ABSTRACT

FINE-SCALE HORIZONTAL AND VERTICAL MOVEMENT OF BARRED SAND BASS, *PARALABRAX NEBULIFER*, DURING SPAWNING AND NON-SPAWNING SEASONS

By

Megan Kline McKinzie

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Habitat use, ecotone edge response, activity space size and associations with the seafloor and thermocline were compared for spawning and non-spawning season barred sand bass. Non-spawning season fish showed affinity with sand/reef ecotone using average activity space areas of 0.003 ± 0.001 km^2 (± SD) and volumes of 0.00001 ± 0.000005 km^3 while remaining 1.9 ± 1.7 m off the seafloor. Spawning season fish used activity spaces areas of 0.139 ± 0.370 km^2 and volumes of 0.001 ± 0.002 km^3. Spawning season individuals displayed two patterns of behavior, one indicative of spawning and another of resting behavior. Resting individuals 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 preferred sand habitats, using significantly larger activity spaces during the day than at night while associating with the thermocline and making vertical dives toward the seafloor.

FINE-SCALE HORIZONTAL AND VERTICAL MOVEMENT OF BARRED SAND BASS, *PARALABRAX NEBULIFER*, DURING SPAWNING AND NON-SPAWNING SEASONS

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CHAPTER 1

INTRODUCTION

Aggregate spawning is the most commonly observed mating style among large and economically important reef fish (e.g., snappers, groupers, sea basses) where tens to thousands of conspecific 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 aggregate behavior is most commonly observed, where individuals travel great distances (ten to hundreds of km) away from home reefs to assemble at spawning grounds for weeks to months each year. In addition, aggregate spawners typically exhibit strong site fidelity to their individual spawning grounds (Colin 1992; Johannes et al. 1999; Jarvis et al. 2010). Spawning aggregations likely represent all the reproductive activity for a given year and it is critical for population maintenance that these aggregations persist (Shapiro et al. 1993; Rhodes and Sadovy 2002).

The predictable nature of these annual spawning aggregations in both time and space, and high fish aggregation density, makes transient aggregate spawners highly susceptible to overfishing (Rhodes and Sadovy 2002; Erisman et al. 2008; Erisman et al. 2011). Fishing pressure by both commercial and recreational fisheries on spawning aggregations reduces overall biomass, decreases size and age at sexual maturity, alters sex ratios and potentially disrupts the social structure necessary for successful reproduction (Rhodes and Sadovy 2002; Nemeth 2005; Erisman et al. 2007). These spawning aggregations may be solely responsible for replenishing local fisheries through recruitment and larval retention, thereby targeted overfishing can cause population level impacts through a reduction in species abundance (Sadovy and Domeier 2005; Nemeth 2005). Many aggregating serranid species are important predators within tropical and rocky reef communities during their non-reproductive seasons. Reduction in abundance of these predators could ultimately result in a shift in community structure. Therefore, ecosystem level effects could also be seen if stocks continue to decline because of overfishing (Sadovy and Domeier 2005).

Unfortunately, overfishing of aggregate spawners can be masked by hyperstability, where catch-per-unit effort (CPUE) remains high or even increases while true population abundance actually declines. This hyperstable state often continues until the population reaches critically low levels (Sadovy and Domeier 2005; Jarvis et al. 2010; Erisman et al. 2011). Regional stocks of one of California's largest recreational fishery species, barred sand bass (*Paralabrax nebulifer*) have shown signs of decline in recent years due to decades of fishing known seasonal spawning aggregations and unfavorable oceanographic conditions (Chih-hao et al. 2005; Erisman et al. 2011). This has lead to a growing concern over the sustainability of the stock.

Peak barred sand bass spawning season is from June-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 to 40 m (Turner et al. 1969; Love et al. 1996a; Hovey et al. 2002; Jarvis et al. 2010). Historical barred sand bass spawning aggregation sites include the Ventura Flats, inner Santa Monica Bay, Huntington Beach Flats, San Onofre and Silver Strand (Love et al. 1996a; Jarvis et al. 2010). Tag and recapture data suggest that individuals 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).

While the timing and location of barred sand bass spawning aggregations is well documented, very little is known about their spawning related movement once individuals reach their seasonal spawning sites. It is possible that they will behave similarly and exhibit patterns of behavior consistent with other *Paralabrax* species. Closely related congeners, kelp bass (*P. clathratus*) and spotted sand bass (*P. maculatofasciatus*) are reported to display spawning behavior throughout their spawning period. In these species, behavioral observations and histological data reveal that courtship behavior begins in the late afternoon continuing through the day with spawning commencing shortly before sunset (Oda et al. 1993; Martinez-Diaz et al. 2001; Erisman and Allen 2006). In contrast to other *Paralabrax* species, 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 (Martinez-Diaz et al. 2001; Erisman and Allen 2006; Miller and Allen 2006). Males and females also spawn multiple times during the course of a single evening (Martinez-Diaz et al. 2001; Erisman and Allen 2006).

Gathering detailed information about how barred sand bass utilize their spawning grounds as well as spawning-related movement and behavior is essential to better understand the temporal and spatial dynamics of barred sand bass spawning aggregations. The purpose of this study was to characterize fine-scale horizontal and vertical movement patterns of tagged barred sand bass during the spawning and non-spawning seasons and to quantify activity space size (area and volume), habitat use and preference, and diel patterns of activity. Movement patterns believed to be indicative of spawning and/or courtship were determined through the comparison of spawning and non-spawning season individuals.

CHAPTER 2

MATERIALS AND METHODS

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) (Figure 1). The HBF is one of the largest and most heavily targeted spawning aggregation sites for barred sand bass (*Paralabrax nebulifer*) in California (Love et al. 1999a; Jarvis et al. 2010). 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^2 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^2 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 Harbor, 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).

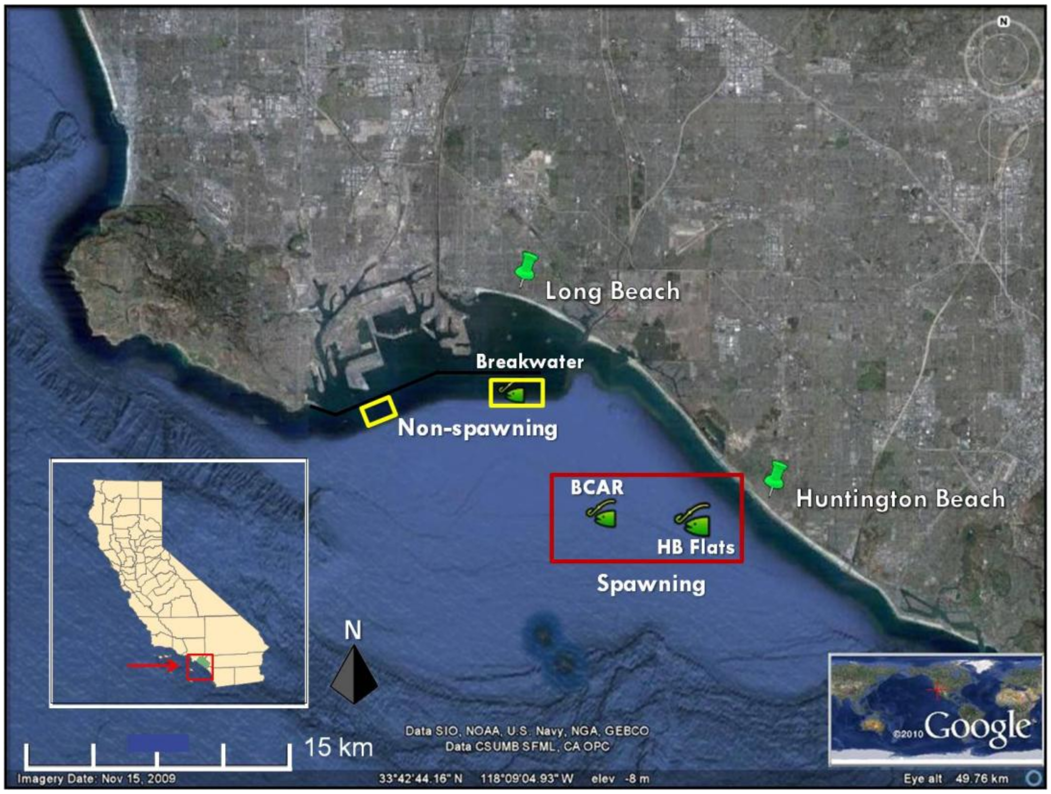


FIGURE 1. Reference map of 2009-2010 spawning (red) and 2011 non-spawning season (yellow) study sties.

Tagging Procedure

Seventeen adult barred sand bass (> 31 cm total length, TL) were collected along the HBF using hook and line from May-Aug during the 2009 and 2010 summer spawning seasons and along the LAFB from Feb-June, 2011. Both sexes are fully mature by 27 cm TL (Love et al. 1996b). Once on board the tagging vessel, fish were anesthetized by submersion in a saltwater bath containing MS-222 (tricaine methanesulfonate - Finquel™, 0.1 g l^{-1}) for several minutes (Munday and Wilson 1997; Cho and Heath 2000). A small acoustic transmitter (Vemco Ltd.; V13-1L acoustic pinger: 36 mm long x

13 mm diam. or a depth sensing V13P-1L; depth rating: 50 ± 2.5 m; 45 mm long x 13 mm diam.) was surgically implanted within the peritoneal cavity through a 1-2 cm incision made approximately 1 cm from the ventral midline between the pelvic fins and vent. The incision was closed with 2-3 discontinuous dissolvable sutures (Ethicon Inc.; Chromic Gut). Transmitters were covered with a paraffin and beeswax mixture (2.3:1) to reduce the risk of an immune-rejection response. An antibiotic ointment was also spread over the wound to further reduce the risk of infection (e.g., Lowe et al. 2003; Topping et al. 2005; Mason and Lowe 2010). Upon completion of surgical procedures, 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., Lowry and Suthers 1998; Lowe et al. 2003; Topping et al. 2005). Individuals were then transferred to a bin of fresh seawater for recovery (5-10 min) and released at the site of capture.

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.; VH100) 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 sec 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 substratum type, sea conditions and water depth at a gain of 0 dB and signal strengths of 86-105 dB. For data analysis, the boat geographic position was assumed equal to fish position (Brill et al. 1999; Cartamil and Lowe 2004). Seafloor depth and presence of other fish were manually recorded every 10 min along with the geolocations of the target fish via the vessel depth sounder (1kW 50 and 200 kHz transducers).

Oceanographic Measurements and 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 verses 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 derivate 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 derivate 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.

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 strength 86-105 dB). Filtered tracking data was plotted on a geo-referenced map of the study area in ArcView 3.3 and ArcMap 10 GIS. ArcView 3.3 Animal Movement Analysis Extension (AMAE) (Hooge and Eichlaub 2000) 95% kernel utilization distribution (KUD) was used to determine the area of individual barred sand bass daily activity spaces. 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 and preference 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 tool near and detection frequency was plotted with 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 was 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 depth 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. To analyze overall levels of activity on a finer temporal scale, kdes for each fish were also determine by hourly bins. Hourly kdes of spawning and non-spawning season fish were compared using a Kruskal-Wallis test. If significant differences were found between hours, the Dunn's method of multiple comparisons was performed as a post-hoc 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.

CHAPTER 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 (Figure 2). Twelve of the seventeen individuals (333-635 mm TL) were tagged within the HBF spawning grounds (14-29 m) from June-Aug 2009 and May-Aug 2010. Five of these fish were tagged with V13 acoustic pingers 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 (13-16 m) from Feb-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 2-20 d and averaged 7.3 ± 5.7 d (± SD). Time between individual successive tracks ranged from 1-59 d with an average of 7.3 ± 17.1 d.

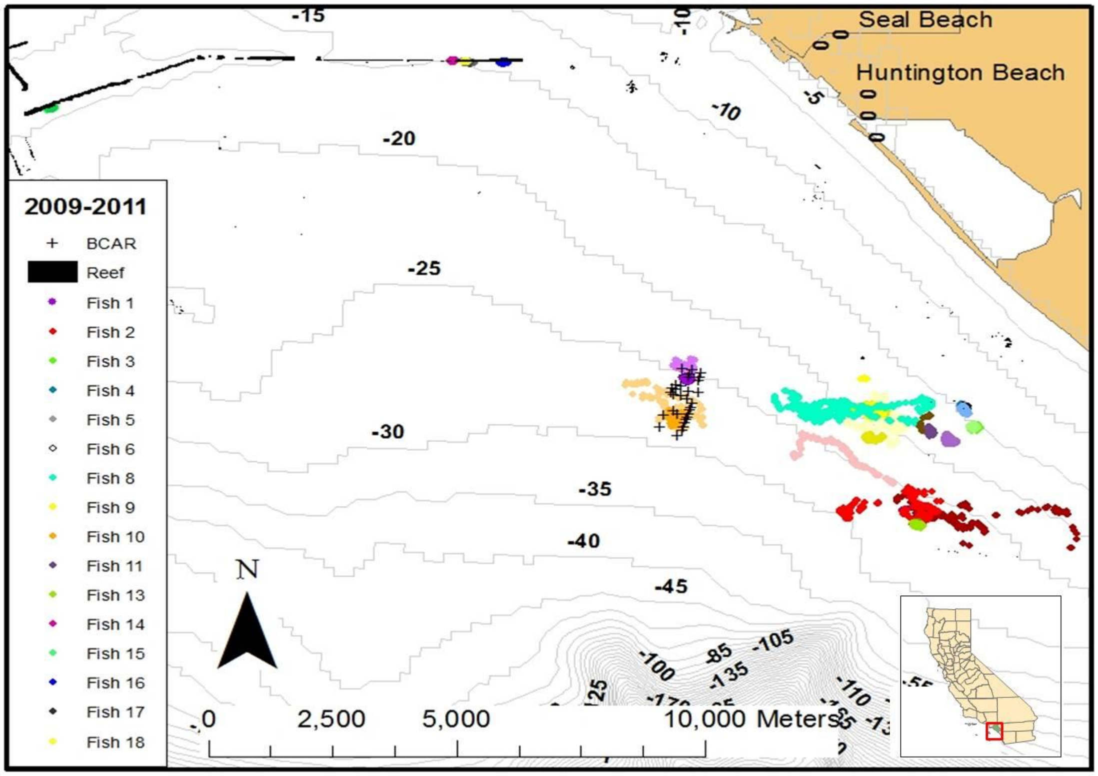


FIGURE 2. Map of the Huntington Beach Flats, including the Bolsa Chica Artificial Reef and Los Angles Federal Breakwater showing completed tracks for all spawning and non-spawning season fish. Track coloration for all fish goes from light to dark with each consecutive track. Natural and artificial reef patches appear in black.

Activity Space Area

Spawning season fish used significantly (4500%) larger daily activity spaces (95% KUD) than non-spawning season fish (Mann-Whitney $U = 13$, $p < 0.001$) (Figure 3). Daily activity space area varied considerably between and among individuals tracked during the spawning season and ranged from 0.002 to 1.89 km^2, averaging 0.139 ± 0.370 km^2 (± SD). These individuals showed distinct diel patterns of activity, utilizing significantly larger areas during the day than at night (Day: 0.136 ± 0.386 km^2, Night: 0.051 ± 0.205 km^2; Mann-Whitney $U = 172$, $p = 0.03$) (Figure 4). Non-spawning season fish used average home range sizes of 0.003 ± 0.001 km^2 (range: 0.002 to 0.006 km^2), with no significant difference between day and night activity space area (Mann-Whitney $U = 36$, $p = 0.89$) (Figure 4). 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.

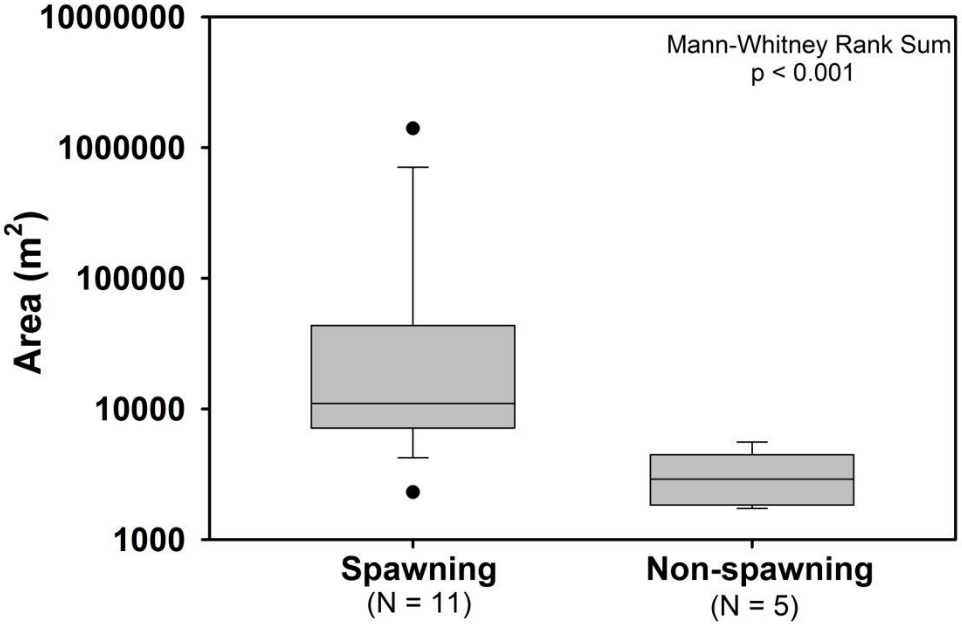


FIGURE 3. Plot comparing daily activity space area for barred sand bass actively tracked during the spawning and non-spawning seasons.

Habitat Utilization

Non-spawning season fish remained strongly associated with the sand/reef ecotone, exhibiting a positive edge response that peaked at 12 m from the edge before decreasing (Figure 5a). There were 52.3% of geolocations that occurred within 60 m

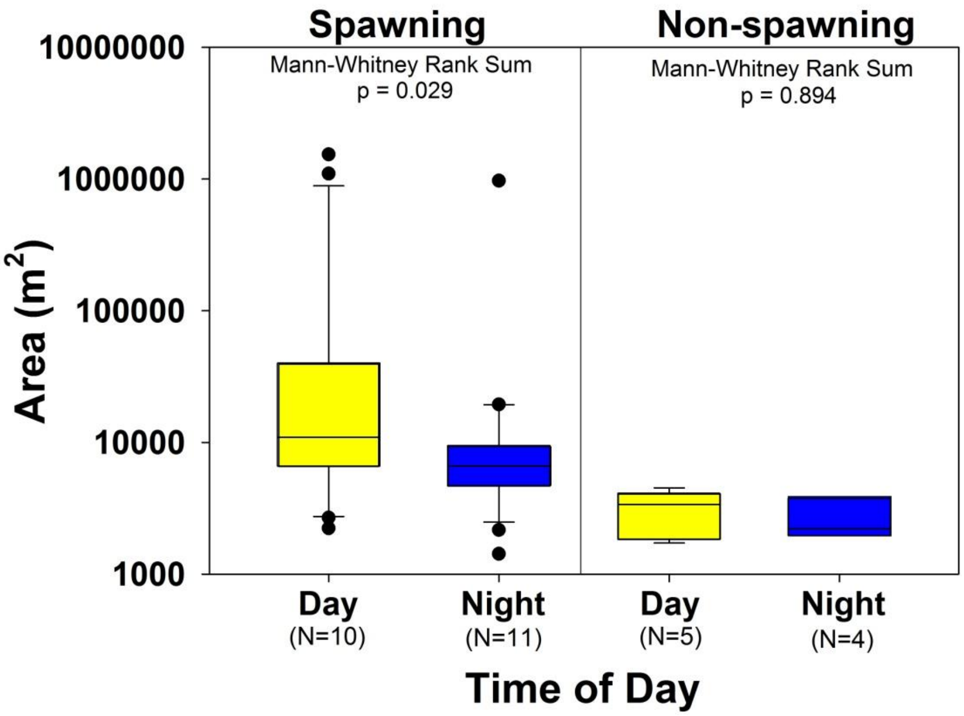
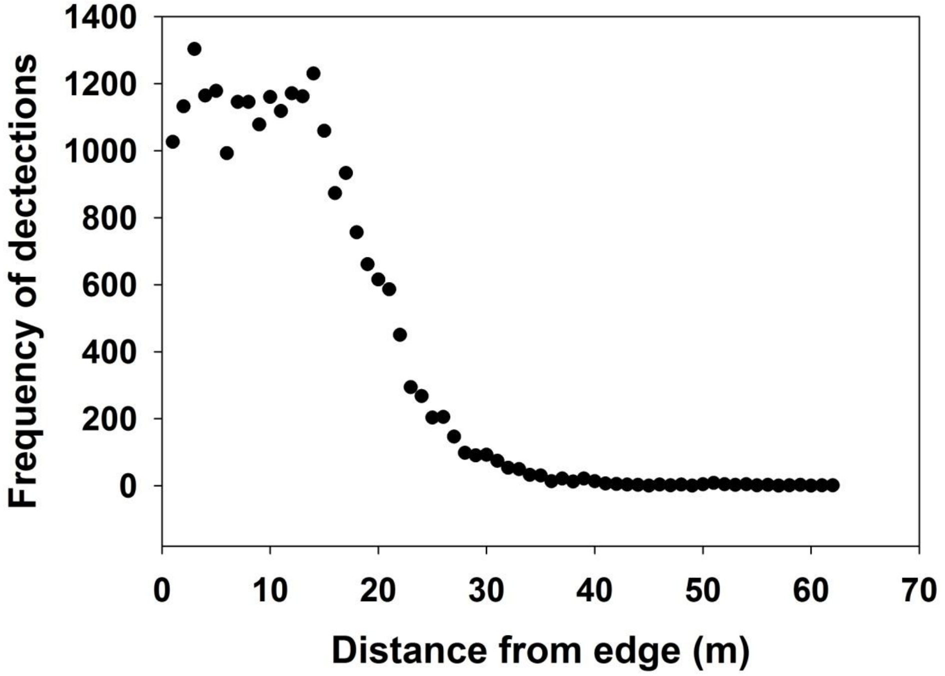


FIGURE 4. Box and whisker plot of barred sand bass day verses night activity space area during spawning and non-spawning seasons.

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 shifts in habitat preference, 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) (Figure 6a, 6b).

(a) LAFB—Non-Spawning



(b) HBF—Spawning Season

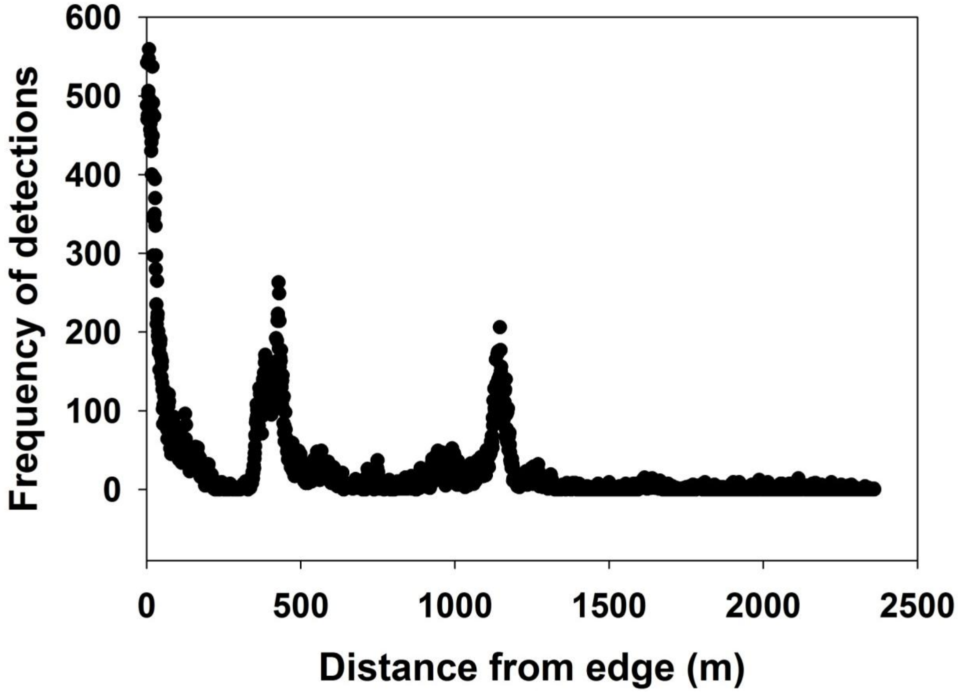


FIGURE 5. (a) The positive edge response of five non-spawning season fish tracked along the Los Angeles Federal Breakwater, California and (b) the sand/reef habitat transitional edge response of eleven actively tracked barred sand bass at one known spawning aggregation site, the Huntington Beach Flats, California.

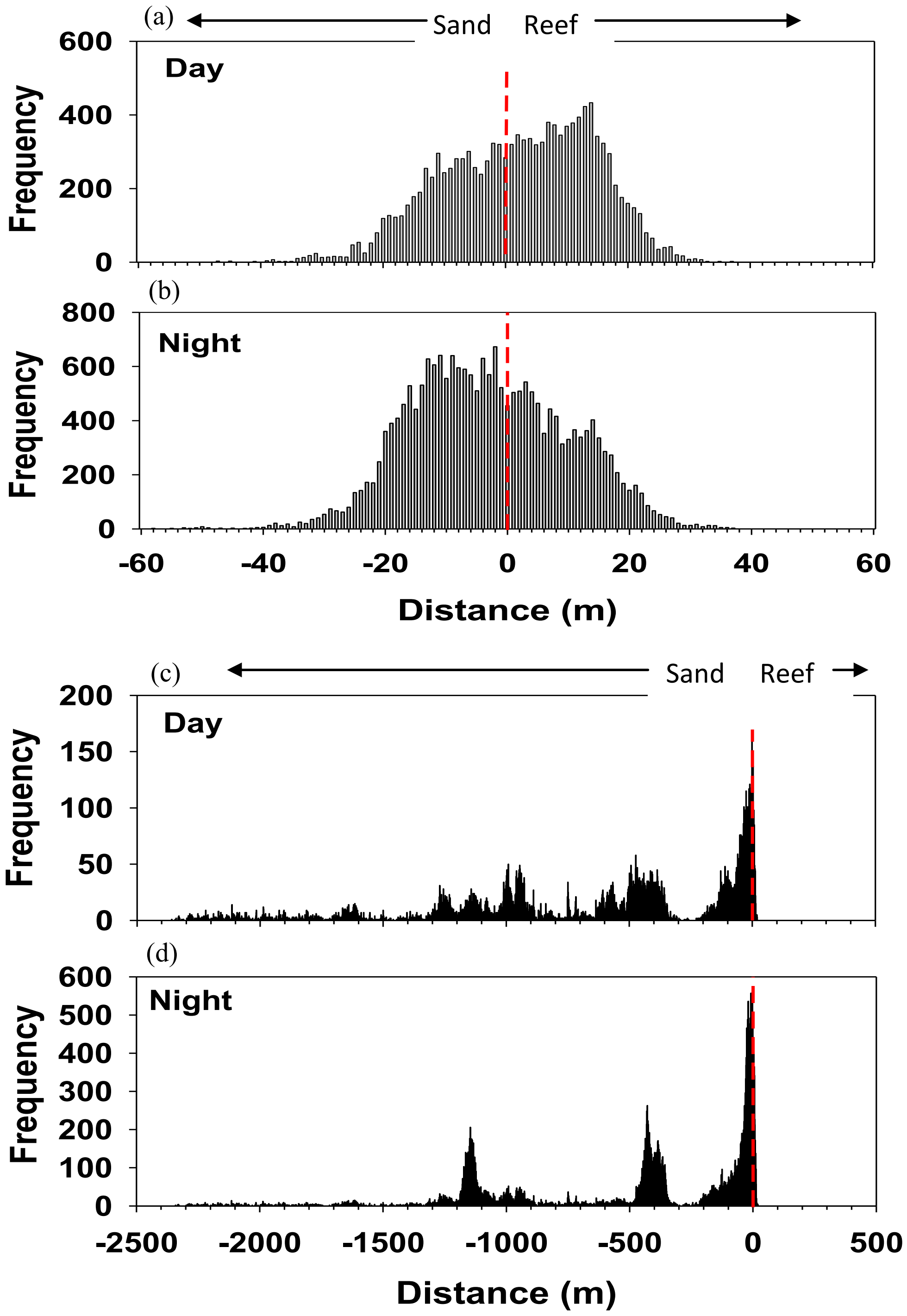


FIGURE 6. Histograms of day and night detections at 1 m bins from sand/reef edge for barred sand bass tracked during the (a, b) 2011 non-spawning season and (c, d) 2009-2010 summer spawning season. Negative distances represent detections in sand habitat and positive distances within reef habitat. Red dashed line indicates location of sand/reef ecotone.

Spawning season individuals preferred sand to available reef habitat in 15-30 m of water, with 94.2 % of geolocations occurring within 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) (Figure 5b). 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 (Figure 6c). 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 (Figure 6d).

Vertical Movement Patterns

All spawning season individuals remained significantly farther from the seafloor during the day than at night (Day: 7.4 ± 5.8 m, Night: 4.2 ± 2.3 m; Mann-Whitney $U = -35176177994$, $p < 0.001$) while non-spawning season fish remained on average 1.9 ± 1.7 m off the seafloor throughout day and night periods (Mann-Whitney $U = 4181178779$, $p = 0.23$) (Fig. 7). Spawning season fish residing in the water column also remained significantly closer to the thermocline (15.8 ± 1.6 °C, 11.7 ± 3.7 m) during the day than at night (Man-Whitney $U = -14487202450$, $p < 0.001$) (Figure 8). Based on time/depth profiles, three main patterns of vertical movement were detected; one pattern representing non-spawning season behavior (Figure 9), one believed to be indicative of spawning/courtship related behavior (Figure 10) and another believed to be spawning season resting behavior (Figure 11). Fish that we believed to be actively participating within the spawning aggregation exhibited diel shifts in vertical movement, remaining approximately 3.6 ± 4.3 m (± SD) off the seafloor at night and moving up into the mid-water column (8.3 ± 6.0 m off substratum) during the day, primarily within or just below the thermocline. During the day, these individuals continually made directed dives towards 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 ± 2.3 m off the seafloor throughout both day and night periods.

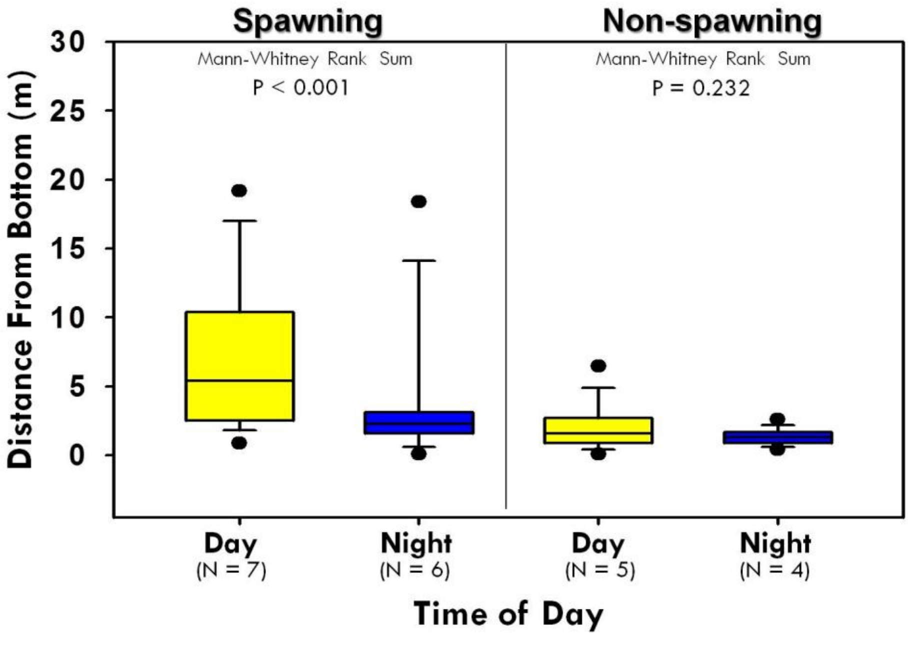


FIGURE 7. Box and whisker plot showing distance from bottom during day and night periods for both spawning and non-spawning season barred sand bass.

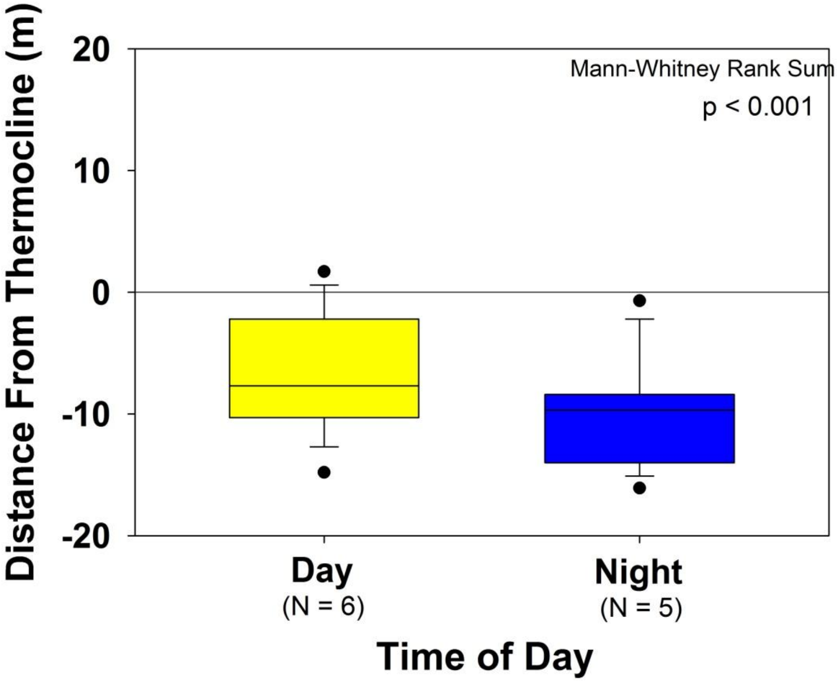


FIGURE 8. Plot showing distance of fish from thermocline during day and night periods for barred sand bass actively tracked during the spawning season.

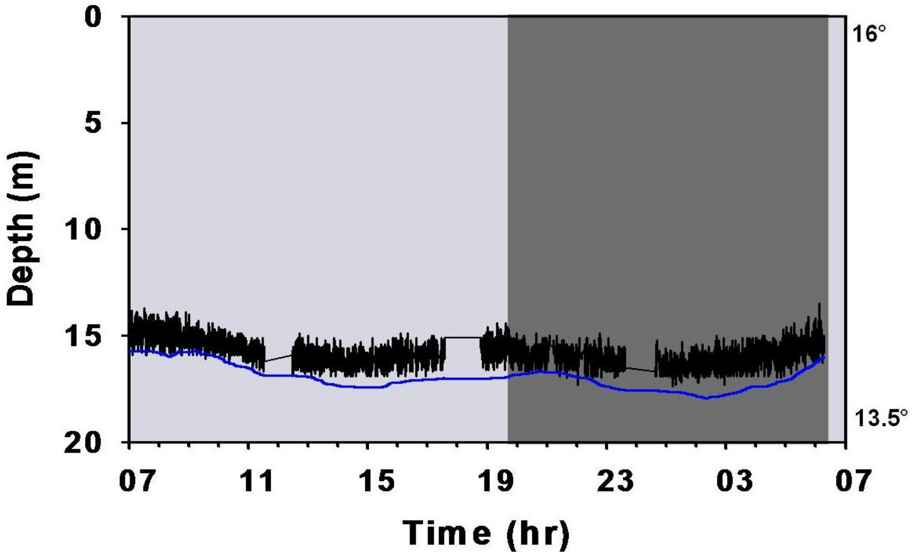


FIGURE 9. Representative depth profile of non-spawning season barred sand bass behavior. Solid blue line represents seafloor. Dashed and solid grey lines indicate location of the thermocline. Day- and nighttime periods are indicated by the light and dark gray boxes, respectively.

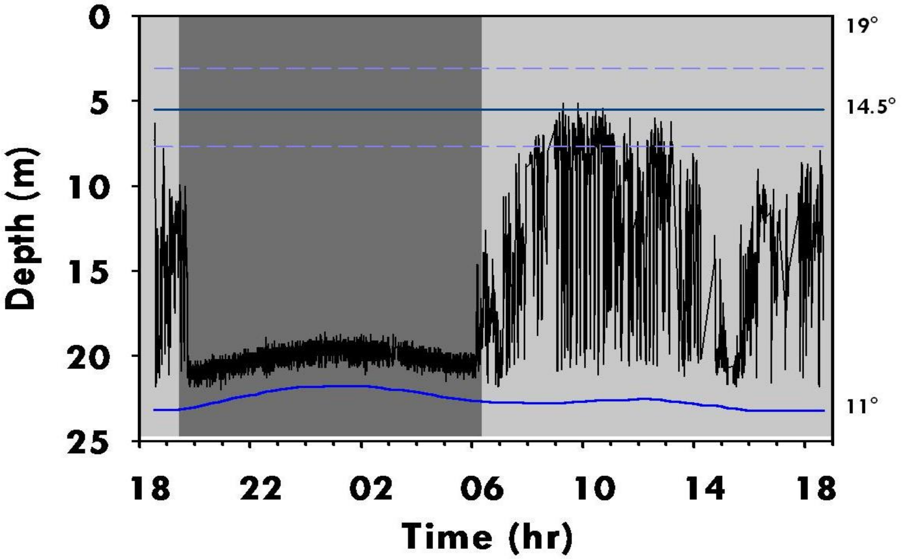


FIGURE 10. Representative depth profile of presumed barred sand bass spawning/ courtship related behavior. Solid blue line represents seafloor. Dashed and solid grey lines indicate location of the thermocline. Day- and nighttime periods are indicated by the light and dark gray boxes, respectively.

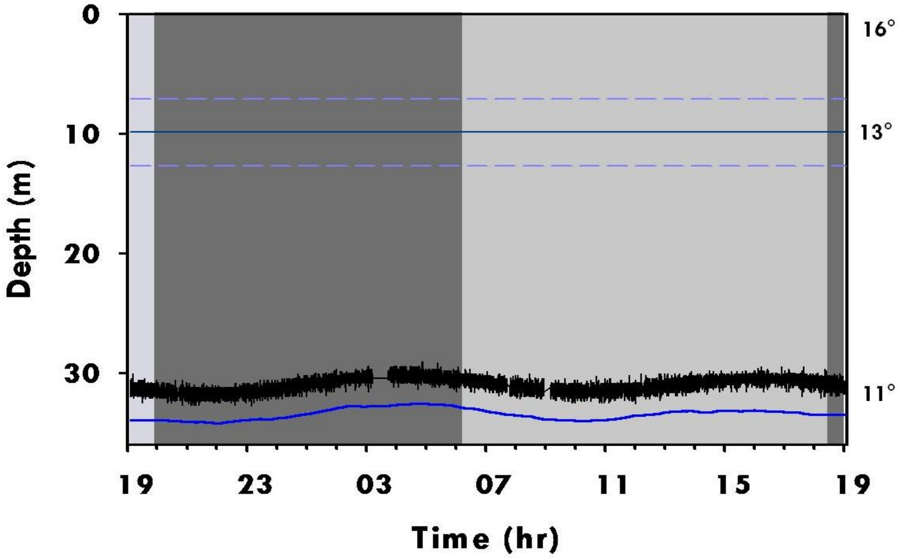


FIGURE 11. Representative depth profile of presumed barred sand bass spawning season resting behavior. Solid blue line represents seafloor. Dashed and solid grey lines indicate location of the thermocline. Day- and nighttime periods are indicated by the light and dark gray boxes, respectively.

Activity Space Volume

Spawning season fish used significantly (7500 %) larger volumes than non-spawning season fish (Mann-Whitney $U = 5, p < 0.001$) (Figure 12). Spawning season individual daily activity space volume averaged 0.001 ± 0.002 km^3 (range 0.00001-0.007 km^3) (Figure 14b, c) and fish used significantly more of the available water column during the day than at night (Day: 0.001 ± 0.002 km^3, Night: 0.0002 ± 0.0007 km^3; Mann-Whitney $U = 38, p = 0.003$) (Figure 13). Spawning season fish were significantly more active during the 11:00 hr then during the 22:00 hr, but the activity space volume used during the 11:00 hr period was not significantly greater than any other hourly period of day (00:00-10:00, 12:00-21:00 or 23:00) and none of the other hours were significantly different from each other (Kruskal-Wallis $H_{23,6} = 53, p < 0.001$). Overall, spawning season fish exhibited the highest levels of activity during the 3rd and 4th weeks of July. Non-spawning season fish used on average 0.00001 ± 0.000005 km^3 (range 0.000007-0.00002 km^3) (Figure 14a), also showing higher levels of activity during the day than at night (Day: 0.00001 ± 0.000006 km^3, Night: 0.000006 ± 0.000003 km^3; Mann-Whitney $U = 29, p = 0.03$) (Figure 13). Non-spawning season fish did not exhibit significantly higher levels of activity during any individual hour of the day or night (Kruskal-Wallis $H_{23,4} = 28, p = 0.22$). 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.

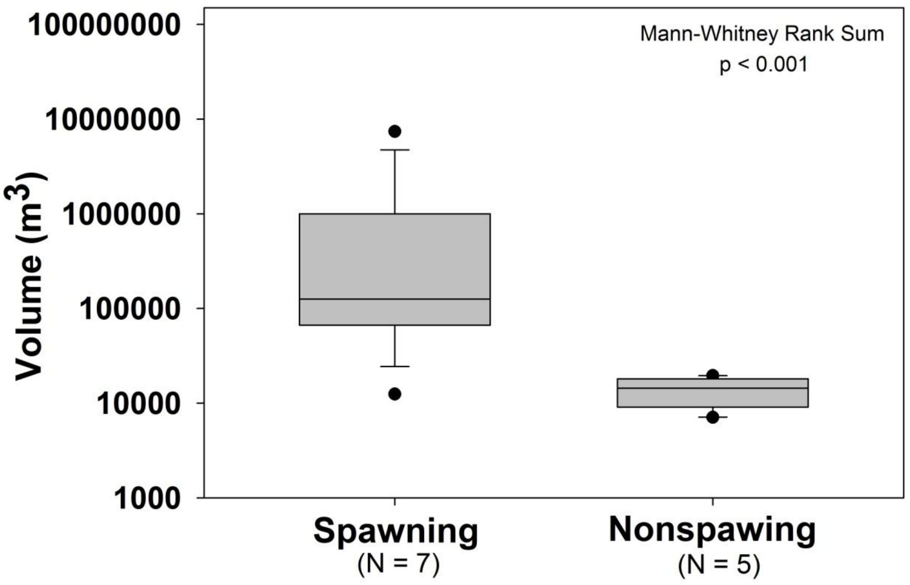


FIGURE 12. Plot comparing daily activity space volume for barred sand bass actively tracked during the spawning and non-spawning seasons.

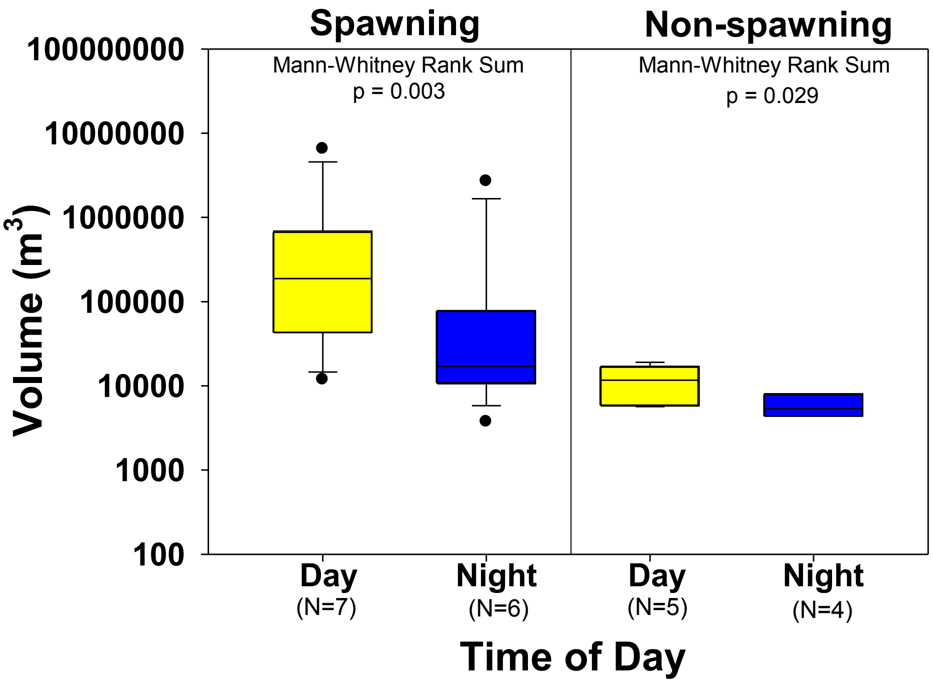


FIGURE 13. Box and whisker plot of day verses night activity space volume for barred sand bass actively tracked during spawning and non-spawning seasons.

(a)

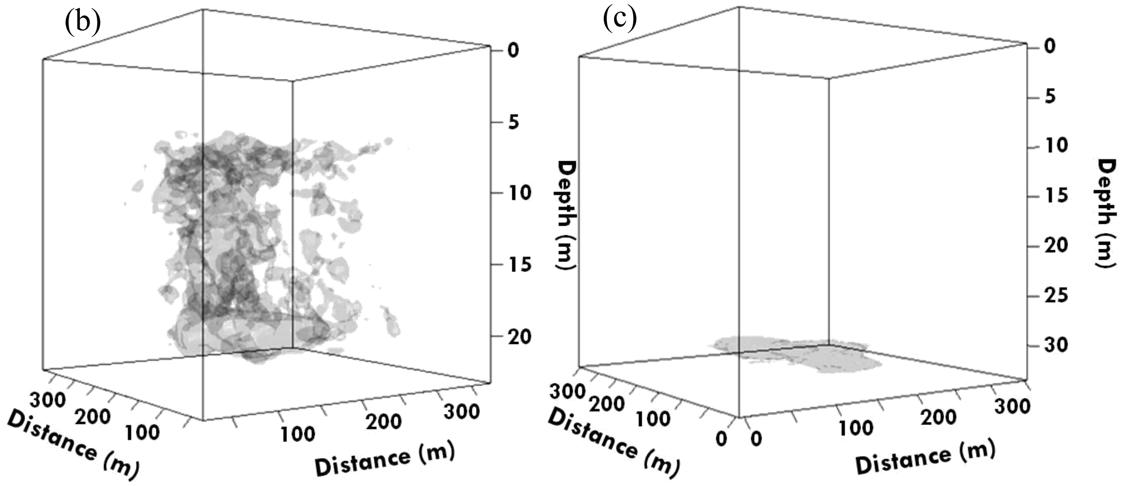


FIGURE 14. Representative barred sand bass 3D daily 95% kde activity spaces depicting (a) non-spawning season behavior, (b) presumed spawning/courtship related behavior and (c) presumed spawning season resting behavior. Maximum depth is representative of actual seafloor depth.

CHAPTER 4

DISCUSSION

The present study is the first report of barred sand bass (*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. While there was typical individual variability in horizontal and vertical movement among actively tracked barred sand bass, 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.

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 barred sand bass 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 preference for sand/reef edge habitat. Previously conducted diver surveys have also directly observed barred sand bass more frequently, and in higher densities associated with sand substratum along reef edges, remaining less than 3 m off the seafloor (Quest 1968; Feder et al. 1974; Anderson et al. 1989; Johnson et al. 1994).

Habitat use and movement patterns of non-spawning season fish may be partially explained by their diet preference. Adult barred sand bass 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 (Roberts et al. 1984; Johnson et al. 1994). 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 barred sand bass (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 (Reis et al. 2004; Mason and Lowe 2010).

Potential differences in the distribution of resources between preferred habitats within the Catalina Island Marine Science Center Marine Life Refuge (CMLR) and along the LAFB may have contributed to the observed differences in diel patterns of habitat selection between the two tracking studies. Mason and Lowe (2010) determined that habitat selection did not differ between day- and nighttime periods, but fish tracked in this study along the LAFB, selected available reef habitat during the day and sand habitat at night. For non-spawning season BSB this suggests that while both habitats contain essential resources, some of the available resources between the two habitat types may be complementary or different (Ries et al. 2004). Along the LAFB, reef habitat may have provided increased access to prey during the day when barred sand bass 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).

Habitat has also been shown to greatly influence activity space size as well as shape (Mathew 1990; Topping et al. 2005). The LAFB creates a natural boundary, which fish cannot cross, resulting in reef habitat with only one useable sand/reef edge causing fish to have more elongated home ranges than the majority of fish tracked at Santa Catalina Island by Mason and Lowe (2010). Elongated home ranges have been shown to result in smaller area use compared to irregular or circular home ranges (Zeller 1997; Eristhee and Oxenford 2001; Topping et al. 2005), which is consistent with what was seen in this study.

Traditional two-dimensional (2D) analyses of horizontal movement have allowed for the comparison of activity space area, habitat selection, and diel patterns of activity between barred sand bass tracked at Santa Catalina Island and the LAFB. However, fish tagged by Mason and Lowe (2010) did not have depth-sensing transmitters, therefore, patterns of vertical movement cannot be compared which limits our ability to understand how or why BSB are utilizing the CMLR and/or any additional differences in behavior. This may be of particular importance when comparing movement patterns and space use between these two distinct populations because fish tracks along the LAFB were primarily conducted during the non-spawning season (Feb-June 2011); fish tagged at Santa Catalina Island were tracked during the 2005 and 2006 summer spawning season. While the formation of known barred sand bass spawning aggregations have not been observed or documented with the CMLR, without the inclusion of depth profiles or additional diver observations, the possibility that fish tracked by Mason and Lowe (2010) exhibited vertical movement patterns indicative of courtship or spawning cannot be excluded. Long-term passive monitoring of acoustically tagged barred sand bass within the CMLR (summer 2005 through summer 2006) revealed that some individuals exhibited year around site fidelity while others remained within the CMLR until the onset of the following spawning season after which time they were not detected within the array (Mason and Lowe 2010). Other transient aggregate spawners have also been observed exhibiting this type of polymorphic behavior (Fitch and Shapiro 1990; Zeller 1998; Egli and Babcock 2004; Semmens et al. 2010).

Both population density and cost of migration may influence an individual's ability to form spawning aggregations (Claydon 2004). The CMLR fish are part of a smaller, more isolated population compared to coastal individuals such as those tracked along the LAFB, which are known to form transient spawning aggregations (Hovey et al. 2002; Jarvis et al. 2010). In small populations, large migration distances may result in prohibitively high migration costs or energy expenditure, reducing the chance that these individuals will undergo such migrations to participate in known transient spawning aggregations (Claydon 2004). This could explain why individuals of species known to form spawning aggregations at one location may not demonstrate aggregate spawning behavior over their entire geographic range (e.g., blue-head wrasse, *Thalassoma bifasciatum*) (Shapiro et al. 1988; Fitch and Shapiro 1990; Warner 1995). Small population size and/or reductions in population size has also been shown to alter mating styles performed by serranids, therefore, it is possible that some CMLR individuals may exhibit alternative mating strategies such as pair-spawning or the formation of smaller resident spawning aggregations (Shapiro et al. 1988; Claydon 2004). Additional tracking studies, diver observations, and/or histological examinations are needed to confirm if reproductively active individuals reside with the CMLR year around and to document evidence of spawning related behavior.

A three dimensional (3D) analysis of barred sand bass movement patterns along the LAFB provided a more detailed representation 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/or habitat selection may be more influential in dictating barred sand bass activity levels and movement patterns then would otherwise be assumed.

Spawning Season Fine-Scale Movement and Habitat Utilization

Histological examinations as well as visual observations and captive breeding studies suggest that while *Paralabrax* species may be capable of daily spawning, the average interval between spawning events is approximately two days (Oda et al. 1993; Martinez-Diaz et al. 2001; Erisman and Allen 2006; Miller and Allen 2006). In addition, for serranid species (e.g., kelp bass, *P. clathratus*; leopard grouper, *Mycteroperca rosacea*) that form long-term breeding aggregations, the proportion of sampled females residing within the surveyed spawning grounds with hydrated oocytes on any given day varied considerably from as low as 10% to greater than 90% (Erisman and Allen 2006; Erisman et al. 2007). This further suggests that not all individuals participating within a spawning aggregation are actively spawning every day. Observations of Mediterranean dusky grouper (*Epinephelus marginatus*) also revealed that individuals did not exhibit sustained spawning activity during consecutive days (Zabala et al. 1997; Hereu et al. 2006). This is consistent with movement patterns of barred sand bass tracked during the summer spawning season at the Huntington Beach Flats (HBF), which were observed exhibiting two primary modes of behavior believed to be indicative of either "resting" or "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 (Sancho et al. 2000a; Hereu et al. 2006). However, sex was unable to be determined for most spawning season individuals, as barred sand bass 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 information collected from fish caught (N = 325) on the Huntington Beach Flats (HBF) spawning grounds during the summer of 2011 suggests that there are both males and females present in roughly equal proportions within the water column as well as on the seafloor (Jarvis et al. unpubl. data). In addition, individuals 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 the sex of individuals tracked explain the different patterns of behavior observed by spawning season barred sand bass in the present study.

Many aggregate spawners, including barred sand bass, exhibit strong site fidelity to their spawning grounds, returning year after year to the same spawning location (Love et al. 1987; Colin 1992; Zeller 1998; Jarvis et al. 2010). 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 (Johannes 1978; Barlow1981; Doherty et al. 1985; Robertson 1991; Colin 1992, Love et al. 1987; Sancho et al. 2000a,b; Claydon 2004). While the majority of aggregate spawning serranids form breeding aggregations over areas of high relief or complexity (Colin 1992; Sadovy et al. 1994; Sancho et al. 2000a; Rhodes and Sadovy 2002; Erisman and Allen 2006; Erisman et al. 2007), spawning season barred sand bass were detected almost exclusively over sand habitat.

By spawning offshore over relatively uniform deeper water sand habitat, barred sand bass may avoid or reduce egg loss that would be expected if they continued to utilized shallow reef habitats due to higher densities of egg predators (Love et al. 1987). Individuals of another local temperate species, California scorpion fish (*Scorpaena guttata*) also move away from reef structures to form long-term summer spawning aggregations over sand habitat (Love et al. 1987). In addition, for individuals of species that spawn over large expanses of featureless sand habitat in at least part of their range and where the precise location of aggregation formation is more variable (e.g., black grouper, *M. bonaci*; camouflage grouper, *E. polyphekadion*; brown-marbled grouper, *E. fuscoguttatus*; leopard coral-trout, *Plectropomus leopardus*; pink snapper, *Pagrus auratus*) (Smith 1972; Samoily and Squire 1994; Johannes et al. 1999; Moran et al. 2003; www.scrfa.org/database), the general location may be of importance to increase reproductive success, but there may be no selective advantage to spawn consistently in any single discrete location (Shapiro et al. 1988; Claydon 2004).

Fish species that utilize habitats of low complexity generally move more and use larger areas to meet their daily requirements then 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 preference for ecotone habitat. Tropical serranid species (e.g., Nassau grouper, *Epinephelus striatus*; red hind, *E. guttatus*; camouflage grouper and leopard grouper) that form large seasonal spawning aggregations of similar densities to those reported for barred sand bass, but over complex reef habitats, utilize areas between 0.5 km^2 - 2.0 km^2 (Colin 1992; Sadovy et al. 1994; Rhodes and Sadovy 2002; Erisman et al. 2007). While this is consistent with the daily activity space area utilized by spawning individuals in this study, the entire spawning aggregation would be assumed to be encompassing a considerably larger area within the HBF spawning grounds, which covers a ~ 55 km^2 area. Consequently, individual BSB may have to travel significantly farther to find conspecifics or to move between discrete aggregations. In addition, presumed spawning individuals were predominately detected higher in the water column. Therefore, these 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. This would also significantly contribute to the larger areas used by presumed spawning individuals.

Reef structures and ecotone habitat may be important during the spawning season for presumed resting individuals. While still preferring 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 the extreme amount of energy that must be expended during spawning, it is possible that for this individual the cost of migration to the nearest reef patch was greater than the benefit of resting within its current location.

Barred sand bass, unlike other serranid species, are not aggregating to a definable geological habitat type such as a reef, but were found to aggregate in mid-water. Therefore, 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 assuring higher reproductive success (Shapiro et al. 1988; Eckmann 1991). Hydroacoustic surveys and video recordings conducted by L.G. Allen (unpubl. data), confirm the daytime presence of large aggregations of barred sand bass associated with the thermocline on the HBF spawning grounds, including the nearby Bolsa Chica Artificial Reef (BCAR).

Barred sand bass may also be seeking out areas within the flats where oceanographic conditions favor successful spawning, provide ideal temperatures/ conditions for eggs and larvae as well as advantageous movement of all ichthyoplankton (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), barred sand bass 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). While adults utilizing the HBF spawning grounds experienced water conditions (19-11 ° C; avg. surface-seafloor) consistent with the physiological limits of barred sand bass 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 assent for positively buoyant eggs. Mediterranean dusky grouper adults also experience wide temperatures ranges (~ 7°) between their territories (20 - 35 m) and spawning depth (5 - 25 m) (Zabala et al. 1997; Hereu et al. 2006).

Individuals are expected to spawn at not only specific locations but also at times that best increase their fitness (Claydon 2004). For many pelagic spawners, spawning times vary from early morning to just after sunset (Shapiro et al. 1988; Sancho et al. 2000b). Spawning season barred sand bass 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; 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 seen throughout the day, the temporal window of actual gamete release may be more restrictive. Histological evidence suggests that barred sand bass exhibit peak spawning during midday (12:00 - 14:00) (Oda et al. 1993); however, fish tracked in the present study did not exhibit increased activity during this period compared to any other point throughout the day. Therefore, additional observations are needed to decisively conclude timing of gamete release in this species.

Periodic diurnal dive behavior displayed by spawning season barred sand bass is believed to be analogous to upward vertical spawning rushes demonstrated by other aggregate 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; Miller and Allen 2006; Erisman et al. 2007). Among these serranid species, gamete release is seen at the apex of short 1-4 m vertical rushes during which time a subset of individuals briefly rises out of the aggregation and quickly returns; however, longer vertical bursts (10 - 15 m) have been reported in Nassau grouper, chocolate hind (*C. boenack*), Pacific creole fish (*Paranthias colonus*) and dusky grouper. In addition, 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 to 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; Zabala et al. 1997; Sala et al. 2003; Erisman and Allen 2006; Erisman et al. 2007). Also, courtship behavior terminating in a spawning event in kelp bass and Nassau grouper can last 15 sec to several min, which is consistent with the duration of dives exhibited by barred sand bass in this study (Erisman and Allen 2006; Erisman et al. 2007). While barred sand bass are exhibiting downward vertical dives compared to upward vertical rushes, they are within the range of magnitude and duration reported for other serranids. It could also be argued that gamete release is occurring at comparable depths or distance from either the surface or seafloor to other aggregate spawning serranids, if in fact gamete release is taking place at the nadir of a dive compared to the apex of a rush. It is also possible that spawning individuals are releasing gametes near the thermocline upon returning to the aggregation post dive.

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 (Moyer 1987; Robertson 1991; Sancho 2000; Sancho et al. 2000a; Claydon 2004; Habrun and Sancho 2012). Therefore, predation pressure may also be the mechanism driving the observed dive behavior of spawning season barred sand bass. Adult barred sand bass 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 water layer of the Huntington Beach Flats (HBF) spawning ground, thereby reducing predation risks. In addition, dive behavior typically terminated 5 - 15 m below the thermocline. If eggs are released at the bottom 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*) and Pacific sardines (*Sardinops sagax*).

Evidence for Large-Scale Spawning Related Movements

The majority of spawning season individuals remained on the HBF spawning ground for their entire tracking period (20 - 150 d), which is consistent with tag and recapture data and residency times reported by Jarvis et al. (2010). However, four of the twelve spawning season individuals appeared to have left the HBF for several days up to two weeks, but were relocated on the spawning grounds 0.5 - 3.0 km from last known detection. Two other individuals, Fish 4 and Fish 7 tagged in May and June, respectively, were either caught and unreported or left the spawning grounds during the second week of July. It is possible that these individuals were transitioning between their home range site and spawning habitat, or potentially utilizing more than one spawning area throughout the summer breeding season. Tag and recapture data collected by the California Department of Fish and Game (CDFG), also showed evidence of emigration from spawning grounds with barred sand bass being recaptured away from the HBF during peak spawning at both known spawning and non-spawning sites (Jarvis et al. 2010).

During the summer months (June-Aug), barred sand bass are known to move offshore away from coastal rocky reef habitats to sand flats to spawn (Love et al. 1996; Hovey et al. 2002). Tag and recapture data, along with previous tracking data, also suggests that barred sand bass are transient aggregate spawners, with aggregations that may be comprised of both migrant and resident individuals (Jarvis et al. 2010; Mason and Lowe 2010). Fine-scale movement data collected during this study, along with observed edge responses and habitat associations, provide additional support for this theory. Several individuals tagged during the summer spawning season (Fish 3, 5 and 6) remained positively associated with reef structures over their entire tracking period (150 d; May-Sept), regardless of whether vertical movement indicative of spawning was detected. It is possible that some of these fish are resident individuals whom reside at their preferred reef patch year around. Evidence of migrant individuals participating within the aggregation is also present. One non-spawning season individual (fish 18) tagged on 22 June 2011, disappeared from the LAFB after its first tracking period on 25 June 2011. It unclear whether this individual was caught and never reported or potentially left the breakwater and headed to one of several nearby spawning aggregation sites such as Horseshoe Kelp or the Huntington Beach Flats (HBF) (Jarvis et al. 2010). However, the timing of its absence is consistent with the onset of peak spawning (July) (Love et al. 1996a; Hovey et al. 2002; Jarvis et al. 2010) and this individual was milting throughout the tagging procedure suggesting that is was mature and developing gametes for the spawning season. Barred sand bass that were acoustically tagged as part of a larger passive monitoring project off the Palos Verde (PV) Peninsula, California located approximately 20 km northwest of the LAFB were also detected leaving their home range site during this time. Several of these individuals were later detected at both Horseshoe Kelp and the HBF spawning grounds during middle to late July and early August before returning to the PV shelf by late August 2011 (Wolfe and Lowe unpubl. data). Another individual tagged within the present study (fish 2) was also detected moving between spawning and non-spawning season habitats. This individual was tagged on the HBF spawning ground on 13 July 2009 and was recaptured 14 km north from the tagging location and 19 km north from its last know detection along the inside of the LAFB on 15 January 2011. Tag and recapture data collected by CDFG also showed that barred sand bass tagged during the non-spawning season and subsequently recaptured on known spawning grounds traveled in a southerly direction with an average migration distance of 17 ± 15 km, while fish tagged in spawning season were primarily recaptured north of their spawning grounds during the non-spawning season (Jarvis et al. 2010).

Management Implications

Due to the significant variation in reproductive behavior and mating styles found among serranid species, it is essential that management measures are tailored to the species in question. 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, thereby promoting population recovery and creating a more sustainable fishery. Typical measures used to reduce fishing pressure on aggregate spawning serranids include further size restrictions or slot limits, decreased bag limits, seasonal closures or bans, and inclusion of important spawning habitat in the development of marine reserves or MPA systems (Sadovy and Domeier 2005; Erisman et al. 2007). Unfortunately, barred sand bass spawning aggregation locations are not currently included in California MPA proposals for the south coast study region (i.e., Pt. Conception to the U.S./Mexican border) (Jarvis et al. 2010). Large-scale movements between home range and spawning sites suggest that barred sand bass are transient aggregate spawners that show high site fidelity to their spawning grounds, with local aggregations comprised of both migrant and resident fish (Jarvis et al. 2010). Therefore, seasonal area closures of a few key spawning aggregation sites such as the HBF could be implemented. However, this may not be feasible and hard to enforce for species such as barred sand bass that associate with multiple habitat types, and utilize huge daily activity spaces while continually moving around even larger spawning grounds with some individuals transitioning between multiple spawning sites. Fine-scale movement data suggests that a short 1-2 week seasonal ban for barred sand bass during the end of July (corresponding to peaks in spawning activity) would be most beneficial. Diel patterns in spawning activity also support this management option because some individuals appear to exhibit spawning related movement patterns throughout the day and night. Therefore, gamete release may be more variable and occur over a longer temporal period then other serranids that spawn exclusively at dusk and the exclusion of barred sand bass for example from only dawn or twilight commercial passenger fishing vessel (CPFV) trips may not effectively protect the entire spawning stock. In addition to a short-term seasonal closure, reductions in bag limits (< 10) and increased size limits (> 31 cm TL) may also help offset current declines and enhance the fishery.

REFERENCES

REFERENCES

Allen LG, Hovey TE (2001) Barred sand bass. In California's living marine resources: A status report. In Leet WS, Dewees CM, Klingbeil R, Larson EJ, editors. California Department of Fish and Game, University of California Agriculture and Natural Resources Publication SG01-11. p. 222-223

Anderson TW, DeMartini EE, Roberts DA (1989) The relationship between habitat structure, body size, and distribution of fishes at a temperate artificial reef. Bulletin of Marine Science 44: 681-697

Barlow GW (1981) Patterns of parental investment, dispersal and size among coral-reef fishes. Environmental Biology of Fishes 6: 65-68

Bedford D, Tarpley J, Palmer-Zwahlen M (1992) Observations of the biological communities at Bolsa Chica Artificial Reef. California Department of Fish and Game Report 19pp

Brill RW, Block BA, Boggs CH, Bigelow KA, Freund EV, Marcinek DJ (1999) Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacores*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. Marine Biology 133: 395-408.

Cartamil DP, Lowe CG (2004) Diel movement patterns of ocean sunfish *Mola mola* off southern California. Marine Ecology Progress Series 266: 245-253

Chih-hao H, Reiss C, Watson W, Allen MJ, Hunter JR, Lea RN, Rosenblatt RH, Smith PE, Sugihara G (2005) A comparison of long-term trends and variability in populations of larvae of exploited and unexploited fishes in the Southern California region: A community approach. Progress in Oceanography 67: 160-185

Cho GK, Heath DD (2000) Comparison of tricaine methanesulphonate (MS222) and clove oil anesthesia effects on the physiology of juvenile chinook salmon *Oncorhynchus tshawytscha* (Walbaum). Aquaculture Research 31: 537-546

Claydon J (2004) Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. Oceanography and Marine Biology: An Annual Review 42: 265-302

Colin PL (1992) Reproduction of the Nassau grouper, *Epinephlus striatus*, (Pisces: Serranidae) and its relationship to environmental conditions. Environmental Biology of Fishes 34: 357-377

Doherty PJ, Williams DM, Sale PF (1985) The adaptive significance of larval dispersal in coral reef fishes. Environmental Biology of Fishes 12: 81-90

Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed. Bulletin of Marine Science 60(3): 698-726

Donaldson TJ (1995) Courtship and spawning behavior of the pygmy grouper, *Cephalopholis spiloparaea* (Serranidae: Epinephelinae), with notes on *C. argus* and *C. urodeta*. Environmental Biology of Fishes 43: 363-370

Duong T (2007) ks: Kernel density estimation and kernel discriminant analysis for multivariate data in R. Journal of Statistical Software 21: 1-16

Eckmann, R (1991) A hydroacoustic study of the pelagic spawning behavior of whitefish (*Coregonus lavaretus*) in Lake Constance. Canadian Journal of Fisheries and Aquatic Sciences 48: 995-1002

Egli DP, Babcock RC (2004) Ultrasonic tracking reveals multiple behavioural modes of snapper (*Pagrus auratus*) in a temperate no-take marine reserve. ICES Journal of Marine Science 61: 1137-1143

Erisman BE, Allen LG (2005) Color patterns and associated behaviors in the kelp bass, *Paralabrax clathratus* (Teleostei: Serranidae). Southern California Academy of Sciences Bulletin 104(2): 45-62

Erisman BE, Allen LG (2006) Reproductive behavior of a temperate serranid fish, *Paralabrax clathratus* (Girard), from Santa Catalina Island, California, U.S.A. Journal of Fish Biology 68: 157-184

Erisman BE, Buckhorn ML, Hasting PA (2007) Spawning patterns in the leopard grouper, *Mycteroperca rosacea,* in comparison with other aggregating groupers. Marine Biology 151: 1849-1861

Erisman BE, Rosales-Casian JA, Hasting PA (2008) Evidence of gonochorism in a grouper, *Mycteroperca rosacea*, from the Gulf of California, Mexico. Environmental Biology of Fishes 82: 23-33

Erisman BE, Allen AG, Claisse JT, Pondella DJ, Miller EF, Murray JH (2011) The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Canadian Journal of Fisheries and Aquatic Sciences 68: 1705-1716

Eristhee N, Oxenford HA (2001) Home range size and use of space by Bermuda Chub *Kyphosus sectatrix* (L.) in two marine reserves in the Soufriere Marine Management Area, St. Lucia, West Indies. Journal of Fish Biology 59: 129-151

Feder, HM, Turner CH, Limbaugh C (1974) Observations on fishes associated with kelp beds in southern California. California Department of Fish and Game, Fish Bulletin 160: 31-32

Fitch WTS, Shapiro DY (1990) Spatial dispersion and non-migratory spawning in the blue-head wrasse *Thalassoma bifasciatum*. Ethology 85: 199-211

Froeschke JT, Allen LG, Pondella DJ (2005) The reef fish assemblages of the Outer Los Angeles Federal Breakwater, 2002-2003. Southern California Academy of Sciences Bulletin 104(2): 63-74

Gadomski DM, Caddell SM (1996) Effects of temperature on the development and survival of eggs of four coastal California fishes. Fishery Bulletin 94: 41-48

Habrun CA, Sancho G (2012) Spawning ascent durations of pelagic spawning reef fishes. Current Zoology 58(1): 95-102

Hereu B, Diaz D, Pasqual J, Zabala M, Sala E (2006) Temporal patterns of spawning of the dusky grouper *Epinephelus marginatus* in relation to environmental factors. Marine Ecology Progress Series 325: 187-194

Hooge PN, Eichenlaub WN (2000) Animal Movements Extension to ArcView. Alaska Biological Center, US Geological Survey, Anchorage

Hooge PN, Eichenlaub WM, Solomon EK (2001) Using GIS to analyze animal movements in the marine environment. In Kruse GH, Bez N, Booth A, Dorn MW, Hills S, Lipcisu RN, Pelletier D, Roy C, Smith SJ, Witherell D, editors. Spatial Processes and Management of Marine Populations Anchorage, Alaska: Alaska SeaGrant. p. 37-51

Hovey CB, Allen LG, Hovey TE (2002) The reproductive pattern of barred sand bass (*Paralabrax nebulifer*) from southern California. CalCOFI Report 43: 174-180

Jarvis ET, Linardich C, Valle CF (2010) Spawning-related movements of barred sand bass, *Paralabrax nebulifer*, in Southern California: interpretation from two decades of historical tag and recapture data. Southern California Academy of Sciences Bulletin 109(3): 123-143

Johannes RE (1978) Reproductive strategies of coastal marine fishes in the tropics. Environmental Biology of Fishes 3: 65-84

Johannes RE, Squire L, Graham T, Sadovy Y, Renguul H (1999) Spawning aggregations of groupers (Serranidae) in Palau. Marine Conservation Research Series Publication #1, The Nature Conservancy 144p

Johnson TD, Barnett AM, Demartini EE, Craft LL, Ambrose RF, Purcell LJ (1994) Fish production and habitat utilization on a southern California artificial reef. Bulletin of Marine Science 55: 65-79

Love MS, Axell B, Morris P, Collins R, Brooks A (1987) Life history and fishery of the California scorpion fish, *Scorpaena guttata*, within the Southern California Bight. Fishery Bulletin 85(1): 99-116

Love MS, Brooks A, Ally JRR (1996a) An analysis of commercial passenger fishing vessel fisheries for kelp bass and barred sand bass in the Southern California Bight. California Department Fish and Game, Fish Bulletin 82: 105-121

Love MS, Brooks A, Busatto D, Stephens J, Gregory P (1996b) Aspects of the life histories of the kelp bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer*, from the southern California Bight. Fishery Bulletin 94: 472-481

Lowe CG, Topping DT, Cartamil DP, Papastamatiou YP (2003) Movement patterns, home range, and habitat utilization of adult kelp bass *Paralabrax clathratus* in a temperate no-take marine reserve. Marine Ecology Progress Series 256: 205-216

Lowe CG, Bray RN (2006) Fish movement and activity patterns. In: Allen LG, Pondella DJ, Horn MH, editors. The Ecology of Marine Fishes: California and Adjacent Waters. University of California Press, Berkeley, CA. p 534-553

Lowry MB, Suthers IM (1998) Home range, activity and distribution patterns of a temperate rocky-reef fish, *Cheilodactylus fuscus*. Marine Biology 132: 569-578

Martinez-Diaz SF, Martinez-Pecero R, Rosales-Velazquez MO (2001) Voluntary spawning, early development and completion of the life cycle of spotted bass, *Paralabrax maculatofasciatus* in the laboratory. Journal of the World Aquaculture Society 32: 122-129

Mason TJ, Lowe CG (2010) Home range, habitat use and site fidelity of barred sand bass within a Southern California marine protected area. Fisheries Research 106: 93-101

Matthews KR (1990) An experimental study of the habitat preferences and movement patterns of copper, quillback, and brown rockfish (*Sebastes* spp). Environment Biology of Fishes 29: 161-178

Miller EF, Allen LG (2006) Observations on the mating behavior of captive spotted sand bass (*Paralabrax maculatofasciatus*). Southern California Academy of Sciences Bulletin 105(1): 17-29

Moran M, Burton C, Jenke J (2003) Long-term movement patterns of continental shelf and inner gulf snapper (*Pagrus auratus*, Sparidae) from tagging in the Shark Bay region of Western Australia. Marine and Freshwater Research 54(8): 913-922

Moyer JT (1987) Quantitative observations of predation during spawning rushes of labrid fish *Thalassoma cupido* at Miyake-Jima, Japan. Japanese Journal of Ichthyology 34(1): 76-81

Munday PL, Wilson SK (1997) Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish. Journal of Fish Biology 51: 931-938

Nemeth RS (2005) Population characteristic of a recovering US virgin Island red hind spawning aggregation following protection. Marine Ecology Progress Series 286: 81-97

Oda DL, Lavenberg RJ, Rounds JM (1993) Reproductive biology of three California species of *Paralabrax* (Pisces: Serranidae). CalCOFI Report 34: 122-132

Quest JC (1968) Observations on the food and biology of the kelp bass, *Paralabrax clathratus*, with notes of the sport fishery in San Diego, California. In: North WJ, Hubbs CL (Eds). Utilization of kelp-bed resources in Southern California. California Department of Fish and Game Report 139: 81-105

Reis L, Fletcher RJ, Battin J, Sick TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annual Review of Ecology, Evolution, and Systematics 35: 491-522

Rhodes KL, Sadovy Y (2002) Temporal and spatial trends in spawning aggregation of camouflage grouper, *Epinephlus polyphekadion*, in Pohnpei, Micronesia. Environmental Biology of Fishes 63: 27-39

Roberts DA, Demartini EE, Plummer KM (1984) The feeding habits of juvenile-small adult barred sand bass (*Paralabrax nebulifer*) in nearshore waters off Northern San Diego County. CalCOFI Report 25: 105-111

Robertson DR (1991) The role of adult biology in the timing of spawning of tropical reef fishes. In: Sale PF, editors. The ecology of fishes on coral reefs. Academic Press. P 356-386

Sadovy Y, Domeier M (2005) Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24: 254-262

Sadovy Y, Rosario A, Roman A (1994) Reproduction in an aggregating grouper, the red hind, *Epinephelus guttatus*. Environmental Biology of Fishes 41: 269-286

Sala E, Aburto-Oropeza O, Paredes G, Thompson G (2003) Spawning aggregations and reproductive behavior of reef fishes in the Gulf of California. Bulletin of Marine Science 72(1): 103-121

Samoilys MA, Squire LC (1994) Preliminary observations on the spawning behavior of coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on the Great Barrier Reef. Bulletin of Marine Science 54(1): 332-342

Sancho G (2000) Predatory behaviours of *Caranx melampygus* (Carangidae) feeding on spawning reef fishes: a novel ambushing strategy. Bulletin of Marine Science 66: 487-496

Sancho G, Petersen CW, Lobel PS (2000a) Predator-prey relations at a spawning aggregation site of coral reef fishes. Marine Ecology Progress Series 203: 275-288

Sancho G, Solow AR, Lobel PS (2000b) Environmental influences on the diel timing of spawning in coral reef fishes. Marine Ecology Progress Series 206: 193-212

Semmens JM, Buxton CD, Forbes E, Phelan MJ (2010) Spatial and temporal use of spawning aggregation sites by tropical sciaenid *Protonibea diacanthus*. Marine Ecology Progress Series 403: 193-203

Shapiro DY, Hensley DA, Appeldoorn RS (1988) Pelagic spawning and egg transport in coral-reef fishes: a skeptical overview. Environmental Biology of Fishes 22(1): 3-14

Shapiro DY, Sadovy Y, McGehee MA (1993) Size, composition and spatial structure of the annual spawning aggregation of the red hind, *Epinephelus guttatus* (Pisces: Serranidae). Copeia 1993: 399-406

Simpfendorfer CA, Olsen EM, Heupel MR, Moland E (2012) Three-dimensional kernel utilization distributions improve estimates of space use in aquatic animals. Canadian Journal of Fisheries and Aquatic Sciences 69: 565-572

Smith CL (1972) A spawning aggregations of Nassau grouper, *Epinephelus striatus* (Bloch). Transactions of the American Fisheries Society 101: 257-261

Topping DT, Lowe CG, Caselle JE (2005) Home range and habitat utilization of adult California sheephead, *Semicossyphus pulcher* (Labridae), in a temperate no-take marine reserve. Marine Biology 147: 301-311

Turner CH, Ebert EE, Given RR (1969) Man-made reef ecology. California Department of Fish Game, Fish Bulletin 146: 176-177

Warner, RR (1995) Large mating aggregations and daily long-distance spawning migrations in the bluehead wrasse, *Thalassoma bifasciatum*. Environmental Biology of Fishes 44: 337-345.

Zabala M, Garcia-Rubes A, Loisy P, Sala E. (1997) Spawning behavior of the Mediterranean dusky grouper, *Epinephelus marginatus* (Lowe, 1834) (Pisces, Serranidae) in the Medes Islands Marine Reserve (NW Mediterranean, Spain) Scientia Marina 61: 65-77

Zeller DC (1997) Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). Marine Ecology Progress Series 154: 65-77

Zeller DC (1998) Spawning aggregations: patterns of movement of the coral trout *Plectropomus leopardus* (Serranidae) as determined by ultrasonic telemetry. Marine Ecology Progress Series 162: 253-263