BRIEF COMMUNICATION

Network analysis reveals aggregation behaviour for an endangered predator at an offshore island

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Abstract

Site fidelity and aggregation behaviour were assessed for giant sea bass *Stereolepis gigas* (GSB) at Santa Barbara Island, California, USA, from 2018 to 2020. Results indicate seasonal variation in GSB presence, and network analyses revealed a preferred location in a spatially constrained pattern, indicative of aggregation behaviour. Results show GSB aggregated annually during spawning months in the same location, confirming the first known aggregation of GSB at Santa Barbara Island. Identifying and monitoring aggregation sites is vital to ensuring proper protection and ultimate recovery for this protected species in a changing climate.

KEYWORDS
fishery recovery, site fidelity, spatiotemporal distribution, spawning aggregation, giant sea bass

Ranging from Humboldt Bay, California, through Baja California, Mexico, and into the Gulf of California, giant sea bass (*Stereolepis gigas*) R Core Team 2020 (hereafter GSB) were nearly extirpated in southern California during the 20th century due to fishing pressure and habitat loss (Chabot *et al*., 2015; Pondella & Allen, 2008). Growing up to 2.2 m (TL) and weighing 250 kg (Allen & Andrews, 2012; Domeier, 2005), GSB are considered a top predator in kelp forest and rocky reef communities. Individuals are able to migrate long distances over short time periods (*e.g.*, >400 km in 140 days) and aggregate annually during summer months, presumably to spawn (Clevenstine & Lowe, 2021; House *et al*., 2016). Documentation of spawning has yet to be confirmed for the species, whereas aggregations have been documented at only a few specific sites in southern California (Clevenstine & Lowe, 2021; Domeier, 2005; House *et al*., 2016). GSB have strong site fidelity to aggregation sites in summer months and return to these same locations inter-annually, making them important areas to consider for conservation as the US population rebounds (Clevenstine & Lowe, 2021; Pondella & Allen, 2008). As oceanic conditions (*i.e.*, sea surface

temperature, productivity) change, aggregation cues may cause shifts in the timing and location of these aggregation events. Although recent genetic analyses have shown fish in Mexican waters may have helped US populations recover (Chabot *et al*., 2015; Gaffney *et al*., 2007; Ramírez-Valdez *et al*., 2021), there is no evidence to date documenting movement of fish between Mexico and the US. Currently, the only confirmed aggregation sites in U.S. waters are around Anacapa Island (Domeier, 2005), Santa Catalina Island (Clevenstine & Lowe, 2021; House *et al*., 2016) and La Jolla, California (Blincow, unpubl. data). These studies suggest that GSB often aggregate at promontories around offshore islands during the summer months; therefore, the authors hypothesise GSB will show fidelity to similar features and conditions at an offshore island within their native range.

To test this, the authors utilised an acoustic telemetry array around Santa Barbara Island (hereafter SBI). A small offshore island off the coast of California totalling roughly 1 mile[2] and made of mostly basaltic rock, SBI has a short nearshore shelf with rocky reef and sand habitats for approximately 1 nm from the shore before dropping into deep water. The nearshore habitat is diverse, with highly dynamic macroalgal cover dominated by giant kelp (*Macrocystis pyrifera*) and
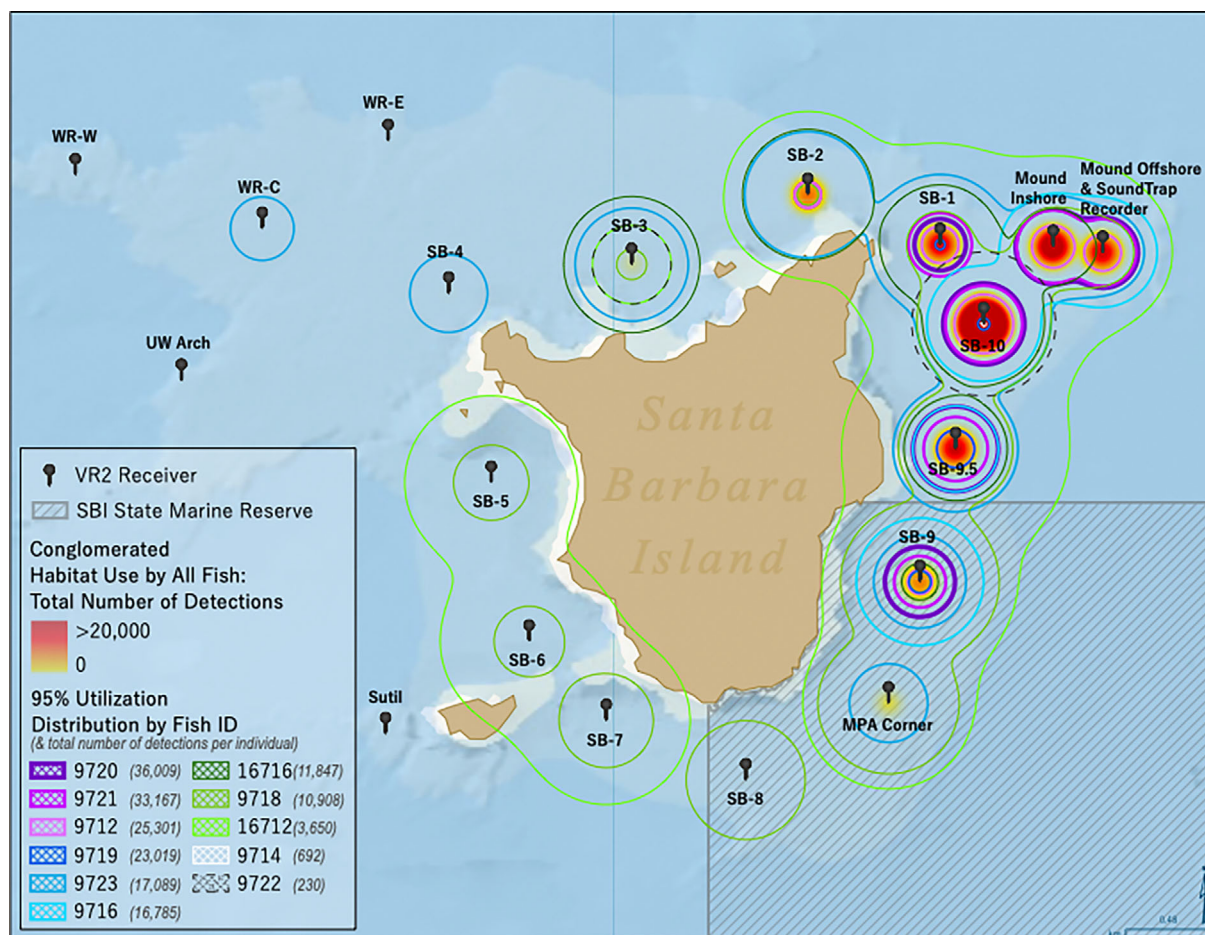

FIGURE 1　A map of Santa Barbara Island, the Conglomerated Habitat Use for 11 giant sea bass across study years (2018–2020). Note that only the 95% utilisation space is shown here. Each site is labelled with its corresponding name. Colour bands indicate individual fish IDs; a heat map indicates fish use (aka presence) within each site

strong tidal currents that move across various geological features, including a rocky promontory in the northeast corner, and a small islet in the southwest corner (Figure 1; Supporting Information Figure S1).

Twelve adult (>100 cm TL) GSB were tagged by divers with acoustic transmitters (V13-1H, 69 kHz, 36 mm length, 13 mm diameter; Vemco Ltd., Halifax, Canada) coated in antifouling paint around SBI at roughly 6 month intervals from 2018 to 2020 (Supporting Information Table S2). Tags were affixed to a short 14 cm monofilament tether with a stainless-steel anchor dart (FH-69, 3.5 cm long, 0.9 cm wide; Floy Tag & Mfg. Inc., Washington, USA) and inserted into the dorsal musculature using a modified handheld pole spear. Fish tagging methods were approved by the California Department of Fish and Wildlife (CDFW Scientific Collecting Permit #SC-1627). Prior to tagging, bait [*i.e.*, Pacific mackerel (*Scomber japonicus*)] was encased in vexar mesh attached to a drop line and allowed to soak for 20–60 min to attract GSB prior to divers entering the water.

Static, omnidirectional acoustic receivers (VR2W 69 kHz; Vemco; hereafter receivers) were moored *c.* 2 m above the seafloor at nine distinct sites around SBI in 2018, and another nine were added in 2019, forming a ring around the island's coastline (Figure 1). Seventeen sites occurred in depths ranging from 15 to 25 m, and one receiver was co-

deployed on a deep-water mooring (Mound Offshore) in *c.* 35 m with a SoundTrap, in conjunction with an affiliated project (McKenna *et al.*, 2021). Of the 18 sites monitored, 10 were located on kelp-dominated rocky reefs, and seven were in sand channels between patches of rocky reef (Supporting Information Figure S1). A rocky promontory dominates the northeast corner of SBI; here, the authors placed three receivers on, and near, the promontory at depths between 15 and 25 m (SB-1, SB-10, Mound Inshore). The co-deployed deep-water mooring was located offshore (east) of the rocky promontory. Range testing conducted in August 2018 estimated a detection range across the array between 0.25 and 0.8 km. Receivers were swapped at 6–8 month intervals by divers on scuba, and acoustic telemetry data were downloaded into Vemco VUE v 2.6.0. Further processing and analyses were carried out using R 4.0.2 (R Core Team 2020). Map images and associated data were processed and rendered using ArcGIS 10.6.1 (ESRI). To delineate drivers of daily fish presence, linear mixed effects models were constructed to explore daily differences in GSB presence across seasons (fixed effect), locations (random effect) and individuals (random effect) (Supporting Information Table S1).

Using a conglomerated habitat use (CHU) distribution, the authors calculated habitat use area (in km²) for each GSB using the

TABLE 1 A table showing unique fish IDs, the year each fish was tagged, the time standard detections per day per individual (gross number detections over the course of the entire study, filtered by hour), 75% and 95% utilisation distribution, and the first and last dates each individual was detected within the array

Individual ID	Tagging date	Time standard detections per day	75% Distribution km^2	95% Distribution km^2	Date first detected	Date last detected
9712	8/13/18	25,301	0.049338	0.217552	8/14/18	4/11/20
9714	8/13/18	692	0.00009	0.000427	8/16/18	3/18/20
9716	8/13/18	16,785	0.481511	1.139002	8/14/18	11/27/19
9718	8/13/19	10,908	0.789118	2.602393	8/14/18	9/25/18
9719	7/2/19	23,019	0.011064	0.043153	7/2/19	10/1/20
9720	7/2/19	36,009	0.265273	0.640714	7/2/19	8/28/20
9721	7/2/19	33,167	0.214549	0.541848	7/2/19	11/2/20
9722	9/9/18	230	0.195472	0.553077	9/10/18	4/9/19
9723	7/2/19	17,089	0.938236	2.426459	7/2/19	10/12/20
16712	10/17/19	3650	2.848669	6.071156	10/17/19	10/8/20
16715	10/14/20	19	10.348755	20.429134	10/17/19	10/27/20
16716	5/30/19	11,847	0.670573	1.701058	5/30/19	8/3/20

adehabitatHR package (Calenge, 2006). A CHU distribution is a metric of habitat use that approximates habitat utilisation space between detections at given receivers, factoring in the time step between detections (Benseman & Allen, 2018; Silverman, 1986). The CHU distribution was constructed using all detections per individual GSB, binned by day, across the entire study period (Table 1). Following the CHU distribution calculation, utilisation distribution probabilities were calculated for 75% and 95% utilisation of space around SBI (Table 1; Figure 1). The 95% CHU distribution was used to compare spatial and temporal variation in individual GSB presence; habitat use (*i.e.*, occupancy) varied greatly (3.03 ± 5.7 km^2) by individual fish, but use was highly concentrated on the northeast corner of the island.

To understand spatial variability and movement patterns of tagged GSB, movement network analyses (MNAs) were constructed for all individuals across the entire study period (Supporting Information Figure S3). An MNA was used to identify patterns of movement during the presumed spawning season (July–October; Clark & Allen, 2018, Clevenstine & Lowe, 2021) across study years (Supporting Information Figure S3). Taking a similar approach to capture-mark-recapture studies (Silk *et al.*, 2021), the authors constructed MNAs using a framework of nodes (*i.e.*, receiver locations) and edges (*i.e.*, direction of movement) within the *CMRnet* package (Silk *et al.*, 2021). An MNA models patterns of movement within an array, with directionality of movement indicated by arrows pointing to and from nodes (Supporting Information Figure S3). A visualisation of GSB presence at each site by month revealed that summer and early fall (July–September) showed the highest and most consistent concentration of individuals (Supporting Information Figure S3). Due to the COVID-19 pandemic, sampling efforts were constrained in 2020 and thus reduced the number of complete networks shown here.

A linear mixed effects model revealed significant differences in the number of transmitter detections across seasons ($F_{3,51} = 3.406$, $P = 0.01749$; Supporting Information Table S1). Seasonally, GSB presence varied spatially across all sites (Figure 1); nonetheless, season was a better predictor of GSB presence compared to location (Supporting Information Table S1). GSB presence increased in April and May, with peak presence from June to October, after which the number of detections dropped precipitously (Supporting Information Figure S2). During winter months (*i.e.*, December–February), GSB presence was low across all sites with no detections at most sites. Nonetheless, all individuals were found to return inter-annually to the array at least once across this study period. Although detections peaked in summer months, the northeast corner of SBI had the highest and most consistent presence of individuals across the entire study period (Figure 1; Supporting Information Figure S2). GSB were present around the southeast corner of the island, as well, but in varying degrees throughout the year. The peak in detections during summer to fall months (*i.e.*, July–October) was used to constrain further analyses to provide the highest level of inference (Supporting Information Figures S2 and S3).

Detection data, CHU and MNAs indicate an aggregation site for GSB at a specific promontory on the northeast corner of SBI. While the patterns of movement around the island changed from 2019 to 2020, the nexus of movement coalesced around receiver locations within the northeast corner on the rocky promontory. In both 2019 and 2020, peak movement around the promontory occurred in July and August, with a reduction in detections and movement beginning in September and October (Supporting Information Figure S2). Individuals showed preferences for this site despite similar geomorphological features at other areas around SBI (*i.e.*, the northwest corner). This could be due to several biotic (*e.g.*, increased prey availability), reduced disturbance by competitors [*i.e.*, California sea lions (*Zalophus californianus*)] and abiotic factors (*e.g.*, vertical promontory, strong currents). Aggregation behaviour was associated with a promontory, not a specific benthic type (*e.g.*, rocky reef, sand), and was neither spatially nor temporally uniform (Figure 1). Selection of outcroppings may benefit broadcast spawning species by allowing larvae to disperse more easily in strong currents that are often present around promontories compared to sheltered reefs (Barlow, 1981; Claydon, 2004; Johannes, 1978). Given the high co-occurrence of adult

GSB during the presumed spawning season, this location is likely used for spawning during the summer months, although gametic evidence and video surveillance is necessary to confirm. These findings are consistent with GSB courtship and aggregation behaviour documented at other offshore islands (Clark & Allen, 2018; Clevenstine & Lowe, 2021).

Although a large portion (73%) of the species range is in Mexican waters, little is known of the extent of population connectivity and transboundary movement (Chabot et al., 2015; Gaffney et al., 2007; Ramírez-Valdez et al., 2021). Recent research suggests continued recovery of GSB in California waters while the species' decline may not have occurred in the southern portion of its range in Mexican waters (Clevenstine & Lowe, 2021; House et al., 2016; Ramírez-Valdez et al., 2021). Nonetheless, as the population continues to recover in California, it is increasingly important to assess whether offshore islands, like SBI, act as population sources or sinks. More work is needed to determine how valuable the aggregation site at SBI is compared to those around Santa Catalina Island, Anacapa Island and La Jolla. Long-term oceanographic monitoring paired with population modelling efforts may be the best way to determine which types of habitats are important predictors of GSB population recovery (Dias, 1996; Paquet et al., 2020). It will be important for future studies to assess habitats that are beneficial across different life stages, such as documented nursery sites (Benseman & Allen, 2018) and foraging grounds (Burns et al., 2020), that likely differ from aggregation sites.

Although GSB can move long distances, not all individuals exhibit this behaviour. The 12 individuals tagged in this study were detected only at SBI and no other receivers in southern California or Mexico (Lowe, Nosal, Semmens, & Blincow, pers. comm.). Previous research shows GSB can move long distances, even across deep ocean basins, to access preferred coastal habitats (Burns et al., 2020; Clevenstine & Lowe, 2021). Other studies have found that individual movement patterns varied, with some individuals moving very little and others migrating long distances (>400 km; Clevenstine, pers. Comm., Blincow, unpubl. data). Based on prior observed migrations (Clevenstine & Lowe, 2021) and inter-annual site fidelity seen in this study, there appears to be potential for connectivity between subpopulations, possibly across international and other management boundaries (e.g., conservation areas and reserves). Nonetheless, more work is needed to understand the existence and extent of subpopulations and the realised connectivity between known aggregation sites (i.e., Anacapa Island, Santa Catalina Island, La Jolla) as numbers continue to increase in southern California. At present it is unclear how much transboundary movement occurs, and if such behaviours are unique to individuals or ubiquitous among the species. To adequately manage GSB, it will be important to quantify connectivity and movement using multinational telemetry networks, network analyses and data-logging transmitters [i.e., pop-off archival tags (PAT)]. Acoustic telemetry and network analyses, as demonstrated here, can be used to quantify the movements of individuals and pinpoint aggregation behaviour, which serves an important function in a species' life history, but may also increase the risk of overfishing (Dayton et al., 2003; Pauly et al., 1998; Sadovy & Eklund, 1999; Salinas-de-León et al., 2015). These data can help inform managers as to what type of management action

(e.g., spatio-temporal closures at aggregation sites, minimum or maximum size limit) may be most beneficial for GSB in California and Mexico.

The necessity of multinational collaborative species management will only increase as climate change continues to impact the marine environment. The marine heatwave of 2013–2015 is a recent example of an unusual climatic event that significantly impacted habitats and species movement throughout the range of GSB and other important game fish in California and Mexico (Cavole et al., 2016; Freedman et al., 2020; Logan & Lowe, 2018; Thompson et al., 2022). The authors found geomorphology to be an important indicator for aggregation and, although that will likely not be impacted by a changing climate, biotic cues to aggregate and spawn, and spawning and reproductive success, are often temperature dependent (Bolden, 2000; Erisman et al., 2012; Semmens et al., 2010; Whaylen et al., 2004). The ability of adult GSB to migrate long distances (Clevenstine & Lowe, 2021) may provide some resilience to climate change and highlight the importance of assessing transboundary movement to ensure effective management. As oceanic conditions continue to change and unusual events become more frequent, GSB range may shift, potentially expanding into new regions (Hastings et al., 2020; Pinsky et al., 2018; Tanaka et al., 2021). Recent studies suggest species range shifts are far less predictable than originally thought (Gaylord & Gaines, 2000, Fredston-Hermann et al., 2020, Fredston et al., 2020), further increasing the need for collaborative research that allows for adaptive management solutions.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.