

# Fine-scale horizontal and vertical movement of barred sand bass, *Paralabrax nebulifer*, during spawning and non-spawning seasons



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## ARTICLE INFO

### Article history:

Received 26 June 2013

Received in revised form 12 October 2013

Accepted 20 October 2013

### Keywords:

Barred sand bass

Acoustic telemetry

Active tracking

Aggregative spawning behavior

Fisheries management

## ABSTRACT

Habitat use, ecotone edge response, activity space size and association with seafloor and thermocline were compared for spawning and non-spawning season barred sand bass (*Paralabrax nebulifer*). Non-spawning season fish showed affinity with sand/reef ecotone using average activity space areas of  $0.003 \pm 0.001 \text{ km}^2$  ( $\pm$ SD) and volumes of  $0.00001 \pm 0.000005 \text{ km}^3$  while remaining  $1.9 \pm 1.7 \text{ m}$  off the seafloor. Spawning season fish used activity space areas of  $0.139 \pm 0.370 \text{ km}^2$  and volumes of  $0.001 \pm 0.002 \text{ km}^3$ . Spawning season individuals displayed two patterns of behavior, one indicative of spawning and another of resting behavior. Resting individuals tracked during spawning season behaved similarly to fish tracked during the non-spawning season, using smaller activity space areas while associating with reef structures and the seafloor. Presumed spawning individuals utilized sand habitats, using significantly larger activity spaces during the day than at night while associating with the thermocline and making repeated vertical dives toward the seafloor.

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## 1. Introduction

Barred sand bass (*Paralabrax nebulifer*) continues to rank as one of southern California's largest recreational fisheries; however, catches have steadily declined for several years due to fishing and unfavorable oceanographic conditions (California Fish and Game Commission, 2012; Chih-hao et al., 2005; Erisman et al., 2011). This popular sport fish forms large spawning aggregations that are predictable in both time and space, making them highly susceptible to overfishing. In addition, the spawning aggregations likely represent all of the reproductive activity for a given year and it is critical for population maintenance that the aggregations persist (Rhodes and Sadovy, 2002; Shapiro et al., 1993). This combined with recent catch declines has led to a growing concern that the fishery may not be sustainable at current levels of take and to consideration of alternative management options for barred sand bass (California Fish and Game Commission, 2012). Spawning behavior and movements are fundamental pieces of 'essential fishery information' for managers particularly for aggregative fish species. Aggregative spawning is the most commonly observed mating strategy among large and economically important reef fishes (e.g. snappers, groupers, sea basses) where tens to thousands of conspe-

cific individuals congregate at specific locations for brief periods each year to reproduce (Colin, 1992; Domeier and Colin, 1997; Rhodes and Sadovy, 2002; Sadovy and Domeier, 2005). Spawning aggregations are classified as either 'resident' or 'transient' based on the frequency and duration of the aggregation, the site specificity and distance traveled by individuals to aggregation sites (Domeier and Colin, 1997). Among serranid species, transient aggregative behavior is most commonly observed, where individuals travel considerable distances (ten to hundreds of km) away from home reefs to assemble at spawning grounds for weeks to months each year. Tag and recapture data suggest that barred sand bass are transient aggregative spawners that show high site fidelity to their spawning grounds, may travel more than 10 km to the site and remain there for several weeks (Jarvis et al., 2010). Peak barred sand bass spawning season is from June to August, when individuals move offshore away from coastal ecotone habitats to form large transient breeding aggregations comprised of several thousand migrant and resident fish over sand flats, in depths of 20–40 m (Hovey et al., 2002; Jarvis et al., 2010; Love et al., 1996; Turner et al., 1969). While the timing and location of barred sand bass spawning aggregations is well documented, virtually nothing is known about barred sand bass spawning behavior and spawning habitat utilization.

It is possible that barred sand bass behave similarly and exhibit patterns of spawning behavior consistent with other *Paralabrax* species. Two southern California congeners, kelp bass (*P. clathratus*) and spotted sand bass (*P. maculatofasciatus*) are reported to display spawning behavior throughout their spawning period. In these

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species, behavioral observations and histological data reveal that courtship behavior begins in the late afternoon continuing throughout the day with spawning commencing shortly before sunset (Erisman and Allen, 2006; Martinez-Diaz et al., 2001; Oda et al., 1993). In contrast, Oda et al. (1993) reported that barred sand bass may exhibit peak spawning activity during midday (12:00–14:00) based on histological analysis of gonads; however, this has never been confirmed by behavioral observations. During spawning, kelp bass and spotted sand bass were seen exhibiting short 1–4 m vertical spawning rushes while releasing gametes just a few meters below the surface (Erisman and Allen, 2006; Martinez-Diaz et al., 2001; Miller and Allen, 2006). Males and females also spawn multiple times during the course of a single evening (Erisman and Allen, 2006; Martinez-Diaz et al., 2001).

Gathering detailed information about barred sand bass spawning habitat utilization and spawning-related movement and behavior is essential to understand the temporal and spatial dynamics of barred sand bass spawning aggregations and may have important management implications. The purpose of this study was to characterize fine-scale horizontal and vertical movement patterns of acoustically tagged barred sand bass during the spawning and non-spawning seasons and to quantify activity space size (area and volume), habitat use, and diel patterns of activity. Movement patterns believed to be indicative of spawning and/or courtship were determined through the comparison of fine-scale vertical and horizontal movements for spawning and non-spawning season individuals.

## 2. Methods

### 2.1. Study site

This study was conducted at one known spawning aggregation location, the Huntington Beach Flats (HBF), California (33°39'18"N, 118°03'12"W), including the Bolsa Chica Artificial Reef (BCAR; 33°39'02"N, 118°06'05"W) as well as representative non-spawning season rocky reef habitat along the outer Los Angeles Federal Breakwater (LAFB; 33°43'01"N, 118°09'38"W) (Fig. 1). The HBF is one of the largest and most heavily targeted spawning aggregation sites for barred sand bass (*Paralabrax nebulifer*) in California (Jarvis et al., 2010; Love et al., 1996). HBF is characterized as primarily sand substratum with sporadic shelves of flat shale and small low-relief natural and artificial reef habitat. It encompasses an approximately 55 km<sup>2</sup> area with depths of 10–40 m. BCAR is located at the far northwest corner of the HBF in 25–30 m of water and its 0.90 km<sup>2</sup> area contains 31 small artificial reefs comprised of over 160,000 tons of concrete rubble, rock quarry, telephone poles and eight steel and concrete barges (Bedford et al., 1992). The LAFB is 13.8 km long and forms the outer edge of the Los Angeles–Long Beach Harbors, making it the largest artificial reef in southern California. It forms a sloping high-relief reef constructed of quarry rock, which extends from the surface down to 15 m, terminating into a sand/mud substratum (Froeschke et al., 2005).

### 2.2. Tagging procedure

Seventeen adult barred sand bass (>310 mm total length, TL) were collected along the HBF using hook and line from May–August during the 2009 and 2010 summer spawning seasons and along the LAFB from February–June, 2011. Once on board the vessel, fish were anesthetized by submersion in a saltwater bath containing MS-222 (tricaine methanesulfonate – Finquel™, 0.1 g l<sup>-1</sup>) for several minutes (Cho and Heath, 2000; Munday and Wilson, 1997). A small acoustic transmitter (Vemco Ltd.; V13-1L continuous pulse or V13P-1L depth sensing; depth rating: 50 ± 2.5 m) was surgically



**Fig. 1.** Reference map of southern California study sites at the Huntington Beach Flats and the Los Angeles Federal Breakwater (solid black line) during the 2009–2010 spawning (red box) and 2011 non-spawning season (blue box), respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

implanted within the peritoneal cavity through a 1–2 cm incision and closed with 2–3 discontinuous dissolvable sutures (Ethicon Inc.; Chromic Gut). Transmitters were coated with a paraffin and beeswax mixture (2.3:1) to reduce the risk of an immune-rejection. A thin film of antibiotic ointment was also spread over the wound to further reduce the risk of infection (e.g. Lowe et al., 2003; Mason and Lowe, 2010; Topping et al., 2005). Fish were measured (TL mm) and externally tagged in the dorsal musculature with a nylon-tipped dart tag (Floy Tag & Manufacturing, Inc.) containing a unique identification number, “do not consume fish” warning and contact information (e.g. Lowe et al., 2003; Lowry and Suthers, 1998; Topping et al., 2005). Fish were then transferred to a bin of fresh seawater for recovery (5–10 min) and released at the site of capture.

### 2.3. Active acoustic tracking

Tagged fish were immediately tracked upon release for an initial 2–10 h period using a gunwale-mounted directional hydrophone (Vemco Ltd.; VH110) and an acoustic receiver (Vemco Ltd.; VR100) for preliminary monitoring and to ensure fish survival. Data collected during this initial tracking period was not included in any subsequent analyses. To assess individual fine-scale horizontal and vertical movement and habitat use during spawning and non-spawning seasons, tagged fish were actively tracked for up to three additional non-consecutive 24 h periods over the length of their transmitter battery life (20–150 d). Transmitters pulsed at a single frequency (60, 63, 75, 78, 81 or 84 kHz) every 1–2 s depending on transmitter type. The receiver automatically recorded the tracking vessel’s geographical location and depth-sensor data (when available) every time a transmitter pulse was detected. Based on range

tests conducted at HBF, highest positional accuracy was determined to be 10–15 m depending on water depth, substratum type, and sea conditions at a gain of 0 dB and signal strengths of 86–105 dB. For data analysis, the tracking vessel's geographic position was assumed equal to fish position (Brill et al., 1999; Cartamil and Lowe, 2004). Water depth and presence of conspecifics was manually recorded every 10 min along with the geolocations of the tagged fish via the vessel depth sounder (Furuno: 1 kW, 50 and 200 kHz transducers).

#### 2.4. Thermocline computation

A sonde (YSI, Model 6600) was deployed every 2–6 h when conditions allowed, from the surface to the seafloor to measure water column temperature profiles during the course of each track. To determine location of thermocline when present, water temperature versus depth profiles were generated and a nonlinear four parameter sigmoidal regression was fitted to the data. Using the output parameters and corresponding nonlinear regression equation ( $f = y_0 + a / (1 + \exp(-(x - x_0) / b))$ ), temperature was calculated at every 0.1 m. Then, the first derivative of water temperature based on changing depth was taken to determine the point with the fastest rate of change, corresponding to the thermocline mid-depth and temperature. Next, the second derivative was computed to find the inflection points to determine the thermocline min and max depths and corresponding water temperatures. The calculated mid-thermocline depth was used in subsequent fish distance from thermocline analyses.

#### 2.5. Data analysis

For horizontal movement and habitat use analyses, positional fixes derived from active tracking were filtered to include only detections of highest positional accuracy (gain 0 dB, signal strengths 86–105 dB). Filtered tracking data were plotted on a georeferenced map of the study area in ArcView 3.3 and ArcMap 10 GIS. A 95% kernel utilization distribution (KUD) was used to determine the area of individual barred sand bass daily activity spaces using ArcView 3.3 Animal Movement Analysis Extension (AMAE) (Hooge and Eichenlaub, 2000). KUD is a probabilistic approach to estimating activity space area, where the region defined represents a 95% probability of locating a fish within the respective area during the tracking period (Hooge et al., 2001). When calculating the KUD using the AMAE, the ad hoc value was used as the smoothing function.

Habitat utilization within the HBF and along the LAFB was determined by plotting fish position over habitat maps and calculating the proportion of time each fish spent associated with each habitat type (Lowe et al., 2003; Mason and Lowe, 2010). To examine a possible edge response, the Euclidean distance from each detection location to the nearest known reef edge was calculated using the ArcMap 10 proximity analysis tools and detection frequency was plotted relative to distance from reef edge (Mason and Lowe, 2010). Observed edge responses may include positive, negative, transitional and neutral. We refer to individuals with detection frequencies that increase near the edge as having a positive edge response, individuals with detection frequencies that decrease near edges as having a negative response, individuals with detection frequencies that peak both close to and far from edge habitats as exhibiting a transitional response, and individuals that exhibit no pattern as having neutral response (Reis et al., 2004). To characterize the spatial extent of sand/reef edge associations during day and night periods, histograms of geolocation frequency at 1 m intervals from the reef/sand edge were created. Kurtosis and skewness, a measure of the peakedness and the distribution of data, were used to describe the shape of the histograms (Mason and Lowe, 2010).

To analyze patterns in vertical movement, depth data were first filtered to remove erroneous depth readings (e.g. negative depth values or values deeper than known seafloor depth). Depth profiles for each tracking period and fish were created by plotting depth readings against time of day to analyze diel patterns of vertical movement. Seafloor and thermocline depths were overlaid upon depth profiles to evaluate possible interactions between seafloor and thermocline position. Patterns of vertical movement were determined for spawning and non-spawning season individuals by calculating fish distance from bottom (DFB) and fish distance from thermocline (DFT), for all filtered (gain 0 dB) geolocations, for each individual.

To determine overall levels of activity, all available horizontal and vertical movement data (gain 0 dB, signal strengths 74–105 dB) were incorporated into 3-dimensional multivariate kernel density estimates (kdes). To ensure all data were in comparable units (m), horizontal data (latitudes and longitudes) were converted to a Universal Transverse Mercator (UTM) projection and vertical movement data remained in meters. Kdes were calculated in 'R' using KS and Spatstat packages (Duong, 2007). To estimate the smoothing factor matrix for 3D kernel estimation a plug-in bandwidth selector was used. The generated kdes were used to calculate daily activity space volume at the 95% contour level, by determining the number of voxels contained within the contour shell and multiplying it by the volume of each voxel (Simpfendorfer et al., 2012).

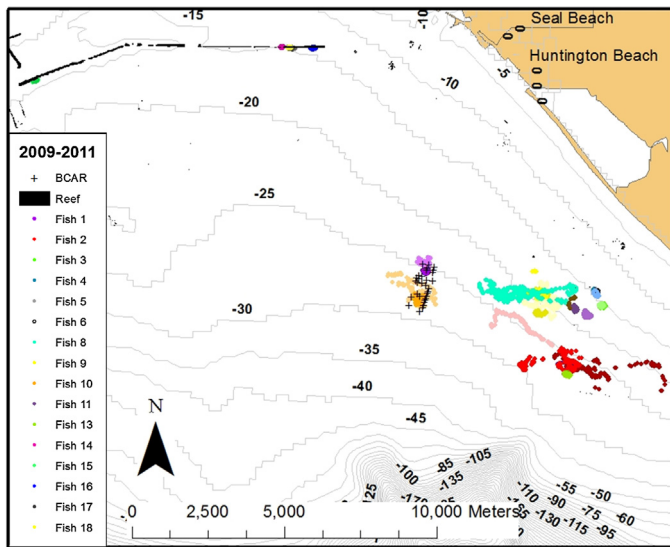
Daily activity space area and volume of spawning and non-spawning season fish were compared using a Mann–Whitney *U* test and a linear regression analysis was used to examine the relationship between fish total length and activity space size (area and volume). For each fish, KUDs and kdes were calculated for day- and nighttime periods to establish any diel patterns in space use. Day and night KUDs and kdes of spawning and non-spawning season fish were compared using a Mann–Whitney *U* test. In addition, spawning and non-spawning season DFB as well as day and night DFB and DFT (spawning season only) were compared with a Mann–Whitney *U* test.

### 3. Results

Sixteen of the seventeen tagged adult barred sand bass (*Paralabrax nebulifer*) (333–635 mm TL) were actively tracked for up to three non-consecutive 24 h periods (24–72 h) to quantify individual horizontal and vertical movement patterns, space use and spawning/courtship related behaviors (Fig. 2). Twelve of the seventeen individuals (333–635 mm TL) were tagged within the HBF spawning grounds (water depth: 14–29 m) from June–August 2009 and May–August 2010. Five of these fish were tagged with V13 acoustic continuous pulse transmitters and seven with V13P depth sensing transmitters. One of the 2010 spawning season fish (Fish 7, V13) was either caught or disappeared from spawning grounds before any 24 h tracks could be completed and therefore excluded from all analyses. Five additional barred sand bass (359–429 mm TL) were tagged within representative non-spawning season habitat along the LAFB (water depth: 13–16 m) from February–June, 2011. All non-spawning season fish were tagged with V13P depth sensing transmitters. For all individuals, the number of days between capture and first track ranged from 2 to 20 d and averaged  $7.3 \pm 5.7$  d ( $\pm$ SD). Time between individual successive tracks ranged from 1 to 59 d with an average of  $7.3 \pm 17.1$  d.

#### 3.1. Activity space area

Spawning season fish used significantly (4500%) larger daily activity spaces (95% KUD) than non-spawning season fish

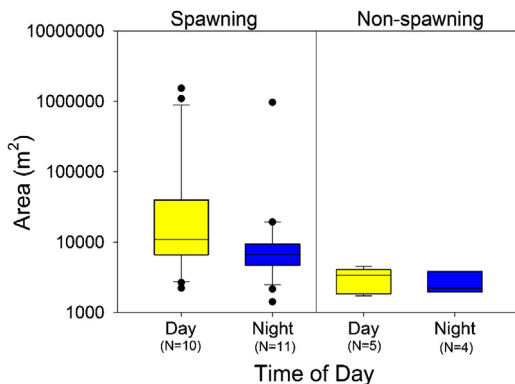


**Fig. 2.** Map of the Huntington Beach Flats, including the Bolsa Chica Artificial Reef and Los Angeles Federal Breakwater showing completed tracks for all spawning and non-spawning season fish. Please include study site labels in your map for HBF and the Breakwater.

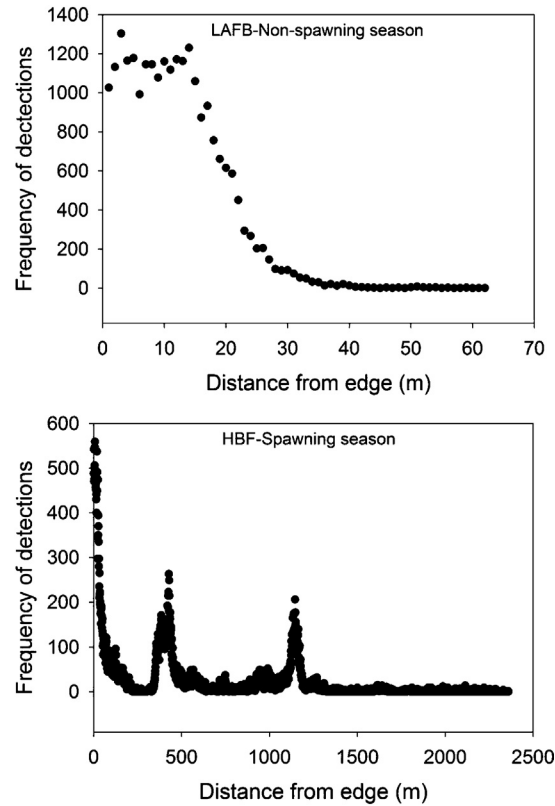
(Mann–Whitney  $U = 13$ ,  $p < 0.001$ ). Daily activity space area varied considerably between and among individuals tracked during the spawning season and ranged from 0.002 to 1.89 km<sup>2</sup>, averaging  $0.139 \pm 0.376$  km<sup>2</sup> ( $\pm$ SD). These individuals showed distinct diel patterns of activity, utilizing significantly larger areas during the day than at night (Day:  $0.136 \pm 0.386$  km<sup>2</sup>, Night:  $0.051 \pm 0.205$  km<sup>2</sup>; Mann–Whitney  $U = 172$ ,  $p = 0.03$ ). Non-spawning season fish used average home range sizes of  $0.003 \pm 0.001$  km<sup>2</sup> (range: 0.002–0.006 km<sup>2</sup>), with no significant difference between day and night activity space area (Mann–Whitney  $U = 36$ ,  $p = 0.89$ ) (Fig. 3). There was no significant relationship between daily activity space area and fish total length for spawning ( $R^2 = 0.003$ ,  $p = 0.78$ ) or non-spawning ( $R^2 = 0.103$ ,  $p = 0.37$ ) season individuals.

3.2. Habitat utilization

Non-spawning season fish remained closely associated with the sand/reef ecotone, exhibiting a positive edge response that peaked at 12 m from the edge before decreasing (Fig. 4). There were 52.3% of geolocations that occurred within 60 m from the edge into sand habitat and 47.7% of geolocations that occurred within 40 m of the edge into reef habitat. These individuals also exhibited diel



**Fig. 3.** Box and whisker plot of barred sand bass day versus night activity space area during spawning and non-spawning seasons. Note log scale on y-axis.



**Fig. 4.** The positive edge response of five non-spawning season barred sand bass tracked along the Los Angeles Federal Breakwater (LAFB) and the sand/reef habitat transitional edge response of 11 actively tracked spawning season barred sand bass at one known spawning aggregation site, the Huntington Beach Flats (HBF).

shifts in habitat use, with a wide peak in geolocations at approximately 16 m into reef habitat during the day (kurtosis =  $-0.338$ , skewness =  $-0.345$ ) and approximately 12 m out into sand habitat at night (kurtosis =  $-0.192$ , skewness =  $0.059$ ) (Fig. 5).

Spawning season individuals utilized sand over available reef habitat in water depths ranging from 15 to 30 m, with 94.2% of geolocations occurring over sand habitat. When grouping all spawning season individuals together they showed a transitional edge response (i.e., detection frequencies peaked both close and far from edge habitats) (Fig. 4). However, individual fish exhibited one or two primary modes of edge response (e.g., either positive, negative and/or transitional). Diel patterns in spatial habitat use were also detected. During the day, pooled data showed a multimodal distribution of geolocations with detection frequencies peaking along the sand/reef ecotone, as well as occurring 300–1300 m away from the nearest reef edge. At night, pooled data showed a tri-modal distribution of geolocations with sharp peaks occurring along the sand/reef ecotone as well as at 450 and 1150 m into sand habitat (Fig. 5).

3.3. Vertical movement patterns

All spawning season individuals remained significantly farther from the seafloor during the day than at night (Day:  $7.4 \pm 5.8$  m, Night:  $4.2 \pm 2.3$  m; Mann–Whitney  $U = -35176177994$ ,  $p < 0.001$ ), while non-spawning season fish remained on average  $1.9 \pm 1.7$  m above the seafloor throughout day and night periods (Mann–Whitney  $U = 4181178779$ ,  $p = 0.23$ ) (Fig. 6). Spawning season fish residing in the water column also remained significantly closer to the thermocline ( $15.8 \pm 1.6$  °C,  $11.7 \pm 3.7$  m) during the day than at night (Mann–Whitney  $U = -14487202450$ ,  $p < 0.001$ ).



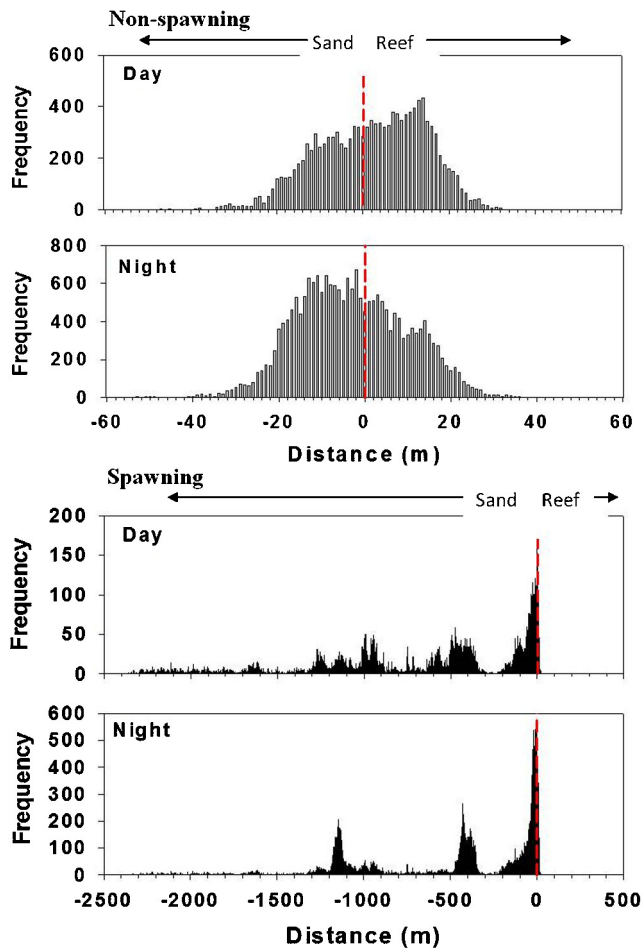


Fig. 5. Histograms of day and night detections in 1 m bins from sand/reef edge (red dashed line) for barred sand bass tracked during the 2011 non-spawning season and 2009–2010 summer spawning season. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Based on time/depth profiles, three main patterns of vertical movement were detected; one pattern representing non-spawning season behavior (Fig. 7a), one believed to be indicative of spawning/courtship related behavior (Fig. 7b) and another believed to be spawning season resting behavior (Fig. 7c). Fish that we believed to be actively participating within the spawning aggregation exhibited diel shifts in vertical movement, remaining approximately  $3.6 \pm 4.3$  m ( $\pm$ SD) off the seafloor at night and moving up into the

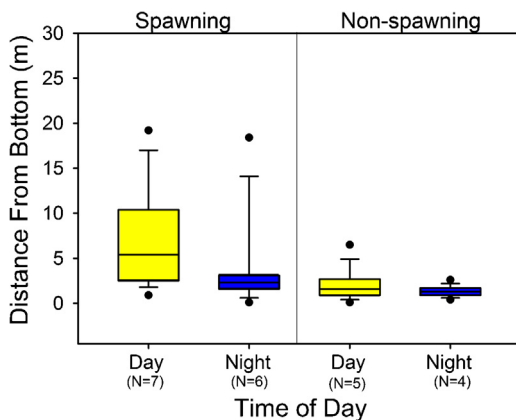


Fig. 6. Plot showing fish distance from the seafloor during day and night periods for both spawning and non-spawning season barred sand bass.

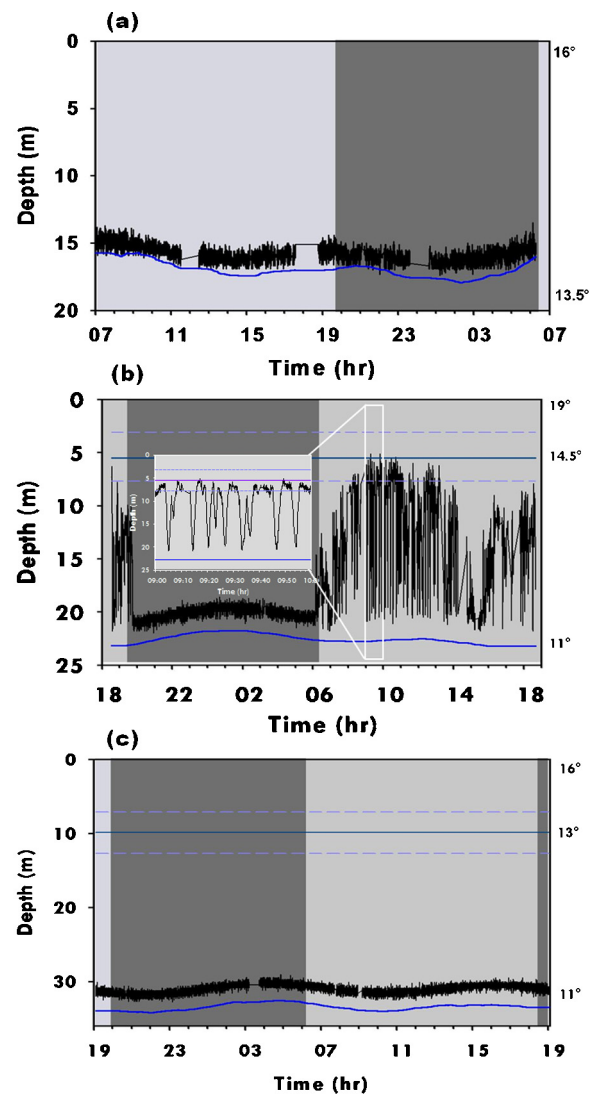
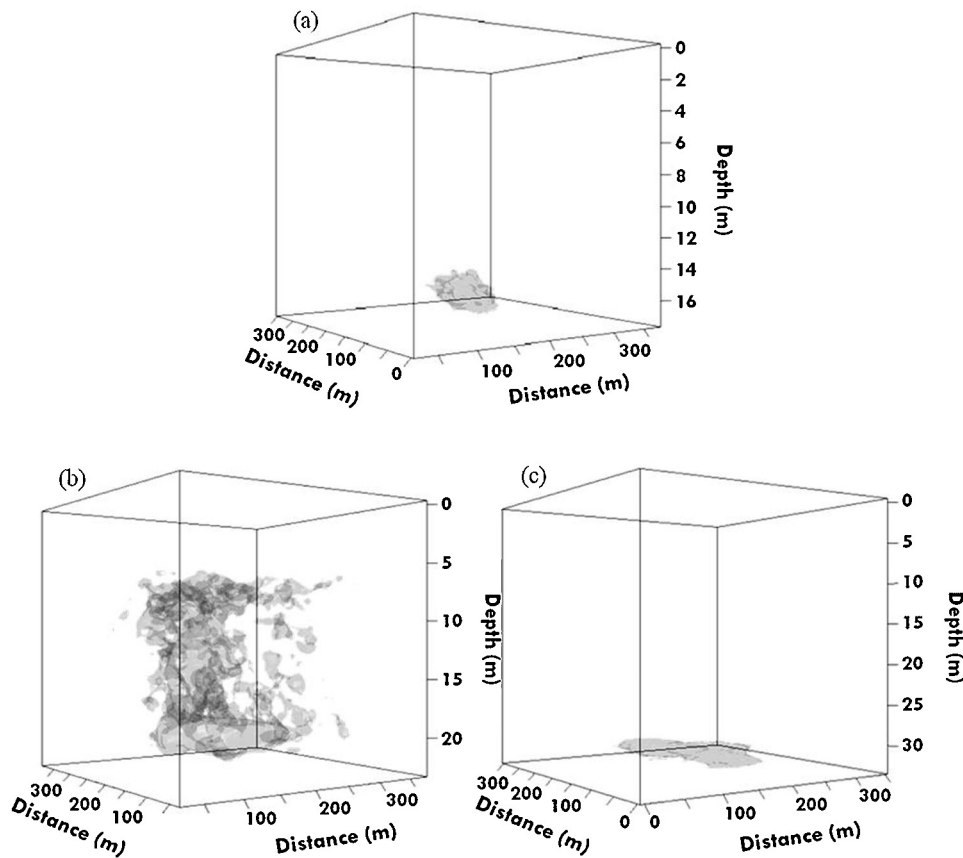


Fig. 7. Representative depth profiles of barred sand bass (a) non-spawning, (b) presumed spawning/courtship and (c) spawning season resting behavior. Insert used to illustrate spawning-related dive behavior.

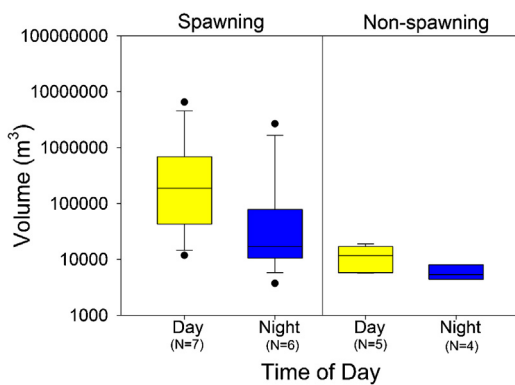
mid-water column ( $8.3 \pm 6.0$  m off substratum) during the day, primarily within or just below the thermocline. During the day, these individuals continually made directed dives toward the seafloor that covered a variety of distances, culminating within a few meters of the thermocline to just above the substratum, and lasting 15 s to several minutes. Individuals that displayed “resting” behavior or non-spawning related behavior were fish presumably not actively participating within the aggregation during that particular tracking period, but remained on the spawning ground. These individuals behaved similar to non-spawning season fish and remained on average  $2.5 \pm 2.3$  m above the seafloor throughout both day and night periods.

#### 3.4. Activity space volume

Three-dimensional activity space estimates provide more detailed representations of the three main patterns of observed behavior: (a) non-spawning, (b) presumed spawning/courtship and (c) resting (Fig. 8). Overall, spawning season fish were significantly more active using (7500%) larger volumes than non-spawning season fish (Mann–Whitney  $U = 5$ ,  $p < 0.001$ ). Spawning season individuals with tracks conducted during the 3rd and 4th weeks of July



**Fig. 8.** Representative barred sand bass 3D daily 95% kde activity spaces depicting (a) non-spawning season, (b) presumed spawning/courtship and (c) presumed spawning season resting behavior.



**Fig. 9.** Box and whisker plot of day versus night activity space volume for barred sand bass actively tracked during spawning and non-spawning seasons.

exhibited the highest levels of activity during this period, consistently utilizing the largest activity space volumes. Spawning season individual daily activity space volume averaged  $0.001 \pm 0.002 \text{ km}^3$  (range  $0.00001\text{--}0.007 \text{ km}^3$ ) and fish used significantly more of the available water column during the day than at night (Day:  $0.001 \pm 0.002 \text{ km}^3$ , Night:  $0.0002 \pm 0.0007 \text{ km}^3$ ; Mann–Whitney  $U=38$ ,  $p=0.003$ ). Non-spawning season fish used on average  $0.00001 \pm 0.000005 \text{ km}^3$  (range  $0.000007\text{--}0.00002 \text{ km}^3$ ), also showing higher levels of activity by using a greater volume of habitat during the day than at night (Day:  $0.00001 \pm 0.000006 \text{ km}^3$ , Night:  $0.000006 \pm 0.000003 \text{ km}^3$ ; Mann–Whitney  $U=29$ ,  $p=0.03$ ) (Fig. 9). There was no significant relationship between daily activity

space volume and fish total length for spawning ( $R^2=0.002$ ,  $p=0.87$ ) or non-spawning ( $R^2=0.365$ ,  $p=0.07$ ) season individuals.

#### 4. Discussion

The present study is the first report of barred sand bass (BSB) (*Paralabrax nebulifer*) fine-scale horizontal and vertical movement contrasting spawning and non-spawning season behavior. Although fish could not be directly observed, the use of active acoustic telemetry allowed for the comparison of several movement parameters including edge response, activity space area and volume, as well as associations with the seafloor and thermocline that could be used to infer patterns of behavior. While there was typical individual variability in horizontal and vertical movement among actively tracked individuals, three distinct patterns of behavior were identified and believed to be representative of non-spawning season behavior, spawning season resting behavior and spawning/courtship related behavior.

##### 4.1. Non-spawning season fine-scale movement and habitat utilization

During the non-spawning season, individuals tracked along the Los Angeles Federal Breakwater (LAFB) exhibited patterns of behavior consistent with adult BSB tracked at Santa Catalina Island, California by Mason and Lowe (2010). Fish tracked in the previous study used small, defined activity spaces and showed a strong association with sand/reef edge habitat. Previously conducted diver surveys have observed BSB more frequently and in higher densities associated with sand substratum along reef edges, remaining less

than 3 m off the seafloor (Anderson et al., 1989; Feder et al., 1974; Johnson et al., 1994; Quast, 1968).

Habitat use and movement patterns of non-spawning season fish may be partially explained by their diet preference. Adult BSB are ambush predators that feed almost exclusively on benthic and epibenthic sand and reef associated invertebrate and fish species, with 45% of their total diet consisting of reef species and 55% from sand associated species (Johnson et al., 1994; Roberts et al., 1984). Overall, fish tracked along the LAFB remained closely associated with the seafloor spending roughly equal proportions of time over available sand (52.3%) and reef habitat (47.7%) while remaining positively associated with the ecotone. This behavior likely results from the concentration of resources located along the ecotone edge (Reis et al., 2004). Edge associated species such as BSB may benefit from using both habitat types by having access to higher prey abundance and diversity while being in close proximity to both resting and refuge areas (Mason and Lowe, 2010; Reis et al., 2004). Along the LAFB, reef habitat may have provided increased access to prey during the day when BSB are known to actively forage (Roberts et al., 1984), as well as, refuge from other diurnally active piscivores, while at night, sand habitat may be of higher quality for resting when they are shown to exhibit the lowest levels of activity (Mason and Lowe, 2010).

A three dimensional (3D) analysis of barred sand bass movement patterns along the LAFB provided a more comprehensive estimation of space use than 2D approaches. A 2D approach alone suggests that time of day and habitat selection did not influence non-spawning season barred sand bass space use (e.g., activity space area or distance from seafloor); however, 3D analysis elucidated diel differences in activity space volume. This suggests that time of day and habitat selection may be more influential in dictating BSB activity levels and movement patterns than would otherwise be assumed.

#### 4.2. Spawning season fine-scale movement and habitat utilization

The movement patterns of BSB tracked throughout the summer spawning season at the Huntington Beach Flats (HBF) suggests that while individuals continue to reside on the spawning grounds they may not spawn every day. Although *Paralabrax* species are capable of daily spawning (Erisman and Allen, 2006; Martinez-Diaz et al., 2001; Miller and Allen, 2006; Oda et al., 1993), previously collected histological data suggest the average interval between barred sand bass spawning events is approximately two days (Oda et al., 1993), while data collected throughout the 2011 spawning season found significant differences in spawning interval by month, with July and August having significantly smaller intervals than June and September (Jarvis et al., unpubl. data). In addition, it has been documented across other serranid species that the proportion of sampled females present on a spawning ground with hydrated oocytes on any given day varies from 10 to greater than 90% (kelp bass, *P. clathratus*, Erisman and Allen, 2006; leopard grouper, *Mycteroperca rosacea*, Erisman et al., 2007). This further suggests that not all females residing on the spawning ground are actively spawning every day. Observations of Mediterranean dusky grouper (*Epinephelus marginatus*) also revealed that individuals did not exhibit spawning activity during consecutive days (Hereu et al., 2006; Zabala et al., 1997). Thus, we believe the two primary modes of behavior that we identified during spawning season are likely indicative of “resting” and “spawning/courtship” related behavior.

Males and females of the same species often exhibit distinct patterns of spawning and courtship behavior as well as differences in the frequency of spawning events (Hereu et al., 2006; Sancho et al., 2000a). However, we could not determine sex for most spawning season individuals, as BSB do not show obvious sexual dimorphism,

with the exception of some males that exhibit minor seasonal color pattern changes during spawning (Allen and Hovey, 2001; Erisman and Allen, 2005). Nevertheless, reproductive data collected from 325 barred sand bass caught on the HBF spawning grounds during the summer of 2011 suggests that males and females were present in roughly equal proportions within the water column as well as along the seafloor (Jarvis et al., unpubl. data). In addition, the BSB we tracked during the summer spawning season frequently exhibited more than one of the observed patterns of behavior over successive tracking periods. Therefore, it is unlikely that sex explains the different patterns of BSB spawning season behavior; however, additional research is needed to definitively discern if any sex-based spawning behavior is exhibited at aggregation sites.

Many aggregative spawners, including barred sand bass, exhibit strong site fidelity to their spawning grounds, returning year after year to the same spawning location (Colin, 1992; Jarvis et al., 2010; Love et al., 1987; Zeller, 1998). Thus, it is assumed that the location of these spawning sites are not random and are chosen because they provide some reproductive advantage, reduce predation risks, enhance gamete mixing and fertilization success or chance of successful recruitment (Barlow, 1981; Claydon, 2004; Colin, 1992; Doherty et al., 1985; Johannes, 1978; Love et al., 1987; Robertson, 1991; Sancho et al., 2000a,b). While most aggregative spawning serranids form breeding aggregations over areas of high relief or complexity (Colin, 1992; Erisman and Allen, 2006; Erisman et al., 2007; Rhodes and Sadovy, 2002; Sadovy et al., 1994; Sancho et al., 2000a), spawning season BSB were detected almost exclusively over sand habitat. By spawning over relatively uniform deeper water sand habitat, individuals may avoid or reduce egg loss that would be expected if they continued to utilize shallow reef habitats that contain higher densities of egg predators (Love et al., 1987). Individuals of another local temperate species, California scorpionfish (*Scorpaena guttata*) also move away from reef structures to form long-term summer spawning aggregations over sand habitat (Love et al., 1987).

Fish species that utilize habitats of low complexity generally move more and use larger areas to meet their daily requirements than species that inhabit areas of high relief or complexity (Lowe and Bray, 2006). In the current study, presumed spawning individuals used considerably larger areas than either presumed resting or non-spawning season fish that showed a strong association with ecotone habitat. Tropical serranid species (e.g., Nassau grouper, *Epinephelus striatus*; red hind, *E. guttatus*; camouflage grouper, *E. polyphekadion* and leopard grouper) that form large seasonal spawning aggregations of similar densities to those reported for BSB, but over complex reef habitats, utilized considerably smaller areas (0.5–2.0 km<sup>2</sup>) (Colin, 1992; Erisman et al., 2007; Rhodes and Sadovy, 2002; Sadovy et al., 1994) during the spawning season than barred sand bass. While this is consistent with the daily activity space area utilized by spawning individuals in the present study, BSB spawning aggregations occur throughout the HBF spawning grounds, which encompasses a ~55 km<sup>2</sup> area. Consequently, individual barred sand bass may have to travel significantly farther to find conspecifics or move between discrete aggregations. In addition, presumed spawning individuals were predominately detected higher in the water column. Therefore, individuals no longer have a fixed benthic reference point and are at the mercy of the longshore currents that are characteristic within the HBF spawning ground. Without prominent benthic features, the aggregations meander over large areas throughout the course of a day, resulting in a much larger activity space. During nighttime tracking periods presumed spawning individuals were relatively sedentary while remaining closely associated with the seafloor. The sharp peaks in distribution of nighttime geolocations over sand habitat were driven by dispersal patterns of sporadic reef structures located within the Huntington Beach spawning grounds (Mason and Lowe, 2010).

Reef structures and ecotone habitat may be important during the spawning season for presumed resting individuals. While still utilizing primarily sand habitat these individuals displayed a positive association with reef edges. This more direct ecotone association may provide additional benefits or resources for resting individuals in the form of increased access to foraging, resting and refuge areas. One exception to this pattern was fish 13, which exhibited horizontal and vertical movement consistent with other presumed resting individuals, but it remained exclusively within sand habitat and unassociated with any known reef structures, ultimately exhibiting a negative edge response. Due to high spawning energy requirements, it is possible that for this individual the cost of migration to the nearest recognizable reef patch was greater than the benefit of resting at its spawning location or that this individual was associated with structured habitat not identified on the bathymetry maps. Turner et al. (1969) reported seeing “gaunt and outwardly inactive” BSB resting on reefs or sand ecotone after spawning.

Barred sand bass, unlike other serranid species, did not aggregate to a definable geological habitat feature such as a reef or pinnacle, but were found to aggregate in mid-water over relatively featureless substratum (sand). Hydroacoustic surveys and video recordings on the HBF also confirmed the daytime presence of BSB associated with the thermocline (L.G. Allen, unpubl. data<sup>1</sup>). The thermocline may provide a recognizable habitat feature to which individuals can orient. This may increase their chance of encountering other reproductively active individuals and might help synchronize spawning activity, ultimately ensuring higher reproductive success (Eckmann, 1991; Shapiro et al., 1988).

Barred sand bass may also be seeking out areas within the HBF where oceanographic conditions favor successful spawning, provide ideal temperatures/conditions for eggs and larvae, as well as advantageous areas of ichthyoplankton dispersal/movement (Colin, 1992; Sancho et al., 2000b). For example, while in warmer strata of the water column, females may benefit from more rapid egg development and hydration (Gadomski and Caddell, 1996; Hereu et al., 2006). According to Gadomski and Caddell (1996), BSB eggs hatched at 12 °C, but the larvae abnormally developed and soon died. Successful hatching of viable embryos occurred only at 16–28 °C, with a median survival temperature of 20 °C, which is consistent with average thermocline to surface summer water temperature off the Southern California coast (Gadomski and Caddell, 1996). Although adult BSB utilizing the HBF spawning grounds experienced average water temperatures ranging from 11 °C (seafloor) to 19 °C (surface) (i.e., temperatures within the physiological limits of BSB eggs), it is likely that eggs and larvae are exposed to a narrower range of temperatures depending on depth of gamete release and rate of vertical ascent for positively buoyant eggs. Mediterranean dusky grouper adults also experience wide temperature ranges (~Δ7°) between their territories (20–35 m) and spawning depth (5–25 m) (Hereu et al., 2006; Zabala et al., 1997).

Fish are hypothesized to spawn at specific locations and times that best increase their fitness (Claydon, 2004). For many pelagic spawners, spawning times vary from early morning to just after sunset (Sancho et al., 2000b; Shapiro et al., 1988). Spawning season BSB believed to be actively participating within the spawning aggregation exhibited distinct diel patterns in space use, with the highest levels of activity observed throughout the day. These individuals were not only using significantly larger activity space areas and volumes during this time, but they also displayed patterns of vertical movement distinct from all other tracked fish by

associating with the thermocline and exhibiting diving behavior. While high levels of activity were detected during all day light hours, the temporal window of actual gamete release may be more constrictive. Histological evidence suggests that barred sand bass exhibit peak spawning during midday (12:00–14:00) (Oda et al., 1993); however, we did not detect a difference in activity during this period relative to other daytime periods. Therefore, additional studies are needed to make conclusions about the actual timing of gamete release in this species.

Periodic diurnal dive behavior displayed by spawning season BSB is believed to be analogous to upward vertical spawning rushes and courtship displays demonstrated by other aggregative spawning serranids (e.g., kelp bass; spotted sand bass, *P. maculatofasciatus*; leopard grouper; pygmy grouper, *Cephalopholis spiloparaea*) (Colin, 1992; Donaldson, 1995; Domeier and Colin, 1997; Erisman and Allen, 2006; Erisman et al., 2007; Miller and Allen, 2006). Among these serranid species, gamete release is seen at the apex of short 1–4 m vertical rushes during which time a group of individuals briefly rises out of the aggregation and quickly returns; however, longer vertical rushes (10–15 m) have been reported in Nassau grouper, chocolate hind (*C. boenack*), Pacific creole fish (*Paranthias colonus*) and dusky grouper. Aggregation formation as well as gamete release has been observed occurring not only within a few meters from the surface (e.g., kelp bass, leopard grouper) but also within just a few meters of the substratum in water depths of 20–30 m (e.g., Nassau grouper, pygmy grouper) as well as in mid-water (e.g., Nassau grouper, chocolate hind, creole fish, dusky grouper) (Colin, 1992; Donaldson, 1995; Erisman and Allen, 2006; Erisman et al., 2007; Sala et al., 2003; Zabala et al., 1997). Courtship behavior terminating in a spawning event in kelp bass and Nassau grouper can last 15 s to several min, which is consistent with the duration of dives exhibited by BSB in this study (Erisman and Allen, 2006; Erisman et al., 2007). BSB tracked in our study exhibited downward vertical dives compared to upward vertical rushes; however, they are within the range of magnitude and duration reported for other serranids. It could be argued that gamete release is occurring at comparable depths or distance from either the surface or seafloor to other aggregative spawning serranids, if in fact gamete release is taking place at the nadir of a dive compared to the zenith of a rush. It is also possible that spawning individuals are releasing gametes near the thermocline upon returning to the aggregation post-dive. While diver observations and video recordings are frequently used to study tropical and sub-tropical serranid spawning behavior and to elucidate timing of gamete release, these methods are not feasible at locations such as the HBF which have extremely poor visibility, strong offshore currents, heavy boat traffic and close proximity to a major shipping channel. Therefore, utilizing a Laser Optical Plankton Counter (LOPC) or a Multiple Opening/Closing Nets and Environmental Sampling System (MOCNESS) to determine egg density at specific depths may be a more feasible option for future studies to address questions related to depth of gamete release in this species.

Piscivorous and planktivorous predation pressure influences spawning behavior and spawning related movement patterns of reef-associated species, specifically the commonly observed ascent or rushing behavior of pelagic spawners (Claydon, 2004; Habrun and Sancho, 2012; Moyer, 1987; Robertson, 1991; Sancho, 2000; Sancho et al., 2000a). Therefore, predation pressure may also be the mechanism driving the observed dive behavior of spawning season BSB. Adult BSB have relatively few predators; therefore, risk of egg predation may be the factor most greatly influencing this spawning related behavior (Sancho et al., 2000a). Diving behavior may facilitate movement away from mobile schooling egg predators that frequent the warmer mixed layer of the water column at the HBF spawning ground, thereby reducing predation risks (Zwolinski

<sup>1</sup> <http://www.usc.edu/org/seagrant/Publications/PDFs/AllenUSCSGFeasibilityRpt9-10-10.pdf>. Accessed 15 March 2012.



et al., 2012; L.G. Allen, unpubl. data<sup>2</sup>). In addition, dive behavior typically terminated 5–15 m below the thermocline. If eggs are in fact released at the nadir of a dive or upon return of some of the exhibited dives, then it may take up to several hours for gametes to reach the surface (Colin, 1992), allowing strong longshore currents to move eggs away from adult aggregations and schooling egg predators such as Northern anchovies (*Engraulis mordax*), Pacific sardines (*Sardinops sagax*) and Pacific mackerel (*Scomber japonicas*).

#### 4.3. Management implications

Knowledge of barred sand bass movement patterns and space use might provide additional information necessary for the development of new management policies that specifically address the vulnerability of spawning aggregation to harvest impacts. For example, increased levels of spawning-related activity gleaned from acoustic telemetry data may allow researchers to determine peak spawning periods during spawning season and thereby identify periods when reproductive output is likely highest and when fish are most vulnerable to fishing. Our fine-scale movement data suggests that presumed spawning activity was highest during the last two weeks in July. Thus, a temporary fishing closure corresponding with this peak in spawning activity could provide relief from fishing pressure while increasing spawning output. To address recent saltwater bass population declines, the California Fish and Game Commission adopted a 14-in minimum size limit and a five fish aggregate bag limit for barred sand bass, kelp bass, and spotted sand bass. While a reduction in the bag limit and an increase in the minimum size limit may help offset recent BSB catch declines, it will likely take several years before regulation effectiveness can be addressed. If further protection is found to be necessary, a spawning season closure may be the most effective management strategy for conserving the stock. Currently, less than 4% of BSB spawning habitat is included in the recently implemented Marine Protected Area (MPA) network in southern California (Fish and Game Commission, 2012). Moreover, seasonal area closures of a few key spawning aggregation sites such as the HBF may not be feasible and would be hard to enforce during spawning season because our data indicate BSB are associated with multiple habitat types, have extremely large daily activity spaces, and utilize even larger spawning grounds. It remains unclear what the direct impacts of sustained fishing pressure are on spawning-related behavior, movement patterns and habitat use of BSB and other closely related temperate serranid species. Further research is warranted and recommended.

#### Acknowledgements

We would like to thank the staff of the California Department of Fish and Wildlife (CDFW) Marine Region particularly Chuck Valle, H. Gliniak, O. Horning and T. Mason who provided logistical and field support; L.G. Allen and K.A. Young for feedback on data analysis and interpretation. We also gratefully acknowledge all of the student volunteers and interns who dedicated their time to help fish and track. Funding for this research was provided by the Federal Aid in Sport Fish Restoration Act (CDFW Grant # F-50-R-24), the CSULB Graduate Research Fellowship, the SCTC Marine Biology Foundation and the LA Rod and Reel Club.

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