

## CHAPTER 1

### INTRODUCTION

The giant sea bass (*Stereolepis gigas*) is thought to be one of the only resident apex predators in the California kelp forest and rocky reef communities (Allen & Andrews, 2012; Domeier, 2001; Horn & Ferry-Graham, 2006). As the largest reef-associated teleost species, giant sea bass (hereby GSB) in the northeastern Pacific and have a maximum recorded total length of 250 cm and weight of 255 kg (Domeier, 2001). The species inhabits nearshore rocky reefs and kelp forests from Humboldt Bay, California, south along the west coast of North America to the tip of Baja California Sur, Mexico, and into the Gulf of California, (Love, 2011; Peterson, Eschmeyer, & Herald, 1999). Because GSB have slow growth rates, are relatively late to mature (11–13 years), and exhibit aggregative behavior during the summer months, the species is susceptible to overfishing (Colin, 1992; Dayton, Thrush, & Coleman, 2003; Domeier, 2001; Leet, Dewees, Klingbeil, & Larson, 2001; Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998; Sadovy & Eklund, 1999).

GSB were fished through the end of the 20<sup>th</sup> century from Point Conception, CA, through Baja California Sur, Mexico, resulting in a 95% and 98% decline in commercial landings in California and Mexico, respectively (Domeier, 2001). The commercial gillnet fishery targeted GSB aggregations and incidentally caught GSB while targeting other nearshore species (e.g., white seabass (*Atractoscion nobilis*), California halibut (*Paralichthys californicus*)) near rocky reefs and kelp beds during the summer months (Pondella II & Allen, 2008). Historic recreational fishing records show landings of multiple GSB at specific sites in southern California and Baja California from June–September, indicating the likelihood of annual aggregations. In the early 1970s, for example, between 70–100 GSB were caught on consecutive fishing trips during the

month of July at Abreojos Point and Magdalena Bay, Baja California, Mexico (Leet et al., 2001).

Aggregating behavior may increase survival through increased vigilance for predators, foraging success, or reproductive opportunities (Parrish & Edelstein-Keshet, 1999).

Environmental factors such as lunar phase, season, and temperature are known signals that cue some species to move purposefully to form aggregations, particularly for spawning (Bolden, 2000; Erisman et al., 2012; Salinas-de-Leon, Rastoin, & Acuna-Marrero, 2015; Semmens, Buxton, Forbes, & Phelan, 2010; Whaylen, Pattengill-Semmens, Semmens, Bush, & Boardman, 2004). A spawning aggregation is defined as a grouping of a single species of fish gathered at a specific location for the purpose of spawning (Domeier, 2012). Because of their conspicuous size, it is unlikely GSB aggregate to feed or protect themselves, so researchers suspect aggregative behavior is related to spawning. Timing and locations of aggregate spawning is thought to occur to reduce egg predation rates, increase mate-encounters, and improve fertilization success (Barlow, 1981; Johannes, 1978; Molloy, Côté, & Reynolds, 2012). Unfortunately, GSB were severely depleted by the mid-1970s before much was learned about the drivers, cues, and movements associated with aggregative spawning behavior.

Dramatic population declines led the State of California to enact a moratorium on recreational fishing for GSB in 1982, and in 1994 commercial take was limited to allow the incidental catch of only one GSB per trip by gill or trammel net (Leet et al., 2001; Pondella II & Allen, 2008). Fishing for GSB in Mexican waters is legal; however, the recreational take of only one GSB is allowed per fisher per day (Secretaría de Agricultura, 2017). Moreover, the International Union for the Conservation of Nature (IUCN) added GSB to their Red List as a critically endangered species in 1996 due to the population being considered “severely fragmented, leading to a continuing decline of mature individuals” (Cornish, 2004; Domeier,

2001). After enacting state-wide protections, the population is likely increasing in California while its status in Mexico is unknown.

Gaffney, Rupnow, and Domeier (2007) suggest there is only one population of GSB that exists throughout its range based on genetic sequencing and mitochondrial data collected from 56 GSB, primarily south of Oceanside, CA ( $n = 46$ ). Chabot, Hawk, and Allen (2015) conducted a similar study in an extended portion of its range, including the northern Channel Islands, CA, and found similar results indicating a low population size, estimated at less than 500 individuals. Both studies point out low genetic diversity and small contemporary population size, likely due to intensive fishing, resulted in a genetic bottleneck for the species across its range (Chabot et al., 2015; Gaffney et al., 2007). Due to its large size, GSB are likely capable of migrating long-distances in search of increased foraging or reproductive opportunities. Such long-distance movements may be migration events, characterized as a highly directional dispersal when fish are cued by seasonal environmental changes. If GSB do migrate long distances to spawning aggregation sites, it is important to understand where and when they move to assess population connectivity as the species recovers (Frisk, Jordaan, & Miller, 2014; Olds, Connolly, Pitt, & Maxwell, 2012).

Historic fishing records and anecdotal scientific evidence suggests GSB aggregate to spawn in southern California, but little is known about where and when, or whether there is fidelity to aggregation sites. On Santa Catalina Island, CA, a historic GSB aggregation site contained promontories and complex *Macrocystis* kelp and rocky reef habitat, which may be advantageous for spawning and larval survival (Farmer et al., 2017; Kobara & Heyman, 2008). As the population has increased during the last several decades, small groups of GSB have been documented in the Southern California Bight during the summer months near kelp beds and

rocky headlands (Pondella II & Allen, 2008). A recent study located two sites at Santa Catalina Island where individuals were seen aggregating: the historic aggregation site and another site where, in 2014, an aggregation of 24 GSB, estimated as a mean biomass density over 40 kg/1000 m<sup>2</sup>, was observed (House, Clark, & Allen, 2016).

Using that observational data, a pilot tagging study was conducted using acoustic telemetry to assess GSB fidelity to an aggregation site at Santa Catalina Island. From 2015–2016, eight mature (> 100 cm TL) individuals were externally tagged with uniquely coded acoustic transmitters (Vemco Ltd., V13-1H) at the historic aggregation site, where an acoustic receiver was deployed at a depth of 20 m. Additional receivers were deployed 4.5 km northwest and 3 km southeast to determine directionality of tagged individuals when they left the aggregation site. All individuals were detected at the aggregation site during both years; however, the number of detections was highly variable between individuals. All tagged GSB were detected leaving and utilizing other areas but some individuals were highly resident to the aggregation site while some individuals had low residency and exhibited movement patterns that were highly diel. GSB detected at the historic aggregation during the day were rarely detected there at night – the suspected time of spawning (App. B, Fig. 1). In addition, not all tagged fish utilized the aggregation site but showed directed movements between receivers (App. B, Fig. 2). One individual left the array at Santa Catalina Island in October 2015, after the end of the suspected spawning season, and was detected on the northern side of Santa Cruz Island in May 2016 (App. B, Fig. 3). This migration indicates a minimum orthogonal distance of approximately 180 km, traversing deep channels and heterogeneous environments.

Considering the population of GSB is still relatively small compared to what it once was, it is unclear whether individuals are utilizing the same aggregation sites as they did pre-

exploitation or if site selection is based primarily on environmental or biological factors. Fish spawning aggregations can occur in transient assemblages of just a few individuals or recurring aggregations of hundreds to thousands of fish (Bolden, 2000; Colin, Shapiro, & Weiler, 1987; Munro, Gaut, Thompson, & Reeson, 1973; Nemeth, Blondeau, Herzlieb, & Kadison, 2007; Sala, Aburto-Oropeza, Paredes, & Thompson, 2003; Whaylen et al., 2004). Other large-bodied reef fish (e.g., grouper and snappers) have been found to migrate long distances to spawn on an annual basis (Bolden, 2000; Mann, Locascio, Coleman, & Koenig, 2009), and, based on anecdotal evidence from the dive and fishing community, GSB may do the same. Because GSB can live nearly 80 years and are capable of long-distance migrations (Allen & Andrews, 2012), there is a possibility individuals remember and return to historic aggregation sites; however, GSB aggregations may not be site-specific at all and aggregation behavior may be density dependent or influenced by social factors. Based on data from the pilot study, GSB are likely using several sites around Santa Catalina Island for different purposes. If some individuals are highly resident to one aggregation site while others are not, it is possible there are multiple sites where aggregating takes place and certain sites may have aggregations for different reasons (e.g., foraging, courtship, spawning).

Quantification and verification of spawning aggregation sites is important to the continued recovery of GSB to understand how aggregative spawning changes as fish densities increase. Spawning has never been documented in the species, and little is known of the temporal and spatial aspects of aggregating or spawning, so it is necessary to examine these patterns of habitat selection, space use, and individual movements to understand how behaviors may change as densities continue to increase. As such, this study aimed to (1) verify GSB aggregation sites at Santa Catalina Island, (2) determine abundance and aggregation size at

aggregation sites, and (3) characterize movement patterns during and outside of spawning season.

## CHAPTER 2

### METHODS

#### Study Site

The study was conducted at Santa Catalina Island, CA, from May 2017 through November 2018. Santa Catalina Island (hereafter Catalina) is located 35 km southwest of Los Angeles, California, and is easily accessible by boat year-round. Anecdotal evidence from the scientific, recreational diving, and fishing communities suggests GSB aggregations are recently reoccurring at Catalina. Eleven sites were monitored covering approximately 4 km<sup>2</sup> of the coast of Catalina (Fig. 1). Ten sites contained *Macrocystis* kelp forests and/or deep rocky reef habitat representative of historic GSB aggregation sites at Catalina (CA MLPA South Coast Project, CA DFW 2009). The recreational dive community reported GSB sightings at all sites but there is neither observational evidence nor fishing records to support potential aggregations at Church Rock, Seal Rocks, Empire Landing, Isthmus Reef, or Arrow Point. Furthermore, while Long Point and Italian Gardens were historically considered aggregation sites, there is a lack of evidence this species is returning en masse to these locations. The historic aggregation site at Goat Harbor and another site, Casino Point, are within no-take Marine Protected Areas (MPAs) but contain different habitats. Goat Harbor is a historic aggregation site on the leeward side of the island with rocky substratum ranging from 10–37 m deep and variable *Macrocystis* kelp stands and complex rocky reefs. Additionally, there is a promontory on the eastern edge of the cove where GSB were historically targeted. Casino Point is primarily a high-relief rocky reef ranging from 5–30 m deep with considerable kelp coverage year-round. The seafloor transitions to sand on the western edge, punctuated by small *Macrocystis* kelp stands and shipwrecks. The east end of Casino Point stops at the end of a jetty, which may serve as a promontory for

spawning.

Based on House et al. (2016), an aggregation ( $n = 24$ ) of GSB was documented at the Palisades in 2014 which they considered a potential aggregation site. The Palisades is located on the windward side of the east end of Catalina with an average depth of 11 m, a maximum depth of 25 m, and sand substratum punctuated by small *Zostera pacifica* eelgrass beds and low-relief rocky reefs. A third site, Little Farnsworth, was chosen as an aggregation site based on anecdotal evidence from the dive community. Little Farnsworth is a nearshore rock pinnacle ranging from 18–40 m deep with two smaller rocks lying adjacent to the promontory and surrounded by sand substratum habitat. No *Macrocystis* kelp stands occur within 1 km of Little Farnsworth and current speeds are highly variable.

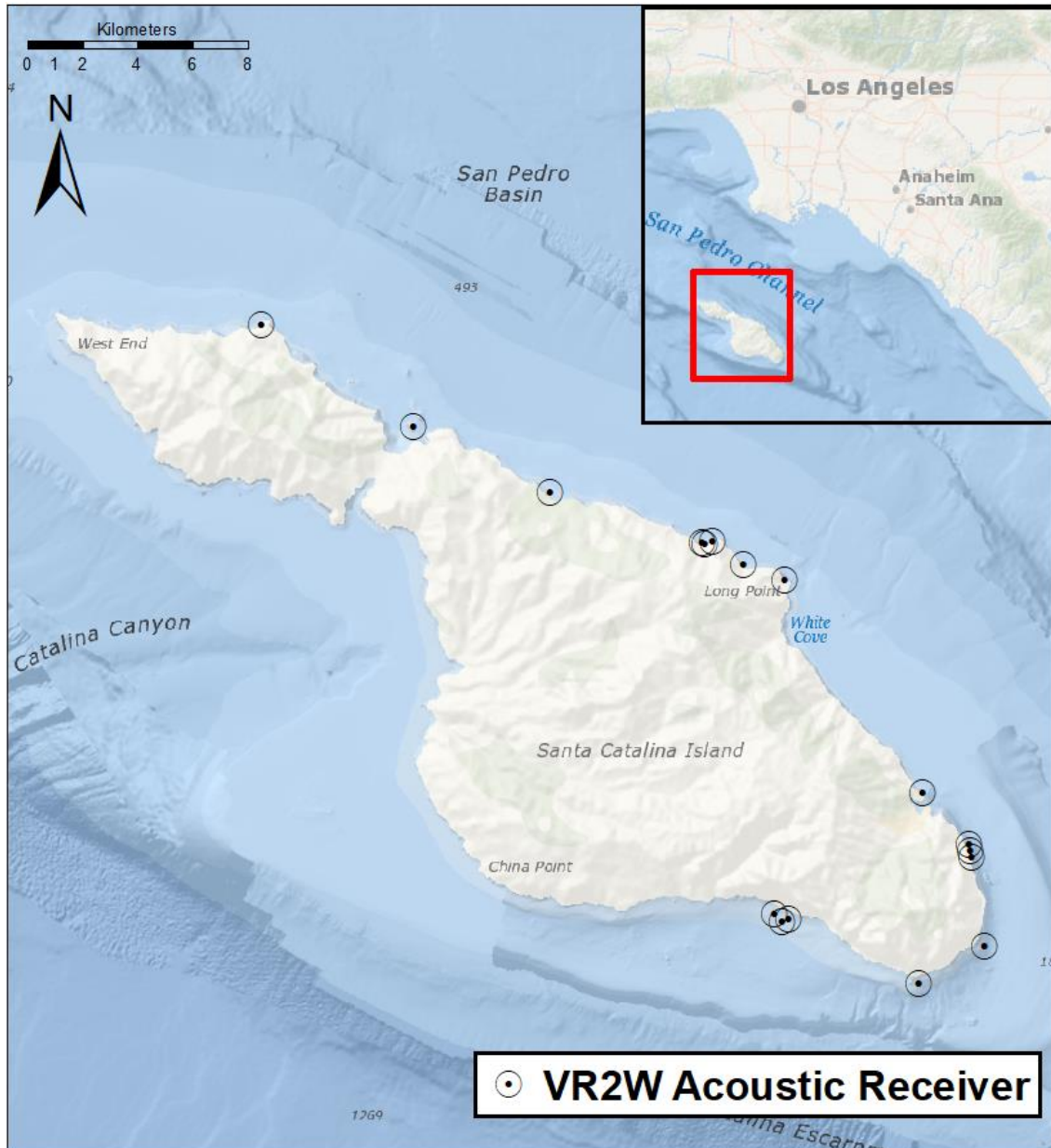
### **Acoustic Receiver Array**

To determine the site fidelity and movement patterns of GSB, a static array of 17 omnidirectional acoustic receivers (Vemco Ltd., VR2W) were moored off the seafloor surrounding Catalina. Receivers recorded detections from acoustic transmitters externally attached to the dorsum of 34 GSB tagged at Catalina. Omnidirectional underwater acoustic receivers (Vemco Ltd., VR2W) were anchored to the seafloor using a 1.2 m sand screw and suspended in the water column using a 2 m line and two trawl floats (2.5 kg buoyancy, 20.3 cm diameter).

To monitor the suspected aggregation sites, three receivers were placed approx. 400 m apart in a triangle formation (App. B, Fig. 4). A single receiver was placed outside *Macrocystis* kelp forests and/or deep rocky reef habitats adjacent to and between aggregation sites (suspect movement pathways) along the coast where migrating tagged fish were most likely to be detected. Receivers recorded the date, time, and individual identification number when a



transmitter emitted a pulse train within the detection range. Water temperature was recorded at the receiver location to the nearest tenth degree °C every hour at depths ranging from 10–27 m with a HOBO temperature datalogger (Onset Computer Corp., Pocasset, MA). Receivers and temperature dataloggers were recovered, downloaded, and redeployed every three months as weather permitted.



**FIGURE 1. Locations of VR2W receivers at Santa Catalina Island, CA. Acoustic receiver 250 m detection radius displayed around each receiver. Inset map shows geographic location of Santa Catalina Island, outlined in red.**

## Range Testing

To determine detection efficiency of acoustic receivers and coded acoustic transmitters, a range test was conducted across a portion of the array on the leeward east end of Catalina. A range test is done to determine a receiver's ability to detect an acoustic transmitter at various horizontal distances from the receiver at multiple depths. Based on the acoustic transmitters used on GSB, the detection range of a receiver can vary from 60–700 m, depending on receiver depth, frequency of detections, signal strength of transmitters, and environmental conditions (Heupel et al., 2006). These variables cause the range of receivers to expand and contract over time and can alter array performance.

An hour-long range test was conducted at a single aggregation site using a range test transmitter with a fixed pulse rate of 5 sec and the same specifications as the transmitters used for tagging (Vemco Ltd., V13-1H coded pinger). The Little Farnsworth aggregation site was chosen based on prior acoustic telemetry data indicating high use by GSB and high variability in environmental conditions. A vessel-borne acoustic receiver equipped with an omnidirectional hydrophone (Vemco Ltd., VR100, 30 dB gain) was used to determine the detection ranges of the three receivers in moderate-to-poor environmental conditions. An 8 m vessel was moved at idle speed through the Little Farnsworth aggregation array at ~1 m/sec, the estimated swimming speed of a mature giant sea bass. The range-testing tag was secured to a polypropylene fishing line 0.5 m above a lead weight using zip ties to maintain vertical orientation. The range-testing transmitter emitted a signal every 5 sec, which was detected by the omnidirectional hydrophone, and the GPS location was recorded for every detection by the surface VR100. These detection times of the VR100 and their associated geolocations were compared to moored acoustic receiver (Vemco Ltd., VR2W) time of detection to determine the distance at which each receiver

would detect the moving range test transmitter. Beginning southeast of the array, the vessel followed the coastline north-northwest along the 20 m depth contour while dragging the range test tag behind the vessel at ~10 m deep. Once the vessel traversed the length of the array northwest, it followed the 30 m depth contour south-southeast while dragging the test tag at ~ 20 m depth along the entire length of the array. This was done to determine the detectability of GSB at the known aggregation location, a pinnacle ~ 75 m east of the middle receiver.

Once range testing was complete, all four receivers (three VR2W, one VR100) were downloaded and detection data was managed using VUE 2.5.0 (Vemco Ltd.) and data analyses were carried out using R 3.5.1 (R Foundation for Statistical Computing). To interpolate GPS locations for the range test tag when it was not detected by the VR100, a continuous-time correlated random-walk model was created using the *crawl* package in R (Johnson & London, 2018). Map images were created using ArcGIS 10.6.1 (ESRI).

### **Acoustic Tagging Procedures**

From 15 June–28 August 2017, a total of 34 mature ( $> 100$  cm TL) GSB were tagged at Catalina across four sites and tagging efforts were focused at suspected aggregation sites ( $> 5$  GSB within  $25\text{ m}^2$ ). Fish were tagged with coded acoustic transmitters (Vemco Ltd., V13-1H; 36 mm long, 13 mm diameter, pulse interval 60–180 sec, 69 kHz, 11 g weight in air, 6 g weight in water, 153 dB power output, estimated battery life 653 d) treated with antifouling coating. Transmitters were attached to a short 14 cm long monofilament tether with a stainless-steel anchor dart (Floy Tag, FH-69; 3.5 cm long, 0.9 cm wide). All fish were approached on SCUBA and the tag was darted into the dorsal musculature using handheld pole spear with modified tag applicator tip (Cressi Co., 2 m long). All fish tagging methods were approved by the California Department of Fish and Wildlife (CDFW Scientific Collecting permit #3450) and the California

State University, Long Beach Institutional Animal Care and Use Committee (CSULB IACUC protocol #382).

## **Visual Surveys**

Dive teams conducted visual surveys for GSB across all sites in 15 of the 18 months of the study. Surveys were conducted monthly during the suspected spawning season (June–October) and bimonthly outside of the spawning season (November–May). Surveys consisted of a 30 min. timed swim at depth to locate GSB and estimate aggregation abundance. All surveys were completed between 07:00–16:00 hr and dive teams counted and measured GSB, when possible. Every dive survey was recorded using a video camera (GoPro, Hero 4) mounted to length calibrated parallel lasers (30 cm spacing). When a fish was seen, the camera captured the profile of the fish and the light of the lasers on the side of the fish. After each survey the video was downloaded and the length of each fish was measured (cm TL) using *ImageJ* software (Schneider, Rasband, & Eliceiri, 2012).

## **Visual Survey Data Analysis**

Visual survey data was used to estimate aggregation abundance based on number of fish counted per site per survey and compared to acoustic telemetry data. To determine if GSB abundance was influenced by time of day, General Linear Models (GLMs) were used considering site, month, time of day, and water temperature as independent factors while the dependent factor was number of fish seen per survey. The number of fish seen on each survey was compared to the number of fish detected during that day to determine whether visual surveys accurately represented the number of fish visiting each site.

## Data Analyses

Acoustic telemetry data were stored and processed in Vemco VUE v 2.6.0 while water temperature data were stored in Onset HOBOWare v 3.7.16. Data analyses were carried out using R 3.5.1 (R Foundation for Statistical Computing). Map images were created using ArcGIS 10.6.1 (ESRI).

## Residency

An attrition curve of GSB to the array at Catalina was calculated as the number of cumulative days ( $\geq 2$  detections in 24 hr) fish were present at any receiver within the array since the date of tagging to the end of the study (498 d). An overall residency index (number of days a fish was detected/total number of days during study) was calculated for each fish at each site over the course of the study to determine the amount of time GSB spent at each site within the array. Time of sunrise and sunset, and lunar phases during the study period were calculated using the *lunar* and *sunphase* packages in R (Agafonkin & Thieurmél, 2018; Lazaridis, 2014). A residency index ranges from 0–1, with 1 indicating the fish spent almost all days it was detectable at that site while 0 indicates the fish was not detected at that site. A Kruskal-Wallis test was used to determine if overall residency was significantly different across sites and a Dunn test was used to determine which sites were different. among the four tagging locations and if residency changed across seasons.

Due to the nature of the acoustic receiver array, residency indices calculated for aggregation sites were biased because there were three receivers per aggregation site compared to one receiver at each corridor area. To account for this bias, the total detection area ( $\text{m}^2$ ) covered by three receivers (at each aggregation site) was scaled to the detection area of a single receiver ( $280,000 \text{ m}^2$ ) by calculating the reciprocal of the aggregation site area divided by the

corridor area. Therefore, 11 site residency indices were calculated for each fish during the study period.

$$\left( \text{scaled detection area} = \frac{1}{\frac{\text{total aggregation area}}{\text{total corridor area}}} \right)$$

Based on the assumption that specific sites were aggregation sites while others were not, residency indices were calculated for each fish to its site of tagging. Tagging site residency was calculated as the number of days a fish was detected at its tagging site divided by the total number of days the fish was detected within the array at Catalina and compared using a Wilcoxon rank sum test.

To determine if there was a seasonal component to site use, seasonal residency indices were calculated. If aggregations only occur during the suspected spawning season, residency should be highest at aggregation sites during the summer and early fall. Seasonal site residency was calculated as the number of days a fish was detected at each site per season divided by the total number of days in that season. Seasons were defined as winter (1 December–28 February), spring (1 March–31 May), summer (1 June–31 August), and autumn (1 September–30 November).

Because little is known of the timing and locations of GSB aggregations, hourly residency values were calculated to determine when fish were utilizing sites and how many fish were at each site during the suspected time of spawning (dusk to dawn). Hourly residency values for each fish were calculated as the number of detections per site per hour divided by the total number of detections for that hour. The relationship between hourly residency and environmental variables was determined using Linear Mixed-Effects (LME) models where the explanatory

variables were site type (aggregation or corridor), water temperature, tidal amplitude, and lunar phase, while daily and hourly residency indices were treated as response variables, and the random factor was individual GSB. Hourly residency indices were logit transformed prior to analysis while daily residency indices were arcsine transformed. Mixed-effects models were performed using a logistic regression approach in the *lme4* package in R (Bates, Mächler, Bolker, & Walker, 2014).

### **Individual Movements**

Based on the pilot study, individual GSB exhibit a variety of movement patterns during the suspected spawning season. To estimate space use of fish during the suspected peak of spawning, diel linear movements were calculated using the *adehabitatHR* package in R (Calenge, 2011). Daily and nightly distance traveled were calculated for each fish during the peak of suspected spawning season to determine if movement patterns differed amongst tagged individuals.

### **Network Analysis**

To characterize movement patterns of individuals and groups of GSB, several social network analyses were conducted using the *asnipe* and *igraph* packages in R (Csardi & Nepusz, 2006; Farine, 2013). Network analyses were used to quantify the associations of individuals as a way to measure individual interactions and groupings (Farine & Whitehead, 2015; Mourier, Jacoby, & Guttridge, 2018). Node-based metrics, where each GSB is a node and each edge is an interaction between another tagged GSB, were used to determine if specific individuals were detected at the same sites at the same times and how this might influence network structure (Jacoby, Brooks, Croft, & Sims, 2012). The larger a node, the more frequently the individual was

detected with other tagged GSB and the more central a node is within the network the more interactions that individual had with other tagged fish. Measures of degree centrality (the node with the most connections), closeness (the node closest to all other nodes), and betweenness (the node between two or more subgroups) were calculated for each network to determine which individuals may be more central within the social structure of aggregating GSB at Catalina.

Detections were binned hourly to create networks and to ensure a large enough timeframe that any tagged individuals would be detected if an aggregating event were to occur. Based on hourly co-occurrences of individuals, a Gaussian mixture model was used to assess aggregating events of GSB at three sites: Goat Harbor, Casino Point, and Little Farnsworth. Networks of interactions amongst tagged individuals were calculated every week during the height of spawning (week 27–35) at each site, separated into daytime and nighttime associations.



## **CHAPTER 3**

### **RESULTS**

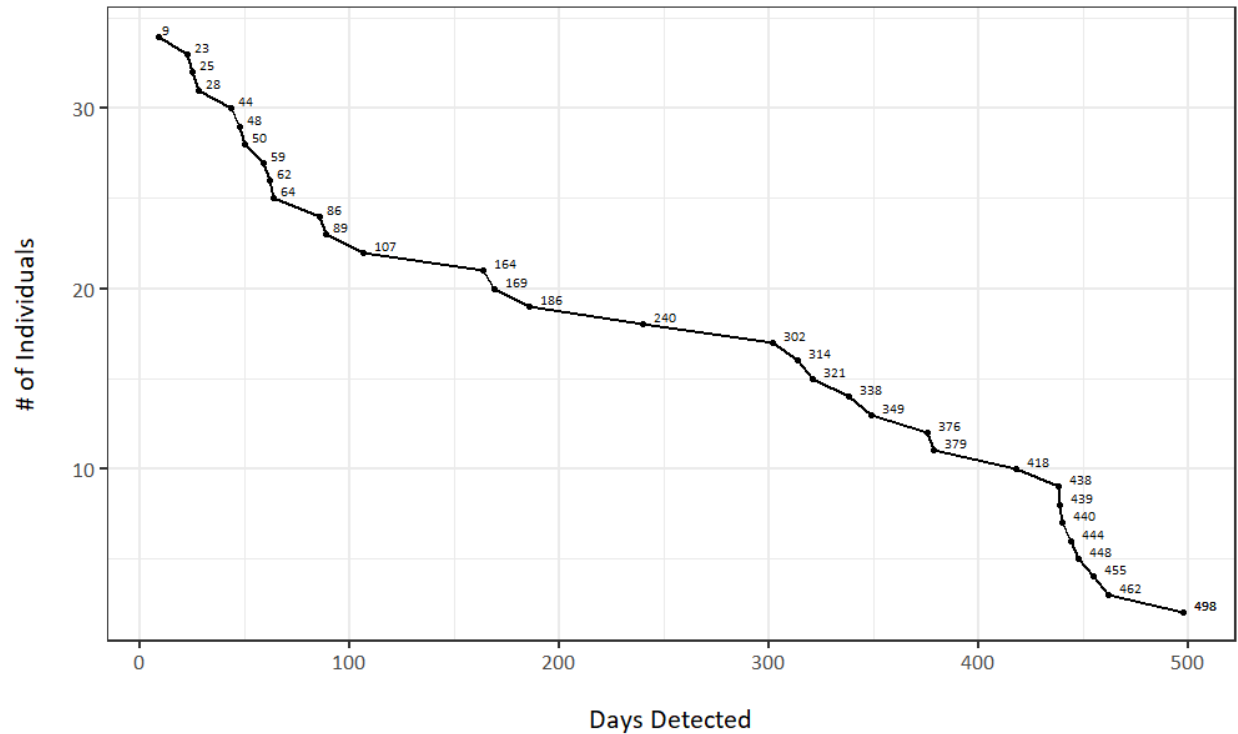
#### **Range Testing**

It was not feasible to conduct a range test at each site, so the site with the most complex habitat was chosen to test for least performance; as such, the detection radii calculated is likely a conservative measure of overall receiver range at Catalina. Due to low VR100 receiver performance, a continuous time-correlated random-walk model was used to interpolate locations of the test tag between VR100 detections (App. B, Fig. 5). Such low performance of the VR100 was not expected but was likely due to high current speed – by moving quickly through the water cavitation occurs around the range test tag, and potentially the omnidirectional hydrophone, inhibiting the ability of the VR100 to detect the tag. Therefore, water movement is likely impacting receiver performance the most. A total of 409 detections were recorded by the VR2W acoustic receiver array at Little Farnsworth, of which 22% occurred at the northwest receiver, 49% at the middle receiver, and 29% at the southeast receiver (App. B, Fig. 6). The average detection radius for each receiver was determined to be 250 m, therefore, single receivers had a detection area of approximately 280,000 m<sup>2</sup>. Due to receiver overlap at aggregation sites, the area covered at each site varied, with the receivers at Goat Harbor covering 521,640 m<sup>2</sup>, while Little Farnsworth covered 551,616 m<sup>2</sup>, and the Palisades covered 645,906 m<sup>2</sup>.

#### **Tagging and Aggregations**

In total, 34 GSB were tagged over the course of this study (App. A, Table 1). Seventeen individuals were tagged at Casino Point, 13 at Little Farnsworth, three at Goat Harbor, and one at Isthmus Reef. In early September 2017, one tag (A69-1601-45710) was continuously detected at

Little Farnsworth and another (A69-1602-2225) at Goat Harbor, indicating these fish shed their tags (Fig. 2). As such, both were removed from analyses from 10 September 2017 onward.



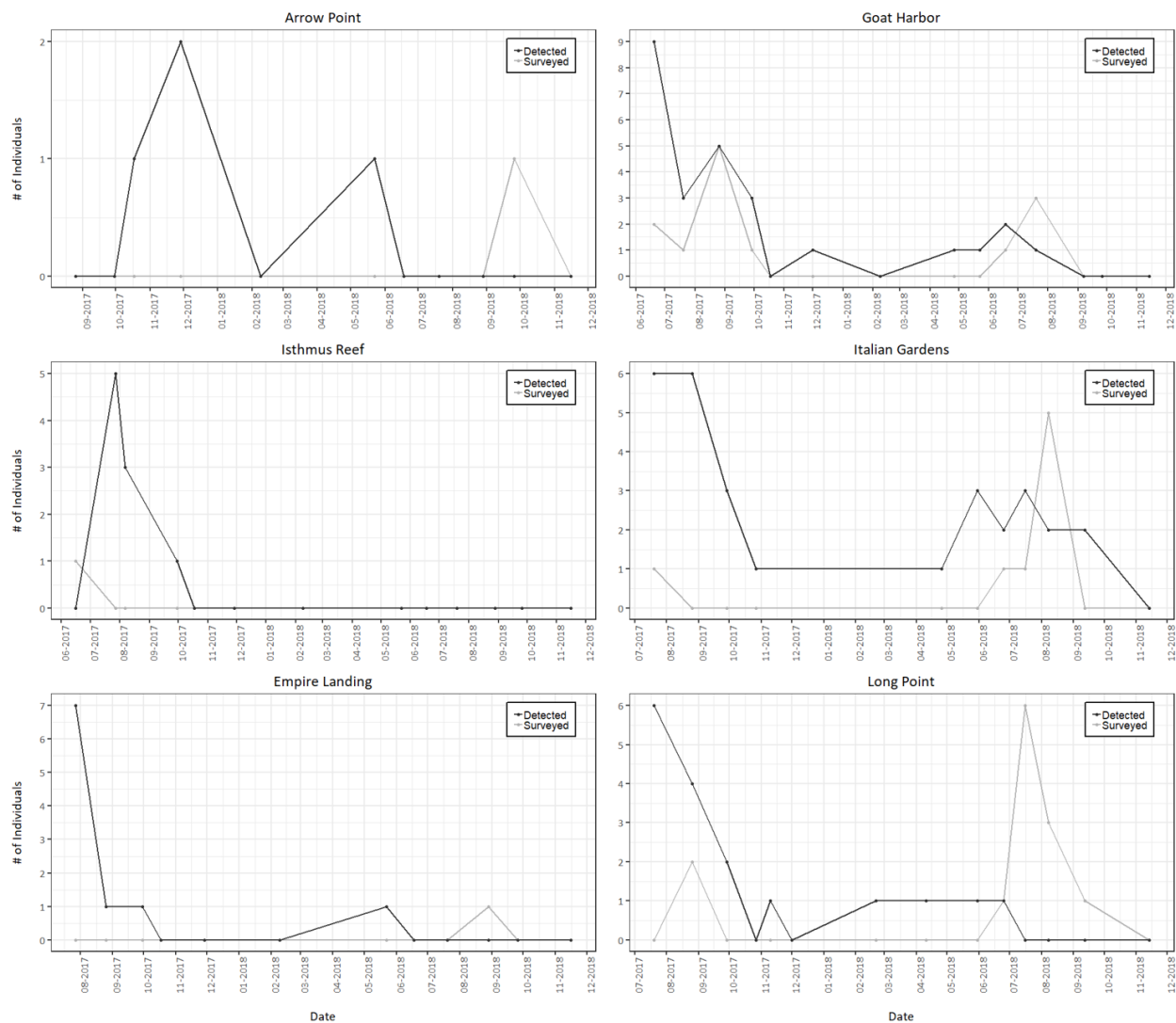
**FIGURE 2. Attrition curve of giant sea bass at Santa Catalina Island. The number next to each point indicates how many days fish were detected within the array.**

Aggregations were documented at Little Farnsworth, Casino Point, Goat Harbor, Seal Rocks, Long Point, and Italian Gardens during the spawning season, but Casino Point was the only site with consistently aggregating GSB outside of the suspected spawning season. Compared to previous observational data from 2014–2015, which found the highest numbers of individuals at the Goat Harbor ( $n = 8$ ) and Palisades ( $n = 24$ ) aggregation sites (House et al., 2016), telemetry data from the present study showed the most tagged fish detected in a single day at Goat Harbor was in late June ( $n = 9$ ) and late August ( $n = 5$ ) 2017, while the highest number of fish detected at the Palisades occurred in late July ( $n = 6$ ) of the same year (Figs. 3, 4). The number of tagged individuals detected during a single day in this study was highest in 2017

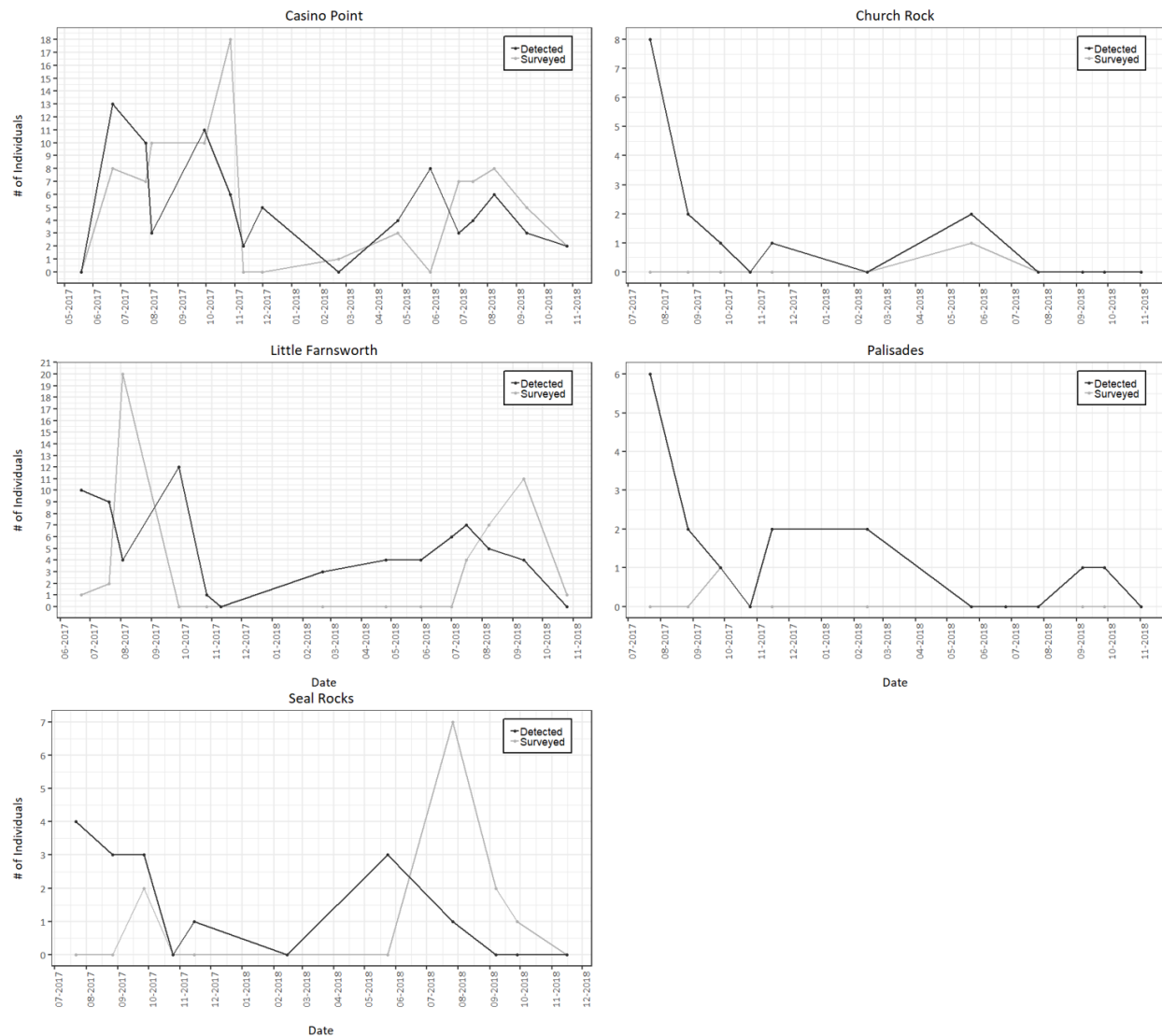
at Little Farnsworth ( $n = 12$ ) in late September and Casino Point ( $n = 13$ ) in late June.

## **Visual Surveys**

Over the course of the study, 183 GSB were seen during SCUBA visual surveys: 92 were seen on 64 surveys in 2017, while 91 individuals were counted on 85 surveys in 2018 (Table 2). The majority of GSB were seen during the summer months (65% in 2017, 70% in 2018; Fig. 3) and most of the sightings occurred at Casino Point (47%) and Little Farnsworth (25%; Fig. 4). Based on GLM results, surveys that occurred just after sunrise (07:00–08:00 hr) had significantly more fish seen ( $p = 0.01$ ) than those that took place throughout all other times of day. Similarly, significantly more fish were seen during the summer months (June–August;  $p = 0.01$ ) than all other months of the year. In addition, there were significantly more fish seen on surveys at Casino Point than all other sites ( $p = 0.001$ ; App. A, Table 3). Of the fish observed on surveys, only 7.7% carried transmitters (11% in 2017, 4% in 2018).



**FIGURE 3.** Line graphs comparing the number of giant sea bass seen on visual SCUBA surveys (gray) to the number detected during that day (black) at Arrow Point, Isthmus Reef, Empire Landing, Goat Harbor, Italian Gardens, and Long Point.



**FIGURE 4. Line graphs comparing the number of giant sea bass seen on visual SCUBA surveys (gray) to the number detected during that day (black) at Casino Point, Little Farnsworth, Seal Rocks, Church Rock, and Palisades.**

## Residency

In total, 982,897 detections from tagged GSB were recorded on 17 receivers over the course of this study (498 days; Fig. 4). Of the 32 GSB that retained their transmitters beyond September 2017, individuals showed significantly different residency to their tagging sites over the course of the study (Kruskal-Wallis,  $p = 0.018$ ; Fig. 5). Tagging site residency was lower for those fish tagged at corridor areas than those tagged at aggregation sites. The only individual tagged at Isthmus Reef spent 20% of its time there, while the three fish tagged at Goat Harbor spent  $61 \pm 13\%$ . The 16 fish tagged at Casino Point spent  $40 \pm 20\%$ , and the 12 fish tagged at Little Farnsworth spent  $65 \pm 18\%$ .

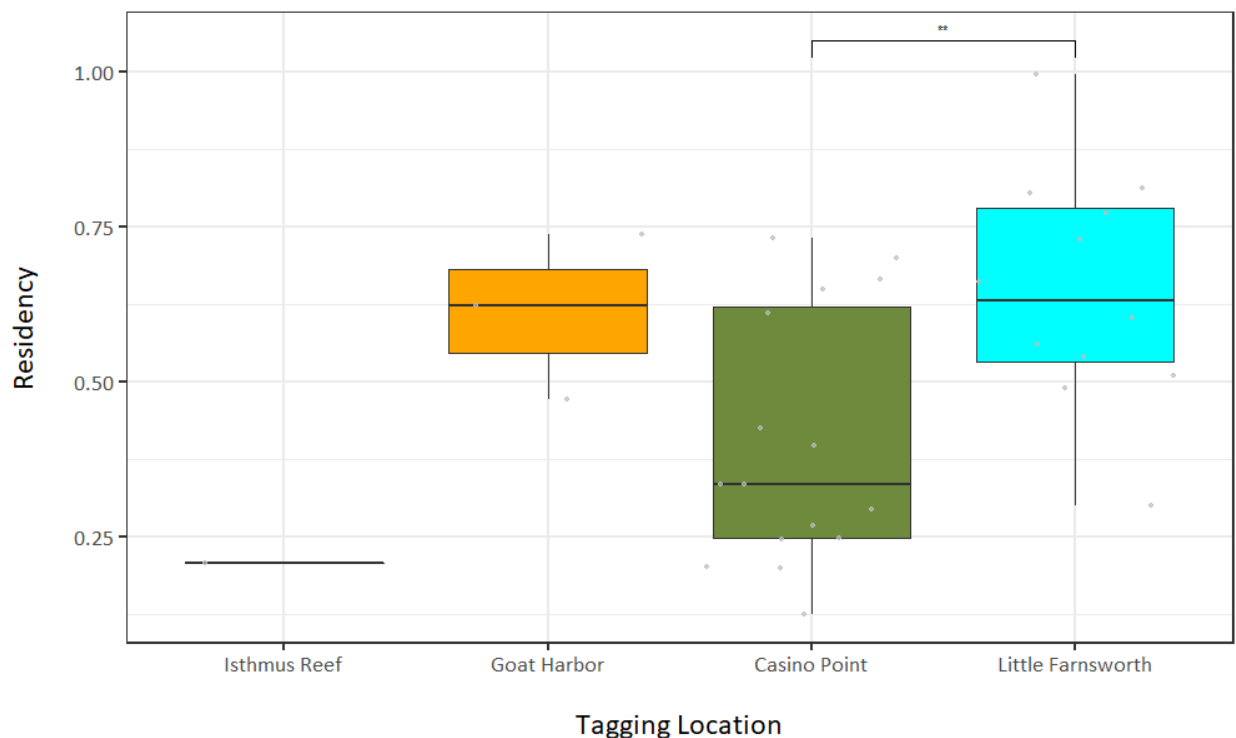
Seasonal site residency varied as did overall site residency (Kruskal-Wallis,  $p < 0.01$ ) (App. A, Tables 3, 4). Residency of tagged GSB across receivers was significantly different overall and changed between summer spawning months and winter non-spawning months (App. B, Figs. 7, 8). Fish showed variable residency across sites and between seasons (Kruskal-Wallis, spring:  $p < 0.01$ ,  $n = 17$ ; summer:  $p < 0.01$ ,  $n = 32$ ; fall:  $p < 0.01$ ,  $n = 29$ ; winter:  $p < 0.05$ ,  $n = 16$ ).

## Individual Movements, and Social Networks

Diel movement patterns varied across fish during the peak of suspected spawning. Using linear distance traveled during daytime and nighttime periods, several patterns were noticeable. The first pattern can be described as very short daytime ( $0.27 \pm 0.79$  km) and nighttime ( $0.35 \pm 0.88$  km) movements of individuals that often ranked highest in terms of degree centrality (e.g., ID #1, A69-1601-45719). Some individual movements were characterized by long daytime ( $11.74 \pm 17.08$  km) and shorter nighttime ( $7.22 \pm 9.96$  km) movements that ranked highly in network betweenness (e.g., ID #10, A69-1601-45721). Other individuals migrated long distances

during the day ( $14.42 \pm 23.78$  km) and swam shorter distances at night ( $4.61 \pm 7.95$  km) and often had the highest closeness values within the entire network (e.g., ID #3, A69-1601-45717; App. A, Table 7). Due to the smaller number of tagged individuals detected at Goat Harbor, the same individual often ranked highest in all centrality, betweenness, and closeness (e.g., ID #14, A69-1601-45716; Fig. 6). Mean values of daytime and nighttime distance traveled by fish tagged at different locations were not significantly different (Kruskal-Wallis,  $p = 0.3916$ ).

During the peak of suspected spawning (3 July–2 September) in 2017, the highest concentration of detections occurred during the final three weeks of August at all three sites (Fig.



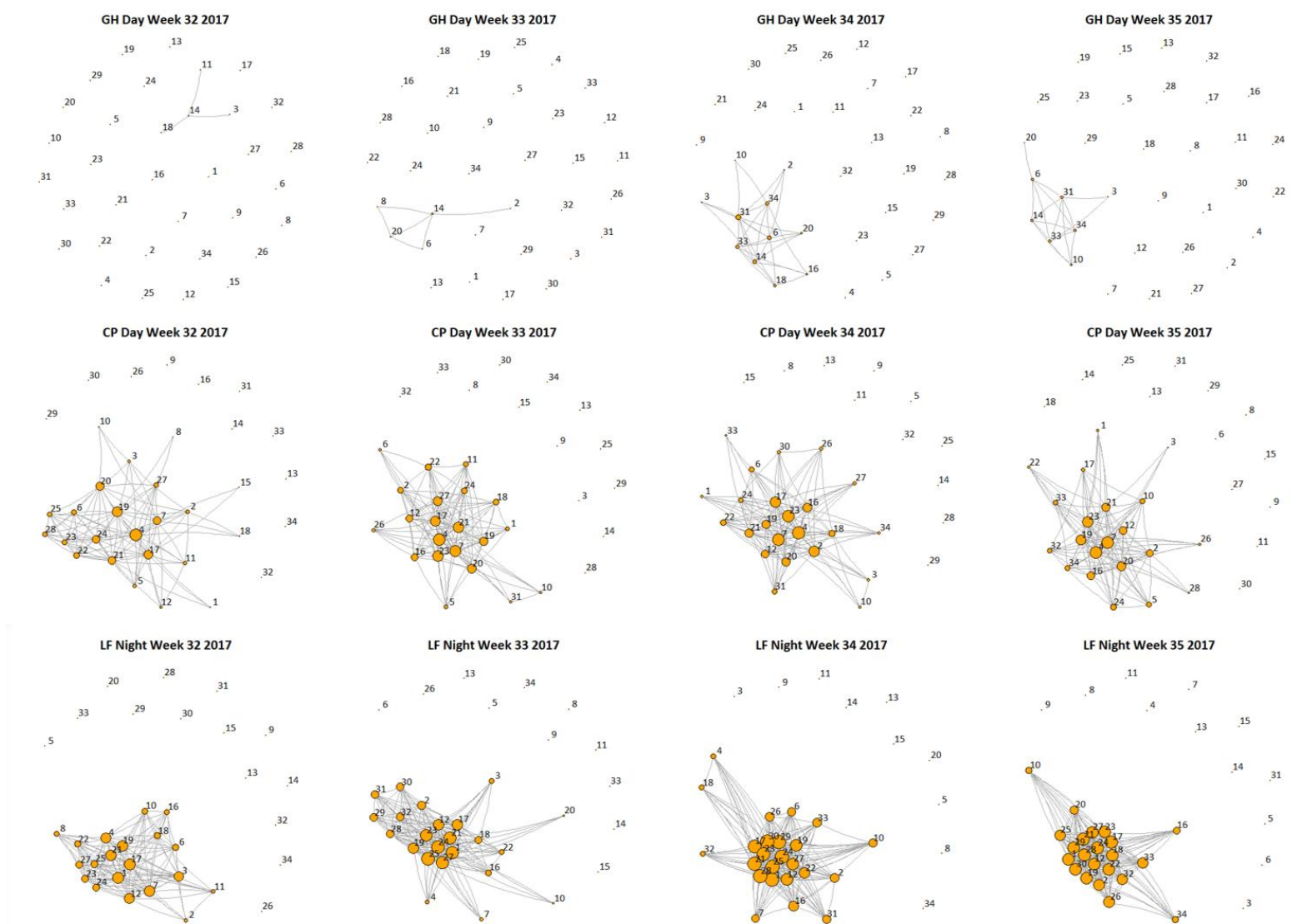
**FIGURE 5. Boxplot of giant sea bass residency by tagging location for the duration of the study. Coloration of stars matches site locations at Santa Catalina Island. Gray dots represent fish tagged at each site. \*\* denote significant differences.**

7). Tagged GSB aggregated at Goat Harbor most frequently during daylight hours in weeks 27 (2–8 July), 28 (9–15 July), and 34 (20–26 August), and both during the day and at night in week

35 (27 August–2 September). Casino Point had aggregations during both day and night in every week of 2017 except week 29 (16–22 July) at night. Little Farnsworth had similar network structures where several individuals were detected during daytime and nighttime periods across all weeks of the peak of suspected spawning except for week 27 at night. Of all networks generated, the most interactions between the most fish occurred during the nighttime hours of weeks 32–35 (6 August–2 September) at Little Farnsworth. Casino Point had similarly high numbers of the same individuals during daytime periods (ID #4, A69-1601-45708; ID #7, A69-1601-45709; ID #23, A69-1602-1536) in those weeks, but nodes (i.e., individuals) were further away from one another when compared to Little Farnsworth (Fig. 6).

In 2018, none of the networks generated at Goat Harbor showed aggregations of GSB, and only four different individuals were detected during the suspected peak of spawning (ID #7; ID #17, A69-1602-1360; ID #20, A69-1602-1534; ID #33, A69-1602-2223). Only two of those individuals were detected consistently at Goat Harbor (ID #20 and ID #33) and all co-occurrences between those two fish were in daytime hours except one during the night of week 27 (9–15 July). Based on observations of daily detections at Casino Point, aggregations occurred every day in weeks 27–31 (9 July–12 August) and nightly weeks 27, 28 (15–21 July), 31 (6–12 August), and 32 (13–19 August), which was supported by the number of individuals within the networks generated for those weeks (ID #7; ID #12, A69-1601-45707; ID #17; ID #20; ID #23; App. B, Fig. 9). Aggregations were still evident every week at Little Farnsworth during daytime and nighttime periods but, like the previous spawning season, the most interactions between the most individuals occurred at night in weeks 27–32 (App. B, Fig. 10).





**FIGURE 6.** Social network plots of giant sea bass at Goat Harbor (day), Casino Point (day), and Little Farnsworth (night) from 7 August – 3 September 2017. Every orange node is a fish with associated ascension number and every gray line in an interaction between two individuals.

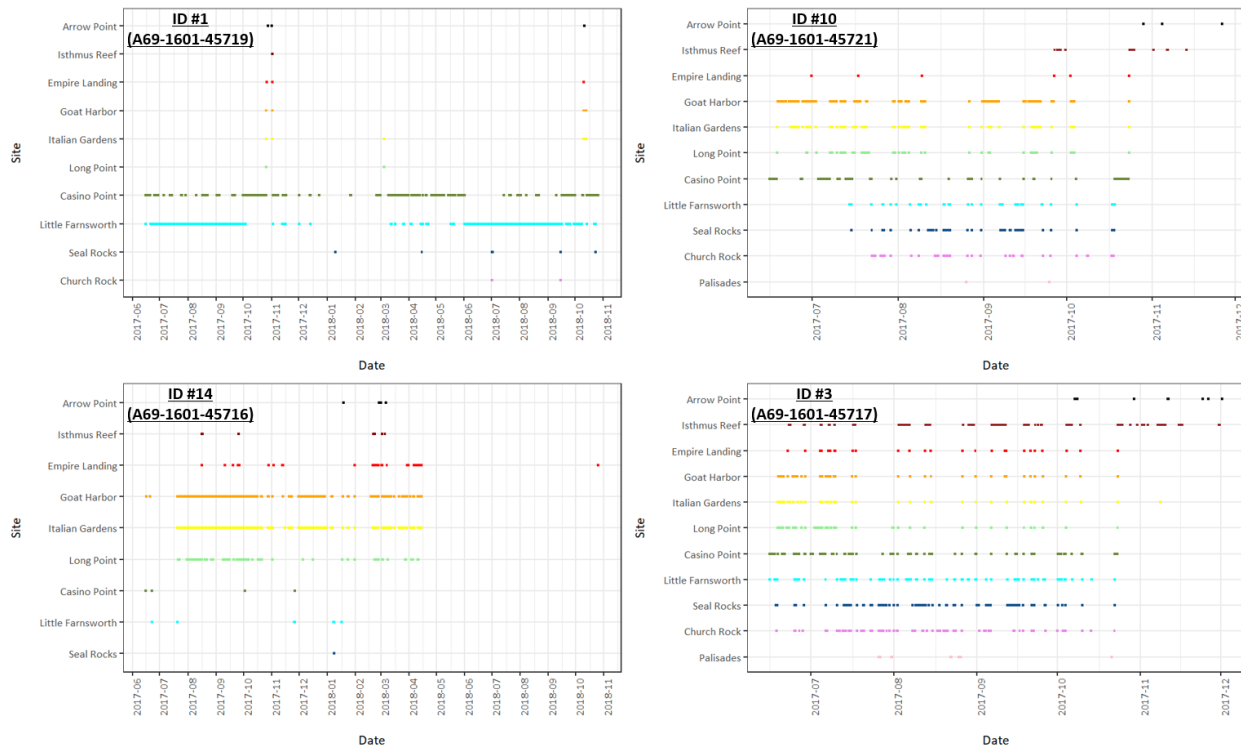
## Long Distance Movements

Only eleven tagged fish were present during the 2018 spawning season at Catalina and, of those, eight fish (23.5%) were present at the end of this study (26 October 2018), calculated as the number of fish having  $\geq 2$  detections at Catalina on or after 1 October 2018. A total of 14 fish left the array at Catalina prior to 2018 and were never detected again. Of those emigrating fish, one (ID #34, A69-1602-2227) was detected for 60 days before leaving the array from the northern-most site, Arrow Point, on 8 October 2017 and was next detected at Point Vicente, CA (33.74283, -118.41317), on 10 October 2017, where it was last detected. This represents a swimming distance of approximately 31 km in 35 hrs. Another fish (ID #29, A69-1602-2220) was detected at Catalina for 65 consecutive days before leaving the array from Casino Point on 22 October 2017, crossing the San Pedro Channel, and was detected off Laguna Beach, CA (33.54440, -117.79850), on 24 October 2017, swimming a minimum distance of approximately 53 km in 56 hrs. Six days after traversing the channel, it was detected approximately 18 km northwest of Laguna Beach, near the Orange County Sanitation District's (OCSD) outfall pipe (Burns, Clevenstine, Logan, and Lowe, unpublished data). A second study was being conducted simultaneously around the OCSD wastewater outfall pipe using an array of 24 acoustic receivers deployed at depths between 35–65 m. The GSB made six additional visits to the outfall pipe until it was last detected on 8 January 2018, and each visit lasted between two and eight days.

Two tagged fish were detected leaving the Catalina array in late 2017 moving north to Point Dume, CA (33.00004, -118.80990). The first (ID #12, A69-1601-45707), left the array from Arrow Point on 12 October, arriving at Pt. Dume on 16 October 2017 before being detected at Morse Point, Santa Cruz Island (33.96657, -119.85468), on 4 November 2017 (Freedman et al., unpublished data). This individual was detected sporadically at Morse Point and Valley

(33.97822, -119.66998) receivers for 29 days before being continually detected for three days at Valley, where it was last detected on 5 December 2017. It was then detected three months later at Pt. Dume on 15 March 2018, returning to the Catalina array via Arrow Point two days later, on 17 March 2018.

The second individuals (ID #17, A69-1602-1360) left Arrow Point on 29 November 2017 and arrived at Pt. Dume six days later on 5 December 2017. This individual also moved offshore to Santa Cruz Island where it was detected on 5 February and 3 April 2018. It was later detected south at Pt. Dume on 14 April 2018 before returning to Catalina via Church Rock on 18 April 2018, swimming approximately 90 km in 74 hrs.



**FIGURE 7. Detection plots of giant sea bass ID #1 (A69-1601-45719), ID #10 (A69-1601-45721), ID #14 (A69-1601-45716), and ID #3 (A69-1601-45717) at Santa Catalina Island.**

## CHAPTER 4

### DISCUSSION

This study found GSB aggregate at specific sites at Catalina during the suspected spawning season. Assuming GSB spawn at night, Little Farnsworth was the most likely spawning aggregation site of all sites monitored (App. B, Fig. 16) and activity peaked during the summer months from June–October, with the most aggregating activity occurring from July–September in 2017 and June–August in 2018.

Based on what little is known of reproductive behaviors of GSB, and that Little Farnsworth was the only site containing an underwater pinnacle surrounded by deep water, Little Farnsworth was the site where aggregative spawning was most likely to occur based on the high number of individuals present at night, the amount of time spent there during nighttime hours, and high residency during the summer months. Observed detection data and patterns of movements for GSB around the approximate time of peak spawning, the selection of promontories and timing of behavior is very similar to that observed in other species, such as Goliath grouper (*Epinephelus itajara*), the only other reef fish close to the same size (2.5 m TL, 360 kg) as GSB, which have been documented to spawn at promontories during the summer months (Collins, Barbieri, McBride, McCoy, & Motta, 2015; Eklund & Schull, 2001; Koenig et al., 2017; Koenig, Coleman, & Kingon, 2011; Mann et al., 2009). Promontories tend to have strong currents which may be beneficial in terms of reducing egg predation and maximizing dispersal (Barlow, 1981; Johannes, 1978), and is suspected to be a reason why several other species including red hind (*Epinephelus striatus*), Nassau grouper (*Epinephelus itajara*), gulf grouper (*Mycteroperca jordani*), sawtail grouper (*M. prionura*), and Pacific yellowtail (*Seriola dorsalis*) spawn at or near promontories (Carter & Perrine, 1994; Sala et al., 2003). Kobara and

Heyman (2008) assessed the geospatial and bathymetric aspects of Nassau grouper spawning sites in the Cayman Islands and found they were all located within 1 km of promontories adjacent to deep water, similar for Nassau grouper throughout the Caribbean (Aguilar-Perera & Aguilar-Dávila, 1996; Carter, Marrow, & Pryor, 1994; Claro & Lindeman, 2003; Colin, 1992). Several other sites at Catalina (Arrow Point, Long Point, Casino Point, Goat Harbor) have similar geomorphologies and were located near promontories but detection data from those sites were dissimilar to Little Farnsworth, with Arrow Point having higher activity during winter months and Long Point, Casino Point, and Goat Harbor having the most activity during daylight hours. This may be due to low GSB abundance or environmental factors that were not ideal for spawning. The size of spawning aggregations naturally varies in time across daily and annual scales (Colin, 1996; Johannes, Squire, Graham, Sadovy, & Renguul, 1999; Samoilys & Squire, 1994). What was documented for GSB during the period of this study will likely change as the population recovers in southern California. In the northern and southern portions of the species range, spawning could be occurring on a more consistent basis, but more studies are needed to address timing and environmental factors associated with spawning.

Little is known about the exact time of spawning in GSB, but it is hypothesized to occur between dusk and dawn (Allen, personal comm.), similar to other groupers and wreckfish (Colin, 1994; Erisman & Allen, 2006). GSB may be similar to Goliath groupers in the western Atlantic and Gulf of Mexico, which have been documented to spawn at night in late summer to early fall during the darkest phase of the lunar cycle, the new moon, supposedly to minimize egg predation by baitfish that are abundant at spawning sites (Koenig et al., 2017). Or GSB aggregation behavior may be similar to species like red hind, which spawn across several days around the full moon and spawning differs across sites and regions (Nemeth et al., 2007). Grouper and snapper

species in the Gulf of California spawn across variable lunar phases, with the large Gulf grouper (*Mycteroperca jordani*) spawning primarily around the full moon (Sala et al., 2003). The leopard grouper (*M. rosacea*) were believed to spawn during both the new and full moon phases but Erisman, Buckhorn, and Hastings (2007) found no significant differences in spawning among lunar phases. It is possible that abundance and densities of GSB at Catalina is too low to support consistent spawning aggregations, regardless of lunar phase or location. As the population continues to recover, aggregation and spawning behaviors may become more predictable in space and time as with other species of large-bodied reef fish. LME results from this study, however, indicated there was no significant difference in hourly residency of fish based on lunar phase as fish were detected during all hours of night across all lunar phases (App. B, Fig. 15).

Although temperature and lunar phase were not a significant drivers of residency over the course of this study, they may play a role in aggregative behavior as densities increase over time. Seasonal residency values indicate both Little Farnsworth and Goat Harbor were visited most frequently in the summer months and may be important sites for spawning or courtship (App. B, Fig. 8). Fish did aggregate at Goat Harbor but numbers were far lower than at Little Farnsworth and aggregating occurred during the day (Fig. 6); therefore, this study confirmed Goat Harbor is an aggregation site but spawning was not likely occurring. Foraging and protection are the two other main drivers of aggregating, but based on what is known of GSB they presumably do not aggregate to search for prey or to reduce risk of predation, as the minimum size of aggregating fish was > 100 cm TL. Suspected courtship behaviors, including pair circling, pair following, ventral nudging (Clark & Allen, 2018), were documented on several daytime surveys in 2017 and 2018 at Goat Harbor, Italian Gardens, and Long Point. Considering all these sites are adjacent to or within the historic aggregation site at Goat Harbor, GSB may be using those areas

for courting and not spawning, based on the number of tagged individuals present during the day versus at night (App. B, Fig. 17).

Casino Point was the site with the highest residency outside of the suspected spawning season (November–April) and consistently had the most individuals seen on visual surveys (Fig. 3); however, Little Farnsworth had the highest overall residency of any site for the duration of the study despite being significantly lower than Casino Point outside of spawning App. B, Fig. 7). GSB were likely aggregating at Casino Point for courting, similar to Goat Harbor; however, aggregations continued outside of the suspected spawning season and fish were detected frequently across all seasons. Casino Point was central to some GSB home ranges within the array at Catalina throughout the year, indicated by relatively high overall residency.

Tagged individuals aggregated at Little Farnsworth from the beginning of the study through November 2017 and aggregations were detected frequently throughout each day during the spawning season despite rarely being seen on surveys after 08:00 hr (App. B, Figs. 11–14). Individuals were detected more frequently from dusk until dawn at Little Farnsworth, but several fish were present during almost every hour of the day, so GSB may aggregate prior to spawning to select mates or establish territories. Similar aggregative behaviors have been observed in tropical snappers, for example, cubera snapper (*Lutjanus cyanopterus*) began to aggregate well in advance of actual spawning (Heyman, Kjerfve, Graham, Rhodes, & Garbutt, 2005). At least 20 aggregating individuals were seen on a single survey around the promontory at Little Farnsworth in the hours just after sunrise (07:00–08:00 hr). This type of behavior has been seen in other species, for example, in Belize, cubera snapper (*Lutjanus cyanopterus*) form annual aggregations at promontories and release their gametes upstream of the prevailing current in the twilight hours (Heyman et al., 2005).

Over the duration of this study, no aggregations of tagged GSB were detected at the Palisades, in contrast to the 24 individuals observed in a previous study (House et al., 2016). GSB may utilize the Palisades under specific environmental conditions that did not occur during the period of this study or aggregations of GSB may move around to areas adjacent to the Palisades (outside of detection range). It is also possible untagged fish were aggregating at or near the Palisades but, based on visual survey and detection data from adjacent Church Rock, it seems unlikely that any aggregations took place in the area during the period of this study.

The connections of GSB within social networks provide information that may be important for understanding individual behaviors within the population at Catalina. The more connections a fish has within a network, the more exposure that individual has to other fish. Highly connected fish, those with the highest degree centrality in any given network, may be more influential within the network or population as a whole. Fish with the highest degree centrality (e.g., ID #1, A69-1601-45719) may be gravid females that spend most of their time close to spawning aggregation sites to conserve energy for reproduction (i.e., egg production). If female movements are short during spawning periods, males may be making daily migrations along Catalina, indicated by highly directed, longer-distance movements (e.g., ID #3, A69-1601-45717). These fish exhibiting diel migration patterns often ranked highest in terms of betweenness because they are connecting different groups, potentially those that are resident to, or aggregate at, different sites.

According to Cornish (2004), GSB are believed to have a “very limited” distribution within California and Mexican waters, increasing its vulnerability to overfishing. However, based on data presented here, GSB travel long distances throughout the year, similar to other large-bodied predatory fish that are capable of long-range movements (Bolden, 2000; Espinoza,



Heupel, Tobin, & Simpfendorfer, 2015, 2016). Other large reef predators, like Nassau grouper, show site fidelity to reproductive and non-reproductive areas throughout the year and their migrations to spawning sites are consistent and predictable (Starr, Sala, Ballesteros, & Zabala, 2007) and the species has been found to migrate 110 km and 240 km to seasonal aggregation sites in the Caribbean (Carter et al., 1994; Colin, 1992). A previous acoustic telemetry study conducted at Anacapa Island, CA, beginning in 2000 found four individual GSB swam to Catalina, a minimum distance of 100 km (Domeier & Maas, 2005). Based on pilot study movement data and data from this study, GSB exhibit long-range movements (> 100 km) that can be characterized as migrations because they are highly directional and likely driven by biological (i.e., reproduction, competition) and environmental changes (i.e., seasonality, resource availability) (Alerstam, Hedenström, & Åkesson, 2003); therefore, the species may have a larger distribution than previously thought.

Due to their large size, GSB may be forced to leave spawning areas due to limited food resources and increased competition after spawning has concluded. Based on seasonal residency data, fish leave Catalina primarily from the northwest end of the island and often return along a similar path. Further studies are needed to determine the fine-scale environmental changes that cause individuals to leave the island and understand potential migratory pathways GSB use in the Southern California Bight.

Although aggregating at specific locales may naturally increase reproductive opportunities (Parrish & Edelstein-Keshet, 1999), GSB became severely depleted before much was learned about the drivers, cues, and movements associated with aggregative behavior (Bolden, 2000; Erisman et al., 2012; Semmens et al., 2010; Whaylen et al., 2004). Like GSB, Goliath grouper were overfished during the latter half of the 20<sup>th</sup> century until regulations

protecting them were put in place in 1990. Four years later, the first aggregations were documented by Colin (1994) but, due to the low number ( $< 10$ ) of aggregating groupers, a “realistic evaluation” of true spawning periodicity could not be assessed for over a decade (Koenig et al., 2011). Due to the estimated 14 year population doubling time of GSB (Musick et al., 2000), accurate assessments of aggregations were not possible until recently and this study provides the first evidence of site-specific residency, annual aggregation site fidelity, and partial migration of GSB at Catalina.

## CONCLUSION

This is the first study to assess movement and aggregations of GSB and provides the first evidence of partial migration of GSB and individual residency to Catalina. Aggregating at Catalina was documented from June–October, and spawning was most likely occurring at a pinnacle promontory in July–September. GSB tagged at Catalina exhibited residency to specific sites throughout the year and individuals showed fidelity to suspected spawning aggregation sites during the summer months. It is possible that, in addition to spawning aggregations, some fish are pair spawning at certain sites because densities may be so low that aggregative spawning is not yet beneficial. This study is not a complete evaluation of GSB aggregation and spawning but it is an important step towards understanding how the behavior of an exploited population may change in light of protection. The identification of a new aggregation site at Little Farnsworth and an annual aggregation site at Casino Point could have implications for the continued recovery of the species; however, more work needs to be done to determine what fish are doing while aggregating at both sites as well as the historic aggregation site at Goat Harbor. Future studies need to confirm the timing of spawning, which may be accomplished by utilizing emerging technologies such as accelerometry tags and remotely operated/autonomous underwater vehicles to capture short-term, fine-scale movements associated with spawning. Proximity tags, if deployed on several GSB in an aggregation, can inform researchers as to whether GSB move together within and outside of the spawning season and, when paired with in-depth social network analyses, may show long-term associations of individuals across the species range. This study provides a baseline of species-specific spatial and temporal movement and behavioral patterns that can be used to improve our understanding of GSB and potentially be used in future management decisions concerning the continued recovery of the species in

California and Mexico.

**APPENDIX A**  
**TABLES**

**TABLE 1. Tagging summary of GSB tagged during this study.**

<b>Date Tagged</b>	<b>Transmitter</b>	<b>ID</b>	<b>Tagging Location</b>	<b>Latitude</b>	<b>Longitude</b>	<b>Depth</b>
15 June 2017	A69-1601-45719	1	Casino Point	33.3492	-118.3235	15
15 June 2017	A69-1601-45720	2	Casino Point	33.3492	-118.3235	15
15 June 2017	A69-1601-45717	3	Casino Point	33.3492	-118.3235	15
15 June 2017	A69-1601-45708	4	Casino Point	33.3492	-118.3235	15
15 June 2017	A69-1601-45711	5	Casino Point	33.3492	-118.3235	15
15 June 2017	A69-1601-45710	6	Casino Point	33.3492	-118.3235	15
15 June 2017	A69-1601-45709	7	Casino Point	33.3492	-118.3235	15
15 June 2017	A69-1601-45712	8	Casino Point	33.3492	-118.3235	15
15 June 2017	A69-1601-457A69-1602-15	9	Casino Point	33.3492	-118.3235	15
15 June 2017	A69-1601-45721	10	Casino Point	33.3492	-118.3235	15
16 June 2017	A69-1601-457A69-1602-13	11	Isthmus Reef	33.4514	-118.4870	16
22 June 2017	A69-1601-45707	12	Casino Point	33.3492	-118.3235	20
22 June 2017	A69-1601-45714	13	Casino Point	33.3492	-118.3235	20
20 July 2017	A69-1601-45716	14	Goat Harbor	33.419	-118.393	20

**TABLE 1. Continued.**

28 July 2017	A69-1601- 45718	15	Casino Point	33.3492	-118.3235	18
28 July 2017	A69-1602- 1356	16	Casino Point	33.3492	-118.3235	18
28 July 2017	A69-1602- 1360	17	Casino Point	33.3492	-118.3235	18
8 August 2017	A69-1602- 1535	18	Little Farnsworth	33.3350	-118.3087	21
8 August 2017	A69-1602- 1357	19	Little Farnsworth	33.3350	-118.3087	21
8 August 2017	A69-1602- 1534	20	Casino Point	33.3492	-118.3235	15
8 August 2017	A69-1602- 1358	21	Casino Point	33.3492	-118.3235	15
9 August 2017	A69-1602- 1359	22	Little Farnsworth	33.3350	-118.3087	22
9 August 2017	A69-1602- 1536	23	Little Farnsworth	33.3350	-118.3087	22
9 August 2017	A69-1602- 1537	24	Little Farnsworth	33.3350	-118.3087	22
9 August 2017	A69-1602- 2219	25	Little Farnsworth	33.3350	-118.3087	21
9 August 2017	A69-1602- 2221	26	Little Farnsworth	33.3350	-118.3087	21
9 August 2017	A69-1602- 2224	27	Little Farnsworth	33.3350	-118.3087	21
18 August 2017	A69-1602- 1538	28	Little Farnsworth	33.3350	-118.3087	22
18 August 2017	A69-1602- 2220	29	Little Farnsworth	33.3350	-118.3087	22

**TABLE 1. Continued.**

18 August 2017	A69-1602- 22A69- 1602-22	30	Little Farnsworth	33.3350	-118.3087	21
18 August 2017	A69-1602- 2225	31	Little Farnsworth	33.3350	-118.3087	21
18 August 2017	A69-1602- 2226	32	Little Farnsworth	33.3350	-118.3087	21
21 August 2017	A69-1602- 2223	33	Goat Harbor	33.419	-118.393	20
21 August 2017	A69-1602- 2227	34	Goat Harbor	33.419	-118.393	20



**TABLE 2. Visual survey count data of giant sea bass across all sites from June 2017 – October 2018. Numbers in parentheses indicate number of tagged fish seen on survey. Dash indicates no survey was conducted. White rows correspond to 2017 surveys, shaded rows correspond to 2018 surveys.**

	AP	IR	EL	GH	IG	LP	CP	LF	SR	CR	P
<b>JUN</b>	-	1	0	2	0	0	8 (1)	1	0	0	0
<b>JUL</b>	-	0	0	1	1	0	7 (1)	2 (1)	0	0	0
<b>AUG</b>	0	0	0	5	0	2	10 (3)	20 (1)	0	0	0
<b>SEP</b>	0	0	0	1	0	0	10 (2)	0	2	0	1
<b>OCT</b>	0	0	0	0	0	0	18 (1)	0	0	0	0
<b>NOV</b>	0	0	0	0	0	0	0	0	0	0	0
<b>DEC</b>	-	-	-	-	-	-	-	-	-	-	-
<b>JAN</b>	-	-	-	-	-	-	-	-	-	-	-
<b>FEB</b>	0	0	0	0	0	0	1	0	0	0	0
<b>MAR</b>	-	-	-	-	-	-	-	-	-	-	-
<b>APR</b>	0	0	0	0	0	0	3	0	0	0	0
<b>MAY</b>	0	0	0	0	0	0	0	0	0	1	0
<b>JUN</b>	0	0	0	1	1	1	7 (2)	0	-	-	0
<b>JUL</b>	0	0	0	3	1	6	7	4	7	-	0
<b>AUG</b>	0	0	1	0	5	3	8	7 (1)	2	0	0
<b>SEP</b>	1	0	0	0	0	1	5	11 (1)	1	0	0
<b>OCT</b>	0	0	0	0	0	0	2	1	0	0	0
Site Total	<b>1</b>	<b>1</b>	<b>1</b>	<b>13</b>	<b>8</b>	<b>13</b>	<b>86</b>	<b>46</b>	<b>12</b>	<b>1</b>	<b>1</b>

**TABLE 3. Results of GLM outputs examining number of fish seen on visual surveys.**

<b>Model Parameters</b>	<b>% deviance explained</b>
* Total ~ Site Type + Site + Month + Time + Temp	76.16%
Total ~ Site + Month + Time	75.84%
Total ~ Site + Month + Temp	69.66%
Total ~ Site + Time + Temp	49.76%

Note: Effects of site type (aggregation or corridor), site, month, time, and water temperature (Temp) on the total number (Total) of giant sea bass seen during visual surveys. \* indicates best fitting model.

**TABLE 4. Residency summary statistics for all sites during each season with associated standard deviation (SD) values.**

<b>Site</b>	<b>Season</b>	<b>Mean</b>	<b>SD</b>	<b>Season</b>	<b>Mean</b>	<b>SD</b>	<b>Season</b>	<b>Mean</b>	<b>SD</b>	<b>Season</b>	<b>Mean</b>	<b>SD</b>
Arrow Point	<i>Summer</i>	0.0%	0.1%	<i>Fall</i>	1.3%	2.3%	<i>Winter</i>	1.2%	3.5%	<i>Spring</i>	0.5%	2.0%
Isthmus Reef	<i>Summer</i>	0.8%	2.3%	<i>Fall</i>	1.1%	3.2%	<i>Winter</i>	0.4%	1.3%	<i>Spring</i>	0.3%	0.7%
Empire Landing	<i>Summer</i>	0.5%	1.4%	<i>Fall</i>	0.5%	1.1%	<i>Winter</i>	0.0%	0.2%	<i>Spring</i>	0.4%	1.3%
Goat Harbor	<i>Summer</i>	3.7%	7.5%	<i>Fall</i>	1.8%	4.4%	<i>Winter</i>	0.4%	2.0%	<i>Spring</i>	0.5%	1.3%
Italian Gardens	<i>Summer</i>	2.9%	10.5%	<i>Fall</i>	2.4%	8.0%	<i>Winter</i>	0.6%	2.9%	<i>Spring</i>	1.8%	7.4%
Long Point	<i>Summer</i>	0.6%	0.8%	<i>Fall</i>	0.2%	0.5%	<i>Winter</i>	0.1%	0.2%	<i>Spring</i>	0.1%	0.1%
Casino Point	<i>Summer</i>	9.8%	14.5%	<i>Fall</i>	12.2%	15.4%	<i>Winter</i>	2.8%	5.7%	<i>Spring</i>	12.1%	19.2%
Little Farnsworth	<i>Summer</i>	16.2%	20.8%	<i>Fall</i>	11.3%	11.6%	<i>Winter</i>	2.0%	4.8%	<i>Spring</i>	4.5%	8.1%
Seal Rocks	<i>Summer</i>	1.2%	1.4%	<i>Fall</i>	1.6%	2.3%	<i>Winter</i>	0.2%	0.6%	<i>Spring</i>	0.3%	0.7%
Church Rock	<i>Summer</i>	1.2%	2.2%	<i>Fall</i>	0.5%	1.1%	<i>Winter</i>	0.1%	0.2%	<i>Spring</i>	0.2%	0.8%
Palisades	<i>Summer</i>	1.3%	2.6%	<i>Fall</i>	2.0%	7.3%	<i>Winter</i>	1.5%	5.4%	<i>Spring</i>	2.3%	10.6%

**TABLE 5. Overall residency statistics from 15 June 2017 – 26 October 2018.**

<b>Overall</b>	<b>Mean</b>	<b>SD</b>	<b>Median</b>
Arrow Point	0.1%	0.3%	0.0%
Isthmus Reef	1.5%	4.2%	0.0%
Empire Landing	1.1%	3.1%	0.1%
Goat Harbor	12.7%	20.4%	1.5%
Italian Gardens	4.6%	10.3%	0.5%
Long Point	1.8%	4.8%	0.2%
Casino Point	29.7%	20.7%	25.8%
Little Farnsworth	39.3%	29.4%	34.7%
Seal Rocks	5.0%	8.4%	1.9%
Church Rock	1.5%	3.4%	0.1%
Palisades	1.2%	2.7%	0.0%

**TABLE 6. Linear distance traveled for giant sea bass during the suspected peak of spawning (6 August – 2 September) in 2017 at Santa Catalina Island.**

<b>Transmitter</b>	<b>ID</b>	<b>Mean Daily Distance Traveled (km)</b>	<b>Daily Standard Deviation</b>	<b>Mean Nightly Distance Traveled (km)</b>	<b>Nightly Standard Deviation</b>	<b>Tagging Location</b>
45707	12	0.937716	1.203111	0.754363	1.139454	Casino Point
45708	04	0.41133	1.369484	0.442011	0.965403	Casino Point
45709	07	0.557352	1.055372	0.767831	1.207422	Casino Point
45710	06	10.28728	11.10762	5.64574	7.995354	Casino Point
45711	05	0.309407	0.875136	0	0	Casino Point
45712	08	3.37	7.19816	0.03143	0.076987	Casino Point
45713	11	9.625798	23.08892	8.992107	12.63797	Isthmus Reef
45714	13	NA	NA	NA	NA	Casino Point
45715	09	NA	NA	NA	NA	Casino Point
45716	14	16.66149	8.259745	13.60145	9.233188	Goat Harbor
45717	03	14.42006	23.7812	4.614322	7.956149	Casino Point
45718	15	6.604626	NA	20.28774	NA	Casino Point
45719	01	0.275029	0.792717	0.353608	0.882054	Casino Point
45720	02	5.28383	9.949051	8.045692	12.7502	Casino Point
45721	10	11.74411	17.0849	7.229216	9.967383	Casino Point
1356	16	2.42925	4.095577	1.395609	2.335808	Casino Point
1357	19	1.347338	1.273054	1.061731	1.235443	Little Farnsworth
1358	21	0.394643	0.886758	0.680922	1.111835	Casino Point
1359	22	0.680922	1.111835	0.127452	0.507869	Little Farnsworth
1360	17	1.428034	1.247113	0.897491	1.198556	Casino Point
1534	20	5.844172	9.820815	1.565796	5.873185	Casino Point
1535	18	5.383012	10.74958	2.214028	6.152268	Little Farnsworth
1536	23	1.428034	1.247113	1.485155	1.23763	Little Farnsworth
1537	24	1.14968	1.252079	0.198021	0.685368	Little Farnsworth
1538	28	0.275029	0.800451	0	0	Little Farnsworth
2219	25	0.556541	1.60334	1.030154	3.290159	Little Farnsworth
2220	29	0.752829	1.839516	0.773822	1.89579	Little Farnsworth
2221	26	0.836202	1.646683	0.512371	1.011429	Little Farnsworth
2222	30	0.154704	0.618815	0.01347	0.0504	Little Farnsworth
2223	33	14.41511	8.778079	12.70286	10.57208	Goat Harbor
2224	27	0.832944	1.18688	0.403585	0.923561	Little Farnsworth
2225	31	11.45013	13.20396	6.75085	7.833547	Little Farnsworth
2226	32	2.32594	2.809175	1.8734	3.057753	Little Farnsworth
2227	34	10.16926	12.00548	4.941909	8.096605	Goat Harbor

**TABLE 7. Network statistics of tagged giant sea bass at Santa Catalina Island during the suspected spawning seasons in 2017 and 2018. Shaded rows correspond to weekly networks assessed in 2018.**

Site	Day/Night	Week	Year	Closeness	Betweenness	Degree Centrality
Casino Point	Day	27	2017	10	10	7, 9
Casino Point	Day	28	2017	5	7	7
Casino Point	Day	29	2017	13	7	7
Casino Point	Day	30	2017	4	4	4
Casino Point	Day	31	2017	3	4	4, 7
Casino Point	Day	32	2017	27	4	4
Casino Point	Day	33	2017	5	23	4
Casino Point	Day	34	2017	31	4	4
Casino Point	Day	35	2017	5	4	4, 7
Casino Point	Night	27	2017	5	7	7
Casino Point	Night	28	2017	2	7	2, 7
Casino Point	Night	29	2017	7	7	7
Casino Point	Night	30	2017	8	4	4
Casino Point	Night	31	2017	15	4	4
Casino Point	Night	32	2017	4	4	4
Casino Point	Night	33	2017	1	7	4, 7
Casino Point	Night	34	2017	5	2	17
Casino Point	Night	35	2017	5	4	4
Casino Point	Day	27	2018	1	1	7, 17, 23
Casino Point	Day	28	2018	7	17, 23	7, 17, 23
Casino Point	Day	29	2018	12	7	7, 12, 23
Casino Point	Day	30	2018	12	12	7
Casino Point	Day	31	2018	32	12, 23	12, 23
Casino Point	Day	32	2018	20	20	20
Casino Point	Day	33	2018	23	23	23
Casino Point	Day	34	2018	20	20	17, 20, 23
Casino Point	Day	35	2018	23	23	17, 20, 23
Casino Point	Night	27	2018	12	12	17, 23
Casino Point	Night	28	2018	20	17, 20	17
Casino Point	Night	29	2018	20	20	20
Casino Point	Night	30	2018	7	NA	7, 17, 20, 23
Casino Point	Night	31	2018	32	20	20
Casino Point	Night	32	2018	12	23	17, 23
Casino Point	Night	33	2018	20	20, 23	23
Casino Point	Night	34	2018	17	17	17
Casino Point	Night	35	2018	23	NA	17, 20, 23

**TABLE 7. Continued.**

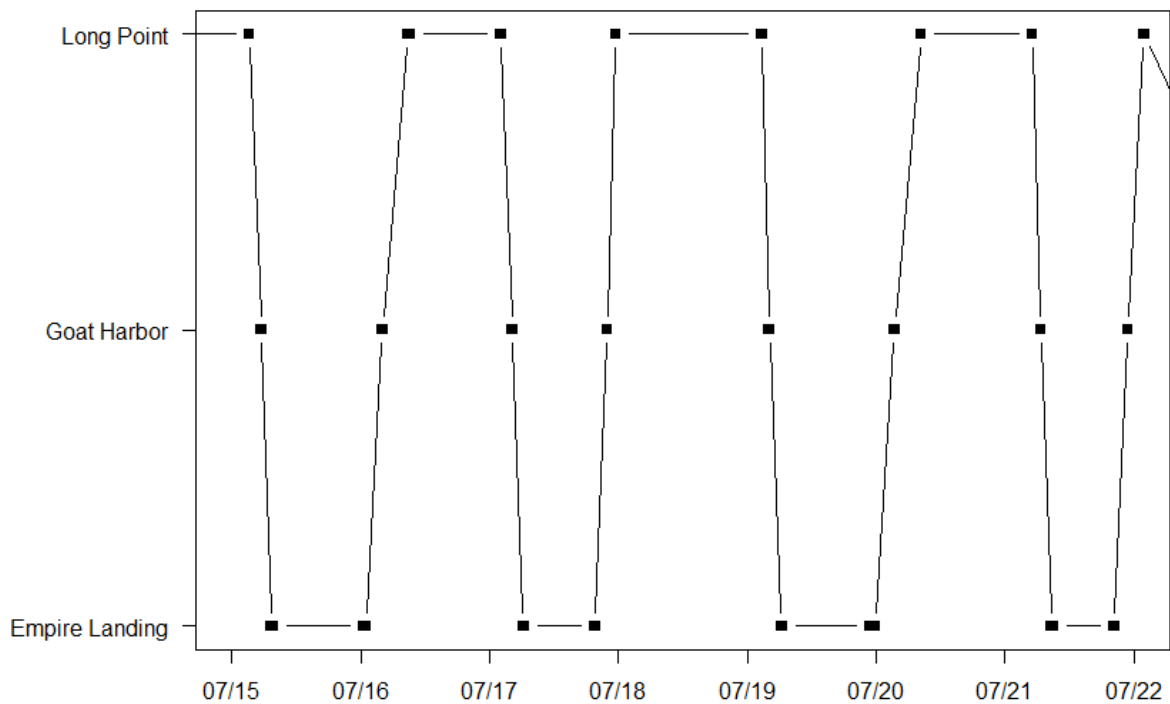
Goat Harbor	Day	27	2017	6	6	6
Goat Harbor	Day	28	2017	2	4	4
Goat Harbor	Day	29	2017	10	10	4, 8, 10
Goat Harbor	Day	30	2017	14	14	14
Goat Harbor	Day	31	2017	14	14	14
Goat Harbor	Day	32	2017	14	14	14
Goat Harbor	Day	33	2017	14	14	14
Goat Harbor	Day	34	2017	20	31	31
Goat Harbor	Day	35	2017	6	6	31, 33
Goat Harbor	Night	27	2017	6	6	6
Goat Harbor	Night	28	2017	4	4	4
Goat Harbor	Night	29	2017	2	NA	2, 10
Goat Harbor	Night	30	2017	2	NA	1, 14
Goat Harbor	Night	31	2017	14	14	14
Goat Harbor	Night	32	2017	2	NA	2, 14
Goat Harbor	Night	33	2017	14	14	14
Goat Harbor	Night	34	2017	33	33	14, 33
Goat Harbor	Night	35	2017	14	14	14
Goat Harbor	Day	27	2018	20, 33	NA	20, 33
Goat Harbor	Day	28	2018	7, 33	NA	7, 20, 33
Goat Harbor	Day	29	2018	NA	NA	NA
Goat Harbor	Day	30	2018	33	33	33
Goat Harbor	Day	31	2018	NA	NA	NA
Goat Harbor	Day	32	2018	20, 33	NA	20, 33
Goat Harbor	Day	33	2018	20, 33	NA	20, 33
Goat Harbor	Day	34	2018	20, 33	NA	20, 33
Goat Harbor	Day	35	2018	20, 33	NA	20, 33
Goat Harbor	Night	27	2018	23	NA	17, 20, 23
Goat Harbor	Night	28	2018	NA	NA	NA
Goat Harbor	Night	29	2018	NA	NA	NA
Goat Harbor	Night	30	2018	NA	NA	NA
Goat Harbor	Night	31	2018	NA	NA	NA
Goat Harbor	Night	32	2018	NA	NA	NA
Goat Harbor	Night	33	2018	NA	NA	NA
Goat Harbor	Night	34	2018	NA	NA	NA
Goat Harbor	Night	35	2018	NA	NA	NA

**TABLE 7. Continued.**

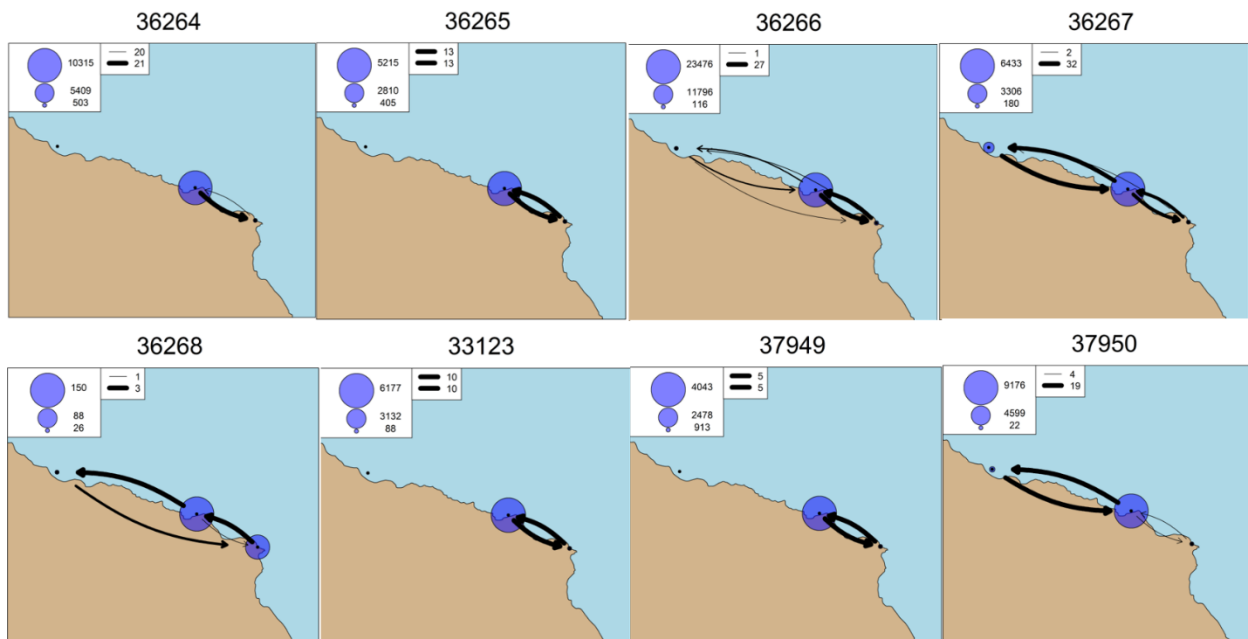
Little Farnsworth	Day	27	2017	7	7	7
Little Farnsworth	Day	28	2017	1	1	1
Little Farnsworth	Day	29	2017	4	1	1
Little Farnsworth	Day	30	2017	3	1	1
Little Farnsworth	Day	31	2017	3	1	1
Little Farnsworth	Day	32	2017	6	25	25, 27
Little Farnsworth	Day	33	2017	16	1	25
Little Farnsworth	Day	34	2017	2	27	25, 27
Little Farnsworth	Day	35	2017	3	29	24, 27, 28
Little Farnsworth	Night	27	2017	13	13	1, 12, 13
Little Farnsworth	Night	28	2017	3	1	1
Little Farnsworth	Night	29	2017	3	1	1
Little Farnsworth	Night	30	2017	7	7	1, 2, 5, 7, 12
Little Farnsworth	Night	31	2017	4	2	1, 12
Little Farnsworth	Night	32	2017	3	3	1, 17
Little Farnsworth	Night	33	2017	3	24, 25	3
Little Farnsworth	Night	34	2017	10	10	1, 21, 24, 25, 28, 29, 30
Little Farnsworth	Night	35	2017	16	10	17, 21, 24, 28
Little Farnsworth	Day	27	2018	23	23	1, 25, 30
Little Farnsworth	Day	28	2018	23	17	1, 25, 30, 32
Little Farnsworth	Day	29	2018	17	17, 25	25
Little Farnsworth	Day	30	2018	23	32	32
Little Farnsworth	Day	31	2018	20	32	1, 25, 32
Little Farnsworth	Day	32	2018	20	20	1, 20, 25
Little Farnsworth	Day	33	2018	17	23	1, 17, 30, 23, 25
Little Farnsworth	Day	34	2018	17	1	1
Little Farnsworth	Day	35	2018	20	20, 23	1, 20, 25
Little Farnsworth	Night	27	2018	23	23	1, 12, 23, 25, 30, 32
Little Farnsworth	Night	28	2018	20	20	1, 12, 25, 30
Little Farnsworth	Night	29	2018	20	20	1, 7, 12, 17, 20, 23, 25, 30, 32
Little Farnsworth	Night	30	2018	17	17	1, 7, 20, 23, 30, 32
Little Farnsworth	Night	31	2018	17	17	1, 12, 23, 25, 32
Little Farnsworth	Night	32	2018	20	20	1, 12, 17, 20, 23, 25, 32
Little Farnsworth	Night	33	2018	32	1	1, 25
Little Farnsworth	Night	34	2018	20	20	1, 17, 20, 23, 25
Little Farnsworth	Night	35	2018	17	17	1, 17, 20, 23, 25



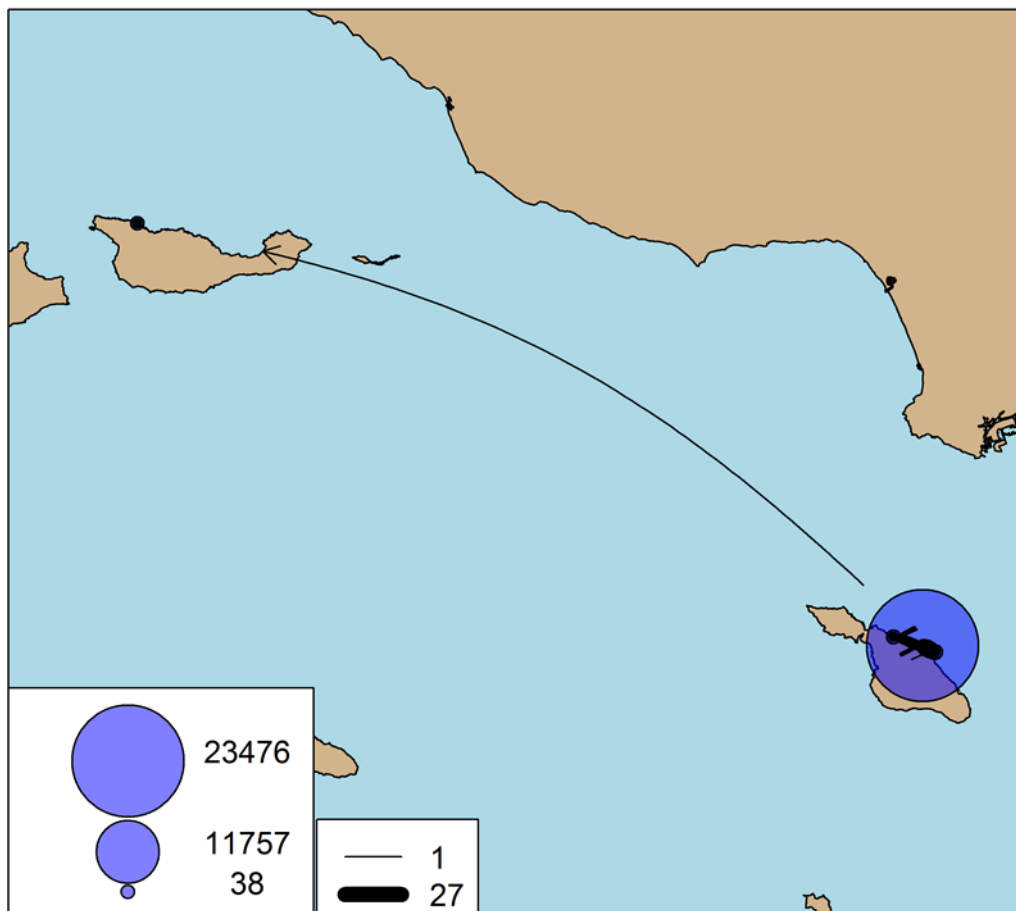
**APPENDIX B**  
**ADDITIONAL FIGURES**



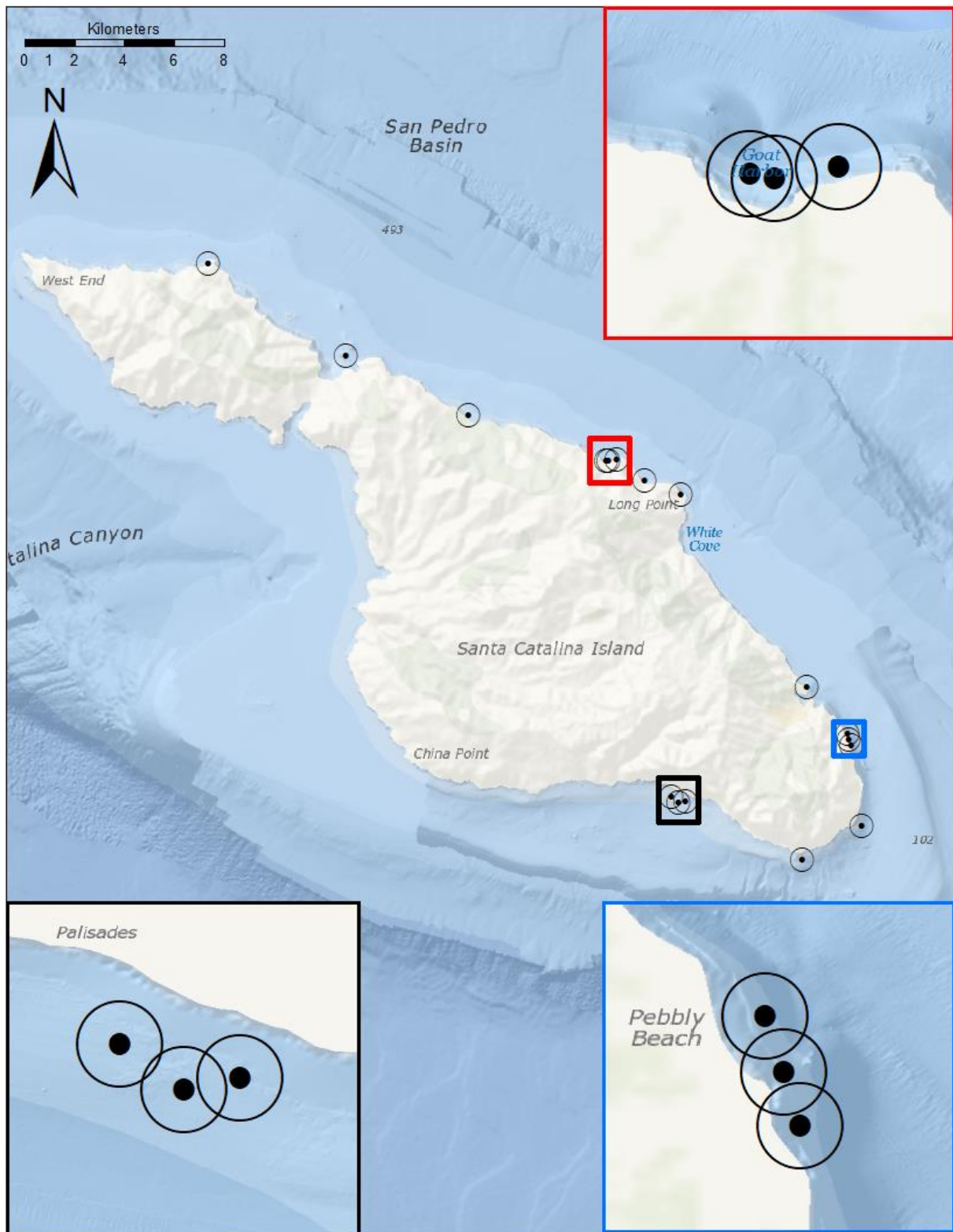
**FIGURE 1. Movements of one giant sea bass tagged during the pilot study at Goat Harbor, Santa Catalina Island, over an 8-day period in July 2015.**



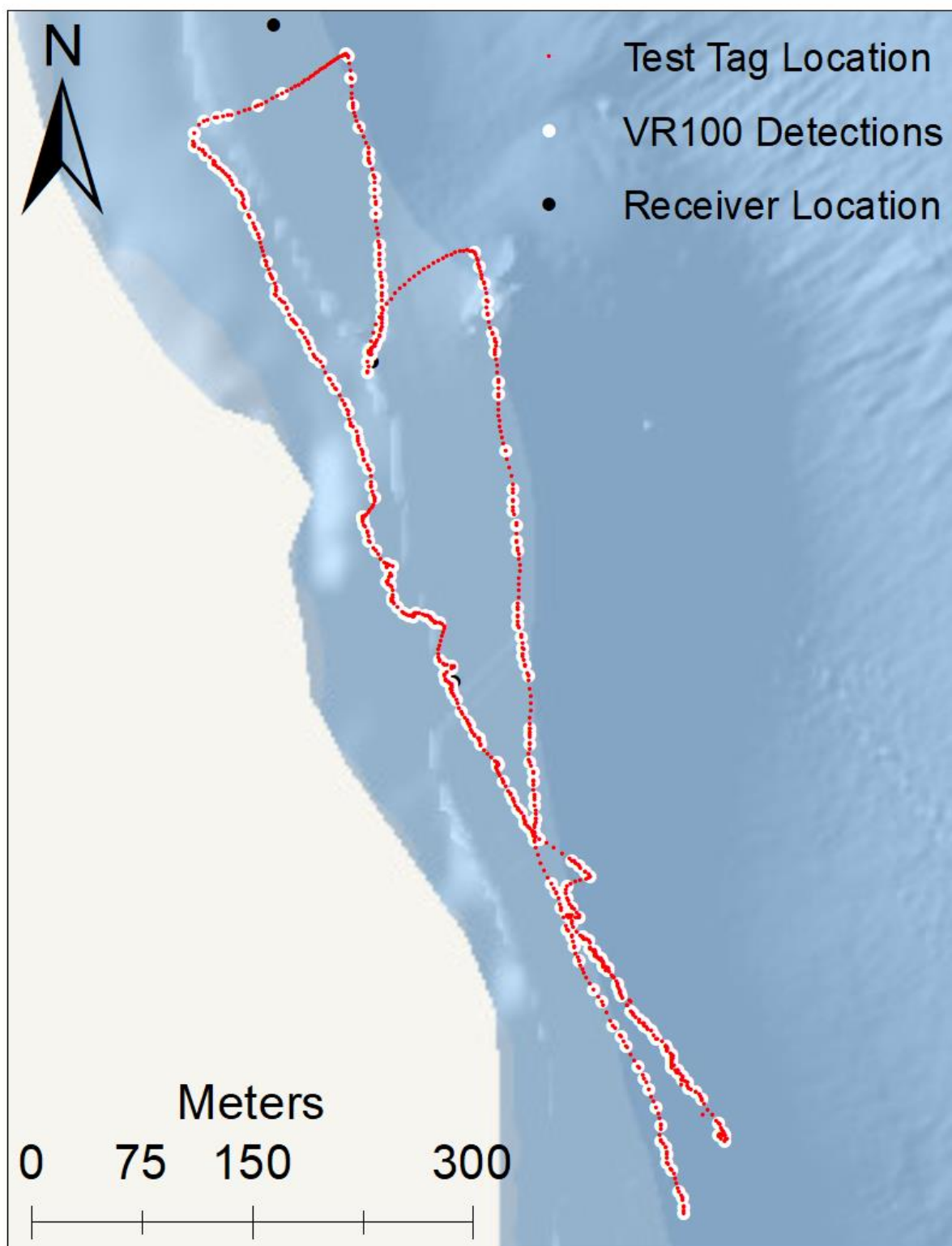
**FIGURE 2. Movements of tagged giant sea bass between receivers on Santa Catalina Island. Size of bubble represents relative number of detections on receiver, and thickness of line between receivers indicates the number of transitions between the two receivers. Tag ID is listed above each figure.**



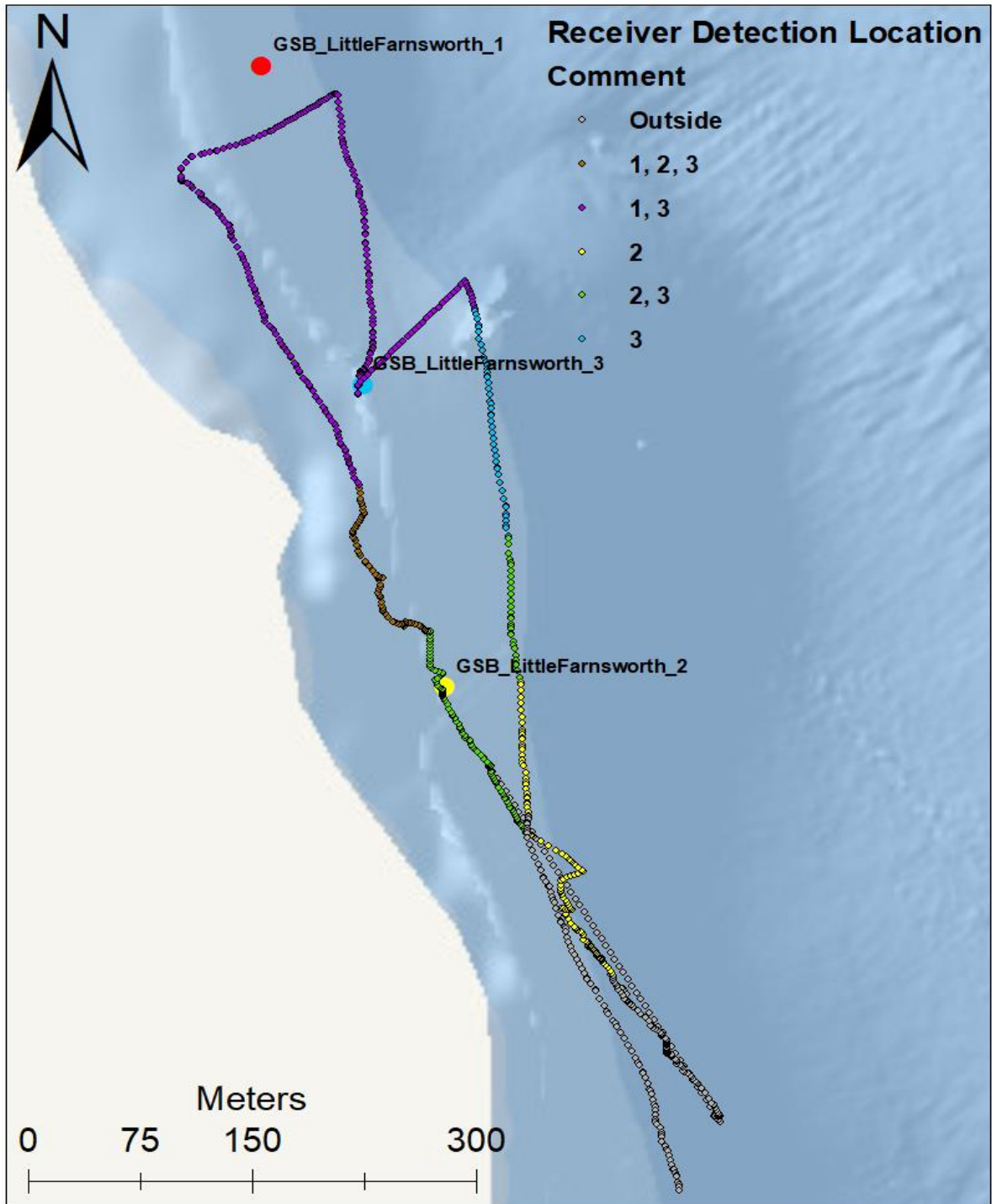
**FIGURE 3.** Bubble plot of one giant sea bass tagged during the pilot study that left the array at Santa Catalina Island in October 2015 and was detected in May 2016 at Santa Cruz Island. Size of the bubble is proportional to the number of detections at each site; thickness of line indicates the number of transitions the individual made between receivers.



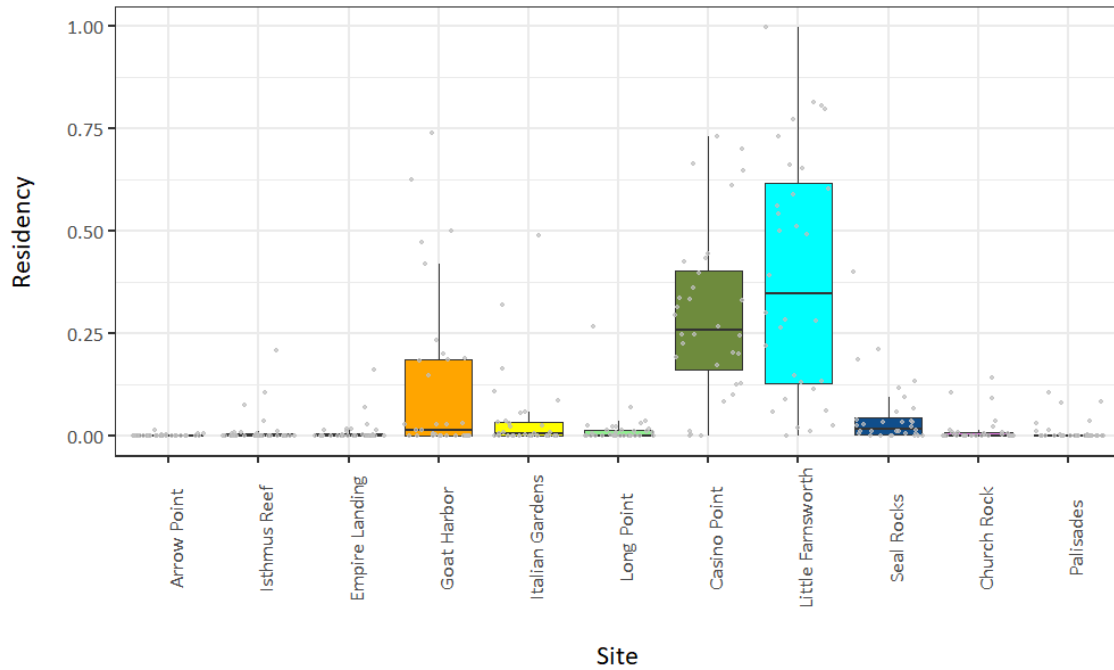
**FIGURE 4. Locations of VR2W receivers at Santa Catalina Island. Acoustic receiver 500 m detection range displayed around each receiver. Inset maps show aggregation sites (red: Goat Harbor; blue: Little Farnsworth; black: Palisades).**



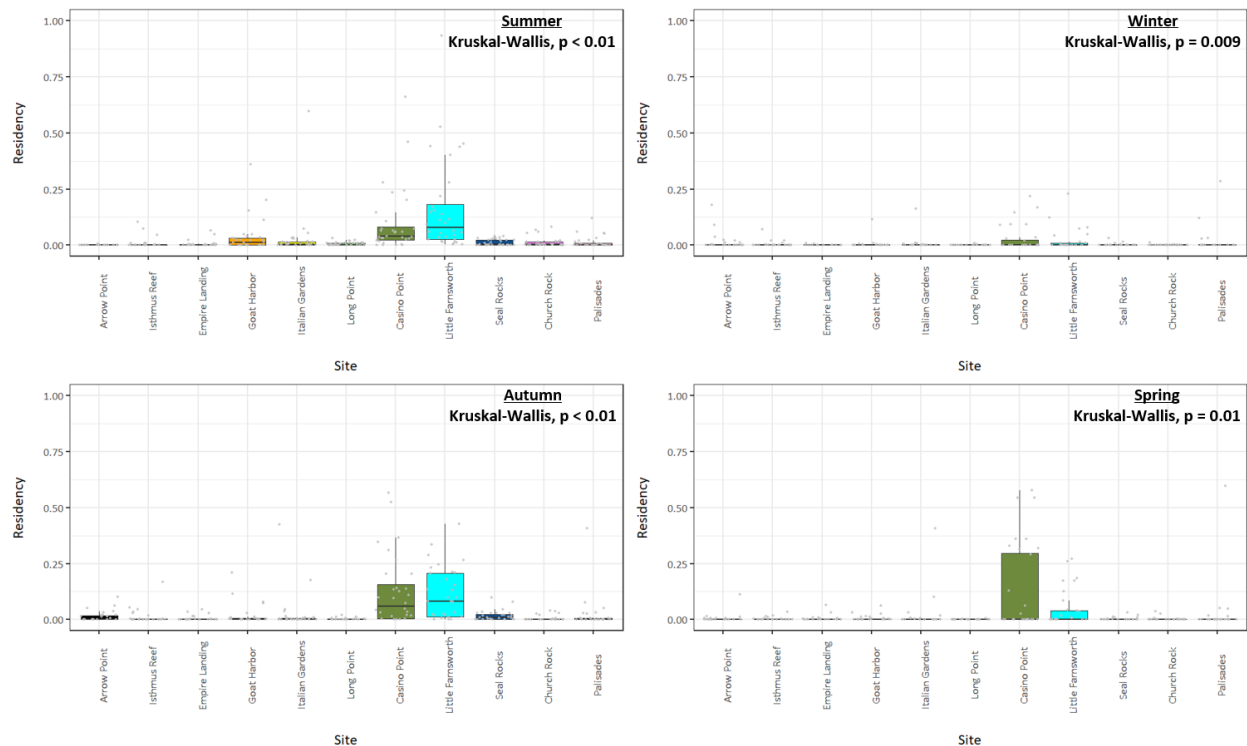
**FIGURE 5.** Results from Little Farnsworth aggregation site array range testing. VR100 acoustic receiver detections (white) are overlaid on map of receiver locations (filled black circles) with approximate locations of the coded pinger (red dots).



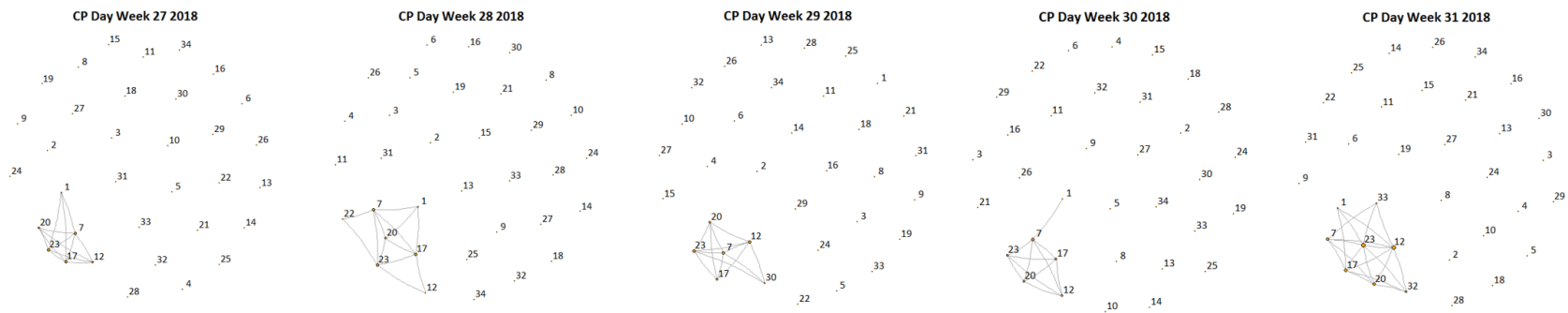
**FIGURE 6.** Map showing maximum detection ranges (m) and detection efficiencies (%) of VR2W acoustic receivers. Each circle represents a receiver and is designated a different color (1: red, 2: yellow, 3: blue). Each dot represents a pulse emitted by the range test tag with different colors associated with the receiver(s) where it was detected (1: red\*, 2: yellow, 3: blue, 1 and 3: purple, 1, 2, and 3: brown, 2 and 3: green) or if it was not detected by any receiver (gray). \*The tag was never detected at receiver 1 only.



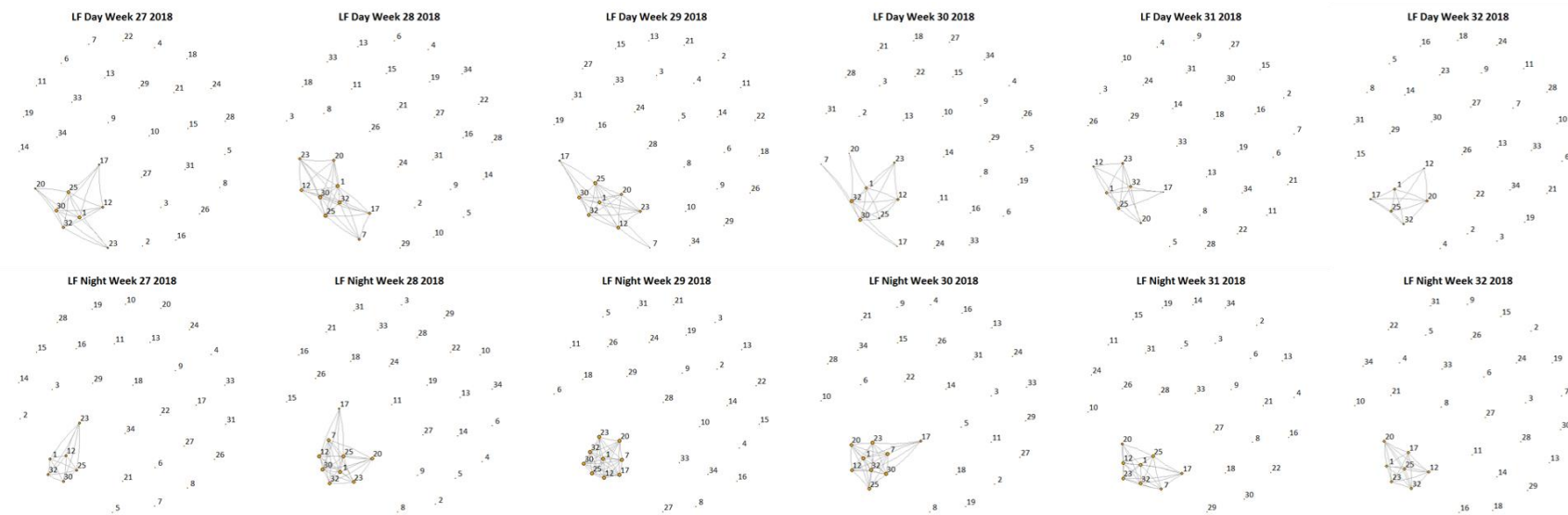
**FIGURE 7.** Boxplot of giant sea bass residency by site for the duration of the study (15 June 2017–27 October 2018) at Santa Catalina Island.



**FIGURE 8.** Boxplot of giant sea bass residency by site during summer (1 June–31 August), (1 September–30 November), winter (1 December–28 February), and spring (1 March–31 May) at Santa Catalina Island.

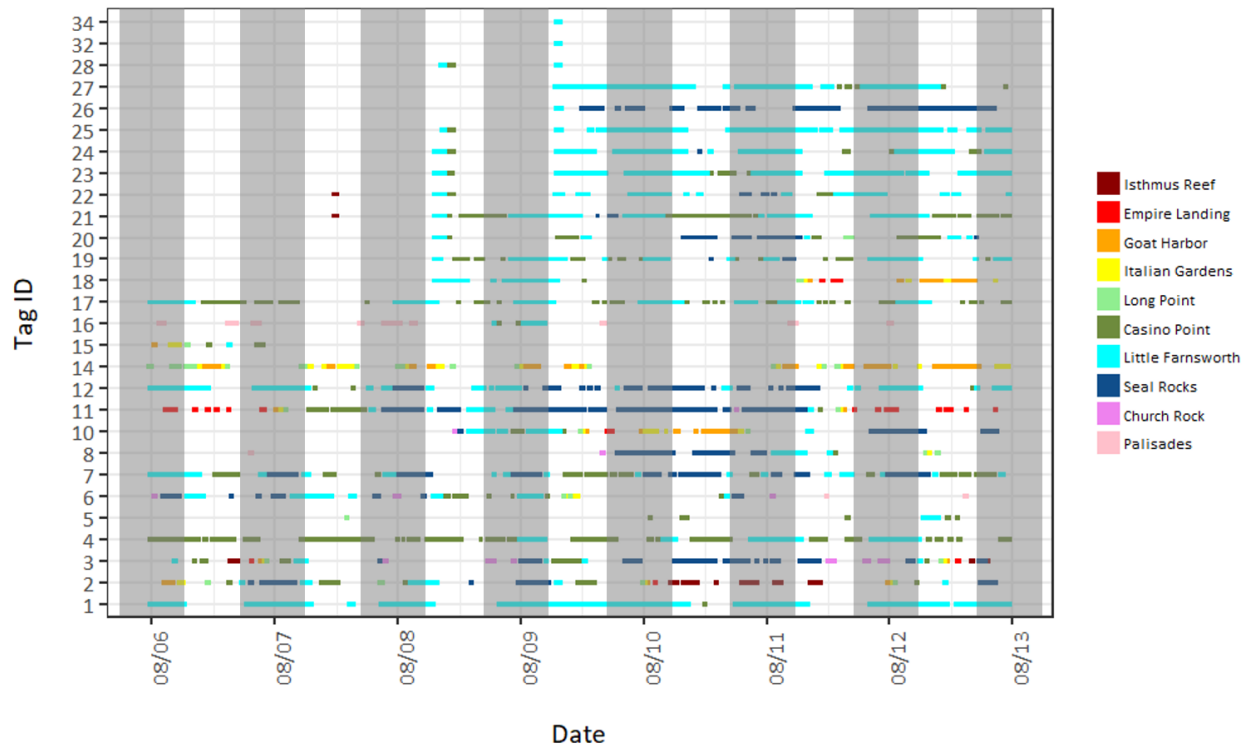


**FIGURE 9. Social network plots of GSB during the day at Casino Point for four weeks during the 2018 spawning season. Every orange node is a fish with associated ascension number and every gray line in an interaction between two individuals.**

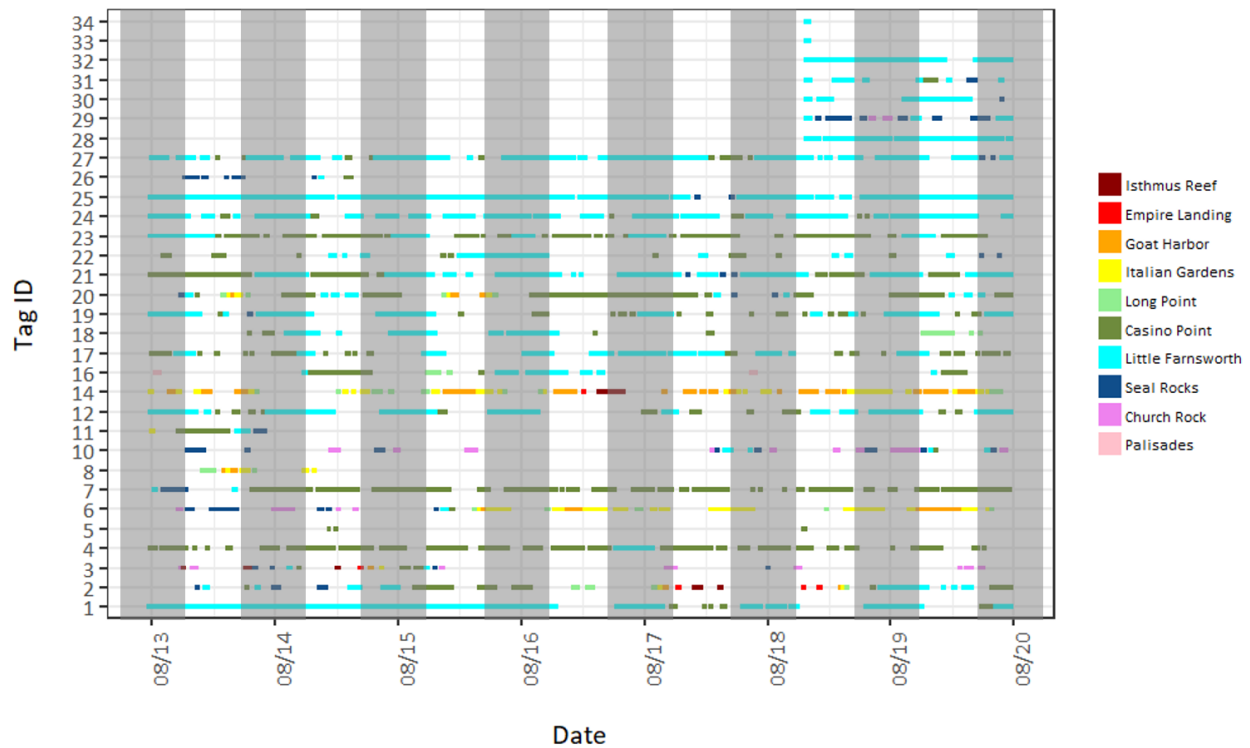


**FIGURE 10. Social network plots of GSB during the day (top row) and at night (bottom row) at Little Farnsworth from 2 July–12 August 2018. Every orange node is a fish with associated ascension number and every gray line in an interaction between two individuals.**

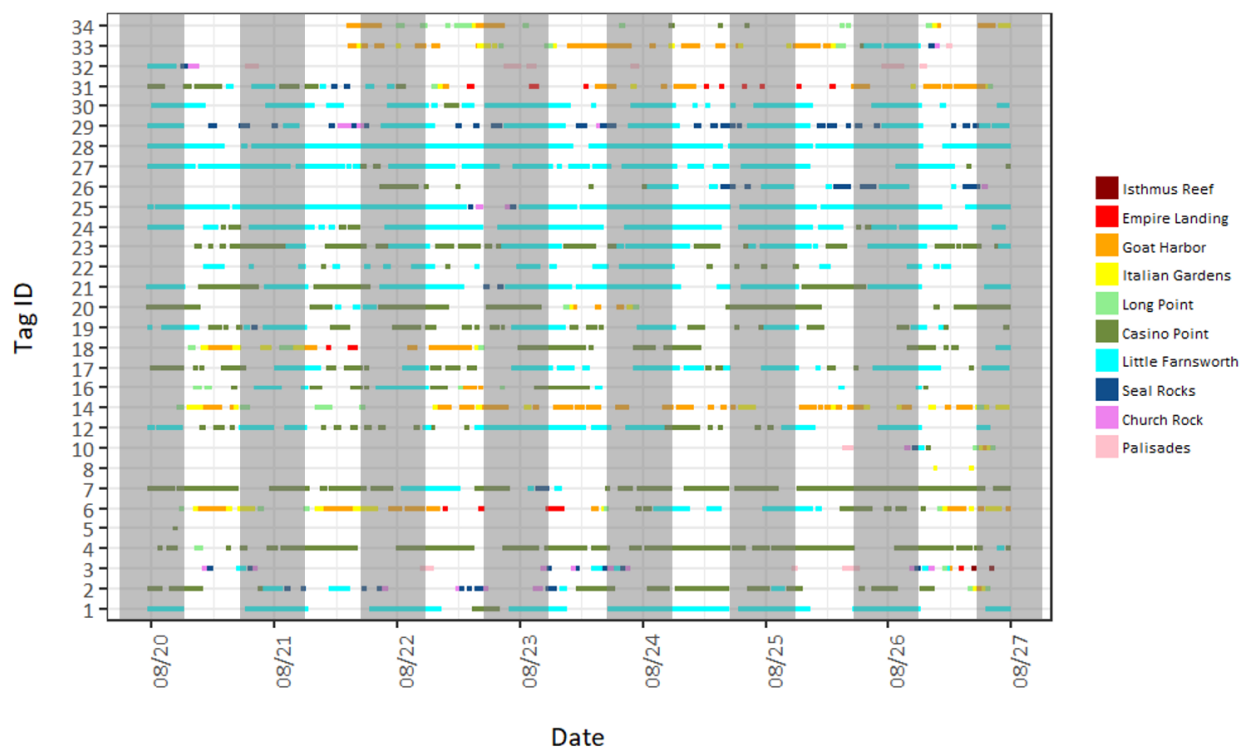




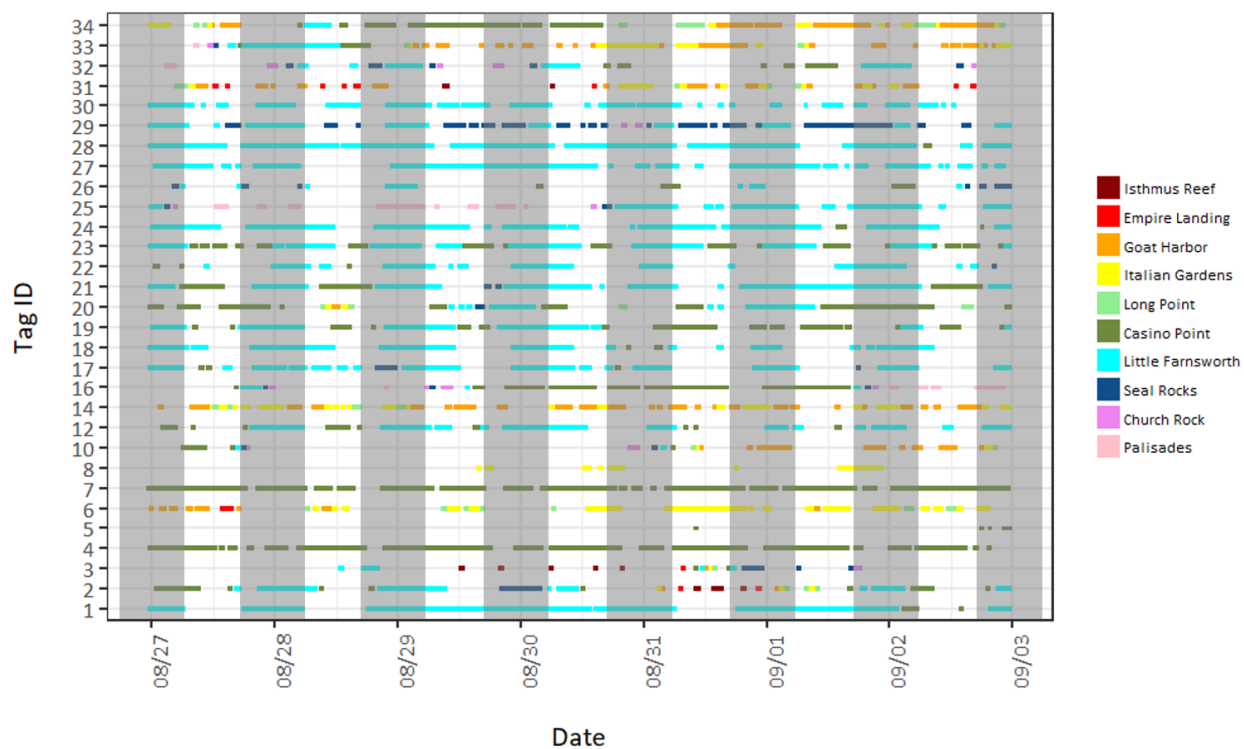
**FIGURE 11. Detection plot of tagged giant sea bass during week 32 (6–12 August) in 2017. Color indicates site, shaded bars represent night.**



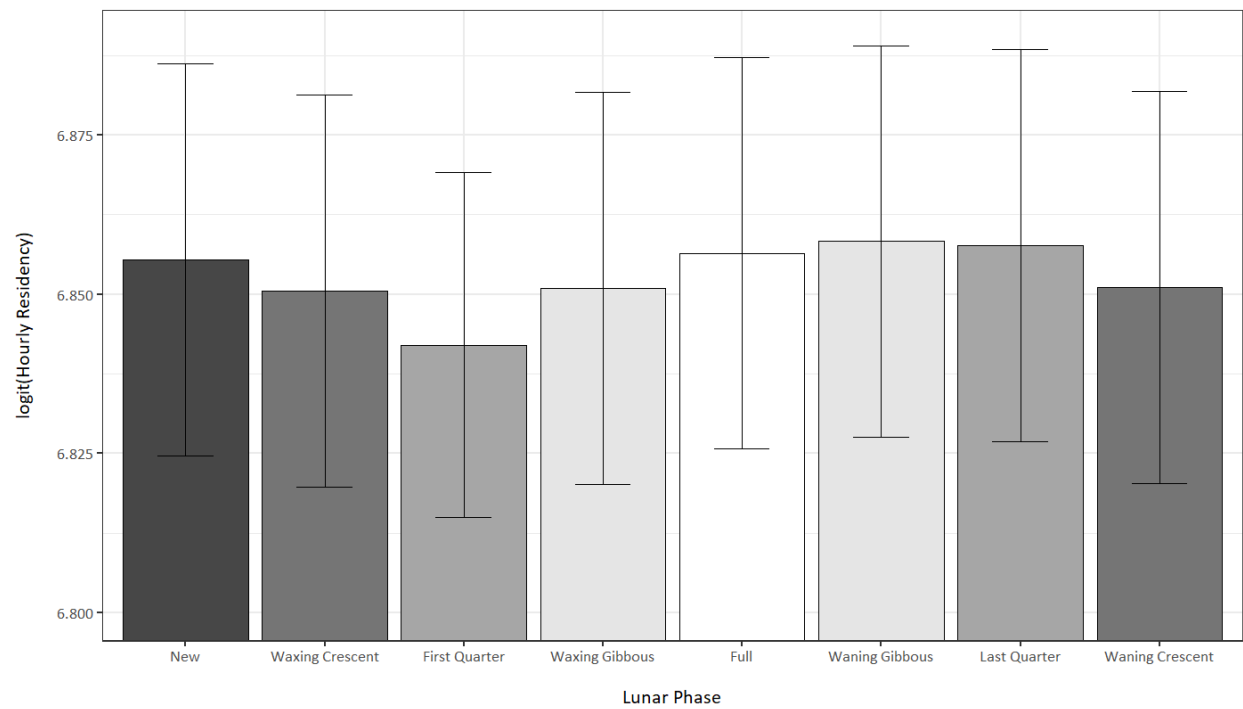
**FIGURE 12. Detection plot of tagged giant sea bass during week 33 (13–19 August) in 2017. Color indicates site, shaded bars represent night.**



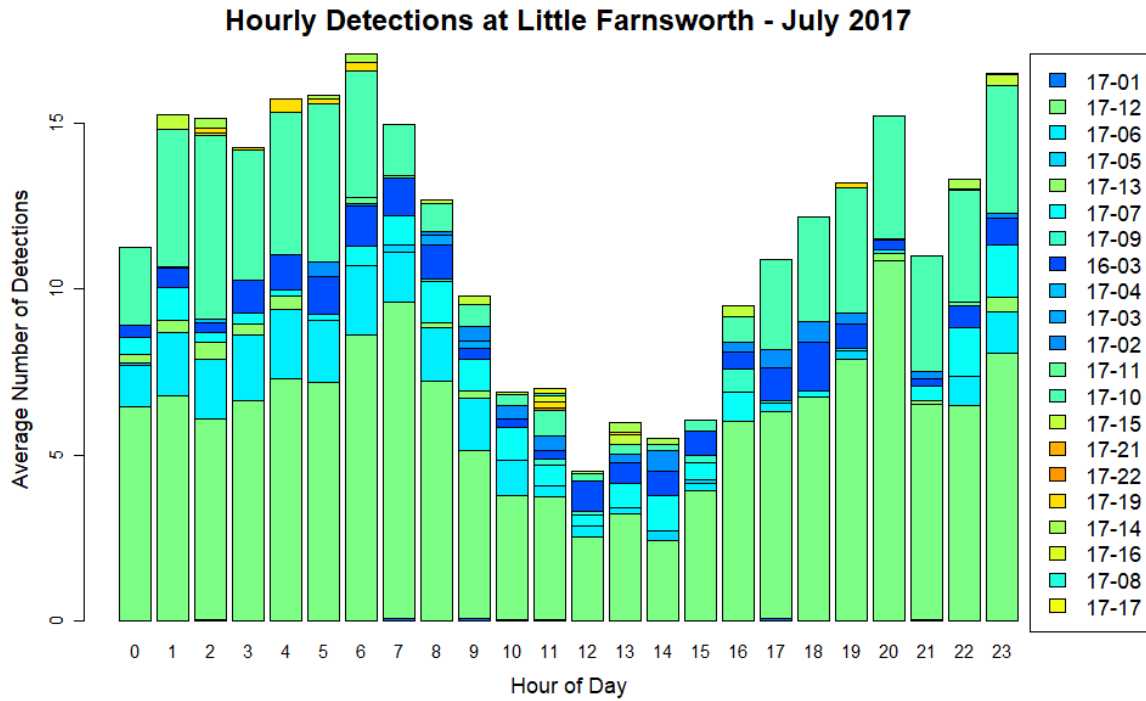
**FIGURE 13.** Detection plot of tagged giant sea bass during week 34 (20–26 August) in 2017. Color indicates site, shaded bars represent night.



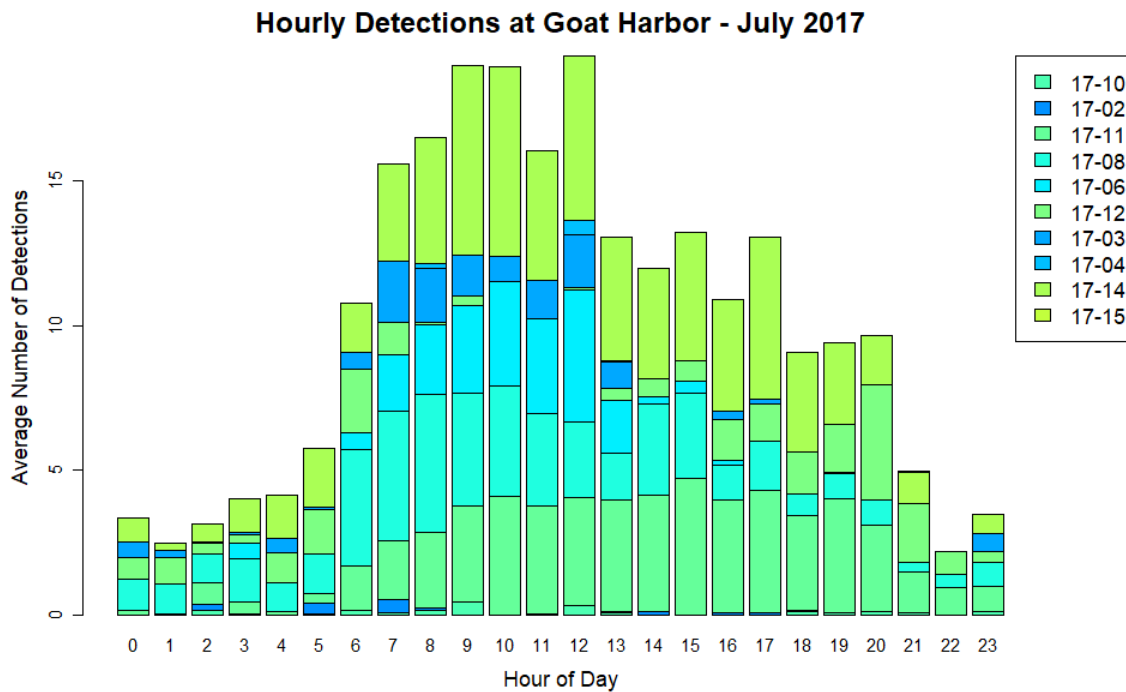
**FIGURE 14.** Detection plot of tagged giant sea bass during week 35 (27 August–2 September) in 2017. Color indicates site, shaded bars represent night.



**FIGURE 15. Boxplot of linear mixed-effects model values comparing hourly residency to lunar phase with 95% CI. Coloration of bars signifies lunar illumination.**



**FIGURE 16.** Average hourly detections of giant sea bass at the Little Farnsworth aggregation site during the peak of suspected spawning. Each color represents a different fish within an hour of day.



**FIGURE 17.** Average hourly detections of giant sea bass at the Goat Harbor aggregation site during the peak of suspected spawning. Each color represents a different fish within an hour of day.

## REFERENCES

## REFERENCES

- Agafonkin, V., & Thieurmél, B. (2018). suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. R package version 0.4.
- Aguilar-Perera, A., & Aguilar-Dávila, W. (1996). A spawning aggregation of Nassau grouper *Epinephelus striatus* (Pisces: Serranidae) in the Mexican Caribbean. *Environmental Biology of Fishes*, 45(4), 351-361.
- Alerstam, T., Hedenström, A., & Åkesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos*, 103(2), 247-260.
- Allen, L. G., & Andrews, A. H. (2012). Bomb radiocarbon dating and estimated longevity of Giant Sea Bass (*Stereolepis gigas*). *Bulletin, Southern California Academy of Sciences*, 111(1), 1-14.
- Barlow, G. W. (1981). Patterns of parental investment, dispersal and size among coral-reef fishes *Ecology and ethology of fishes* (pp. 65-85): Springer.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using *lme4*. *arXiv preprint arXiv:1406.5823*.
- Bolden, S. K. (2000). Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to a spawning aggregation in the central Bahamas. *Fishery Bulletin-National Oceanic and Atmospheric Administration*, 98(3), 642-645.
- Calenge, C. (2011). Home range estimation in R: the adehabitatHR package. *Office national de la classe et de la faune sauvage: Saint Benoist, Auffargis, France*.
- Carter, J., Marrow, G. J., & Pryor, V. (1994). Aspects of the ecology and reproduction of Nassau grouper (*Epinephelus striatus*) off the coast of Belize, Central America.
- Carter, J., & Perrine, D. (1994). A spawning aggregation of dog snapper, *Lutjanus jocu* (Pisces: Lutjanidae) in Belize, Central America. *Bulletin of Marine Science*, 55(1), 228-234.
- Chabot, C. L., Hawk, H. A., & Allen, L. G. (2015). Low contemporary effective population size detected in the Critically Endangered giant sea bass, *Stereolepis gigas*, due to fisheries overexploitation. *Fisheries Research*, 172, 71-78.
- Clark, B. L., & Allen, L. G. (2018). Field Observations on Courtship and Spawning Behavior of the Giant Sea Bass, *Stereolepis gigas*. *Copeia*, 106(1), 171-179.
- Claro, R., & Lindeman, K. C. (2003). Spawning aggregation sites of snapper and grouper species (*Lutjanidae* and *Serranidae*) on the insular shelf of Cuba. *Gulf and Caribbean Research*, 14(2), 91-106.

- Colin, P. L. (1992). Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fishes*, 34(4), 357-377.
- Colin, P. L. (1994). *Preliminary investigations of reproductive activity of the jewfish, Epinephelus itajara* (Pisces: Serranidae). Paper presented at the Proceedings of the Gulf and Caribbean Fisheries Institute.
- Colin, P. L. (1996). Longevity of some coral reef fish spawning aggregations. *Copeia*, 1996(1), 189-192.
- Colin, P. L., Shapiro, D. Y., & Weiler, D. (1987). Aspects of the reproduction of two groupers, *Epinephelus guttatus* and *E. striatus* in the West Indies. *Bulletin of Marine Science*, 40(2), 220-230.
- Collins, A., Barbieri, L. R., McBride, R. S., McCoy, E. D., & Motta, P. J. (2015). Reef relief and volume are predictors of Atlantic goliath grouper presence and abundance in the eastern Gulf of Mexico. *Bulletin of Marine Science*, 91(4), 399-418.
- Cornish, A. (2004). Giant sea bass. *Stereolepis gigas*. The IUCN Red List of Threatened Species 2004 (Publication no. 10.2305/IUCN.UK.2004.RLTS.T20795A9230697.en). from IUCN
- Csardi, G., & Nepusz, T. (2006). The *igraph* software package for complex network research. *InterJournal, Complex Systems*, 1695(5), 1-9.
- Dayton, P. K., Thrush, S., & Coleman, F. C. (2003). Ecological Effects of Fishing. *Report to the Pew Oceans Commission, Arlington, Virginia (USA)*.
- Domeier, M. L. (2001). Giant sea bass. *California's Living Marine Resources: A Status Report*, 209-211.
- Domeier, M. L. (2012). Revisiting spawning aggregations: definitions and challenges. In Y. S. de Mitcheson & P. L. Colin (Eds.), *Reef fish spawning aggregations: biology, research and management* (pp. 1-20): Springer.
- Domeier, M. L., & Maas, T. (2005). Black seabass return? Retrieved from <http://www.freedive.net/Blacks/Article/bsb.htm>
- Eklund, A.-M., & Schull, J. (2001). A stepwise approach to investigating the movement patterns and habitat utilization of goliath grouper, *Epinephelus itajara*, using conventional tagging, acoustic telemetry and satellite tracking *Electronic tagging and tracking in marine fisheries* (pp. 189-216): Springer.
- Erisman, B. E., Aburto-Oropeza, O., Gonzalez-Abraham, C., Mascareñas-Osorio, I., Moreno-Báez, M., & Hastings, P. A. (2012). Spatio-temporal dynamics of a fish spawning aggregation and its fishery in the Gulf of California. *Scientific Reports*, 2, 284.

- Erismann, B. E., & Allen, L. G. (2006). Reproductive behaviour of a temperate serranid fish, *Paralabrax clathratus* (Girard), from Santa Catalina Island, California, USA. *Journal of Fish Biology*, 68(1), 157-184.
- Erismann, B. E., Buckhorn, M. L., & Hastings, P. A. (2007). Spawning patterns in the leopard grouper, *Mycteroperca rosacea*, in comparison with other aggregating groupers. *Marine Biology*, 151(5), 1849-1861.
- Espinoza, M., Heupel, M. R., Tobin, A. J., & Simpfendorfer, C. A. (2015). Residency patterns and movements of grey reef sharks (*Carcharhinus amblyrhynchos*) in semi-isolated coral reef habitats. *Marine Biology*, 162(2), 343-358.
- Espinoza, M., Heupel, M. R., Tobin, A. J., & Simpfendorfer, C. A. (2016). Evidence of partial migration in a large coastal predator: opportunistic foraging and reproduction as key drivers? *PloS one*, 11(2), e0147608.
- Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using *asnipe*. *Methods in ecology and evolution*, 4(12), 1187-1194.
- Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, 84(5), 1144-1163.
- Farmer, N. A., Heyman, W. D., Karnauskas, M., Kobara, S., Smart, T. I., Ballenger, J. C., . . . Lindeman, K. C. (2017). Timing and locations of reef fish spawning off the southeastern United States. *PloS one*, 12(3), e0172968.
- Frisk, M. G., Jordaan, A., & Miller, T. J. (2014). Moving beyond the current paradigm in marine population connectivity: are adults the missing link? *Fish and Fisheries*, 15(2), 242-254.
- Gaffney, P., Rupnow, J., & Domeier, M. (2007). Genetic similarity of disjunct populations of the giant sea bass *Stereolepis gigas*. *Journal of Fish Biology*, 70, 111-124.
- Heyman, W. D., Kjerfve, B., Graham, R., Rhodes, K., & Garbutt, L. (2005). Spawning aggregations of *Lutjanus cyanopterus* (Cuvier) on the Belize Barrier Reef over a 6 year period. *Journal of Fish Biology*, 67(1), 83-101.
- Horn, M. H., & Ferry-Graham, L. A. (2006). Feeding Mechanisms and Trophic Interactions. In L. G. Allen, D. J. Pondella II, & M. H. Horn (Eds.), *The Ecology of Marine Fishes: California and Adjacent Waters* (pp. 387-410): University of California Press, Berkeley.
- House, P. H., Clark, B. L., & Allen, L. G. (2016). The Return of the King of the Kelp Forest: Distribution, Abundance, and Biomass of Giant Sea Bass (*Stereolepis gigas*) off Santa Catalina Island, California, 2014-2015. *Bulletin, Southern California Academy of Sciences*, 115(1), 1-14.
- Jacoby, D. M., Brooks, E. J., Croft, D. P., & Sims, D. W. (2012). Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. *Methods in ecology and evolution*, 3(3), 574-583.



- Johannes, R. E. (1978). Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes*, 3(1), 65-84.
- Johannes, R. E., Squire, L., Graham, T., Sadovy, Y., & Renguul, H. (1999). Spawning aggregations of groupers (Serranidae) in Palau. *The Nature Conservancy Marine Research Series Publication*, 1, 1-144.
- Johnson, D., & London, J. (2018). Crawl: an R package for fitting continuous-time correlated random walk models to animal movement data. *Zenodo*.
- Kobara, S., & Heyman, W. D. (2008). Geomorphometric patterns of Nassau grouper (*Epinephelus striatus*) spawning aggregation sites in the Cayman Islands. *Marine Geodesy*, 31(4), 231-245.
- Koenig, C. C., Bueno, L., Coleman, F. C., Cusick, J., Ellis, R., Kingon, K., . . . Stallings, C. (2017). Diel, lunar, and seasonal spawning patterns of the Atlantic goliath grouper, *Epinephelus itajara*, off Florida, United States. *Bulletin of Marine Science*, 93(2), 391-406.
- Koenig, C. C., Coleman, F. C., & Kingon, K. (2011). Pattern of recovery of the goliath grouper *Epinephelus itajara* population in the southeastern US. *Bulletin of Marine Science*, 87(4), 891-911.
- Lazaridis, E. (2014). lunar: Lunar Phase & Distance, Seasons and Other Environmental Factors (Version 0.1-04).
- Leet, W. S., Dewees, C. M., Klingbeil, R., & Larson, E. J. (2001). Giant sea bass (C. D. o. F. a. Game, Trans.) *California's Living Marine Resources: A Status Report* (pp. 209-211): California Department of Fish and Game.
- Love, M. S. (2011). *Certainly more than you want to know about the fishes of the Pacific Coast: a postmodern experience*: Really Big Press.
- Mann, D. A., Locascio, J. V., Coleman, F. C., & Koenig, C. C. (2009). Goliath grouper *Epinephelus itajara* sound production and movement patterns on aggregation sites. *Endangered Species Research*, 7(3), 229-236.
- Molloy, P. P., Côté, I. M., & Reynolds, J. D. (2012). Why spawn in aggregations? In Y. S. de Mitcheson & P. L. Colin (Eds.), *Reef fish spawning aggregations: biology, research, and management* (pp. 57-83): Springer.
- Mourier, J., Jacoby, D. M., & Guttridge, T. L. (2018). Network Analysis and Theory in Shark Ecology - Methods and Applications: Taylor and Francis.
- Munro, J., Gaut, V., Thompson, R., & Reeson, P. (1973). The spawning seasons of Caribbean reef fishes. *Journal of Fish Biology*, 5(1), 69-84.

- Musick, J., Harbin, M., Berkeley, S., Burgess, G., Eklund, A., Findley, L., . . . Huntsman, G. (2000). Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries*, 25(11), 6-30.
- Nemeth, R. S., Blondeau, J., Herzlieb, S., & Kadison, E. (2007). Spatial and temporal patterns of movement and migration at spawning aggregations of red hind, *Epinephelus guttatus*, in the US Virgin Islands. *Environmental Biology of Fishes*, 78(4), 365-381.
- Olds, A. D., Connolly, R. M., Pitt, K. A., & Maxwell, P. S. (2012). Habitat connectivity improves reserve performance. *Conservation Letters*, 5(1), 56-63.
- Parrish, J. K., & Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science*, 284(5411), 99-101.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres, F. (1998). Fishing down marine food webs. *Science*, 279(5352), 860-863.
- Peterson, R. T., Eschmeyer, W. N., & Herald, E. S. (1999). *A field guide to Pacific coast fishes: North America*: Houghton Mifflin Harcourt.
- Pondella II, D. J., & Allen, L. G. (2008). The decline and recovery of four predatory fishes from the Southern California Bight. *Marine Biology*, 154(2), 307-313.
- Sadovy, Y., & Eklund, A.-M. (1999). Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichenstein, 1822).
- 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.
- Salinas-de-Leon, P., Rastoin, E., & Acuna-Marrero, D. (2015). First record of a spawning aggregation for the tropical eastern Pacific endemic grouper *Mycteroperca olfax* in the Galapagos Marine Reserve. *Journal of Fish Biology*, 87(1), 179-186. doi:10.1111/jfb.12703
- Samoilys, M. A., & Squire, L. C. (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.
- Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature methods*, 9(7), 671.
- Secretaría de Agricultura, G., Desarrollo Rural, Pesca y Alimentación. (2017). <http://www.sportfishinginmexico.com/licences/>.
- Semmens, J. M., Buxton, C., Forbes, E., & Phelan, M. (2010). Spatial and temporal use of spawning aggregation sites by the tropical sciaenid *Protonibea diacanthus*. *Marine Ecology Progress Series*, 403, 193-203.

- Starr, R. M., Sala, E., Ballesteros, E., & Zabala, M. (2007). Spatial dynamics of the Nassau grouper *Epinephelus striatus* in a Caribbean atoll.
- Whaylen, L., Pattengill-Semmens, C. V., Semmens, B. X., Bush, P. G., & Boardman, M. R. (2004). Observations of a Nassau grouper, *Epinephelus striatus*, spawning aggregation site in Little Cayman, Cayman Islands, including multi-species spawning information. *Environmental Biology of Fishes*, 70(3), 305-313.