

# Connectivity and movements of juvenile predatory fishes between discrete restored estuaries in southern California

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**ABSTRACT:** Establishing connectivity via fish movements among restored estuaries is important for maintaining community structure, but data on the degree to which animals efficiently move among estuaries are limited. To test estuarine connectivity potential, we translocated 5 species of juvenile predatory fishes between 2 discrete estuaries approximately 10 km apart, and using passive acoustic telemetry, measured their ability to home back to their estuary of capture. Individuals from all species except *Paralabrax maculatofasciatus* (spotted sand bass) moved between the sites after translocation. Feeding guild and associated foraging behavior were found to greatly influence a species' connectivity potential, with estuarine resident ambush predators moving between sites less frequently compared to roving forager marine migrant predators. Time spent moving between sites was not significantly different among species, and 67% of homing fish completed the transit in <3 d. Fish showed no preference for one site over the other and returned to each site equally. Stable isotope analysis revealed that the availability of food (as indicated by diets) in each restored estuary could have affected *Mustelus californicus* (gray smoothhound) habitat use. Roving forager juvenile predatory fishes displayed high connectivity over a large scale, which suggests that newly restored estuaries should attract these species quickly. However, long-term use may depend on environmental conditions and succession of the prey community.

**KEY WORDS:** Acoustic telemetry · Restoration · Elasmobranch · Behavioral ecology · Habitat selection

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## INTRODUCTION

Estuaries are often regarded as fish nurseries because they support juvenile fishes at higher densities compared to other coastal habitats (Allen et al. 2006, Dahlgren et al. 2006, Fodrie & Mendoza 2006). High prey abundances, seasonally warmer conditions, and limited numbers of large predators in estuaries are thought to contribute to high carrying capacities, increased survivorship and increased growth rates for juvenile predatory fishes (JPF) in these habitats (Allen et al. 2006, Fodrie & Mendoza 2006, Espinoza et al. 2011). As a result, estuaries can contribute more individuals to adult populations per unit area compared to other coastal habitats (Fodrie

& Mendoza 2006). Because of this, suitable estuarine habitat may be essential for rebuilding overfished coastal fish stocks for populations that are known to use estuaries as nurseries (Irlandi & Crawford 1997, Valentine-Rose et al. 2007).

In coastal systems, population connectivity due to movements of individuals between habitats facilitates important ecological functions such as the transport of energy and nutrients (Irlandi & Crawford 1997). Establishing connectivity through the exchange of individuals among areas that serve as nurseries (such as estuaries) could benefit juvenile fishes by increasing their diversity and biomass (Irlandi & Crawford 1997, West & Zedler 2000, Valentine-Rose et al. 2007, Thrush et al. 2008).

Additionally, predator populations with high connectivity can exert top-down trophic control across different habitats through which they move, and can spatially alter community structure (McCauley et al. 2012). Thus, it is no surprise that when connectivity is limited, aspects of ecological functionality are also hindered (Valentine-Rose et al. 2007).

Connectivity between populations depends heavily on the ability of individuals to travel between habitats (Knowlton & Graham 2010, McCauley et al. 2012). For marine fishes, research has largely been focused on connectivity through larval dispersal; however, pelagic larvae have a limited ability to move independently of bulk water flow (Siegel et al. 2008). In contrast, juvenile, sub-adult, and adult fishes can actively move among different coastal habitats; at these life stages, connectivity is largely a product of the distance over which an individual can successfully orientate, and an individual's ability to cross large habitat gaps (Knowlton & Graham 2010, Papastamatiou et al. 2011, McCauley et al. 2012). The connectivity potential of estuarine JPFs is likely determined by their physiology (e.g. orientation ability, mobility, and vagility) as well as by habitat features within the coastal landscape (e.g. distances between estuaries, and microhabitat variability within an estuary); both are important to consider when managing estuaries on a regional scale.

Physiological traits are often shaped by life history (e.g. foraging strategy and patterns of estuarine use), and species with analogous life history traits likely display similar connectivity patterns (Cooper 2000, 2007). Species with high mobility are likely to have a higher chance of maintaining connectivity compared to species that are adapted to a more sedentary lifestyle (Cooper 2000, 2007, Knowlton & Graham 2010). Foraging marine migrants—estuarine species that utilize estuaries for parts of the year, and employ an active feeding strategy where individuals search for food—may have a higher connectivity potential compared to ambush resident predators, which spend the majority of their lives or life history stages in estuaries, and adopt a lie and wait predation strategy (Haaker 1975, Allen et al. 2006, Espinoza et al. 2011).

Another factor influencing connectivity potential for JPFs is the patchiness of estuarine habitats within the coastal landscape, and it is generally believed that connectivity between 2 estuarine patches is directly related to the distance between them (Zedler & Langis 1991, Zedler 1996). In California, extensive coastal development has resulted in the loss or degradation of approximately 90% of the available

wetland habitat (Zedler & Langis 1991, Zedler 1996, Larson 2001) and has created large gaps between available habitats that can potentially limit connectivity and isolate groups of estuarine fish populations along the California coastline (Zedler & Langis 1991, Zedler 1996, Fulford et al. 2011). The decline in overall biodiversity and in certain gamefish populations along coastal California has often justified restoration of estuaries in areas of historical estuarine coverage, although information about how functionally similar these restored estuaries are compared to their natural counterparts is limited (Zedler 1996, Zedler et al. 2001).

Creating a landscape of restored estuaries that maintains connectivity for JPFs would be ideal for regional estuary managers and is both ecologically and economically important (Espinoza et al. 2011, Farrugia et al. 2011, Espasandin 2012). In southern California, limited space is available for restoration, and restored estuaries are usually located far apart, possibly restricting their ability to attract and support JPF populations (Zedler 1996, Allen et al. 2006). Differences in habitat quality due to variation in restoration design, size, and shape may affect fish behavior and habitat use within estuaries (Irlandi & Crawford 1997, Nicolas et al. 2010a,b), which in turn can alter JPF connectivity if individuals do not use certain restored estuaries (Resetarits 2005). Understanding how far JPF are able to travel between sites, how frequently inter-estuary travel occurs, and how restoration design affects these movements is critical for restoration purposes; however, this information is poorly understood. Identifying limits to connectivity can better inform the placement and design of restored estuaries in California.

Our project addresses some of these knowledge gaps by measuring the ability of 5 different JPF species to move between 2 discrete, uniquely designed restored estuaries located approximately 10 km apart. We tagged fishes from 2 groups with similar life histories: the mobile roving forager marine migrants and the estuarine resident ambush predators. We then translocated fishes between the study sites to induce a forced homing response in order to test for connectivity potential and habitat preferences. Because individuals were translocated, we measured the potential for connectivity through animal movements instead of the realized connectivity. We used acoustic telemetry to assess individuals' movements after translocation, as well as stable isotope analysis to identify if individuals were foraging solely within their home estuaries or if foraging occurred across multiple estuaries prior to translocation. We hypothe-

sized that ambush predators would be less likely to move between sites compared to roving foragers because of their life history, but that all species would prefer the open format (i.e. nonchannelized), full tidal basin to the smaller tidal creek estuary due to its increased sub-tidal area.

## MATERIALS AND METHODS

### Study sites

The Bolsa Chica Full Tidal Basin (BCFTB) and the Huntington Beach Wetlands Complex (HBWC) are 2 restored estuaries with ocean inlets that are situated approximately 10 km apart along the southern California coastline (Fig. 1). BCFTB is a 1.48 km<sup>2</sup> full tidal basin that was opened to tidal influence in 2006, and has a 4 m maximum basin depth with sub-tidal areas composed of a mix of eelgrass *Zostera marina* and mud/sand substrata. HBWC is composed of 3 distinct tidal creek marshes: a fully draining creek restored in 1989 (Talbert Marsh), a 1.8 m deep, full inundation

creek opened in 2009 (Brookhurst Marsh), and a small tidal 0.5 m deep basin with connecting marsh creeks that opened in 2011 (Magnolia Marsh). All marshes in the HBWC are connected to each other and ultimately to the ocean via a fortified flood control channel. In total, the complex contains 0.77 km<sup>2</sup> of restored sub-tidal habitat. HBWC marsh channels are composed primarily of fine-grained sediments (mud/silt), while the flood control channel is dominated by sand and shell hash; eelgrass is found throughout the HBWC. HBWC has more intertidal vegetation compared to BCFTB, which is mostly surrounded by rip-rap. Both sites have similar mixes of microhabitat features, are mainly flushed through tidal action, and are no-take reserves where all fishing is prohibited.

### Tagging and translocation

All capture, tagging and translocation occurred between June and October 2011. Two guilds of species were tagged based on feeding behavior and resi-

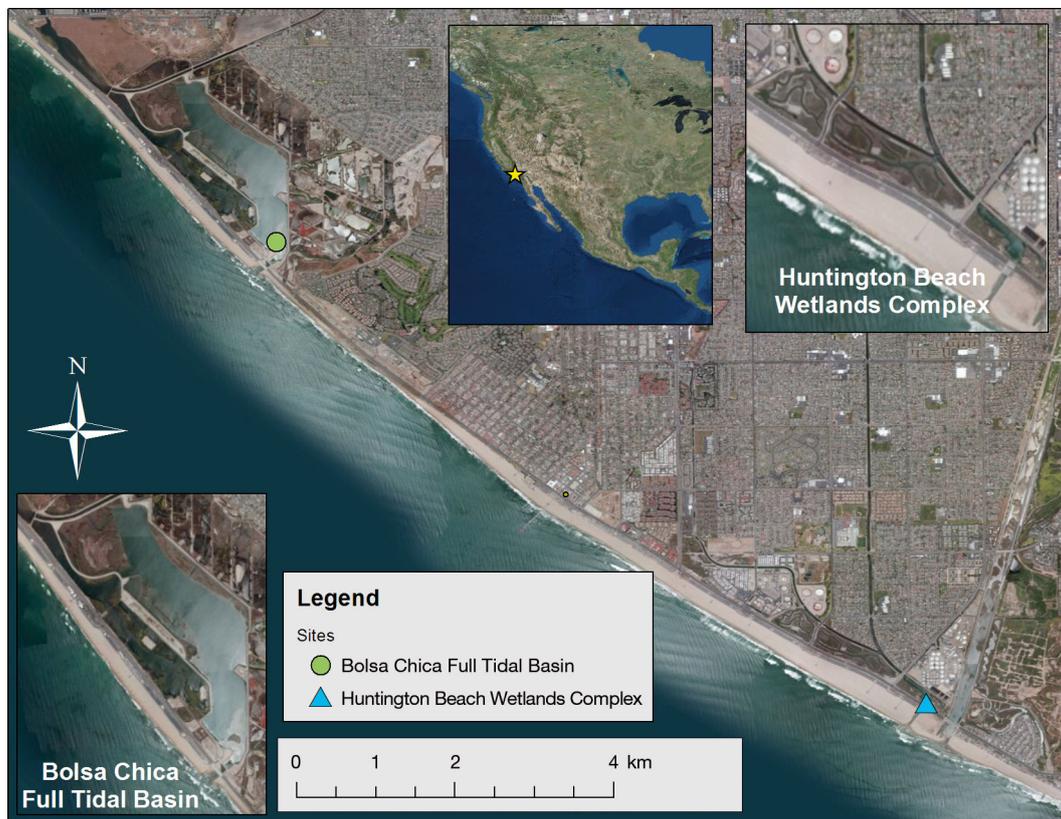


Fig. 1. Study sites at Bolsa Chica Full Tidal Basin (BCFTB, 33.6836° N, 118.0347° W) and Huntington Beach Wetlands Complex (HBWC, 33.6324° N, 117.9608° W), 2 restored estuaries located approximately 10 km apart in Huntington Beach, CA. The insets show differences in habitat design between BCFTB (a full tidal basin) and HBWC (a tidal creek estuary)

dence time classifications created in Allen et al. (2006). Roving forager marine migrant elasmobranchs (gray smoothhounds *Mustelus californicus*, leopard sharks *Triakis semifasciata*, and shovelnose guitarfish *Rhinobatos productus*) were captured on a 10 hook longline with 5/0 barbless circle hooks baited with frozen squid (see Table 1). Ambush predator species (California halibut *Paralichthys californicus*, a facultative estuarine resident as a juvenile, and spotted bay bass *Paralabrax maculatofasciatus*, an estuarine resident) were caught with rod and reel using 1/0 circle hook leadheads with plastic lures.

After capture, all fishes were measured for total length (TL) and fork length (FL; see Table 1) and individuals too small for acoustic transmitter tagging were externally tagged with a nylon dart tag and immediately released. Fish large enough to carry an acoustic transmitter (i.e. the transmitter was less than 2% of fishes' estimated body weight) had transmitters surgically implanted according to procedures approved in the California State University Long Beach IACUC protocol #290. Acoustic transmitters (V9-2x; 9 mm diam. × 29 mm long with a pseudorandom pulse interval of 110 to 250 s, power output = 145 to 151 dB, battery life = 738 d, weight in air = 4.7 g) for all species were covered in beeswax/paraffin (1:2.3) prior to surgical implantation into the body cavity to reduce immune-rejection (Lowe et al. 2003). Transmitters for *P. californicus* were smaller in order to fit into their body cavity (9 mm diam. × 24 mm long with a pseudo-random pulse interval of 50 to 130 s, power output = 145 to 151 dB, battery life = 222 d, weight in air = 22 g), but were prepared in the same manner. Incision wounds were closed with 2 dissolvable sutures (5.0, 36 mm needle chromic gut suture, Ethicon). A small piece of skin and dorsal musculature was removed using a biopsy needle for stable isotope analysis and a nylon dart or T-bar tag was inserted into the biopsy wound for external identification. Excised muscle tissue was stored in glass vials. After tagging, fishes were placed in a cooler of fresh seawater with constant aeration, transported to the other study site, and released at least 200 m from the ocean inlet inside of each estuary.

#### Acoustic data monitoring and analysis

Vemco omnidirectional acoustic receivers (model VR2W) were deployed as 'gates' inside the entrances of each estuary in June 2011. Each receiver was determined to have an average detection range of

175 m, providing up to 0.20 km<sup>2</sup> receiver detection coverage at the entrance to each estuary. When tagged fish were within the detection range of a receiver, the time, date, and transmitter identification were recorded. Receivers were placed in such a way that when fish passed through the array, the time stamps of detections could be used to determine directionality of movements in or out of the estuary. Acoustic detections were used to determine which individuals returned to their estuary of capture after translocation (hereafter referred to as 'homing'). Residence time was determined as the time between translocation release and the last detection before exiting the translocation site. If individuals did not leave the estuary, then their residence time was considered to be continuous until their exit or the end of the study. Homing time was defined as the time between the last detection before exiting the translocation site and the first detection upon entering the estuary from which the fish was originally captured.

Receiver arrays were maintained at each site for 2 yr; however, transmitters from a subset of smaller individuals (mostly *P. californicus*) only lasted for a single year. Acoustic detections of individuals that returned to the estuary the following year were used to determine inter-annual site fidelity to BCFTB and HBWC for marine migrant species (i.e. 2012 and 2013). The number of estuarine residents that remained in estuaries was determined only through 2012, as batteries in the smaller transmitters for a number of these individuals would not have lasted after the summer of 2012.

#### Stable isotope analysis

In this study, stable isotope analysis (SIA) of white muscle tissue from translocated fish was used to provide time-integrated information that increased our ability to interpret fish movement between spatial locations (Hobson 1999). Stable isotope data were not collected to describe trophic structure within the 2 systems, thus food sources were not collected. Only *P. californicus* and *M. californicus* tissues were analyzed because we were able to collect the largest sample sizes of those species, and they acted as representatives for their respective foraging groups. Levels of  $\delta^{13}\text{C}$ , i.e.

$$[(^{13}\text{C}_{\text{sample}} \cdot ^{12}\text{C}_{\text{sample}}) / (^{13}\text{C}_{\text{standard}} \cdot ^{12}\text{C}_{\text{standard}}) - 1] \times 1000$$

and  $\delta^{15}\text{N}$ , i.e.

$$[(^{15}\text{N}_{\text{sample}} \cdot ^{14}\text{N}_{\text{sample}}) / (^{15}\text{N}_{\text{standard}} \cdot ^{14}\text{N}_{\text{standard}}) - 1] \times 1000$$

composition in muscle tissue may be distinct

between BCFTB and HBWC if individuals had unique diets by site or if isotopic signatures of the same prey items reflected a difference in isotope source by site. White axial muscle tissue samples from translocated individuals were washed with Milli-Q and then dried at 50°C for 24 to 48 h ( $n = 24$  for *P. californicus*, size range 30.5–72.7 TL;  $n = 15$  *M. californicus*, size range 55.0–77.6 TL). Dried tissue was then shipped to the University of California Santa Cruz Stable Isotope Lab, where urea was extracted from elasmobranch tissue with petroleum ether and samples were washed with deionized water prior to stable isotope analysis. Isotope abundance is expressed in parts per thousand in a ratio of heavy to light isotopes. Tissues were analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  compositions and corrected delta values were expressed relative to  $\delta^{13}\text{C} = -29.53\text{‰}$  vs. Vienna PeeDee Belemnite Standard, or  $\delta^{15}\text{N} = 1.18\text{‰}$  vs. air  $\text{N}_2$ . Typical sample precision was greater than 0.15‰.

### Data analysis

To estimate degree of connectivity, comparisons of the tendency to home between sites and among species were performed using Pearson's chi-squared tests. Differences in homing and residence times for homing individuals among species were compared using ANOVA with Tukey's post hoc tests. Differences in residence time for non-homing individuals among species, as well as residence times of non-homing versus homing individuals (both species specific and pooled) were analyzed with a Kruskal-Wallis test with post-hoc pairwise Wilcoxon comparisons or 2-sample Wilcoxon tests, respectively. Pearson correlations were performed separately between TL and residence times,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope content and homing times. PERMANOVAs were used to test for differences in muscle tissue  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  between

sites for both *M. californicus* and *P. californicus*. The test statistic of PERMANOVA (pseudo- $F$ ) is a multivariate analogue of Fisher's  $F$ -ratio. If the PERMANOVA was significant, univariate  $t$ -tests were also done on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to determine which factors were responsible for observed differences between sites.

## RESULTS

### Telemetry results

Telemetry data was collected for 30 *Mustelus californicus*, 30 *Paralichthys californicus*, 5 *Triakis semifasciata*, 6 *Rhinobatos productus*, and 9 *Paralabrax maculatofasciatus* (Table 1). Roving forager JPFs homed more frequently than ambush predators (Pearson's  $\chi^2 = 18$ ,  $df = 4$ ,  $p = 0.001$ ). A large portion of tagged *T. semifasciata* (80%), *M. californicus* (73%), and *R. productus* (83%) homed to their original estuary after translocation, while only 17% of *P. californicus* and no *P. maculatofasciatus* homed (Table 1). Homing time ( $\log_{10}$ -transformed) did not vary significantly among species (ANOVA,  $F_3 = 0.97$ ,  $df = 3$ ,  $p = 0.400$ ). However, on average, *P. californicus* tended to take the longest to move between the estuaries (mean  $\pm$  SD =  $18.2 \pm 16.6$  d,  $n = 5$ ) while *R. productus* tended to home the fastest ( $5.5 \pm 7.6$  d,  $n = 5$ ). The majority of fish that exhibited homing behavior returned to their sites of capture relatively quickly, with 67% of homing fish detected in their estuary of capture 3 d or less after leaving the translocation site.

We did not observe a preference in the number of individuals homing to one site over the other; however, *T. semifasciata* were only captured in the BCFTB so the entire translocation as conducted with other species could not be completed. Four of the 5 *T. semifasciata* returned to BCFTB, but 1 individual

Table 1. Numbers of fish tagged and homed by location in 2011. Numbers in parentheses represent the minimum–maximum total length of tagged fish

Species	Guild	No. of fish tagged from BCFTB	No. of fish homing back to BCFTB	No. of fish tagged from HBWC	No. of fish homing back to HBWC
<i>Paralabrax maculatofasciatus</i>	Ambush predator	3 (29.0–37.0 cm)	0	6 (28.2–37.4 cm)	0
<i>Paralichthys californicus</i>	Ambush predator	15 (31.4–70.6 cm)	3 (44.5–72.7)	15 (30.5–72.7 cm)	2 (44.5–50.0 cm)
<i>Rhinobatos productus</i>	Foraging predator	4 (71.4–81.0 cm)	4 (71.4–81.0 cm)	2 (60.2–61.0 cm)	1 (61 cm)
<i>Mustelus californicus</i>	Foraging predator	15 (57.6–77.6 cm)	10 (56–73.5 cm)	15 (55.0–73.5 cm)	12 (57.6–77.6 cm)
<i>Triakis semifasciata</i>	Foraging predator	5 (55.0–110.0 cm)	4 (55.0–110.0 cm)	0	N/A

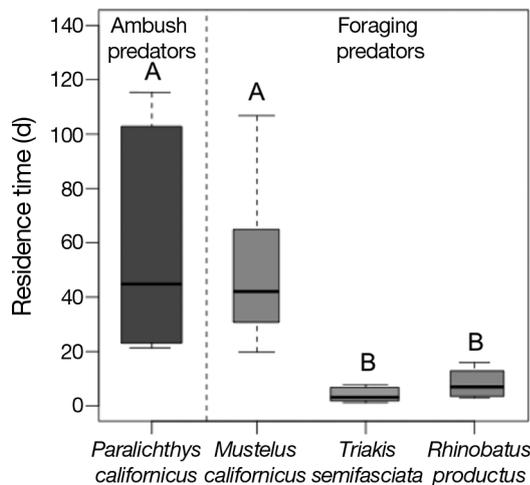


Fig. 2. Residence time spent in the translocation site for homing individuals by species. Black line = median; box = second and third quartiles; whiskers = first and fourth quartiles. *Paralichthys californicus* and *Mustelus californicus* spent significantly longer in the translocation site compared to *Triakis semifasciata* and *Rhinobatos productus*. Letters indicate significant differences

remained in HBWC for over 1 yr. Additionally, 9 *M. californicus* and 1 *R. productus* were detected moving between the estuaries multiple times during the summer immediately following translocation (Jun to Oct 2011).

For fishes that homed, the average ( $\pm$ SD) residence time ( $\log_{10}$ -transformed) in the translocated estuary prior to homing for *M. californicus* ( $50.9 \pm 25.3$  d) and *P. californicus* ( $61.5 \pm 44.6$  d) was significantly longer compared to *T. semifasciata* ( $4.4 \pm 3.4$  d) and *R. productus* ( $7.2 \pm 5.6$  d) (ANOVA,  $F_3 = 31.86$ ,  $p < 0.001$ ; Fig. 2). Residence time prior to homing when all JPF species were pooled was comparable in duration (BCFTB median = 45 d, HBWC median = 41 d) between sites (Wilcoxon test,  $W = 173.5$ ,  $p = 0.5$ ). Although *M. californicus* had the highest number of homing individuals, there was no difference in their residence times spent in BCFTB or HBWC (Wilcoxon test,  $W = 32$ ,  $p = 0.070$ ).

Non-homing fish spent a significantly longer amount of time in the translocation site compared to homing individuals across all species (Wilcoxon Test,  $W = 1008.5$ ,  $p = 0.001$ ). Residence time of non-homing JPFs differed among species (Fig. 3, Kruskal-Wallis = 11.2,  $df = 3$ ,  $p = 0.010$ ) and pairwise comparisons revealed that the only significant difference was between *P. californicus* (median = 144 d, range = 18 to 437 d) and *P. maculatofasciatus* (median = 651 d, range = 284 to 668 d; Wilcoxon test,  $p = 0.009$ ). Of the 9 *P. maculatofasciatus* tagged, 7 were still

detected in the study sites over 2 yr from the original tagging date and remained at their translocation site for the duration of the study. Across all species, the residence times of non-homing fish were not significantly different between BCFTB (median residence time = 225 d, range = 5 to 662 d) and HBWC (median = 215 d, range = 9 to 668 d) (Wilcoxon test,  $W = 163.5$ ,  $p = 0.9$ ).

The majority of JPFs (53 individuals) were not detected in either site after leaving the estuaries in 2011; however, the number of fish detected inter-annually at a study site was greater in BCFTB than in HBWC. From June through September 2012, 1 yr after the original translocation event, 14 marine migrants (*M. californicus*, *R. productus*, and *T. semifasciata*) were detected returning to BCFTB, while only 6 marine migrants were detected returning to HBWC. In addition, 8 marine migrant JPF were detected moving between and utilizing both study sites in the summer of 2012. A greater number of estuarine residents (*P. maculatofasciatus* and *P. californicus*) also remained in BCFTB ( $n = 5$ ) compared to HBWC ( $n = 2$ ) through 2012. In the beginning of summer 2013 (detections in May and June 2013), 14 marine migrants were detected returning to BCFTB, while only 3 marine migrants were detected returning to HBWC. Additionally, 5 *M. californicus* were

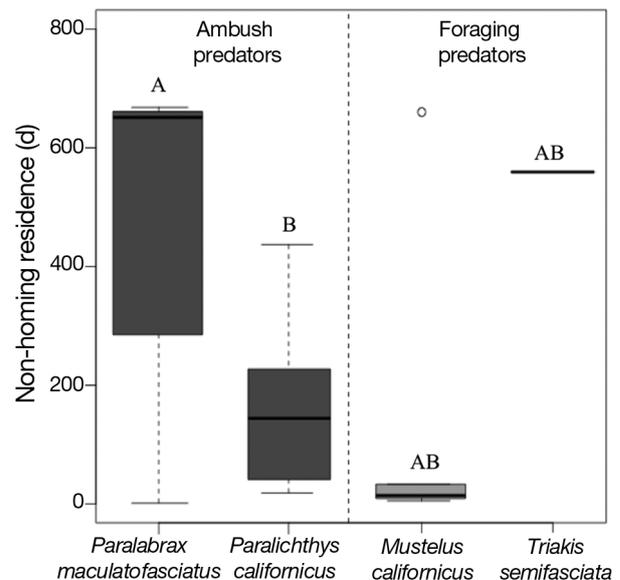


Fig. 3. Residence time spent in the translocation site for non-homing individuals by species. *Paralabrax maculatofasciatus* had the longest residence time, with most individuals remaining in study sites throughout the course of the study. The only significant difference found was between *P. maculatofasciatus* and *Paralichthys californicus*. Letters indicate significant differences

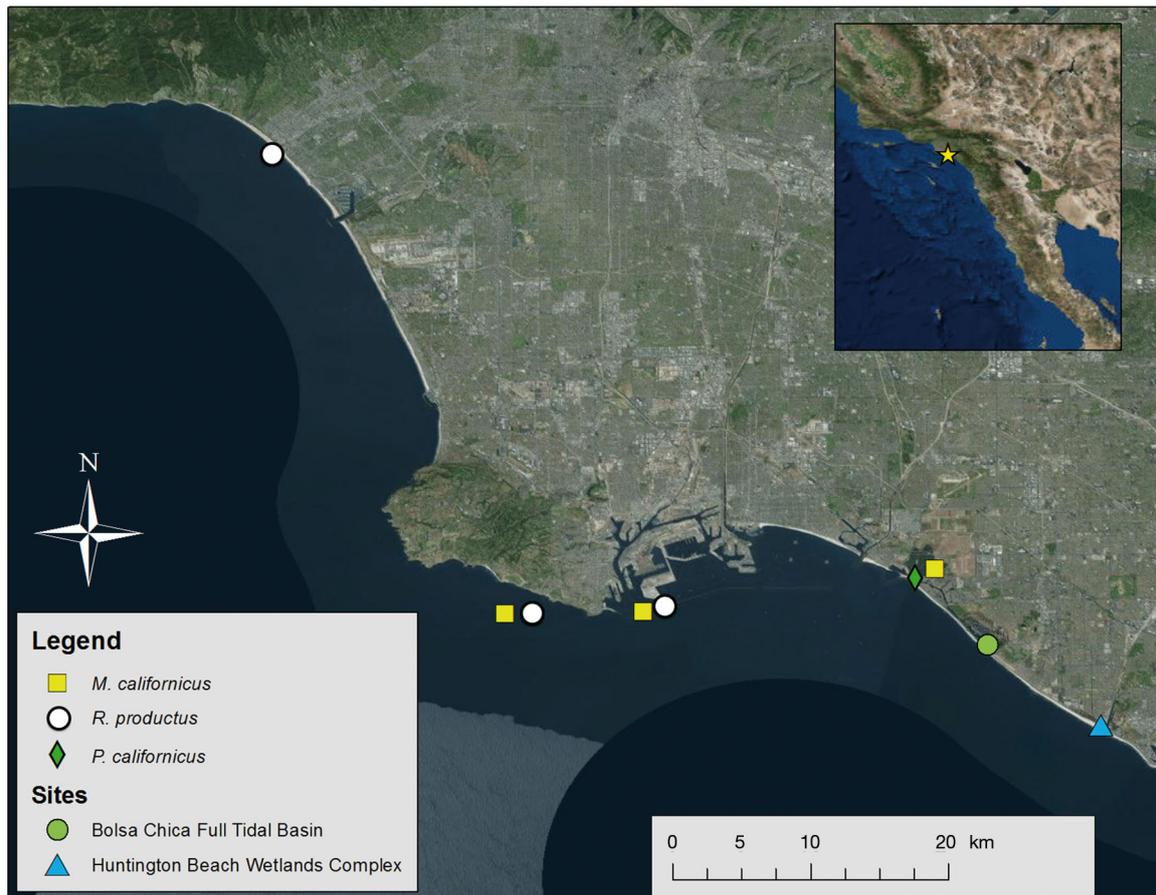


Fig. 4. Other locations where individual *Mustelus californicus*, *Rhinobatos productus*, and *Paralichthys californicus* tagged in this study were detected. An individual *R. productus* was detected at Santa Monica Pier, over 40 km from the study sites. Inset map shows region from central California to Baja California

detected moving between both estuaries in 2013. Most marine migrants returned the following year to the site they had occupied in 2012; however, some individuals switched from the prior year and there was no pattern with respect to the estuary in which they were originally tagged. Some returning marine migrant individuals changed from using a single estuary during 2012 to moving between and utilizing both estuaries in 2013.

Tagged fish were also detected at other locations outside of the 2 study areas. In summer 2012, 2 tagged *M. californicus* were detected by acoustic receivers in Anaheim Bay (33.73031° N, 118.09733° W) and the Seal Beach National Wildlife Refuge (33.73765° N, 118.0739° W), located about 8 km north of BCFTB (Fig. 4). Also in June 2012, a recreational fisherman caught a *P. californicus* in Anaheim Bay that had been tagged with a dart tag in BCFTB in the summer of 2011.

A tagged *R. productus* and 2 *M. californicus* were detected at the entrance to the Port of Los Angeles (33.7234° N, 118.07332° W) and along the southeastern Palos Verdes shelf (33.7100° N, 118.3296° W). The *R. productus* was detected 19 d after leaving BCFTB while the 2 *M. californicus* took 70 and 48 d, respectively, to reach the entrance to the Port of Los Angeles after being last detected at HBWC. These locations are completely exposed shelf habitats (i.e. not embayed or protected by land and totally vulnerable to wave action) and are at least 6 m deeper than the study sites. One of the *R. productus* detected at the entrance to the Port of Los Angeles was later detected at the Santa Monica Pier (34.00716° N, 118.4989° W) in the fall of 2012, over 40 km from its original tagging site at BCFTB. All detections and recaptures of fish outside the study sites occurred during winter months when seasonal migrants typically leave estuaries.

Table 2. Stable isotopes for each species by study site

Species group	Location	n	(TL range cm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Paralichthys</i>	HBWC	10	(72.7–30.5)	$-14.93 \pm 0.87$	$16.91 \pm 0.83$
<i>californicus</i>	BCFTB	14	(52.0–31.4)	$-15.61 \pm 0.91$	$16.42 \pm 0.47$
<i>Mustelus</i>	HBWC	9	(77.6–55.0)	$-15.39 \pm 0.78$	$16.66 \pm 0.35$
<i>californicus</i>	BCFTB	6	(77.6–63.0)	$-15.89 \pm 0.28$	$16.66 \pm 0.22$

### Stable isotope findings

Combined  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  signatures differed significantly between sites for *M. californicus* (PERMANOVA, Pseudo- $F = 4.95$ ,  $df = 1$ ,  $p = 0.020$ ; Table 2), but not for *P. californicus* (PERMANOVA, Pseudo- $F = 2.37$ ,  $df = 1$ ,  $p = 0.110$ ). Univariate  $t$ -tests revealed that  $\delta^{13}\text{C}$  in *M. californicus* was more negative in BCFTB ( $t_9 = -3.18$ ,  $df = 9$ ,  $p = 0.010$ ) than in HBWC, but no differences existed in  $\delta^{15}\text{N}$  between sites ( $t_{13} = 0.87$ ,  $df = 13$ ,  $p = 0.40$ ). TL was not correlated with  $\delta^{13}\text{C}$  ( $r = 0.30$ ,  $p = 0.170$  for *P. californicus*;  $r = -0.06$ ,  $p = 0.84$  for *M. californicus*) or  $\delta^{15}\text{N}$  ( $r = 0.28$ ,  $p = 0.200$  for *P. californicus*;  $r = 0.13$ ,  $p = 0.630$  for *M. californicus*) for either species.

### DISCUSSION

Despite the distance (approximately 10 km) between BCFTB and HBWC, individuals from 4 of the 5 JPF species that had been translocated were found to voluntarily move between these estuaries. Additionally, 9 individuals moved between sites multiple times during the summer of translocation. While translocation was used to test the degree of connectivity potential, it is likely that migratory fishes are moving between southern California estuaries on a scale of at least 10 km, with the potential to reach habitats as far as 40 km away. This means that newly restored estuaries could benefit from this type of connectivity and experience increased recovery rates relative to more isolated estuaries because they have the potential to recruit JPFs from larger distances than previously thought.

As in other studies (e.g. Fodrie & Mendoza 2006), the rapid movements between estuaries in our study highlight the low amount of time individuals spend in exposed coastline habitat as compared to estuarine habitat, suggesting that estuarine habitat may be preferred over exposed habitat. Long residence times in estuaries also indicate that these JPFs may prefer estuaries over other coastal habitats. While *Paralichthys californicus* and *Paralabrax maculato-*

*fasciatus* tended to remain in a single estuary for long periods of time, it is likely the majority of marine migrant JPFs utilized other estuarine habitats in addition to the study sites. Prior studies on *Mustelus californicus* in the BCFTB have shown that individuals remained for approximately 18 to 24 d prior to migrating from the full tidal basin

(Espinoza et al. 2011). Individuals (marine migrants) with longer homing times may be utilizing comparable neighboring estuarine habitats such as Anaheim Bay, the Santa Ana River or Newport Bay before returning to their site of capture. While some individuals have even been detected or captured in these nearby estuaries, we had no receivers in those habitats at the beginning of this study, so we were unable to confirm if individuals visited other neighboring estuaries in the year following translocation. While most homing movements were made during summer months, winter emigrations reveal movements over greater distances and to non-estuarine coastal habitats; thus, connectivity potential may be higher between estuaries in summer months when JPFs consistently use estuaries over other, more exposed habitats.

Species from different foraging guilds exhibited differing connectivity potentials. Within the first year post-translocation, roving foragers moved between sites more frequently than ambush predators. Prior movement studies of terrestrial lizards also found that roving foragers moved more frequently and quickly than ambush predators (Cooper 2000, 2007). In our study, only 5 *P. californicus* (17% of tagged *P. californicus*) and none of the *P. maculatofasciatus* were found to move between sites, which suggests reduced connectivity potential for ambush species. Prior studies using elemental fingerprinting found that *P. californicus* rarely recruit to adult stocks further than 10 km away from their juvenile habitats (Fodrie & Levin 2008), reinforcing the idea of limited connectivity potential. In our study, the few *P. californicus* that did home spent longer periods of time at translocation sites prior to leaving compared to the larger roving foraging species *Triakis semifasciata* and *Rhinobatos productus*. This may indicate that movement between sites may be more difficult or more risky for juvenile ambush predator species with comparatively smaller body sizes, and therefore individuals of these species may avoid moving between sites to reduce predation risk (Abrams 2010). Larger body size has been linked to decreased predation risk; and because foraging species tagged were

larger in size and length (typically over 50 cm), they may encounter less predation risk when moving between sites compared to ambush predators (Gehring & Swihart 2003).

However, it is also possible that these juvenile ambush predators have less of a need to home as long as habitat quality is sufficient and prey demands are met. Prior research on *P. californicus* found that individuals over 25 cm selected high water flow habitat because these areas may increase prey encounter rates through increased tidal delivery (Espasandin 2012). Because ambush predators receive new influxes of prey with each incoming tide, they typically remain in the same area for prolonged periods of time (Haaker 1975, Heidelberg et al. 1997, Kimmerer et al. 1998). In contrast, roving foragers continually search for benthic prey, and thus prior habitat knowledge of areas with high prey densities can increase resource acquisition efficiency (Dingle 1996, Ari & Correia 2008, Bartumeus & Catalan 2009). High densities of roving foragers can also deplete benthic prey resources, forcing individuals to seek out new habitats. Ambush predators may not rely on prior habitat knowledge, and as long as a continual influx of prey is maintained, species with this foraging mode may have a reduced drive to relocate to another habitat or estuary (Haaker 1975, Dingle 1996, Love 2011). The decreased connectivity potential of ambush predators and estuarine residents may isolate these populations, and adaptive management strategies must consider that these types of fishes may be more susceptible to localized population extirpations due to the onset of adverse conditions.

While the conclusions about specific diet composition that can be drawn from the stable isotope data are limited, the fact that ambush predators (*P. californicus*) and roving foragers (*M. californicus*) show contrasting isotopic patterns can be used to support the idea that movement patterns are influenced by perceived habitat quality. First,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures were not different for *P. californicus* between estuaries, suggesting that this species feeds on similar prey items in BCFTB and HBWC. If *P. californicus* are able to consume similar prey items in both BCFTB and HBWC, then they may not perceive a habitat quality difference between sites. Habitats with environmental conditions similar to natal grounds are shown to have an increased likelihood of residency for animals after translocation, and similar prey availability between BCFTB and HBWC may have lead *P. californicus* to remain at their translocation site (Stamps & Swaisgood 2007). Prior studies in HBWC indicated that the diet of *P. californicus* (>23 cm TL) was domi-

nated by fish (Fox 2012). While it is likely that many pelagic prey of *P. californicus* (such as top smelt *Atherinops affinis*) move between estuaries (Deegan 1993, Allen et al. 2006), the interchange of prey species between sites could lead to similar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures in *P. californicus*. Additionally, if *P. californicus* feed on prey items carried into the estuaries on an incoming tide that have similar isotopic signatures, then *P. californicus* in both BCFTB and HBWC would have similar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures.

In contrast, muscle tissue sampled from *M. californicus* captured in BCFTB had lower  $\delta^{13}\text{C}$  values than those from HBWC. While it is difficult to elucidate what caused this isotope shift without supporting prey isotope data from BCFTB and knowledge of the isotope turnover rate, this trend suggests that *M. californicus* is either feeding on different species in each site or that the same prey items were enriched in  $^{13}\text{C}$  in HBWC. Prey isotope data from HBWC indicates that crustaceans and crabs had comparatively less  $^{13}\text{C}$  than gastropods and bivalves (C. Whitcraft unpubl. data). Assuming prey items are not acquiring a site-specific  $\delta^{13}\text{C}$  signal, *M. californicus* in BCFTB may consume more gastropods and bivalves, while those in HBWC consume more crustaceans and crabs. Because HBWC has proportionally more intertidal habitat in which crabs such as *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* are known to burrow, and BCFTB has more sub-tidal habitat better suited to bivalve and gastropod benthic infauna, the designs of these estuaries may influence *M. californicus* diet. Because *M. californicus* homed back to both BCFTB and HBWC equally, this dietary shift may not alter the connectivity potential between sites, especially if individuals readily move between sites.

Habitat patch size and shape has been found to alter fish community composition as well as behavioral patterns (Topping et al. 2005, 2006, Nicolas et al. 2010a,b). Despite large differences in estuary shape and size between sites, relatively equal numbers of individuals from each guild were observed to return to the site of capture. *M. californicus*, which had the largest number of homing individuals, did not have longer residence times at either site, and homed back equally to both BCFTB and HBWC. This suggests that tagged *M. californicus* may find the habitat of BCFTB and HBWC of comparable quality. *T. semifasciata* were only captured in BCFTB, and the majority of *T. semifasciata* returned to BCFTB quickly after translocation. It is possible this species typically requires more space than is available in HBWC, as prior studies have found they can have activity spaces over double the area that HBWC provides

(Carlisle & Starr 2009), although one translocated *T. semifasciata* was found to use HBWC for over 1 yr. Our data suggest that both sites and estuary designs are able to support these JPF species, are seasonally preferred over adjacent coastal ocean-exposed habitats, and that their habitat design differences may not significantly impact habitat connectivity through JPF movements despite prior predictions (Ray 2005, Allen et al. 2006).

Over a multiple year period, more individuals returned to or continued to use BCFTB than HBWC. Although a large number of JPFs ( $n = 53$ ; 66% of all individuals) were never detected in either site after leaving, the inter-annual interchange between estuaries serves as a mechanism of connectivity between estuaries and other coastal habitats for these JPFs (Ray 2005). While we cannot discount the notion that higher inter-annual use of BCFTB could be indicative of higher habitat quality for supporting JPFs, there are instances of individuals moving between BCFTB and HBWC over years that would suggest habitat quality remained similar between the study sites over time. Some individuals utilized both sites within a single summer in both 2012 and 2013, indicating that connectivity between the sites remained high in subsequent years. The observed differences in the number of individuals using BCFTB inter-annually may simply be due to its larger size, thereby allowing this site to support more individuals overall.

Previous studies of *P. californicus* have shown that estuaries have higher densities of juveniles compared to exposed coastal habitats, which translates into an increased potential of these habitats to contribute to adult stocks. However, because southern California estuaries constitute such a small percentage of the available coastal habitat, these estuaries do not contribute significant numbers of halibut to adult populations (Fodrie & Mendoza 2006). Restoration projects can potentially increase the populations of JPFs by increasing estuarine habitat, as our data have shown that JPF select these habitats over other coastal habitats. JPF do not seem to prefer one specific restoration design over another and connectivity between sites appears high regardless of design. In addition, placement of new restoration sites may not be as limited by distance as previously assumed, as some JPFs can travel over 10 km between these habitats. Our data indicates that the connectivity potential between restored estuaries is high, and that these sites could provide a network of protected nursery habitats that allow JPF to easily access a greater area of preferred coastal habitat beyond what a single restoration site could provide.

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