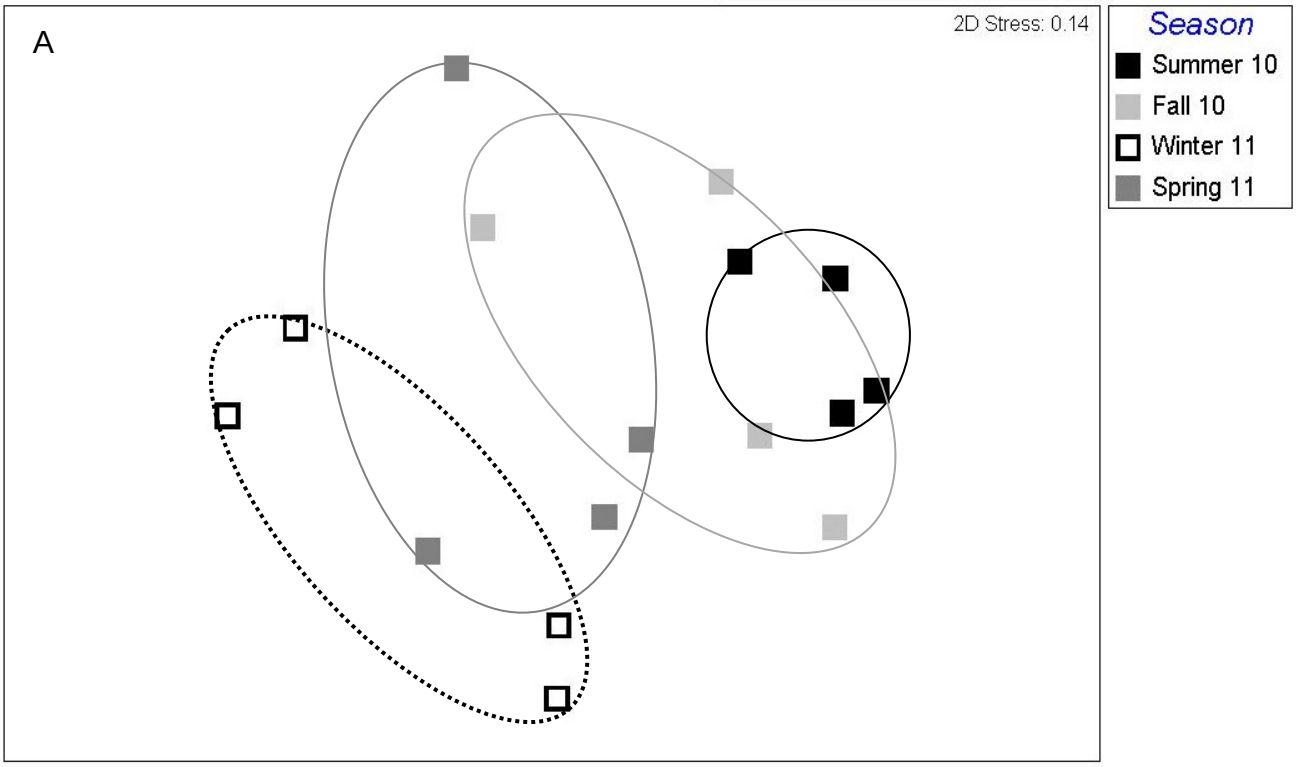


Figure 8. Non-metric multidimensional scaling (MDS) ordination of fish assemblages, based on log(*x*+1) transformed abundances from the 16 samples collected in Year 2, by season (A) marsh within season (B). Ellipses drawn on graphs illustrate seasons. There were too few permutable units to test for differences between marshes by season (details in text).



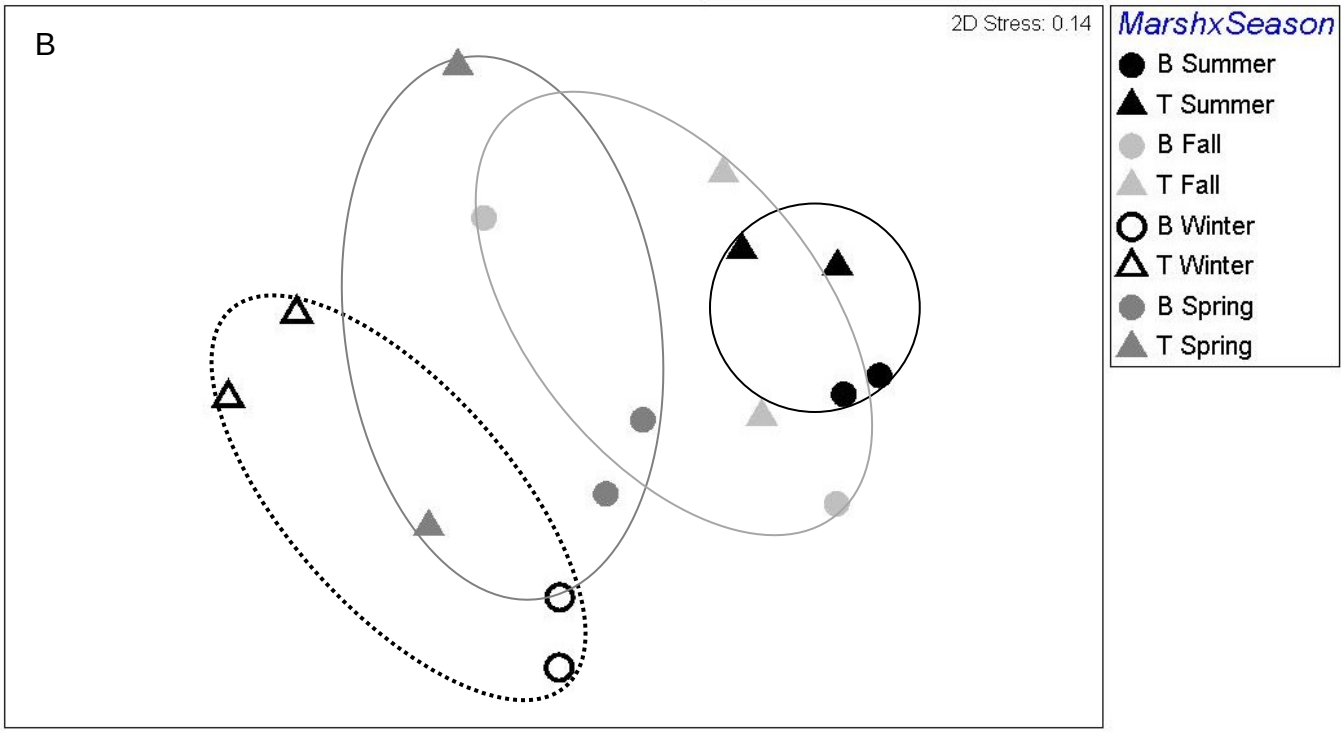


Figure 9. Canonical analysis of principal coordinates (CAP) ordination of fish assemblages, based on log(x+1) transformed abundances from the 16 samples collected in Year 2. Species identified in the SIMPER analysis as contributing at least 5% to the dissimilarity between marshes are indicated, with vector length representing the strength of correlations of each species with the CAP axes (unit circle corresponds to $r = 1$).

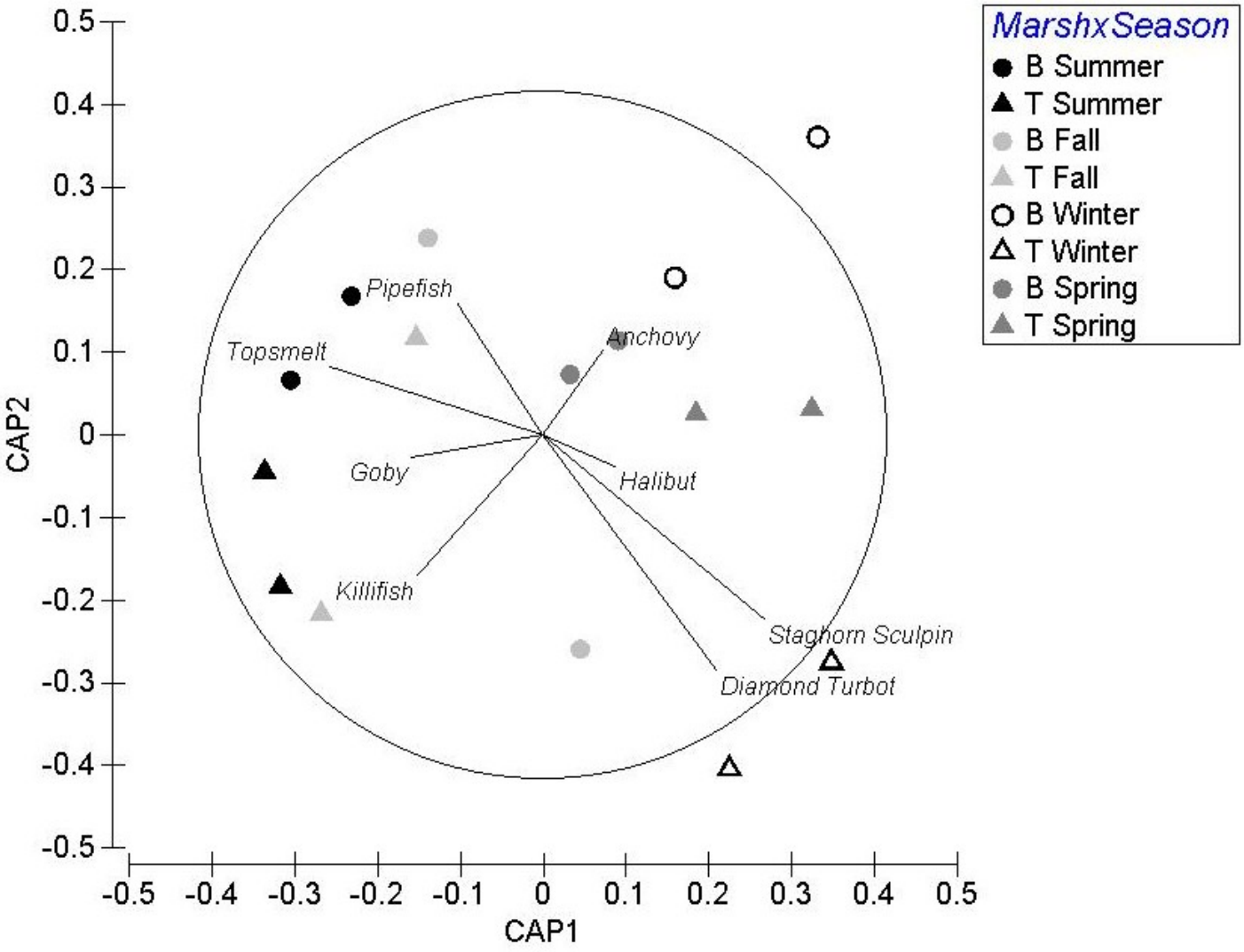


Figure 10. Average (± 1 SE) abundances for eight fish species identified in the SIMPER analysis of Year 2 between marshes by season. Different letters indicate statistically significant differences among seasons while asterisks indicate significant differences between marshes within season (PERMANOVA, $p < 0.05$). Gray bars = Brookhurst Marsh; White bars = Talbert Marsh. (Sample size in each marsh: $n = 8$).

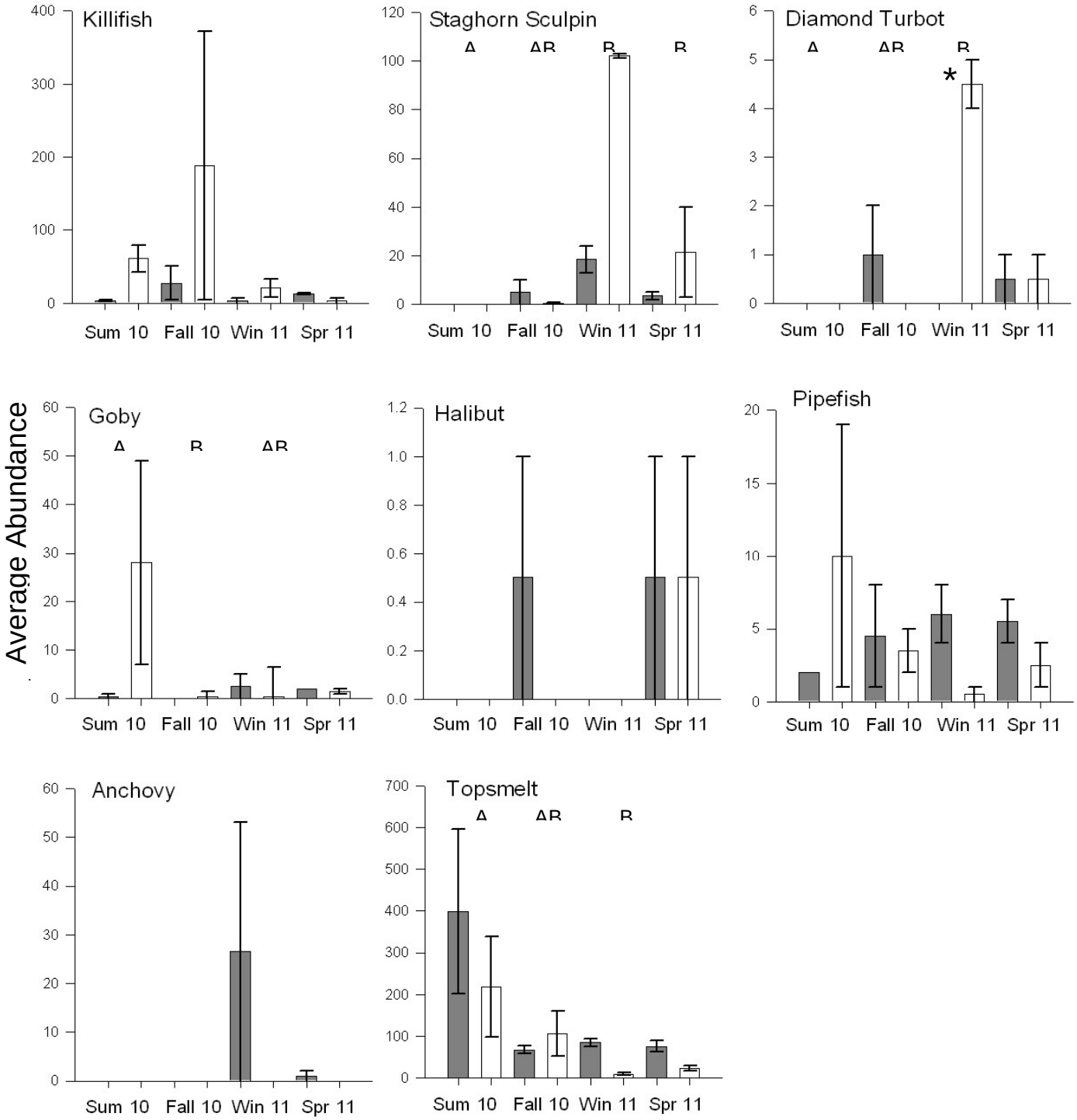


Figure 11. Average seasonal water temperature gradient inside the HBW from December 2009 – December 2010. Background color represents the average water temperature profiles for each season.

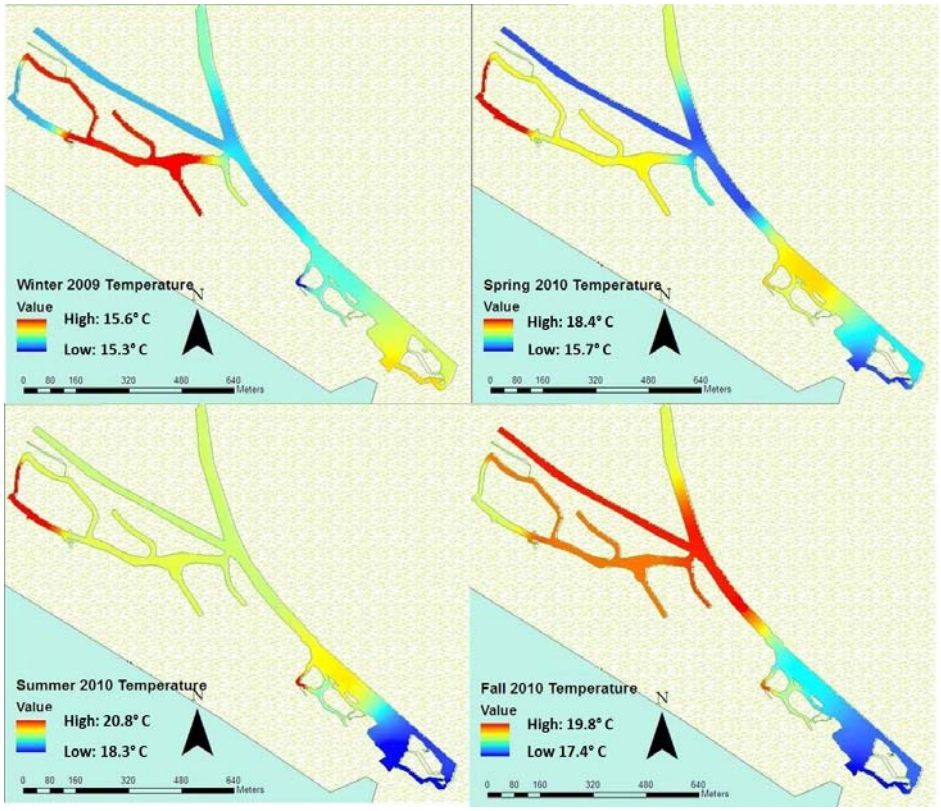


Figure 12. Water temperature profile of the HBW during the 2010 study period. Dark lines indicate average daily temperatures for the HBW and the ocean. Grey lines indicate the absolute maximum and minimum daily temperatures. Average ocean surface temperatures were recorded at NOAA buoy 46230, Newport Beach, CA.

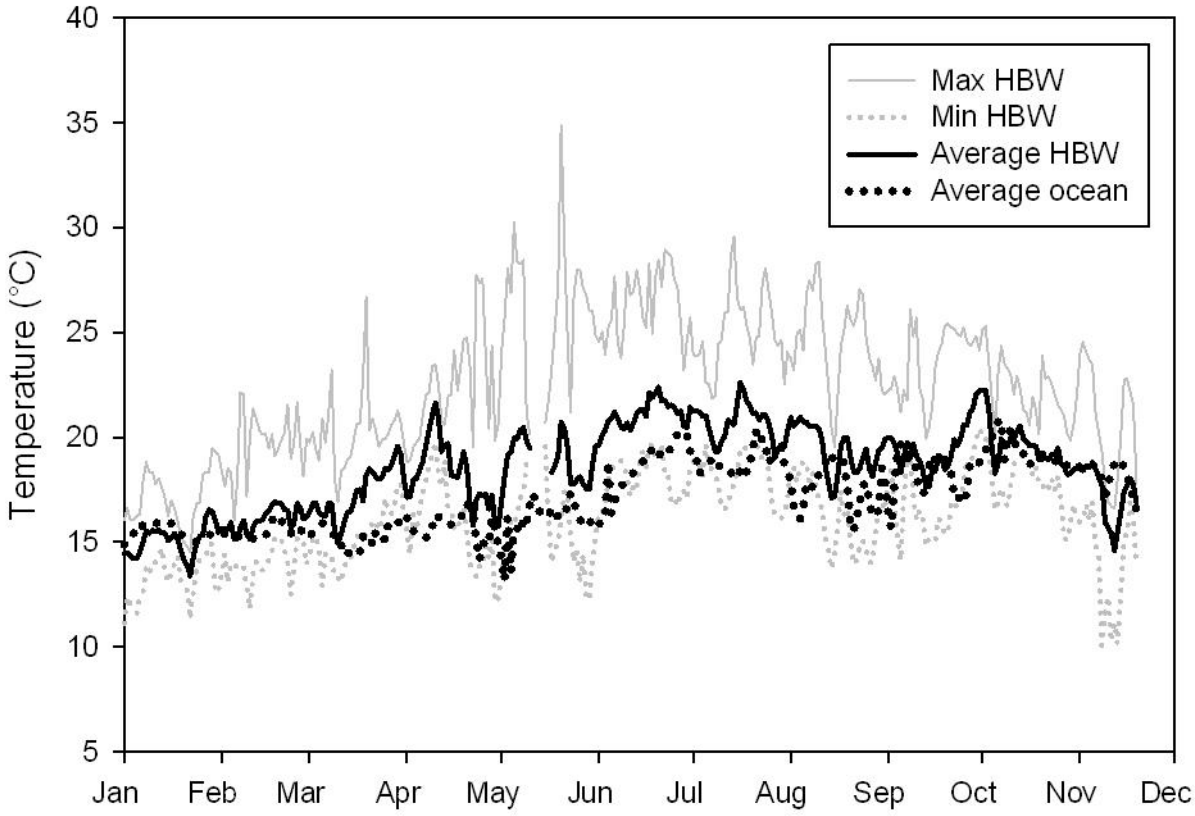


Figure 13. Comparative clod card dissolution (w_2/w_1*100) in the various habitats of the HBW (mean ± SD, $n = 4$ at each site). All sites were significantly different from one another ($F_{7, 24} = 1{,}842.1$, $p < 0.001$). BC (Brookhurst-side Channel) indicates Tidal Channel locations north of the bisecting roadway, TC (Talbert-side Channel) indicates Tidal Channel locations south of bridge.

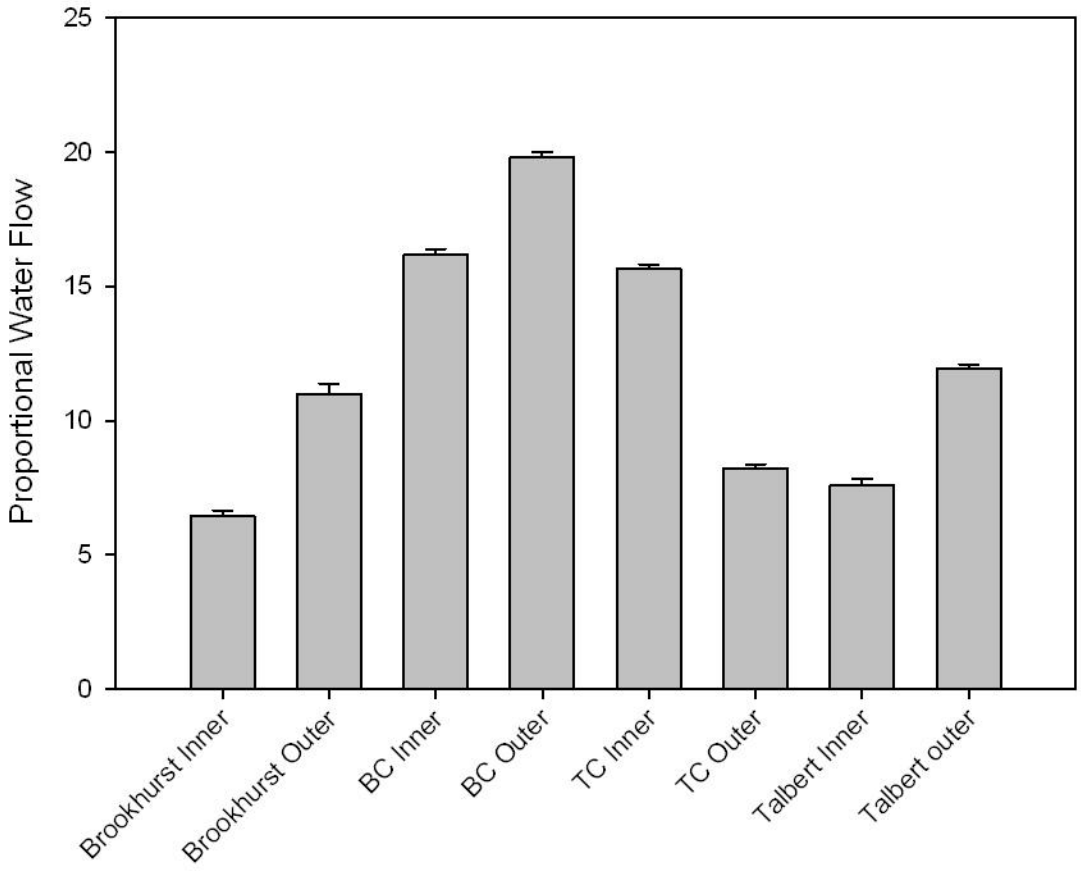


Figure 14. CPUE for hook and line surveys among all sites of the HBW. Halibut were only caught by hook and line within the Tidal Channel (*n* = 5 halibut).

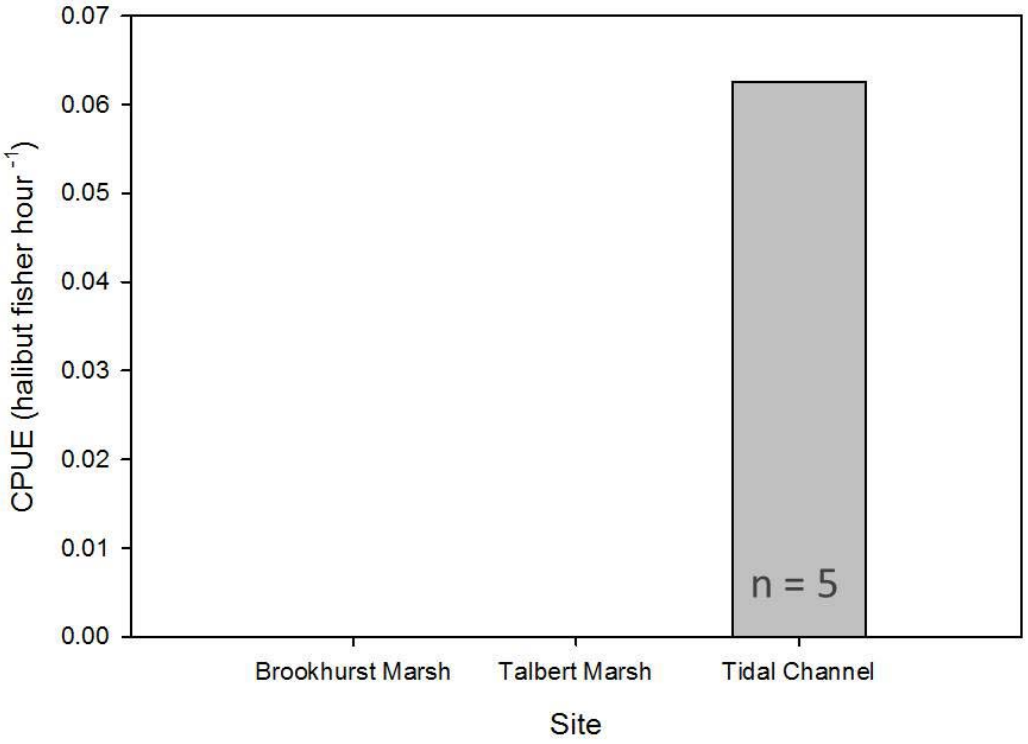


Figure 15. Proportion of all halibut caught per size class by sampling method. Bars represent proportion of catch per size class; colors correspond to sampling method. Total number of halibut caught per size class indicated by line graph and secondary y-axis.

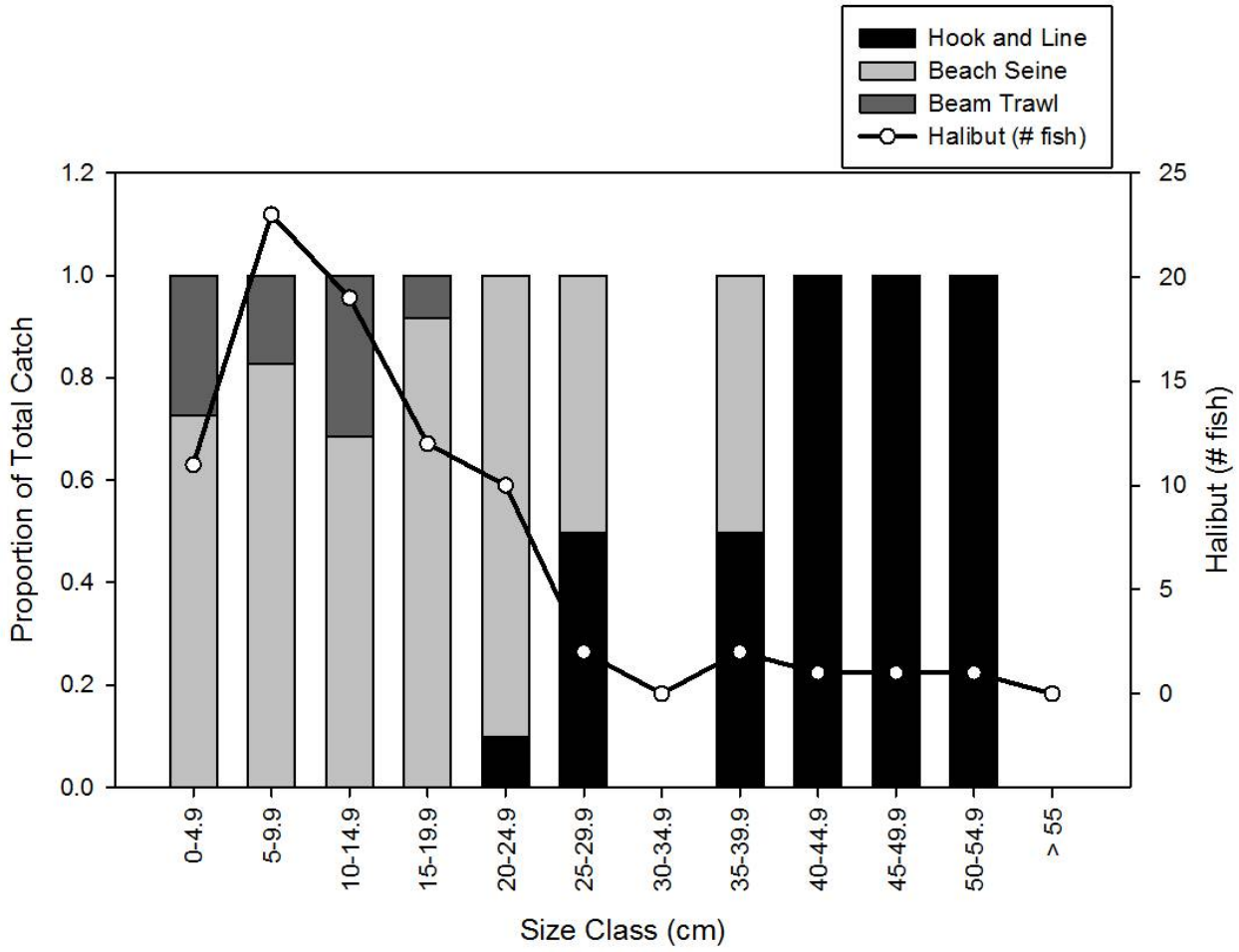


Figure 16. Size (TL) of halibut caught per site in the HBW during the study period. Boxes represent the 25th and 75th percentiles, whiskers represent the 10th and 90th percentiles. Median TL is indicated by the horizontal line inside grey boxes. Black dots indicate outliers.

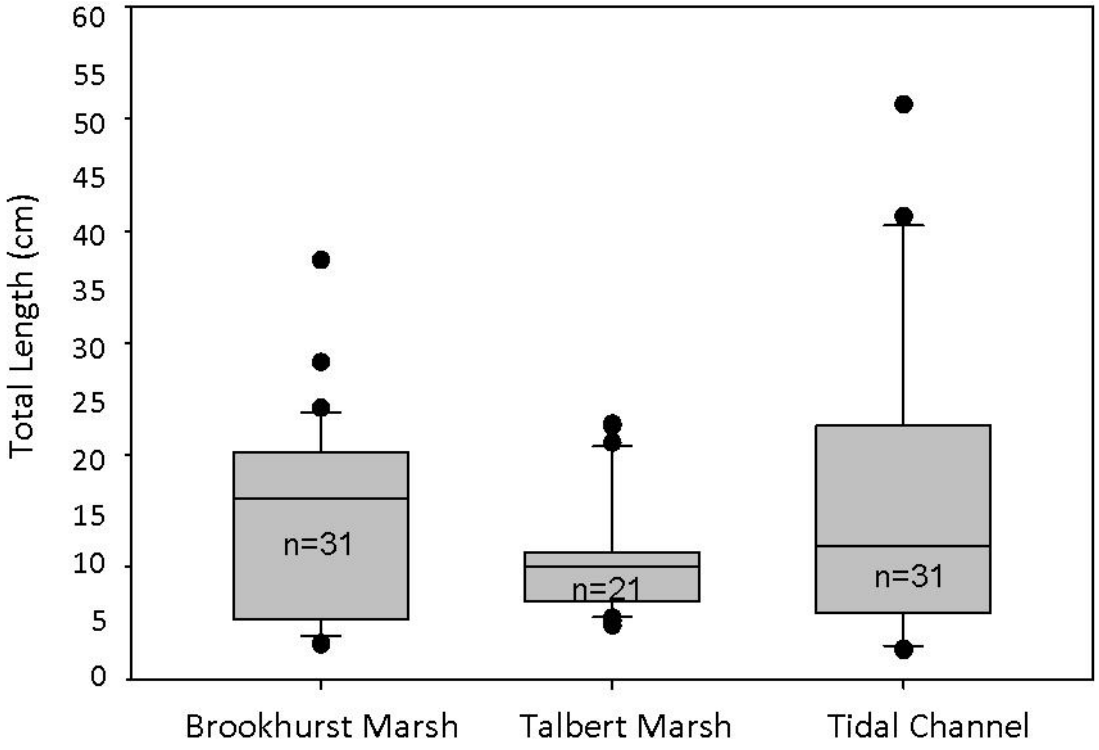


Figure 17. Number of halibut by size class caught among all locations in the HBW during population surveys for all methods. Bar color indicates location of capture.

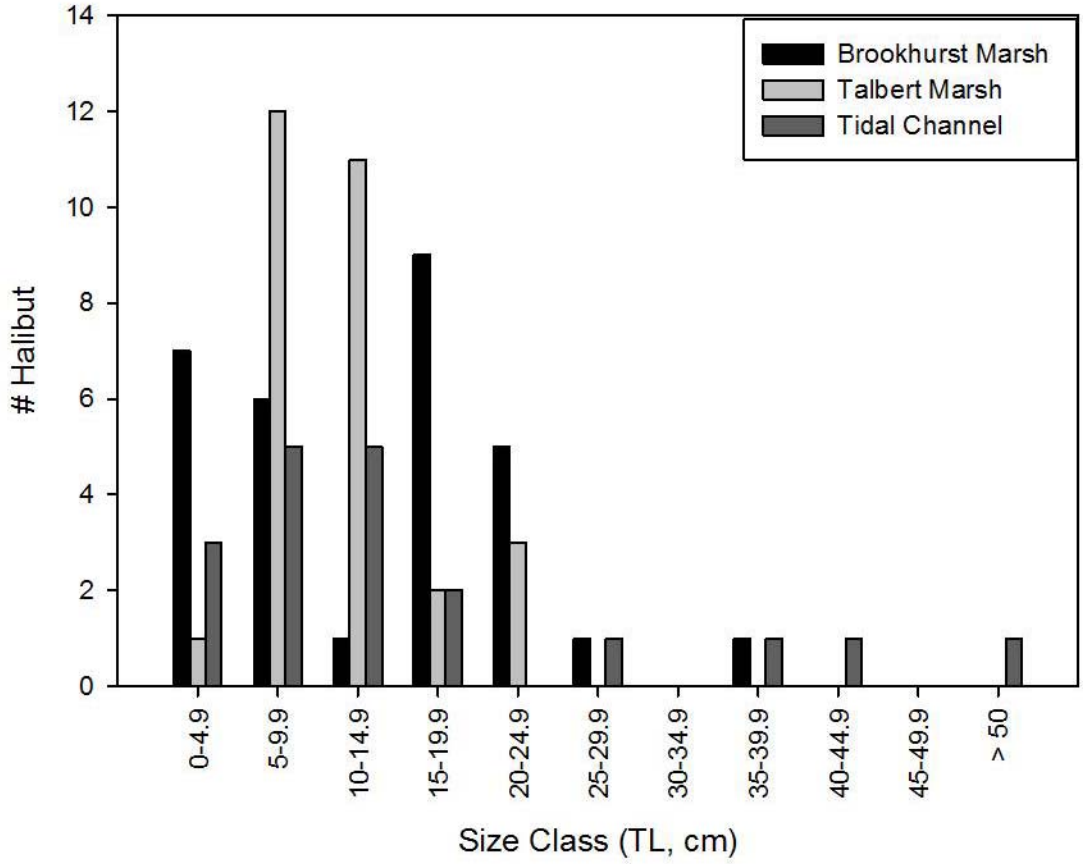


Figure 18. Euclidean Distance Analysis (EDA) ratio (distance between observed fish positions and each habitat type divided by the distance between randomly generated positions and each habitat type) for each individual and population mean to the benthic types within the HBW. Values = 1 indicate habitat use is proportional to availability, values < 1 suggest habitat association; and values > 1 suggest habitat avoidance. Bar colors represent benthic habitat types.

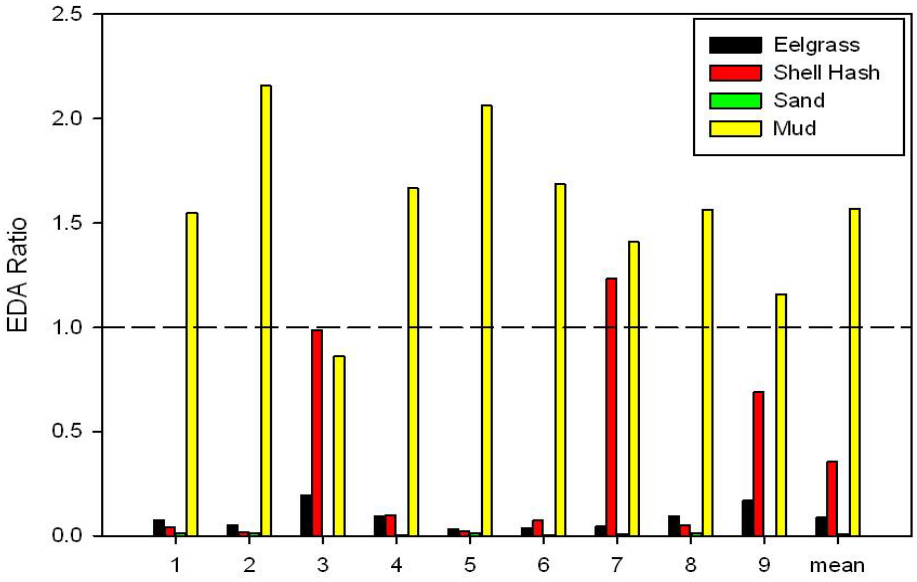


Figure 19. Mean ± S.E. (A) distance traveled (meters) while active and (B) ROM for transplanted and non-transplanted individuals under different time periods. Differing letters indicate non-significance among treatments at the 0.05 level with Tukey's HSD test.

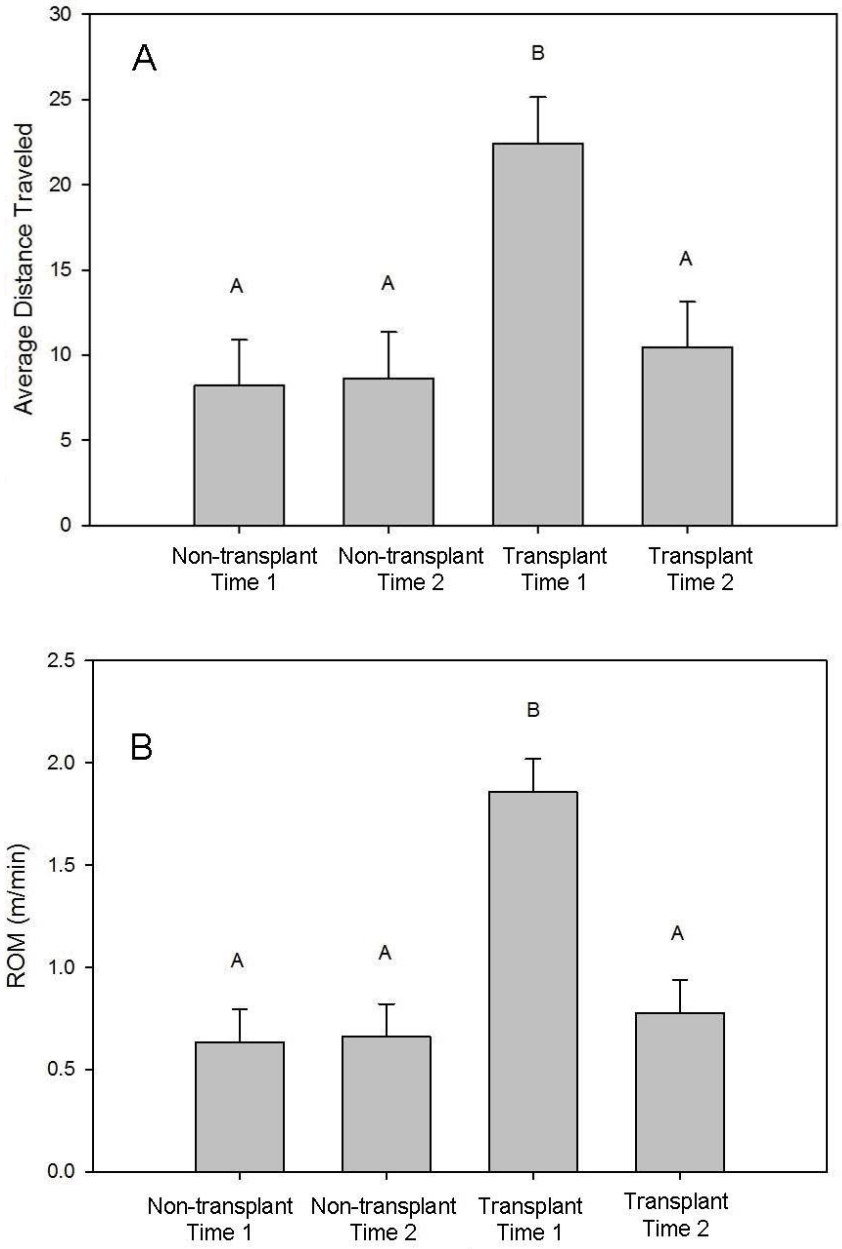


Figure 20. Proportion of total detections by VR2W receivers during passive acoustic monitoring. Size of bubble indicates relative proportion of detections of tagged halibut during the observation period (May 2010 – June 2011).

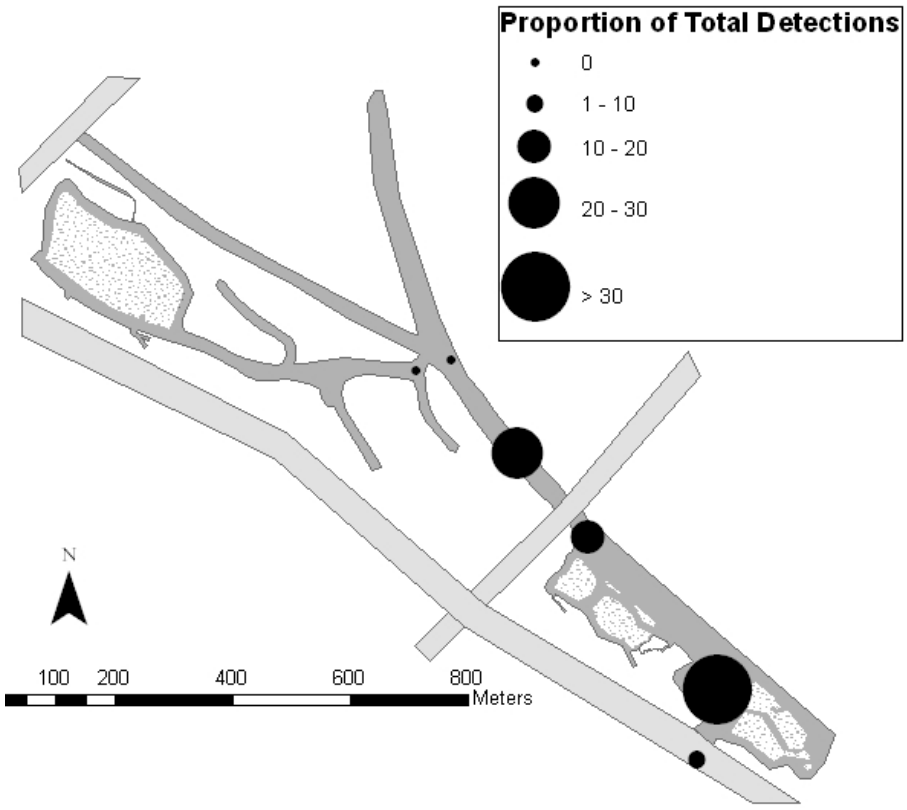


Figure 21. Daily detection plot of tagged halibut in the HBW. Individuals are identified on the *y*-axis by their transmitter number. Colors of each bar correspond to the receiver at which the individual was detected that day. Asterisks indicate individuals that emigrated from the HBW. Light gray bar indicates highest water temperatures, hashed bar indicates period of heavy rainfall.

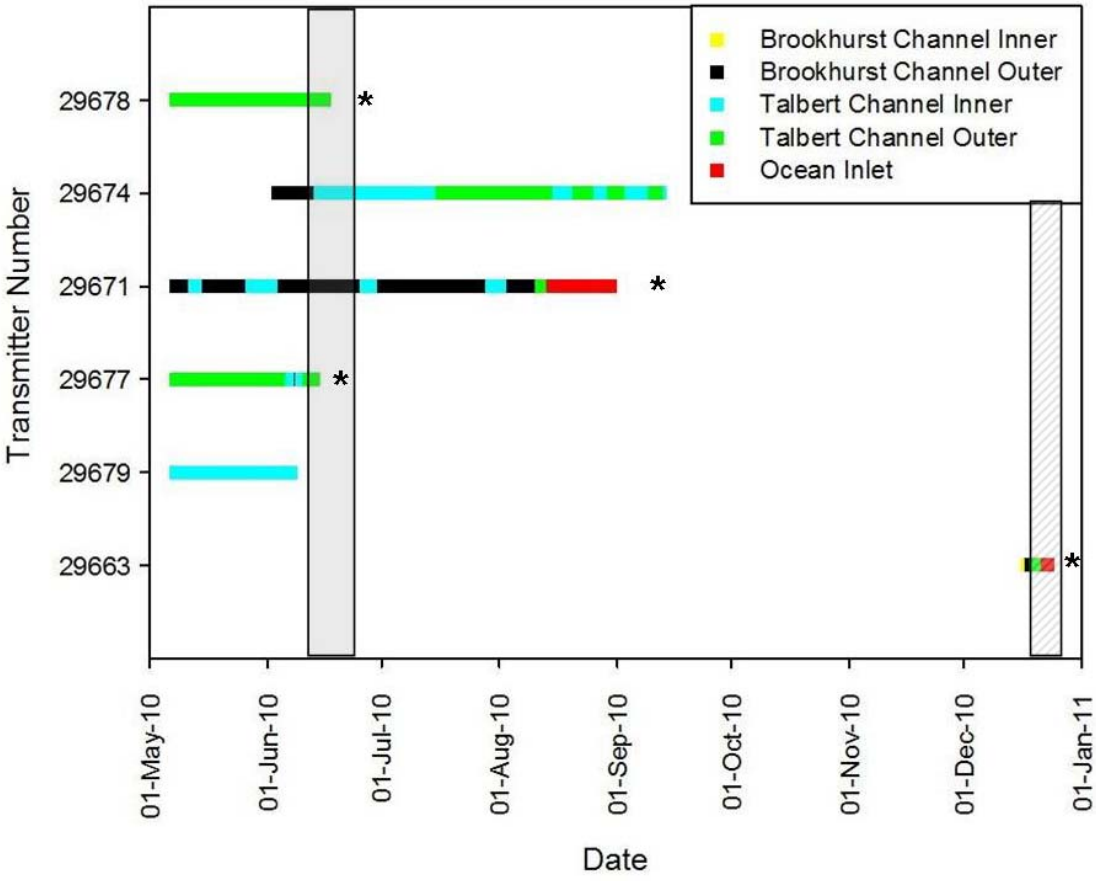


Figure 22. Home range, observed locations, and capture locations for non-transplanted halibut. Light gray dots indicate all observed locations for each individual. Stars indicate capture/release location. Dark gray polygons indicate total home range during observation. Home range size indicated on each panel.

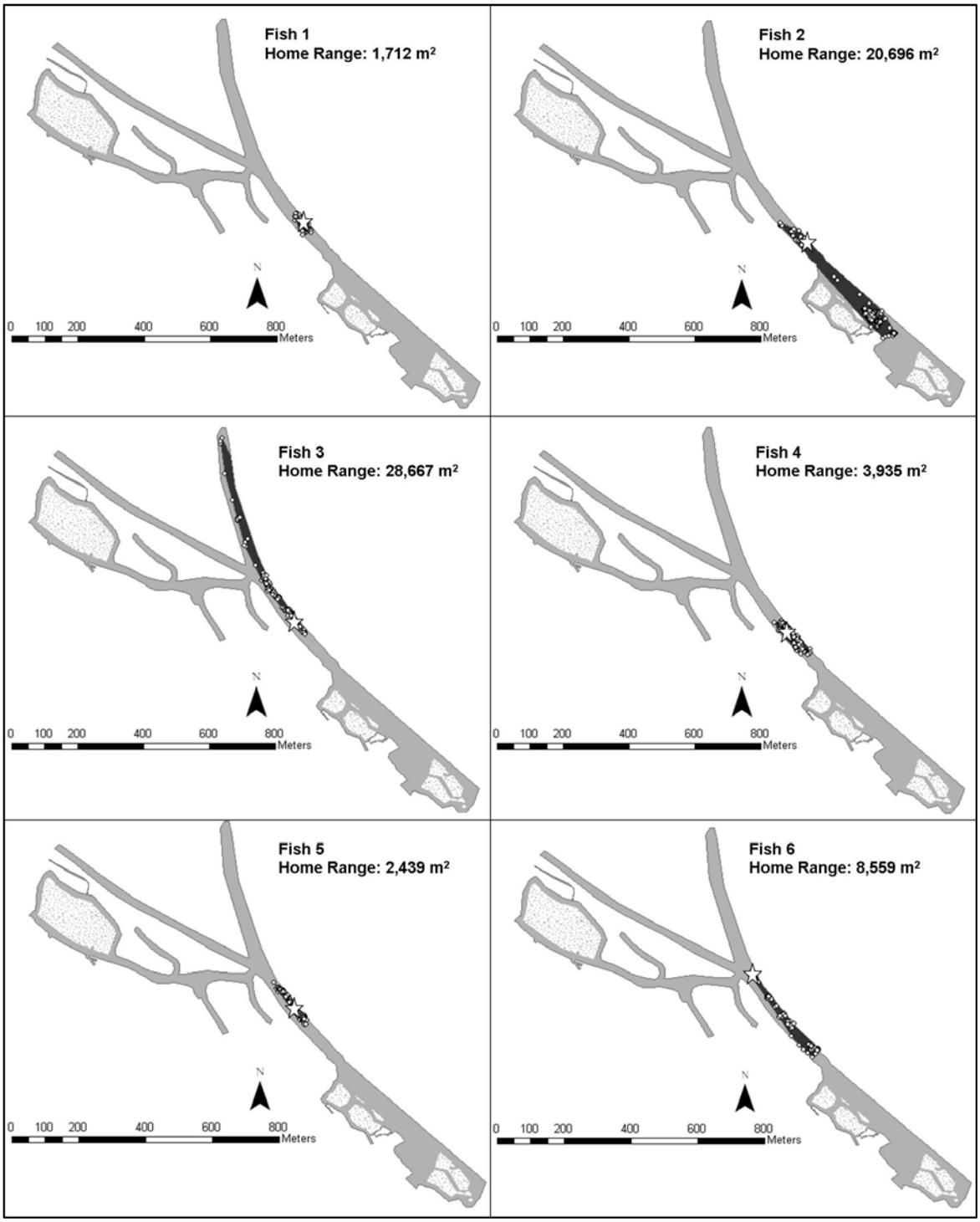


Figure 23. Home range, observed locations, and capture locations for transplanted halibut. Light gray dots indicate all observed locations for each individual. Stars indicate capture location. Dark gray polygons indicate total home range during observation. Home range size indicated on each panel.

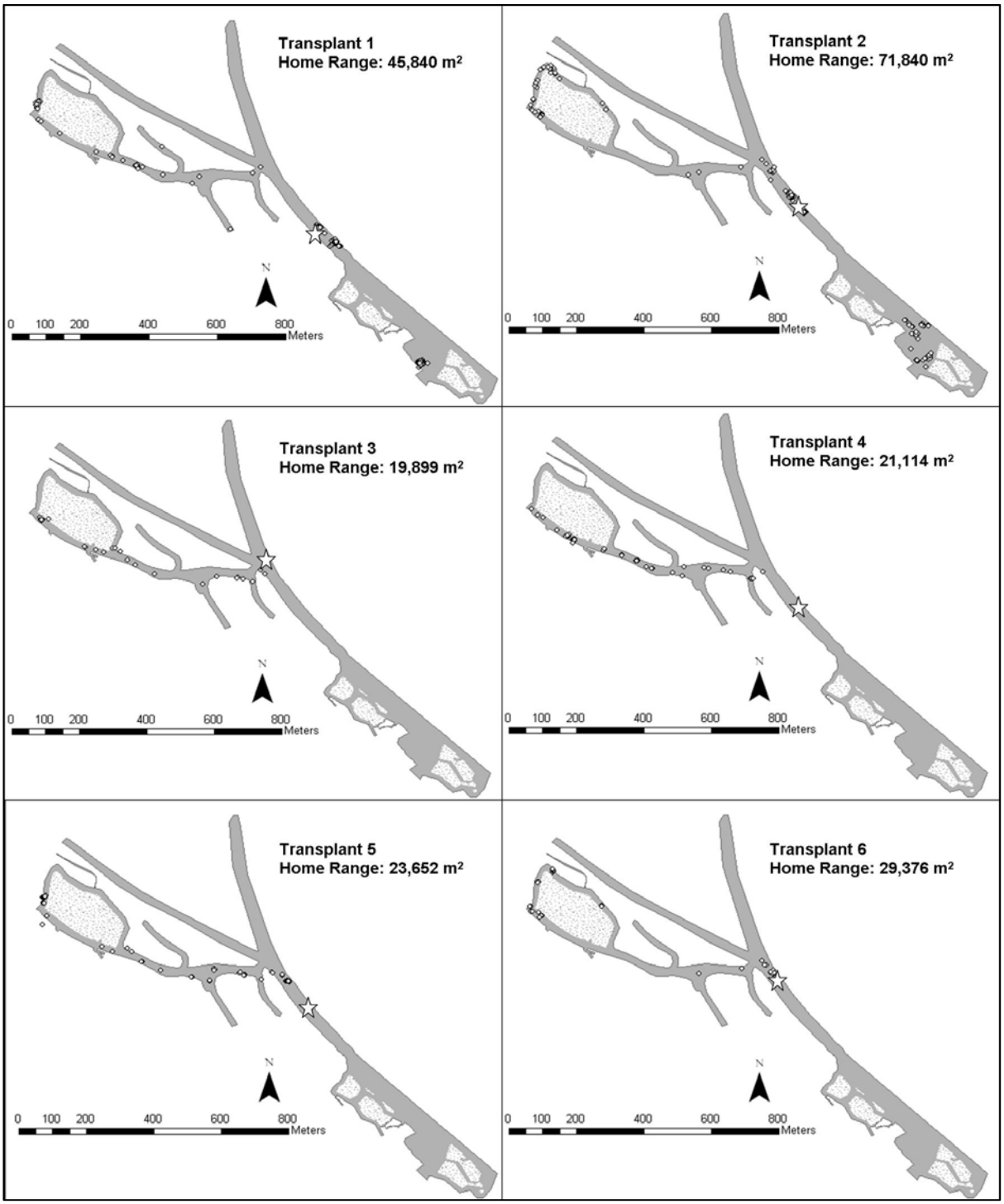


Figure 24. Frequency of diet items or empty stomachs in wild-caught halibut, by habitat. "Unknown" samples were unidentifiable during stomach content analysis. Sample size above each column represents the number of halibut stomachs examined from each habitat.

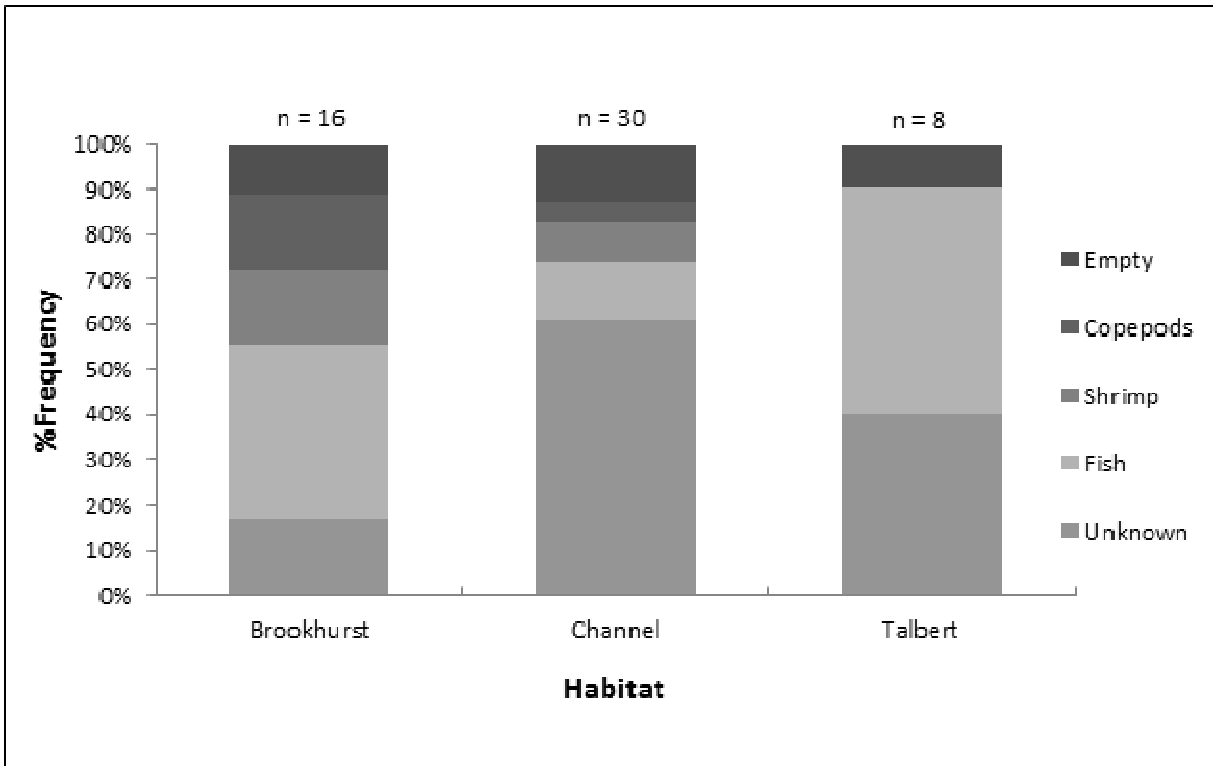


Figure 25. Dual isotope plot of $\delta^{13}C$ versus $\delta^{15}N$ values for diet items removed from the stomachs of wild-caught halibut across habitats, by prey type. "Unknown" samples were unidentifiable during stomach content analysis.

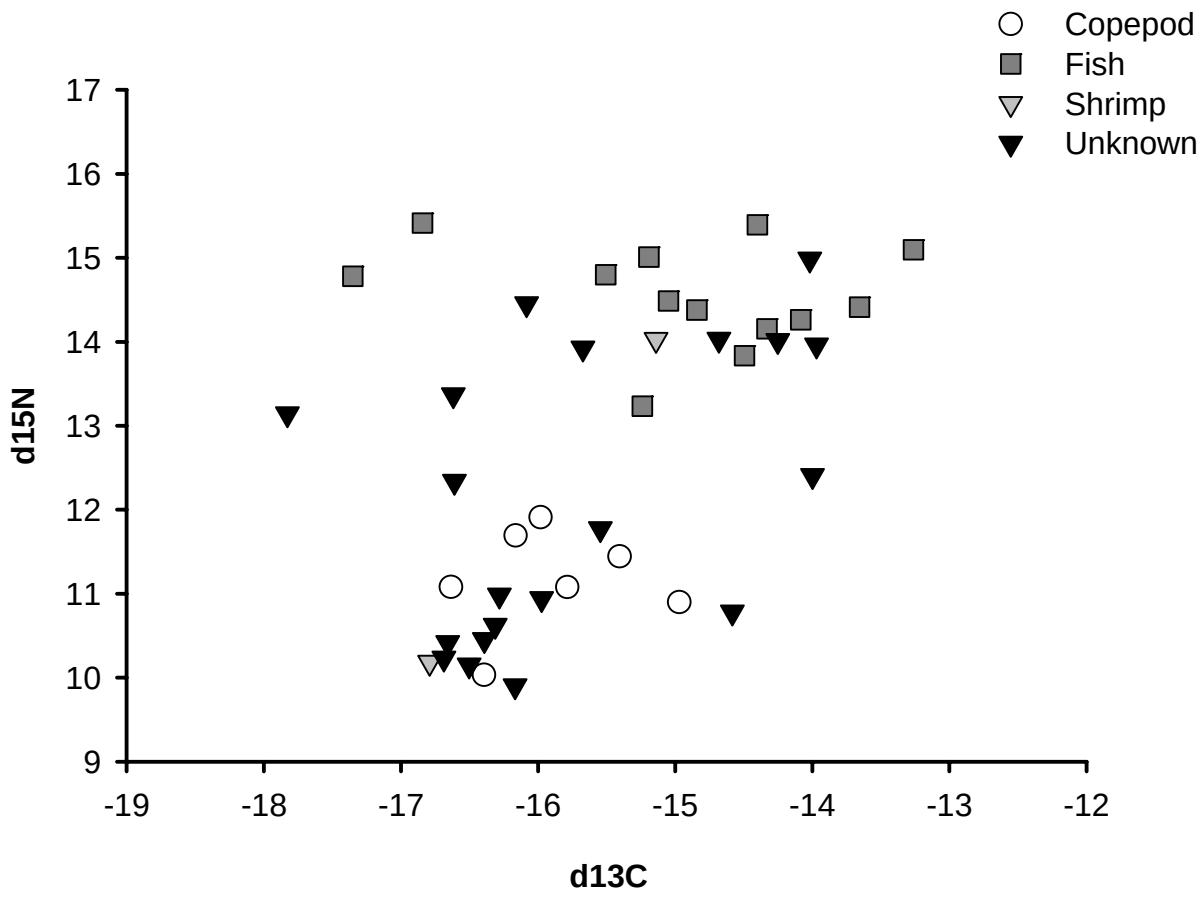


Figure 26. Dual isotope plot of $\delta^{13}C$ versus $\delta^{15}N$ values for diet items of wild-caught halibut across habitats, by prey type. "Unknown" samples (Fig. 25) were classified based on isotopic signatures using the "Add New Samples" option in a Canonical Analysis of Principal Coordinates (CAP) analysis done with the PERMANOVA+ add-on to the PRIMER statistical software package. Ellipses drawn on graph illustrate groups that were statistically significantly different from one another (ANOSIM).

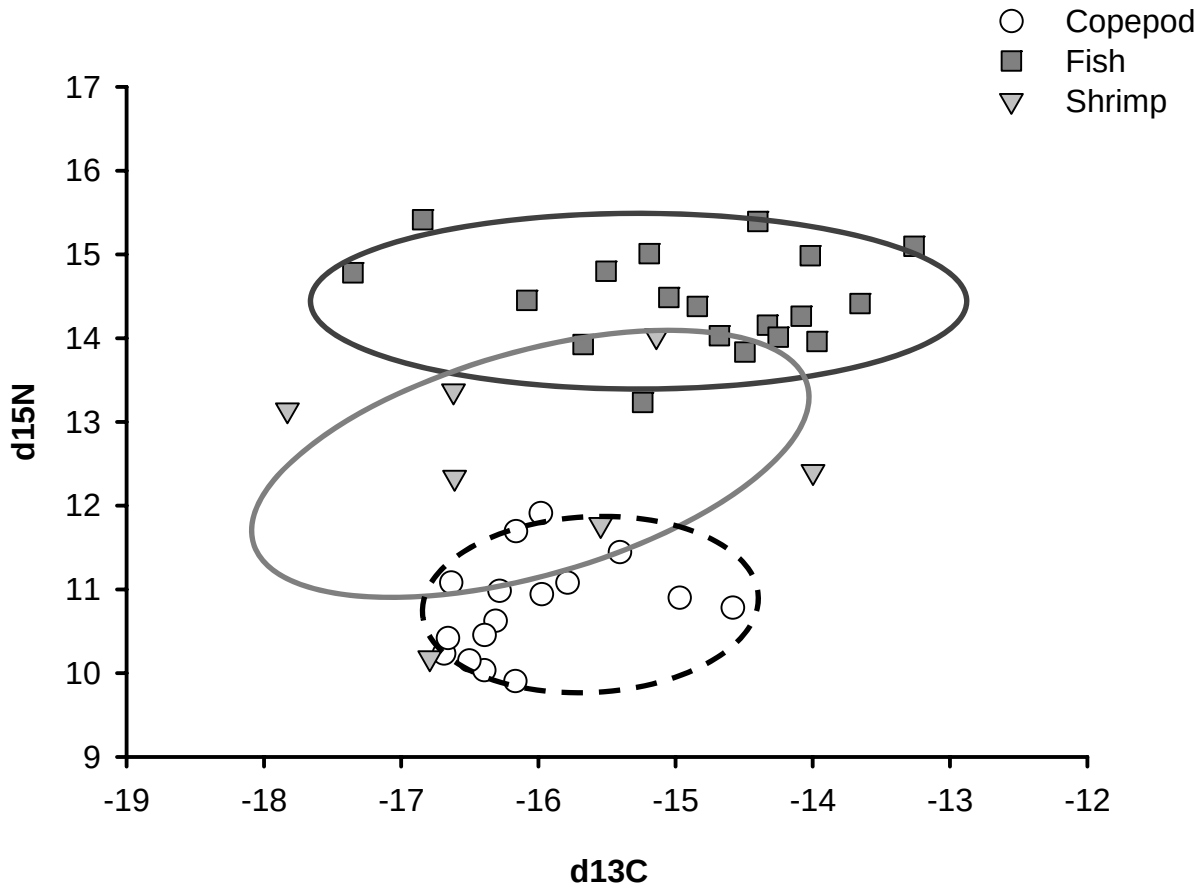


Figure 27. Frequency of diet items or empty stomachs in wild-caught halibut, by habitat. "Unknown" samples were classified based on isotopic signatures using the "Add New Samples" option in a Canonical Analysis of Principal Coordinates (CAP) analysis done with the PERMANOVA+ add-on to the PRIMER statistical software package (Fig. 26). Sample size above each column represents the number of halibut stomachs examined from each habitat.

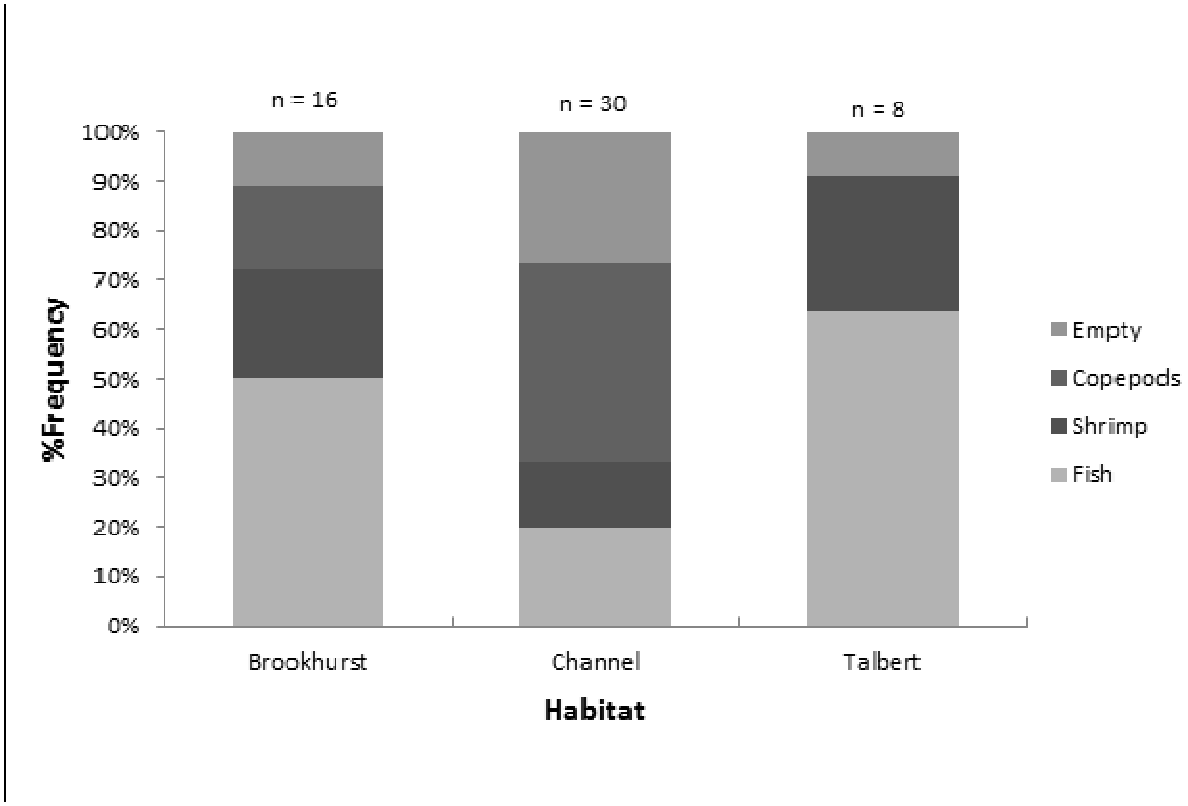


Figure 28. Dual isotope plot of $\delta^{13}C$ versus $\delta^{15}N$ values for muscle tissue of wild-caught halibut, by habitat. Fish collected from the inlet (illustrated by the ellipse drawn on graph) were statistically significantly different from all other habitats, which were not different from one another (ANOSIM).

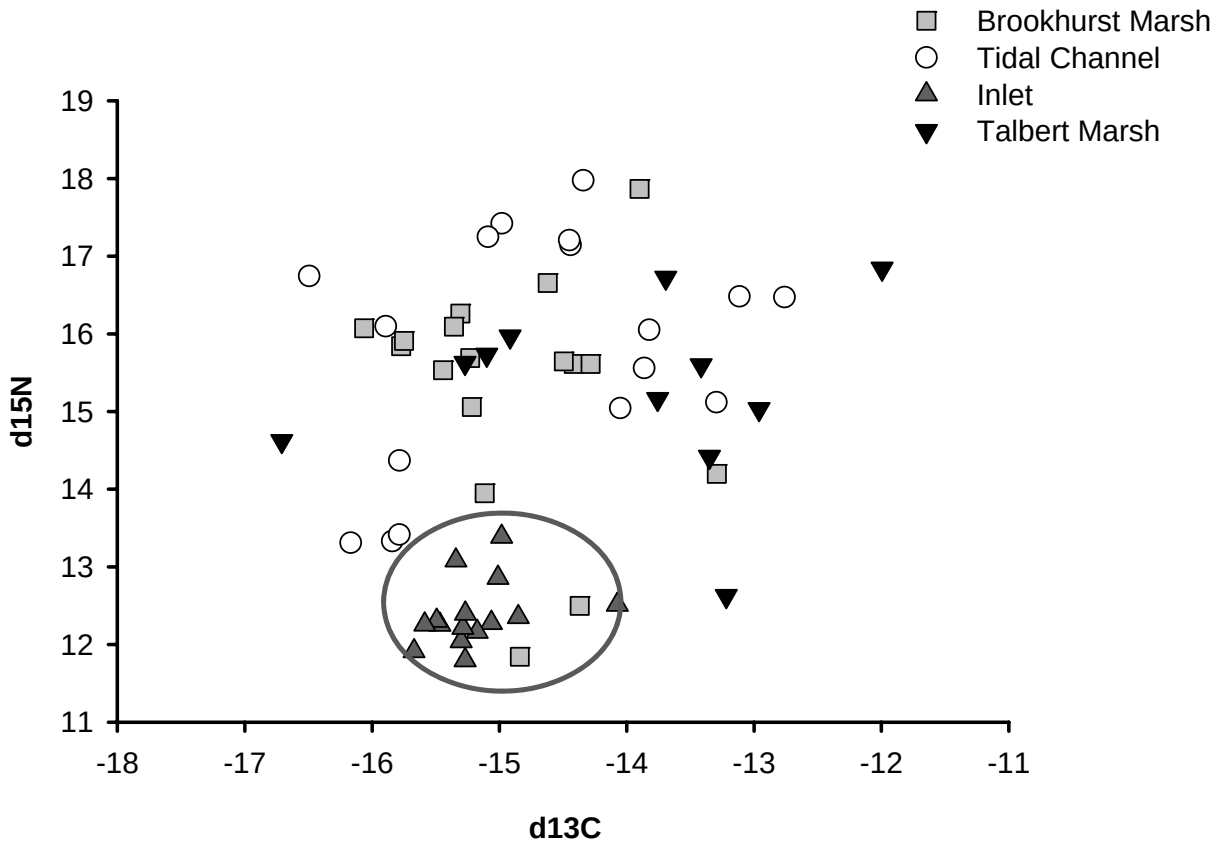


Figure 29. Dual isotope plot of $\delta^{13}C$ versus $\delta^{15}N$ values for muscle tissue of wild-caught halibut across habitats, by size class. Ellipses drawn on graph illustrate groups that were statistically significantly different from one another (ANOSIM).

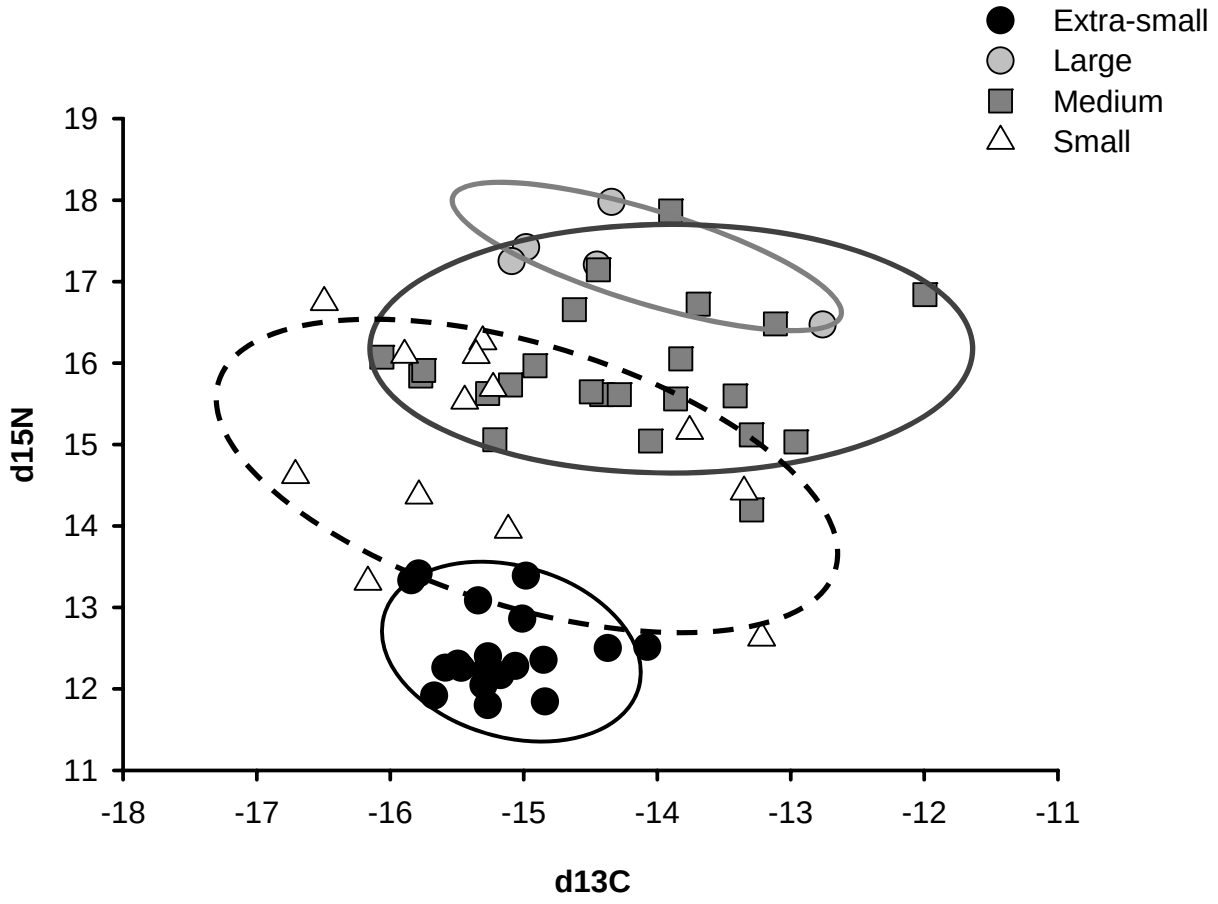


Figure 30. Frequency of diet items or empty stomachs in wild-caught halibut in the small size class, by habitat. "Unknown" samples were classified based on isotopic signatures using the "Add New Samples" option in a Canonical Analysis of Principal Coordinates (CAP) analysis done with the PERMANOVA+ add-on to the PRIMER statistical software package. Sample size above each column represents the number of halibut stomachs examined from each habitat.

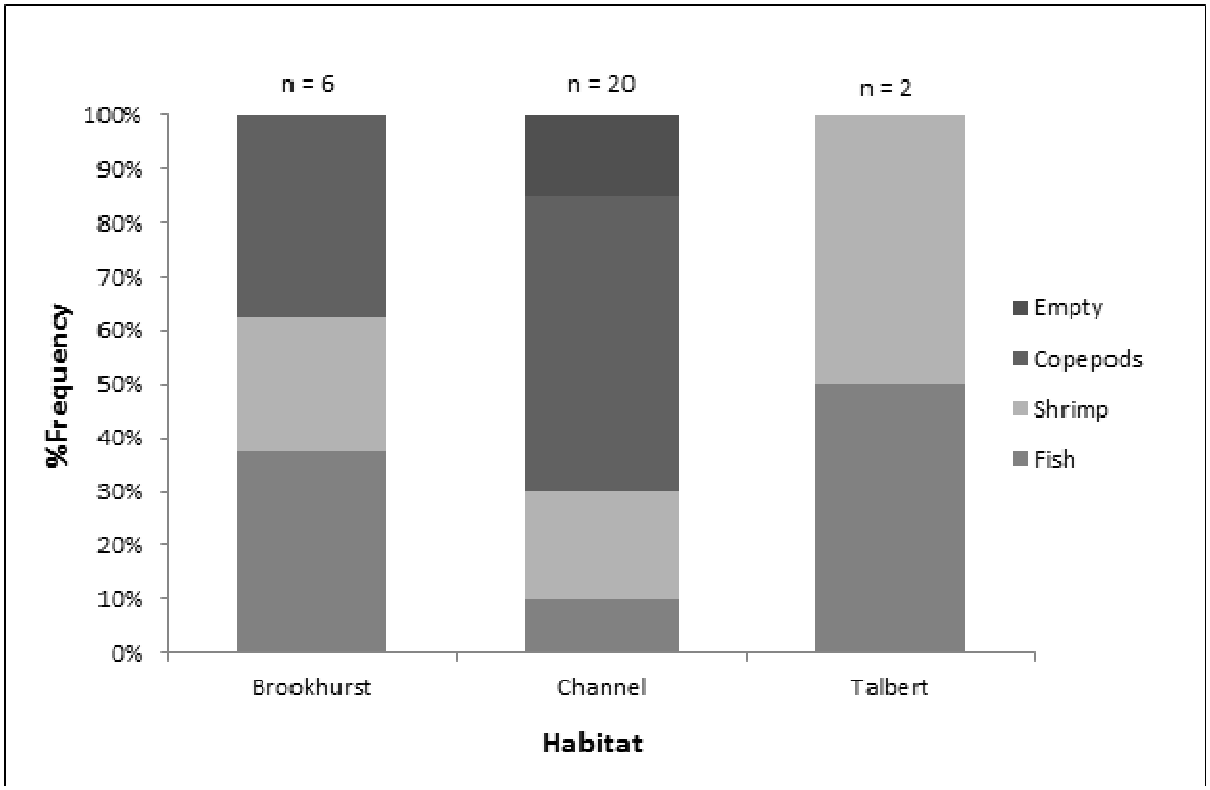


Figure 31. Dual isotope plot of $\delta^{13}C$ versus $\delta^{15}N$ values for muscle tissue of wild-caught halibut in the small size class, by habitat. Ellipses drawn on graph illustrate groups that were statistically significantly different from one another (ANOSIM).

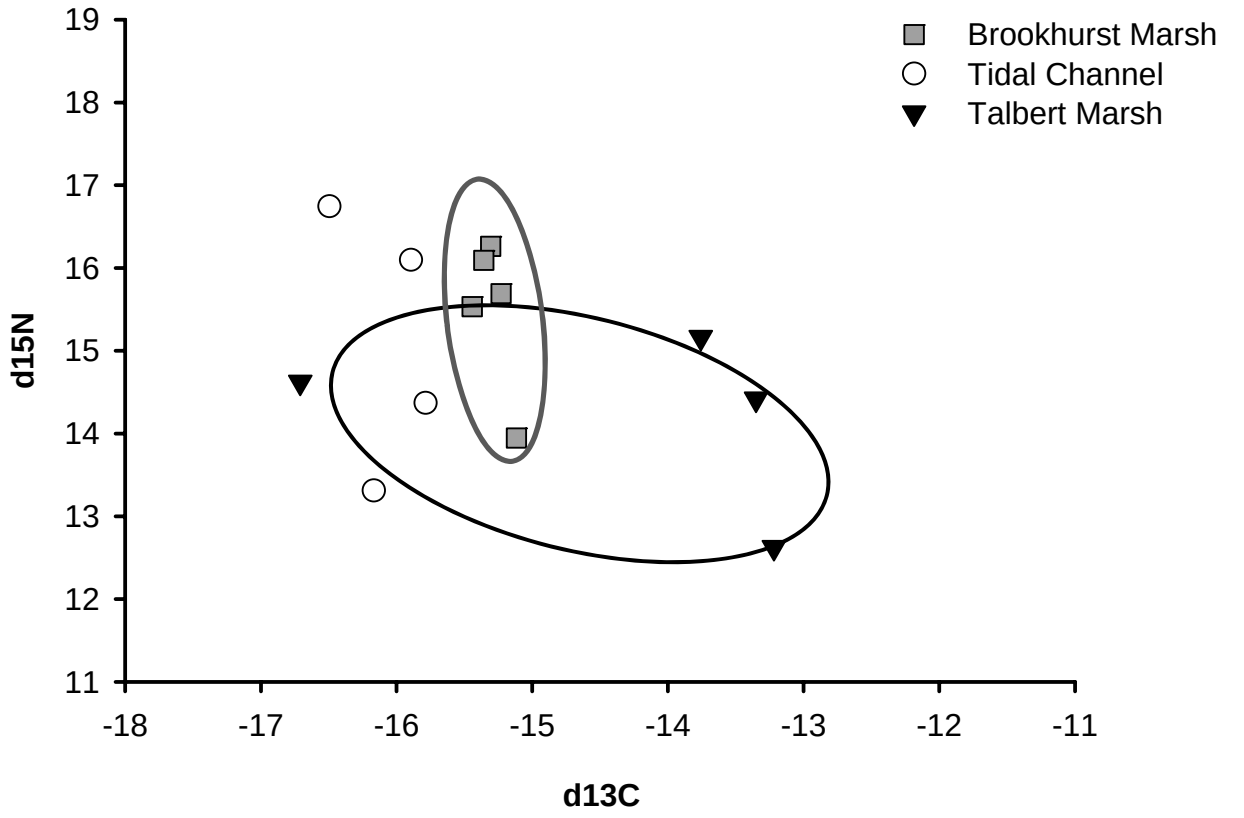


Figure 32. Frequency of diet items or empty stomachs in wild-caught halibut in the medium size class, by habitat. "Unknown" samples were classified based on isotopic signatures using the "Add New Samples" option in a Canonical Analysis of Principal Coordinates (CAP) analysis done with the PERMANOVA+ add-on to the PRIMER statistical software package. Sample size above each column represents the number of halibut stomachs examined from each habitat.

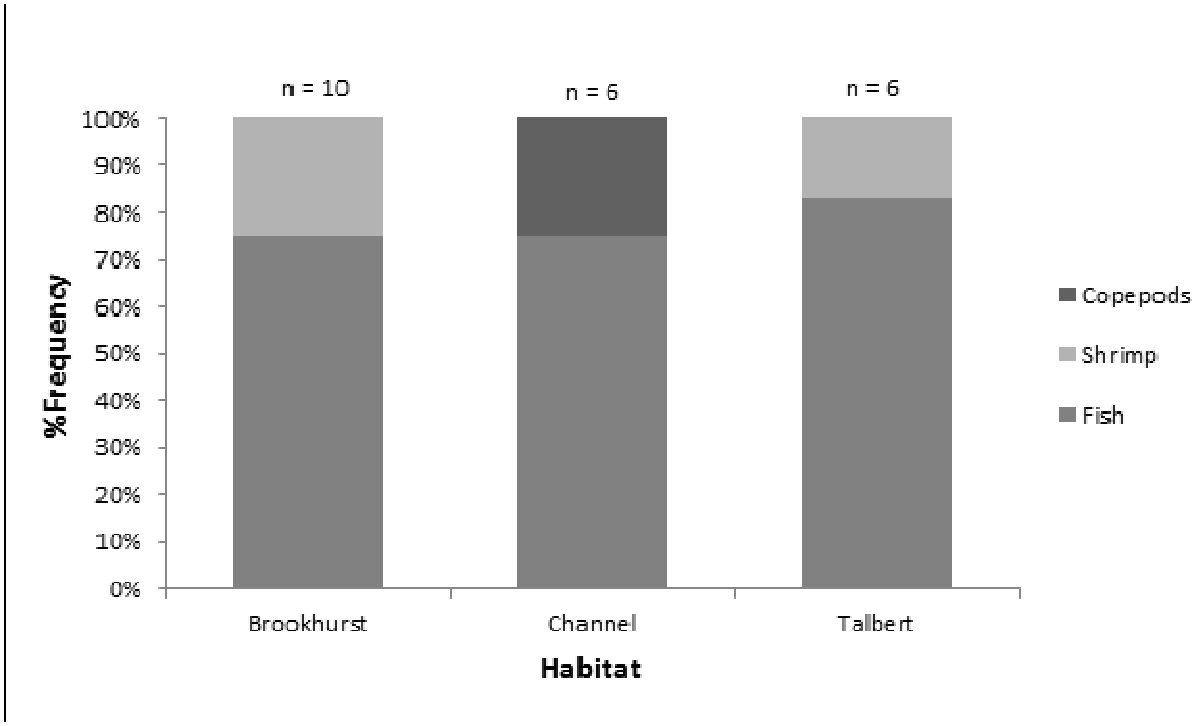


Figure 33. Dual isotope plot of $\delta^{13}C$ versus $\delta^{15}N$ values for muscle tissue of wild-caught halibut in the medium size class, by habitat. None of the groups were statistically significantly different from one another (ANOSIM).

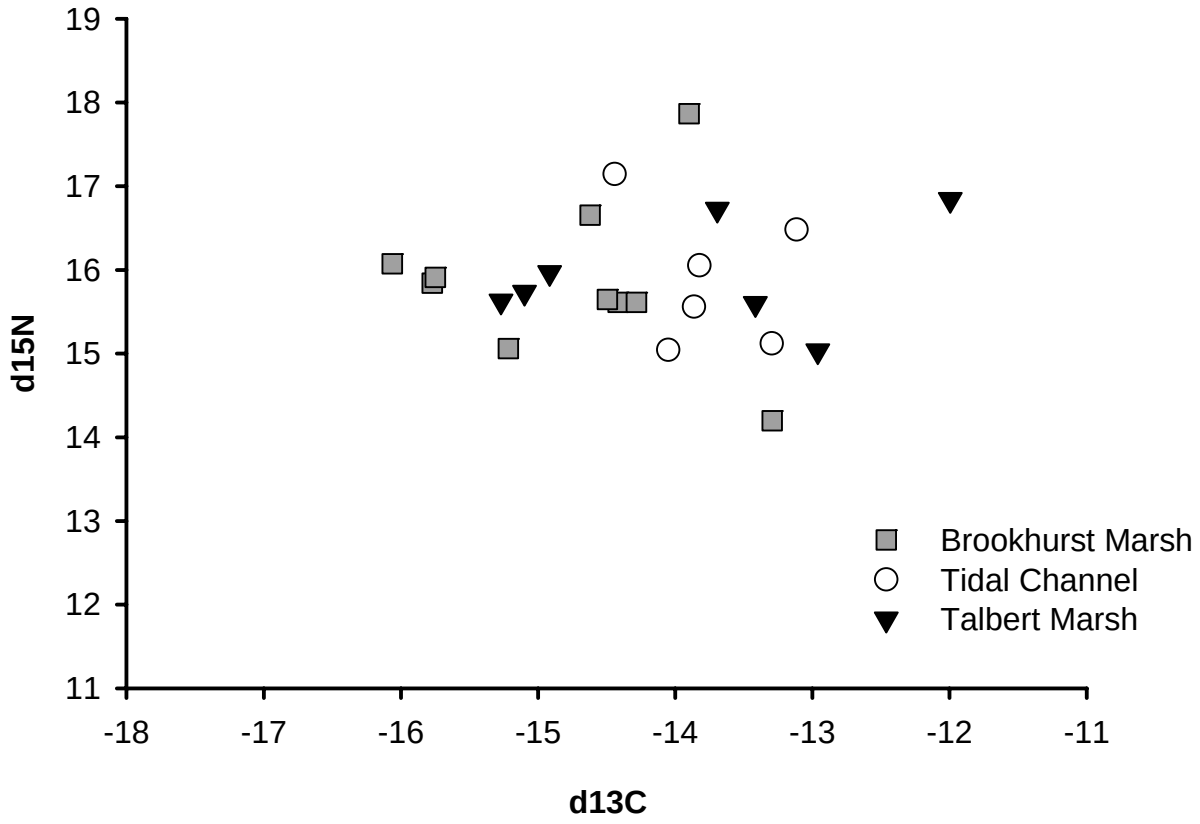


Figure 34. Average relative growth (mm mm^{-1} week^{-1}; ± 1 SE; n = 2 tanks per treatment, 5 fish per tank) of halibut in the lab experiment, by diet. Fish were sampled at 4, 6, 8, 10, and 12 weeks.

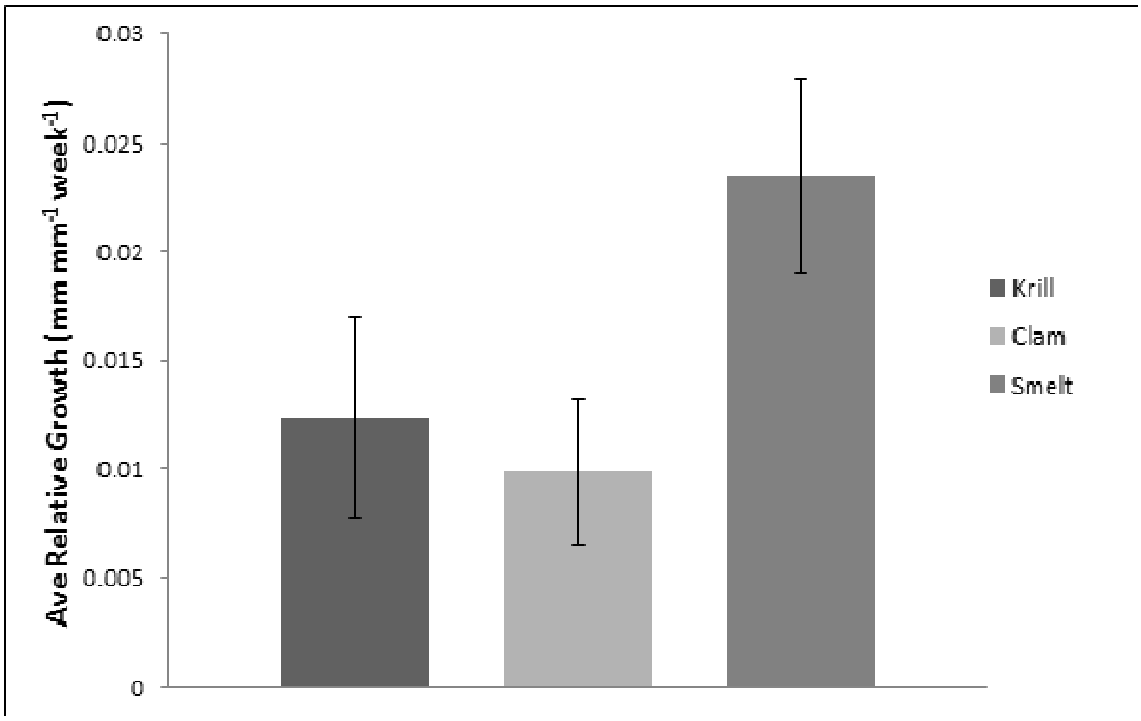


Figure 35. Dual isotope plot of $\delta^{13}C$ versus $\delta^{15}N$ values for muscle tissue of halibut in the lab experiment, by diet. The control group was sampled at the start of the experiment; fish in the treatment groups were sampled at 4, 6, 8, 10, and 12 weeks. Ellipses drawn on graph illustrate groups that were statistically significantly different from one another after 8 weeks (ANOSIM).

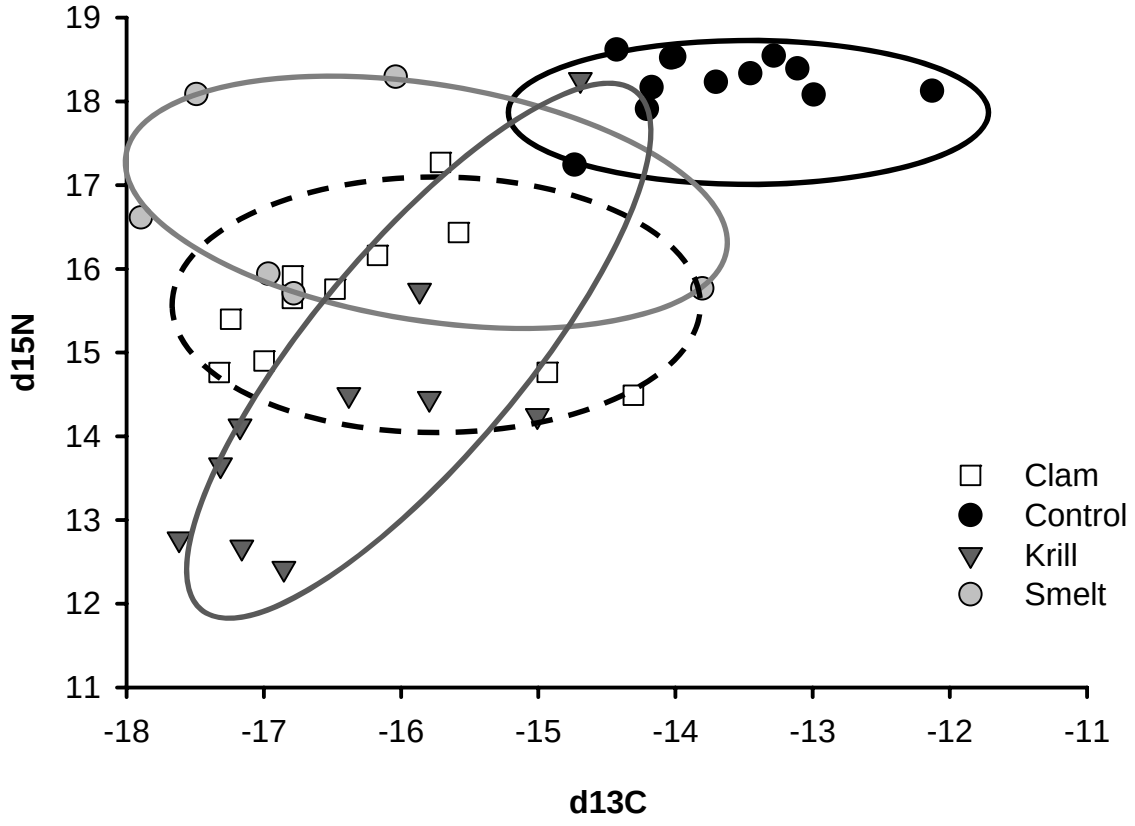


Figure 36. Average relative growth (mm mm^{-1} week^{-1}; ± 1 SE) of halibut in the caging experiments after 8 weeks; by habitat. Sample size above each column represents the number of halibut recovered from cages in each marsh. Dotted line separate caging experiments by year (2010 versus 2011).

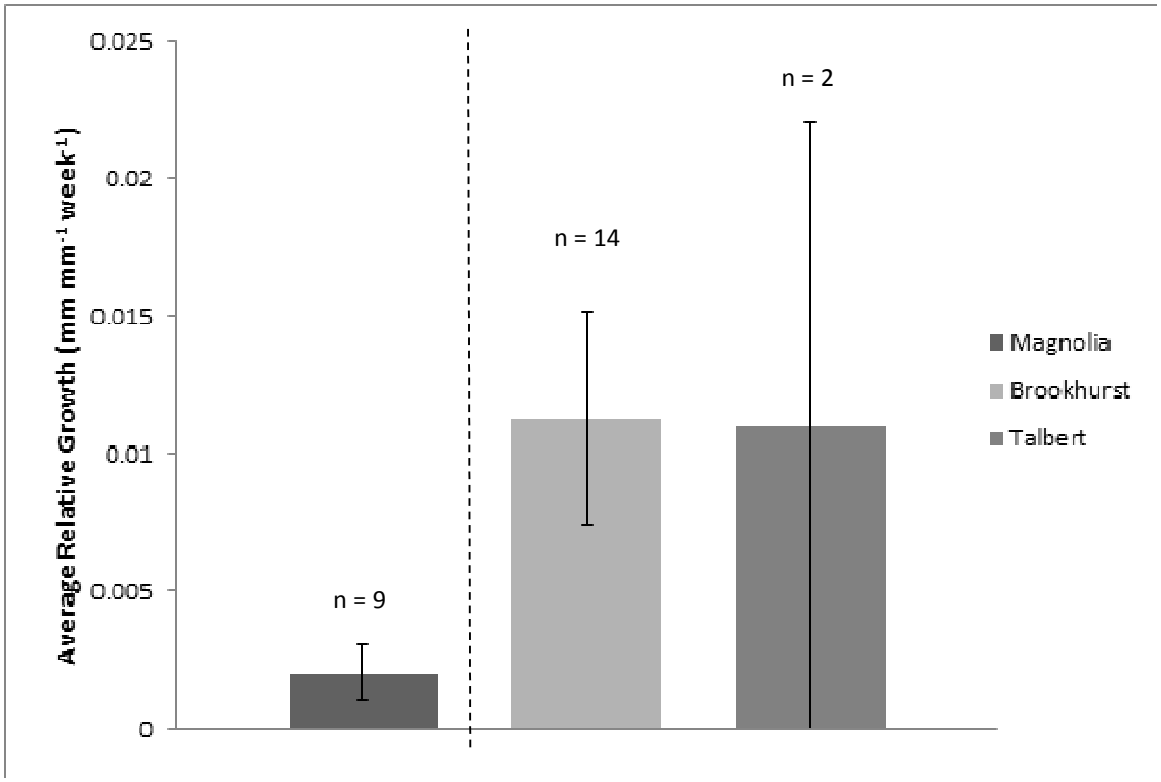


Figure 37. Frequncy of diet items or empty stomachs in caged halibut at 8 weeks; by habitat. Sample size above each column represents the number of halibut recovered from cages in each marsh. Dotted line separate caging experiments by year (2010 versus 2011).

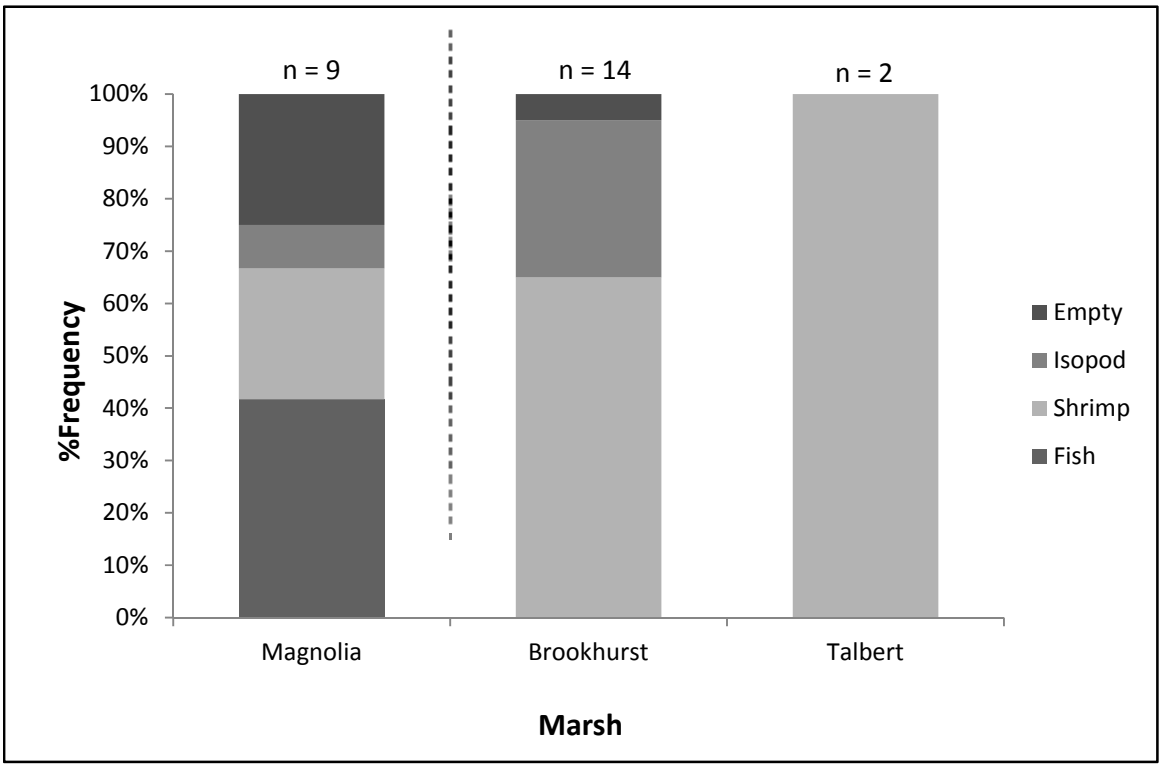


Figure 38. Dual isotope plot of $\delta^{13}C$ versus $\delta^{15}N$ for muscle tissue of halibut caged in Magnolia Marsh for 8 weeks in 2010. The control group was sampled at the start of the experiment. Although separation between the two groups is evident in the scatterplot, isotope signatures of caged fish were not significantly different from those the control group at the 0.05 level at the end of the experiment (ANOSIM, $p = 0.075$).

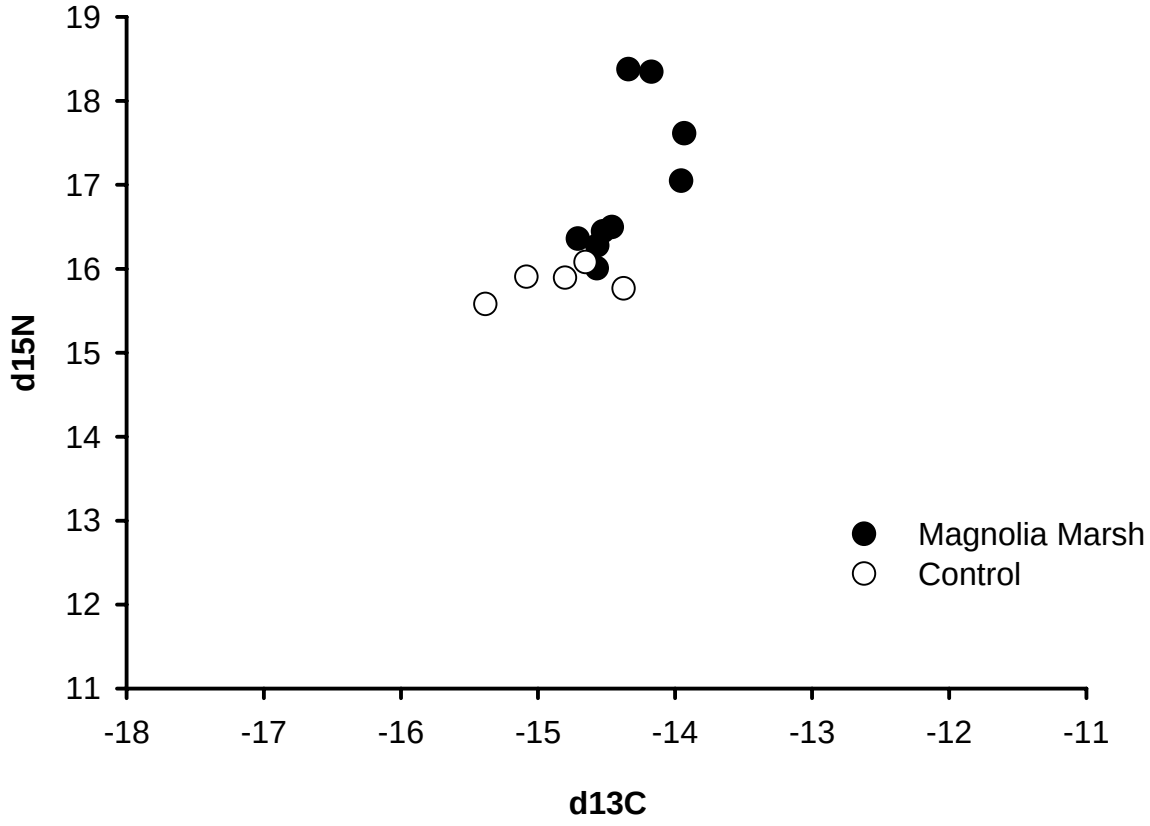


Figure 39. Dual isotope plot of $\delta^{13}C$ versus $\delta^{15}N$ for muscle tissue of halibut caged in Brookhurst and Talbert Marshes for 8-9 weeks in 2011. The control group was sampled at the start of the experiment. Ellipses drawn on graph illustrate groups that were statistically significantly different from one another at the end of the experiment (ANOSIM).

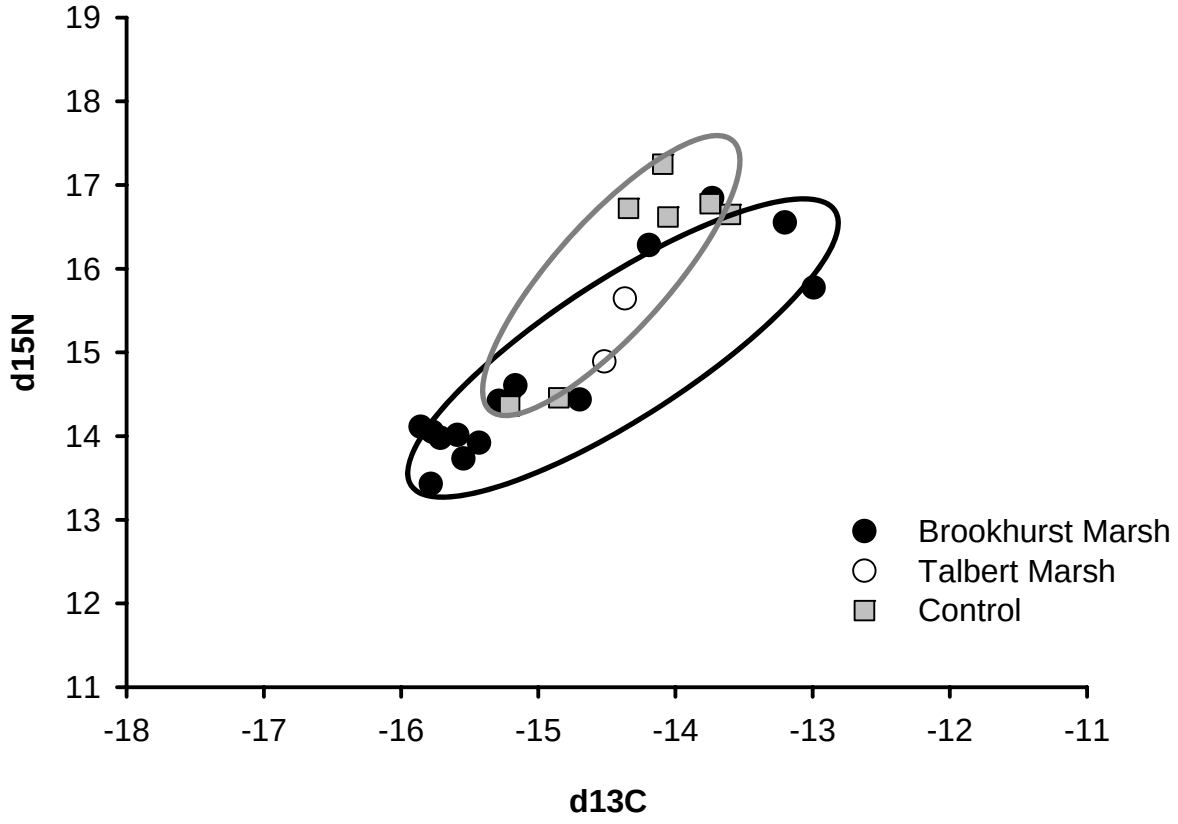


Figure 40. Average change (± 1 SE) in (A) δ15N and (B) δ13C values for halibut caged in each marsh after 8 weeks relative to the control group, by year. The relevant control groups were sampled at the start of each experiment. Sample size in each group: Magnolia Marsh, *n* = 9; Brookhurst Marsh, *n* = 14; and Talbert Marsh, *n* = 2.

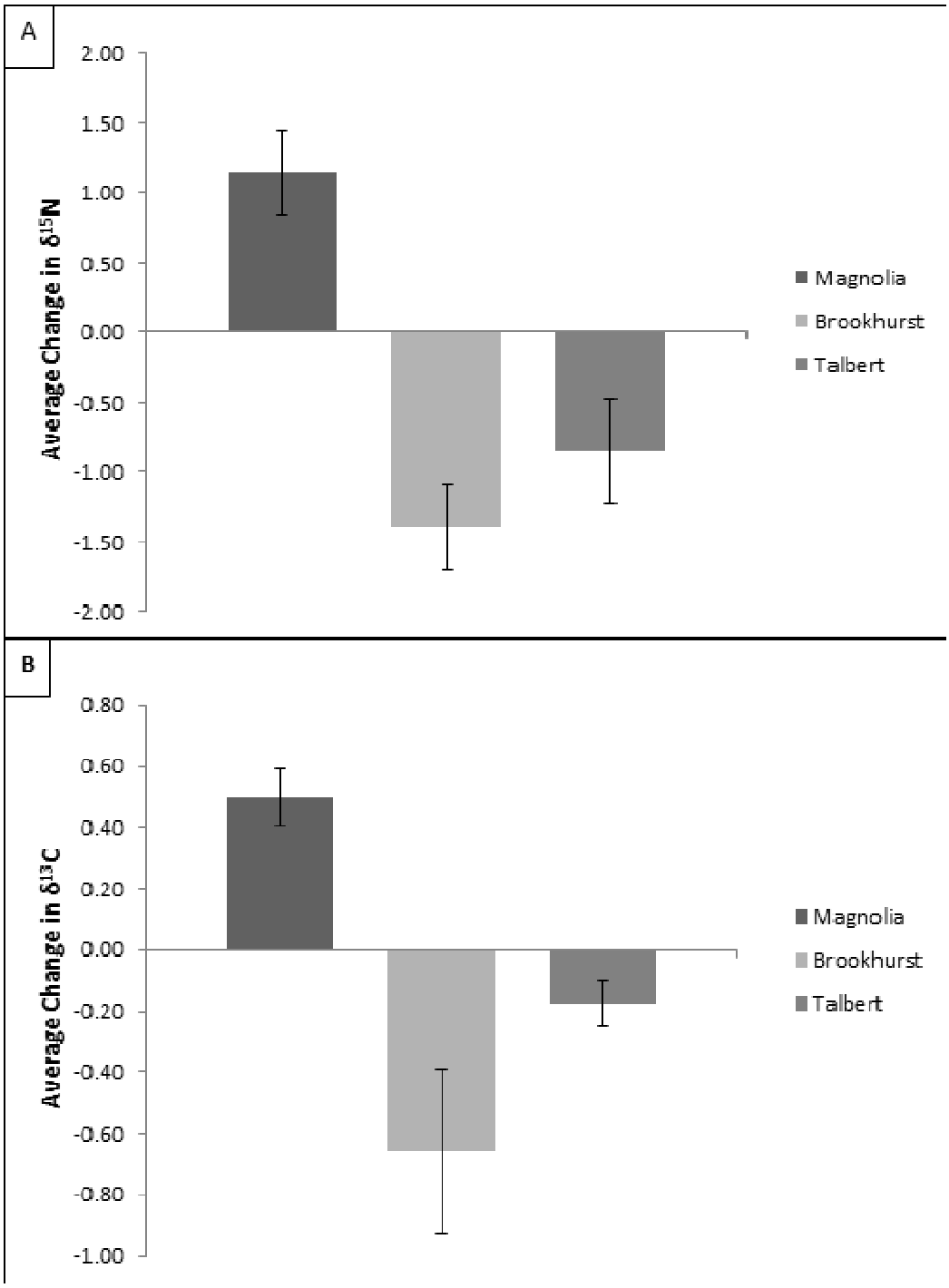


Figure 41. Dendrogram for hierarchical clustering (using group-average linking) of stable isotope ratios (C and N) of muscle tissue from 77 halibut caught in the Huntington Beach Wetlands (both wild-caught and caged, calculated on Euclidean distances between individuals. Clusters are significantly different from one another at the 0.05 level (similarity profile test; SIMPROF).

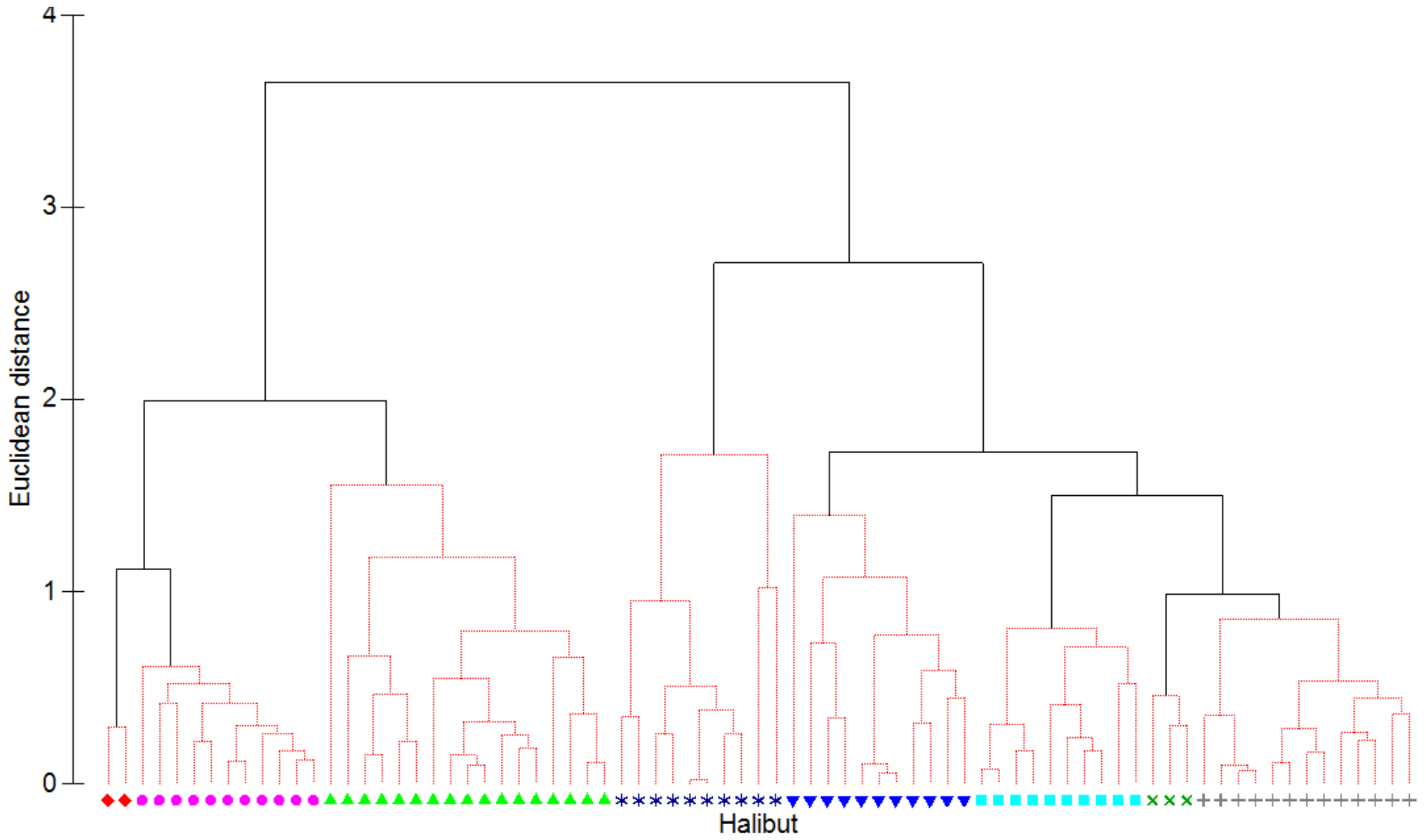


Figure 42. Non-metric multidimensional scaling (MDS) plots of stable isotope ratios (C and N) of muscle tissue (A) and stomach contents (B) from 77 halibut caught in the Huntington Beach Wetlands, calculated on Euclidean distances between individuals. Different colors denote fish significantly different from one another at the 0.05 level with respect to their isotope signatures as calculated with SIMPROF (Fig. 24). Fish muscle tissue isotope ratios were positively correlated with the average isotope ratios of their gut contents ($r_s = 0.55$, $p < 0.001$).