

Residency and inter-reef connectivity of three gamefishes between natural reefs and a large mitigation artificial reef

Ryan K. Logan*, Christopher G. Lowe

Department of Biological Sciences, California State University Long Beach, Long Beach, CA, 90840, USA

ABSTRACT: Understanding the spatial and temporal patterns of residency for mobile gamefish species to artificial reefs (ARs), and connectivity with adjacent natural habitats is critical in quantifying AR productivity. Forty-five kelp bass *Paralabrax clathratus* (KB), 45 barred sand bass *P. nebulifer* (BSB) and 45 California sheephead *Semicossyphus pulcher* (SH) were tracked for 2 yr using passive acoustic telemetry on the Wheeler North Artificial Reef (WNAR), and an additional 20 fish (~7, 7, and 6 KB, SH, and BSB, respectively) were tagged at each of 3 nearby natural reefs (n = 195 fish) in the area of San Clemente, California, USA. SH exhibited significantly higher site fidelity to WNAR, measured as the proportion of days detected since tagging ($74 \pm 27\%$), than KB ($45 \pm 38\%$) and BSB ($30 \pm 26\%$); however, BSB displayed seasonal residency. All species tagged at WNAR showed high affinity to the area of the reef they were tagged. The majority of fish exhibited site attachment to the reef from which they were tagged, as only 13.3% of all fish were detected on a reef other than their respective tagging reef, and usually for short durations. Results of this study suggest that fish are not moving randomly among natural and AR habitats, and there was no evidence of migration of fish to WNAR. In addition, consistent long-term presence of these highly mobile fish suggests that WNAR is providing sufficient resources for the species examined and is thus functioning in much the same way as surrounding natural habitat.

KEY WORDS: Kelp bass · Barred sand bass · California sheephead · Acoustic telemetry · Attraction–production · Serranidae · Labridae

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INTRODUCTION

Many artificial reefs (ARs) are comprised of submerged structures (e.g. ships, tires, steel frames, boulders) placed on the seafloor deliberately, to mimic attributes of a natural habitat (Jensen 1997). These attributes can include serving as breakwaters and controlling local beach erosion (Bohnsack 1989). However, since the development of the National Fishing Enhancement Act of 1984, the majority of AR construction in the USA has focused on enhancing fishery resources and fishing opportunities (Stone 1985). Intensive fishing pressure over the last several decades has led to over-exploitation of many rocky

reef-associated fishes, and has significantly changed species composition and the demography of coastal marine fishes (Lea et al. 1999, Love 2006, Bellquist & Semmens 2016). In theory, ARs provide new habitat for fish and benthic organisms to colonize, increasing food resources, leading to an increase in overall fish biomass in the area, and thereby enhancing commercial and recreational fishing opportunities (Stone 1985, Leitão et al. 2007, Scarcella et al. 2011). For these reasons, when mitigation for anthropogenic habitat loss is required by resource agencies, ARs have generally been well accepted by fishers and other stakeholders (Bombace et al. 1994, Charbonnel et al. 2002, Leitão 2013, Cresson et al. 2014). In many

*Corresponding author: rklogn@gmail.com

cases, ARs around the world have been found to have higher densities of fish than natural reefs (Smith et al. 1979, Matthews 1985, Ambrose & Swarbrick 1989, Cresson et al. 2014), including where this study took place in southern California (Jessee et al. 1985, DeMartini et al. 1994, Stephens et al. 1994).

Two opposing hypotheses have been posited to explain the increased abundance of fish associated with ARs. The first, known as the 'production' hypothesis, states that ARs are effective producers of fish biomass which increase the recruitment of new individuals to the reef and enhance growth due to the availability of abundant food resources and high quality habitat (Bombace et al. 1994, Powers et al. 2003, Cresson et al. 2014). Over time, these structures become a mating, spawning and recruitment zone for high trophic level fishes and a source of larvae for adjacent habitats (Cresson et al. 2014). The other hypothesis, known as the 'attraction' hypothesis, proposes that ARs have a long-term, counterproductive effect because they are known to attract mobile organisms from natural reefs (Bohnsack & Sutherland 1985, Bohnsack 1989, Lindberg 1997, Powers et al. 2003, Bolding et al. 2004). As a result, mobile, reef-associated fish may concentrate on ARs, where they fare more poorly due to slower growth rates caused by crowding, increased predation pressure and higher catch rates (Crowder & Cooper 1982, Matthews 1985, Hixon & Beets 1989, Grossman et al. 1997, Steele 1997), culminating in an overall net loss of fish biomass in an area. Many studies examining fish abundance on ARs assume all fish visually recorded or caught on the AR reside there permanently (Ambrose & Swarbrick 1989, Bombace et al. 1994, Granneman & Steele 2014); however, to determine fish productivity, knowledge of surrounding habitats and fish movements across a range of spatial and temporal scales is required. For example, if fish counted or sampled on an AR do not consistently reside there, then determining accurate estimates of fish production for that AR would be difficult.

The Wheeler North Artificial Reef (WNAR) off the coast of San Clemente in the Southern California Bight is the largest constructed natural rock reef in the USA (Elwany et al. 2011). Southern California Edison Company (SCE) was required to build the reef as mitigation for the loss of the San Onofre Kelp Bed (SOK) resulting from the operation of the San Onofre Nuclear Generating Station (SONGS) (Ambrose 1994). Specifically, discharged cooling water from the plant's once-through cooling system distributed a plume of turbid water over SOK, which restricted giant kelp *Macrocystis pyrifera* growth and

recruitment (Reed et al. 2006). SONGS was decommissioned in June 2013, and kelp growth has since returned to the area; however, SCE is still required to meet the mitigation requirements. For SCE to receive mitigation credit, WNAR must meet or exceed biotic and abiotic performance standards relative to community performance from 2 nearby natural reefs, San Mateo Kelp Bed (SMK) and Barn Kelp Bed (BK). Because of this, there has been extensive monitoring and reef community assessment of WNAR since its construction; however, nothing is known about how reef fish use this habitat and to what extent they move between WNAR and these adjacent natural reefs. There is thus a unique opportunity to use WNAR and the nearby natural reefs as a model system to test where this AR falls on the attraction–production continuum.

While the greater part of WNAR was constructed only 7 yr prior to the start of the study in 2015 (WNAR was constructed in 2 phases, beginning in 1999 and completed in 2008), the community assemblage of WNAR is very similar to the communities reported on SMK and BK (Reed et al. 2015). The species richness and densities of fish, including young-of-the-year fish, invertebrates and algal communities on WNAR are similar or exceed those found on BK and SMK. Therefore, WNAR, which supports a mature kelp bed community, should provide habitat quality, prey resources and refuge habitat similar to those on nearby natural reefs.

In this study, we examined the site fidelity and movement patterns of 3 economically and ecologically important fish species, the kelp bass *Paralabrax clathratus* (KB), barred sand bass *P. nebulifer* (BSB) and California sheephead *Semicossyphus pulcher* (SH). KB and BSB constitute 2 of the most important recreational fisheries in terms of the number of fish taken by recreational fishers and commercial passenger fishing vessel (CPFV) fisheries since 1959 (Dotson & Charter 2003, Erisman et al. 2011). KB are known to be important reef piscivores which can have strong effects on the recruitment patterns of smaller reef fish species and can account for upwards of 50% of mortality attributable to predation in some species (Steele 1997, 1999, Forrester & Steele 2000, Anderson 2001). Where abundant, BSB may assume a similar ecological role (Steele 1997). SH regained commercial interest due to the development of a live-fish trap fishery which began in the early 1990s, and have remained a popular target among spearfishers due to their large size and curious nature (Alonzo et al. 2004). SH are also considered an important keystone species as a reef predator of benthic macro-

invertebrates including sea urchins, which aids in the maintenance of giant kelp forests (Tegner & Dayton 2000).

Recent monitoring of WNAR, SMK and BK has indicated that all 3 species occur in similar densities, and that KB and SH (BSB not measured) recruit and reproduce at similar rates at all reefs (Reed et al. 2015). This could suggest that fish are residing on WNAR and behaving similarly to fish on natural reefs in the area (lending support to the production hypothesis), or that fish are continually moving between WNAR and the natural reefs (suggesting support of the attraction hypothesis). To quantify this, a static array of acoustic receivers was used to monitor the long-term movements of KB, BSB and SH in relation to the AR, in order to elucidate (1) the site fidelity of these species to the AR; (2) how these species differ in their spatial and temporal movement patterns on the AR; and (3) whether fish caught and tagged at adjacent natural reefs move to the AR.

MATERIALS AND METHODS

Study site

WNAR is located approximately 1 km off the coast of San Clemente, CA (33° 23' N, 117° 37' W). The completed reef spans approximately 2.5 km² of seafloor along 3.5 km of coastline through depths of 11 to 17 m. The reef itself was constructed of ~114 000 t of quarry rock distributed in low relief polygons (rising 1 to 1.5 m above the seafloor) with an additional 57 blocks, each composed of 8 modules measuring 40 × 40 × 1 m constructed from concrete rubble and quarry rock from the experimental phase of construction. Roughly 1 km northwest of WNAR is a shallow (~5 to 10 m) natural rocky outcropping that consists of low relief rock with sparse kelp cover. Trestles Reef (TR), nearly 0.6 km directly south of WNAR, is a small rocky reef with dense kelp coverage. SMK, SOK and BK are 1.2, 7.5 and 19 km southeast of WNAR respectively, at similar depths and distance from the coast as WNAR, and separated by sand habitat (Fig. 1).

Acoustic receiver array

To determine the site fidelity and movement patterns of KB, BSB and SH, a static array of 41 omnidirectional acoustic receivers (Vemco, VR2W) moored 2 m off the seafloor recorded the acoustic detections

of transmitters surgically implanted into the 3 species of fish caught on WNAR, as well as the adjacent natural reefs (SMK, SOK and BK). Based on preliminary range testing and the presence of a dense kelp forest, 32 of the 41 receivers were placed in a grid fashion ~400 m apart (Fig. 1). Since the receivers had (conservatively) a 200 m detection range, this ensured a nearly complete coverage of WNAR. A row of 3 receivers placed ~1 km to the northwest and southeast of WNAR formed brackets to monitor directionality of movements to and from the AR. The remaining 3 receivers were placed at adjacent natural reefs (1 receiver per reef) at varying distances south of WNAR. A further receiver was in place as part of an ongoing study on TR; because of its proximity to WNAR, detections at this receiver were included in the results of the study, but no fish were tagged at this reef (labeled 'Trestles' in Fig. 1). A reference transmitter (Vemco V16-4L, 152 dB power output) was placed on a receiver mooring in the interior of the reef to provide calibration for diel and weather-related variability in detection ranges. Receivers were recovered and data downloaded approximately every 3 mo, and batteries replaced annually.

Fish collection and tagging

Between September 2014 and March 2015, 45 KB, 45 BSB and 45 SH were captured and tagged on WNAR. Between March 2015 and December 2015, 22 KB, 20 BSB and 18 SH were caught and tagged on SMK, SOK and BK (4–8 of each species per reef; see Table 1). All fish were captured via hook and line or baited trap. Fish were measured, weighed, sexed (SH only) and surgically implanted with an acoustic transmitter (Vemco, V9-2L; 9 mm diameter × 29 mm long, pulse interval 55 to 155 s, estimated battery life 730 d, power output 145 dB). Fish were anesthetized in a bath of fresh seawater dosed with tricaine methanesulfonate (MS-222, 0.2 g l⁻¹) until reaching a level 4 state of sedation (Lowe et al. 2003, Carter et al. 2011, Wolfe & Lowe 2015). Fish were then removed from the anesthetic and held upside down in a live well of circulating fresh seawater, the transmitter was inserted through a 1.5 cm incision in the abdominal wall into the peritoneal cavity, and the incision was closed with 2 to 3 interrupted sutures (Ethicon, PSD II). Following the surgery, an external dart tag with contact information (Floy Tag & Mfg.) was inserted into the dorsal musculature for angler recapture identification. Fish were then allowed to recover in a live well prior to release at the site

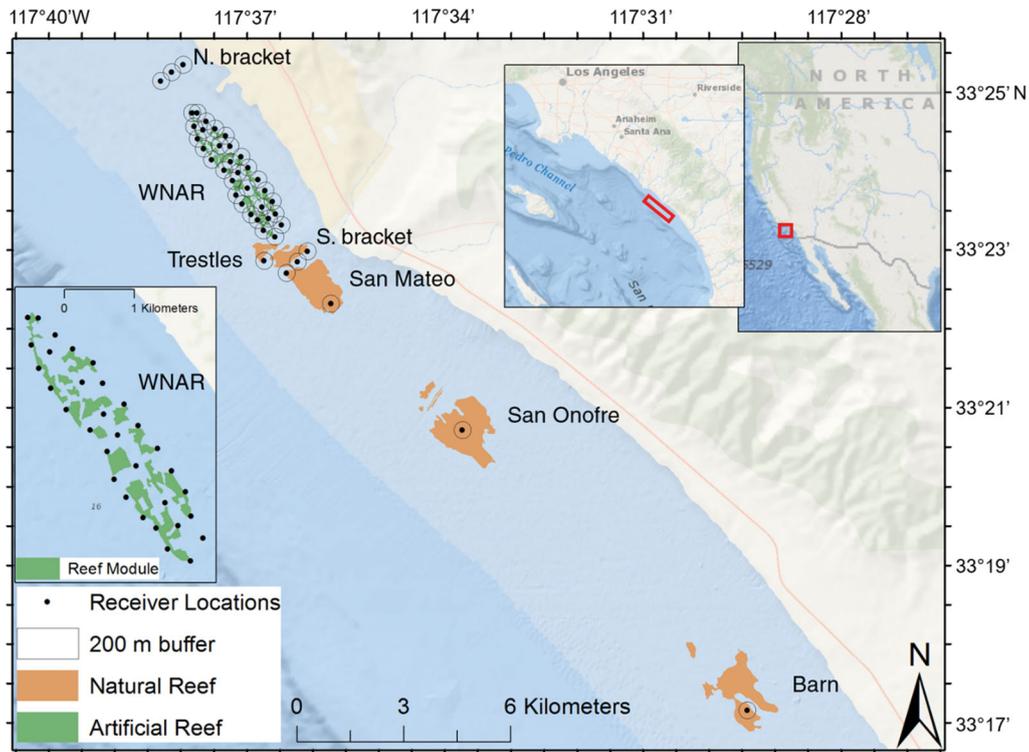


Fig. 1. Locations of VR2W acoustic receivers (black points) deployed on the Wheeler North Artificial Reef (green) in relation to natural reef sites (orange) off San Clemente, CA. Small circles around VR2W locations represent the acoustic receiver 200 m radius detection distance. Inset maps show (top right) geographic location of WNAR (red rectangles) off the California coast, and (bottom left) the WNAR module layout relative to receiver locations

of capture. All fish capture, handling and surgical 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 (IACUC protocol #344).

Residency and array performance

Monitoring of tagged fish began in September 2014 and continued until September 2016. Only fish that were detected for ≥ 10 d post tagging on WNAR were incorporated into analyses. Residency index was calculated as the percentage of cumulative days fish were present at WNAR (at least 2 detections on any receiver within a 24 h period) since their date of tagging. Residency index values ranged from 0 to 100%, where values close to 100 indicate near complete presence throughout the monitoring period. Residency indices were not normally distributed and did not have equal variances (Shapiro-Wilk normality test and Bartlett test of equal variance, $p < 0.05$), therefore, a Kruskal-Wallis test was used to deter-

mine if residency was significantly different among the 3 species, and a Mann-Whitney U -test was used to determine differences in residency between male and female SH. Because the receiver coverage at the natural reef sites was not sufficient to consistently detect fish tagged on the respective reef (even if they were resident; refer to Fig. 1), direct comparison of residency indices within species among reefs could not be assessed. Finally, the relationship between fish size and residency to WNAR was determined for all 3 species using general linear models (GLMs). The independent variable in the models were fish total length (TL) and sex (where applicable), with the residency index as the dependent variable.

Since BSB seasonally migrate to spawning aggregation areas (Jarvis et al. 2010, Teesdale et al. 2015), site fidelity measurements were made for spawning and non-spawning seasons. Additionally, in contrast to KB and SH which generally had long-term and consistent residency patterns to WNAR until complete loss of detections, preliminary analysis revealed that BSB residency to WNAR was inconsistent, even outside of the spawning season. Therefore, to determine whether BSB presence was influenced by envi-

Table 1. Kelp bass *Paralabrax clathratus* (KB), barred sand bass *P. nebulifer* (BSB) and California sheephead *Semicossyphus pulcher* (SH) tagged on natural and artificial reefs off San Clemente, CA, showing numbers of fish tagged and analyzed (fish never detected were not included in analyses), days at liberty and days detected (mean \pm SD, parentheses indicate range), and the mean residency index (\pm SD), calculated as the percentage of cumulative days fish were present, for each species and reef. WNAR: Wheeler North Artificial Reef; SMK: San Mateo Kelp Bed; SOK: San Onofre Kelp Bed; BK: Barn Kelp Bed. Note that residency indices for fish tagged at SMK, SOK and BK are presented for reference, but are likely underestimates of true residency due to the limited receiver coverage present at the natural reef sites

Species	Reef	No. tagged	No. analyzed	Days at liberty	Days detected	Residency index
KB	WNAR	45	41	712 \pm 10 (700–730)	319 \pm 274 (10–729)	0.45 \pm 0.38
BSB	WNAR	45	40	714 \pm 10 (698–730)	215 \pm 188 (10–658)	0.30 \pm 0.26
SH	WNAR	45	40	604 \pm 43 (577–730)	442 \pm 161 (71–636)	0.74 \pm 0.27
KB	SMK	8	8	409 \pm 79 (306–554)	210 \pm 116 (13–296)	0.52 \pm 0.31
BSB	SMK	8	7	426 \pm 92 (306–501)	194 \pm 113 (38–297)	0.46 \pm 0.26
SH	SMK	4	1	502	64	0.13
KB	SOK	7	6	390	47 \pm 26 (22–90)	0.12 \pm 0.06
BSB	SOK	6	2	390	65 \pm 51 (29–101)	0.17 \pm 0.13
SH	SOK	7	0	NA	NA	NA
KB	BK	7	2	371 \pm 24 (355–389)	132 \pm 169 (13–252)	0.37 \pm 0.47
BSB	BK	6	3	355	311 \pm 76 (223–355)	0.88 \pm 0.21
SH	BK	7	0	NA	NA	NA

ronmental (e.g. sea surface temperature, kelp cover, tide height, moon phase, photoperiod) or biological (e.g. TL) parameters, mixed-effects models (restricted maximum likelihood estimation) were performed using a logistic regression approach in the *lme4* package in R (Bates et al. 2014). Because giant kelp *Macrocystis pyrifera* is an important habitat feature for temperate rocky reefs and supports increased community structure (Schiel & Foster 2015), kelp canopy surface area (km²) was estimated in ArcGIS from quarterly aerial infrared photographs of WNAR provided by MBC Applied Environmental Sciences. Daily presence of each BSB was assessed as a binary variable and analyzed using the *glmer* function in R with a binomial distribution. Presence was treated as the response variable, and environmental and biological parameters were modelled as fixed factors. Individual tag IDs were treated as a random effect term to account for the lack of temporal and spatial independence among tagged fish.

Raw receiver detections were examined for individual BSB to determine the occurrence and directionality of emigration movements during the spawning season (June to August). An emigration event was characterized as an individual detected ≥ 2 times by any of the bracket receivers, or receivers on the edge of the AR during a given day with no return detected to the 32 receivers of the main array within 7 d. Emigrations away from WNAR were assigned north or south directions based on sequential receiver detections. Frequencies of observed movement directions were compared to frequencies of a random (50:50) direction of movement with a chi-squared test.

To quantify seasonal changes in residency to WNAR for all species, a seasonal residency index (number of days detected/total number of days in each season; arcsine transformed to meet assumptions of normality) for each fish was compared among seasons using a 1-way analysis of variance (ANOVA) with Tukey's HSD test for pairwise comparisons. Seasons were defined as 28 February to 31 May (spring), 1 June to 31 August (summer), 1 September to 29 November (fall) and 30 November to 27 February (winter). Because not all SH were tagged in the same season, data for all SH were truncated to begin on the date when all SH had been tagged (8 March 2015).

To determine if detection range of receivers was influenced by weather-related variability, hourly presence-absence of the reference transmitter was assessed at each receiver in the WNAR array over the course of the study. The detection distance of the reference transmitter was assessed over time using a GLM with a binomial probability distribution and a logit link function using maximum likelihood estimation. The detection distance curve formed the basis of the analysis and the approach adopted was to determine whether each of several environmental factors shifted the detection curve and, if so, by how much. In order to determine their effects on the detection distance, the environmental parameters included in the model were sea surface temperature ($^{\circ}$ C), wave height (m), rainfall (cm), tide height (cm), and kelp canopy cover (km²). A useful summary of the effects of each environmental factor is the shift (± 1 SD change) in the detection curve at which 50% of the

signals were detected (DP50; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m593/p111_supp.pdf).

Space use

To quantify whether space use of individuals tagged on WNAR was comparable to previously estimated home range sizes of these species, the AR was divided into 6 zones (~0.12 km² each; see Fig. 3 below). Because each zone was large enough to encompass the estimated home range of all tagged species on WNAR (Lowe et al. 2003, Topping et al. 2005, Mason & Lowe 2010), fish could be expected to remain resident to 1 zone. Site fidelity to each zone was assessed using a zonal fidelity index (ZFI), calculated as the proportion of cumulative days detected from any receiver in the respective zone, relative to the total number of days detected from the entire array for each fish. One-way ANOVA was used to compare overall ZFI values (arcsine transformed) among species.

To determine if fish selected habitat on the outer (ocean facing), middle or inner portion (land facing) of WNAR, the proportion of days detected on all outer edge, middle and inner edge receivers was calculated for each fish and averaged by species, and a 1-way ANOVA was run on arcsine transformed values for each species with Tukey's HSD for significant pairwise comparisons.

Dispersal and attraction

Connectivity between all natural reefs and the AR was assessed using a network analysis, which was based on the number of days detected at a given reef, referred to as a 'node', and the number of transitions between each pair of nodes, known as 'edges' (Jacoby et al. 2012). A movement count transition matrix could then be constructed containing movements between each pair of reefs, as well as the movements from each reef onto itself (i.e. residency, when the fish stayed at the respective reef). Bracket receivers were included as separate nodes to display movements toward the brackets that did not reach a separate reef. Because only 1 SH was detected on a reef other than the reef on which they were tagged, SH were excluded from all network analyses.

Direct comparisons of residency and inter-reef transitions of fish tagged at a natural reef and fish

tagged at WNAR are biased due to the unequal receiver coverage and the unequal number of tags deployed on WNAR and the natural reefs. Therefore, 1 receiver in the WNAR array was randomly chosen to represent WNAR (to match receiver coverage at the natural reefs) and 7 fish tagged on WNAR were chosen at random to match the number of fish tagged at the natural reefs (KB and BSB analyzed separately). The number of days detected at each reef and all inter-reef transitions for those 7 fish were calculated and averaged, giving a transition matrix for 1 randomly selected fish. This analysis was repeated 500 times while randomly selecting from the available pool of individuals and WNAR receivers. The average of these 500 matrices was taken, yielding an average number of days detected and an average number of inter-reef transitions for 1 randomly chosen fish on WNAR. To determine the effect of using data from only 1 receiver at a time compared to all 32 receivers, the same method was employed again; however, using pooled data from all 32 receivers in the WNAR array. Then, by constructing a transition matrix for each KB or BSB tagged at the natural reefs, summing those matrices and dividing by the total number of fish tagged there, the average number of days detected and the average number of transitions between reefs was calculated for 1 average natural reef KB and BSB, making direct comparisons between WNAR and natural reef fish possible.

From these average transition matrices, 2 metrics were calculated to assess inter-reef connectivity. First, the probability of transition was determined by dividing the number of transitions made from one reef to another by the total number of transitions, yielding the probabilities of fish moving to or remaining resident at each reef. Second, to understand the long-term dynamics of where fish may reside over time, the dominant eigenvector to the transition probability matrix was rescaled to the proportion of the total, resulting in a regional stable state distribution for fish tagged at WNAR, and fish tagged at the natural reefs. This metric gives an estimate of the average proportion of time individuals tagged at a particular reef are expected to spend on that reef or other reefs over a long timescale. It is important to note that these stable state distribution proportions only apply to fish that remained within the receiver array over the course of the study, and do not include fish that were no longer being detected due to mortality (fishing and natural), tag failure or emigration to areas with no receiver coverage.

RESULTS

Tagging, array performance and residency to wheeler north artificial reef

In total, 195 fish were captured, tagged and released over the course of the study. Using the ≥ 10 d detected post tagging criterion, 4 KB (9%), 5 BSB (11%) and 5 SH (11%) were excluded from residency and movement analyses. The mean (\pm SD) TL of tagged KB, BSB and SH across all sites was 31 ± 4.3 cm (range 24.8–47.6 cm), 32.6 ± 3.9 cm (27.5–42.8 cm) and 35.7 ± 6.2 cm (22.3–50.5 cm), respectively. Fish size was not significantly different among tagging reefs (KB: $F_{3,63} = 0.85$, $p = 0.47$; BSB: $F_{3,61} = 0.34$, $p = 0.79$; male SH: $F_{3,27} = 1.2$, $p = 0.31$; female SH: $F_{3,28} = 2.2$, $p = 0.11$). In total, 6 439 458 transmitter detections were recorded on all 42 receivers over the course of the study period. Five fish (0.03%; 2 SH, 2 BSB and 1 KB) were reported recaptured by local anglers, but all were reportedly released.

GLM results and associated Akaike information criterion (AIC) scores indicated that kelp cover (km^2) had the largest influence on the distance at which 50% of the detections (DP50) were detected. Due to the occurrence of a strong El Niño over the duration of the study period, the increase in water temperature drove a decrease in the abundance of giant kelp. As a result, the distance at which the reference transmitter was detected increased over time, with DP50 increasing by 23.5% (456 to 564 m) with a 1 SD change in the mean kelp cover (Fig. S1). Therefore, receiver performance improved over the course of the study period.

Residency indices to WNAR were significantly different among species (Kruskal-Wallis $H = 0.2$, $p < 0.01$; Fig. 2, Table 1). SH residency was significantly higher ($74 \pm 27\%$) than KB ($45 \pm 38\%$) and BSB ($30 \pm 26\%$), while there was no significant difference between KB and BSB (Table 1). There was no difference in residency between male and female SH (Mann-Whitney $W = 214$, $p = 0.7$). Larger BSB were detected on a higher proportion of days ($r^2 = 0.11$, $F_{1,38} = 4.7$, $p = 0.03$), but there was no relationship between KB TL and residency. No relationship was found between the residency index and body size or sex for SH. Due to the limited receiver coverage at the natural reef sites, the residency indices for the natural reef tagged fish (presented in Table 1) should be interpreted as minimum residency values, as individuals that were detected would move in and out of the detection range of the receiver, or were never detected post tagging. Opportunistic mobile receiver

deployments (Vemco, VR100) at areas on the natural reefs outside the detection range of the single moored receiver on each reef, confirmed the presence of tagged fish that had rarely, or never, been detected on the moored receivers and these fish were therefore still used in connectivity analyses.

Kelp canopy surface area (km^2) was the single environmental parameter examined here that explained the most variation (35%) in the presence of BSB to WNAR (Table 2). However, the best fitting model included average daily sea surface temperature ($^{\circ}\text{C}$) (www.ndbc.noaa.gov), kelp cover (km^2), photoperiod (indication of season) and total length of the fish (cm); this model explained 37.8% of the variation in BSB presence (Table 2).

All tagged BSB were considered to be sexually mature (>27 cm TL; Love et al. 1996). While no mass spawning migration event was observed for all BSB, 15 fish (37.5%) did show detection patterns characteristic of a spawning-related emigration, and the weekly proportion of all BSB present was significantly lower during the spawning season (June to August) than non-spawning (Mann-Whitney $W = 1489$, $p < 0.01$; Fig. 2). Of the 15 BSB that emigrated around the same time period, 8 (53.3%) returned to their respective tagging zone, while 7 (46.6%) were never detected again (Fig. 3A). Detection patterns revealed that 7 fish went north, 4 went south, and the directionality of 4 fish could not be determined; however, the direction of migration was no different from random ($\chi^2 = 0.82$, $df = 1$, $p = 0.37$). The date of departure ranged from 30 June 2015 to 20 August 2015, with a median departure date of 6 August 2015. Median return date to the WNAR array was 3 November 2015. The mean absence time for fish that went north was 120 ± 15 d, while the mean time away from WNAR for fish that went south was 91 ± 9 d; however, this pattern was not significant likely due to the small sample size (Mann-Whitney $W = 9$, $p = 0.1$). BSB that migrated were significantly larger (34.6 ± 4.2 cm) than BSB that did not migrate (31.2 ± 3.7 cm; Mann-Whitney $W = 106$, $p = 0.02$), but there was no difference in mean TL (cm) for fish that moved north (33.3 ± 1.3 cm) compared to fish that moved south (30.8 ± 1.8 cm; Mann-Whitney $W = 8.5$, $p = 0.12$). SH and KB showed no difference in the residency index among seasons ($F_{3,156} = 0.83$, $p = 0.48$ and $F_{3,160} = 1.5$, $p = 0.23$, for SH and KB, respectively) (Fig. 4); whereas, BSB showed a significant difference in the residency index among seasons ($F_{3,152} = 3.6$, $p = 0.01$) with a significantly higher residency in winter (0.41 ± 0.05 , mean \pm SE) than summer (0.25 ± 0.04) (Fig. 4).

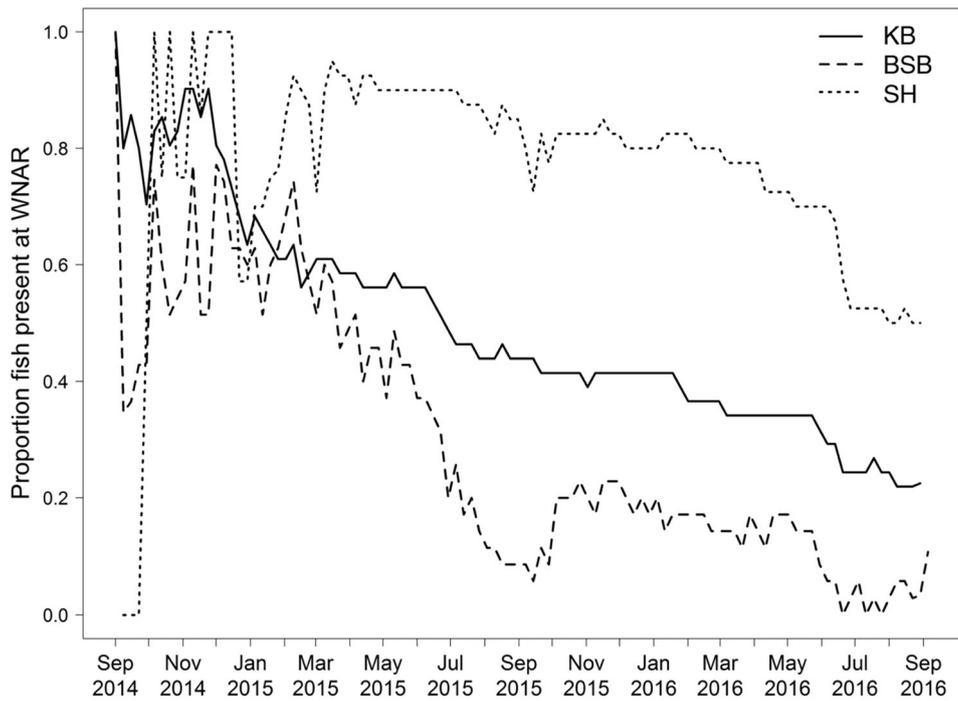


Fig. 2. Weekly proportion of all kelp bass *Paralabrax clathratus* (KB), barred sand bass *P. nebulifer* (BSB) and California sheephead *Semicossyphus pulcher* (SH) present at Wheeler North Artificial Reef (WNAR) between September 2014 to September 2016

Space use while present on WNAR

All species had high overall ZFIs (SH: 0.83 ± 0.25 ; KB: 0.79 ± 0.31 ; BSB: 0.79 ± 0.29), and there was no difference among species ($F_{2,118} = 0.24$, $p = 0.78$). The only species selecting habitat in the outer, middle or inner portion of the reef was SH, which were detected by the middle receivers on significantly more days than by inner or outer edge receivers ($F_{2,29} = 4.8$, $p = 0.01$; proportion of days detected =

0.37 ± 0.13), despite the fact 87% of SH were tagged at locations closest to the outer edge receivers. The majority of KB and BSB (66 and 64%, respectively) were also tagged at locations closest to the outer edge receivers; however, for these species the proportions of days detected did not differ among the 3 groups of receivers ($F_{2,29} = 2.9$, $p = 0.07$ and $F_{2,29} = 1.2$, $p = 0.3$, for KB and BSB, respectively).

Dispersal and attraction: WNAR fish

Of the 121 fish tagged on WNAR that were included in analyses, 20 (16.5%) were detected on a neighboring natural reef during the course of the study. Of these 20 fish, 11 were KB (55%) and 9 (45%) were BSB. No SH tagged on WNAR were detected on any natural reef during the course of the study. Out of the 20 fish detected on TR (90%), 4 were detected on SMK (20%), and 1 was detected on SOK (5%). No fish tagged on WNAR were ever detected at BK. All 11 KB detected on a reef other than WNAR

Table 2. Best fitting models based on Akaike information criterion (AIC) values of generalized linear mixed-effects model examining the effect of sea surface temperature (SST), kelp canopy cover (kelp), moon phase (moon), photoperiod (photo) and fish total length (TL) on the presence (PA) of barred sand bass *Paralabrax nebulifer* at Wheeler North Artificial Reef, off San Clemente, CA, from September 2014 to September 2016. Tag ID was treated as a random effect term (1|TagID) to account for the lack of temporal and spatial independence among tagged fish. The best fitting model is identified in bold

Model parameters	AIC	ΔAIC	% variation explained
PA ~ SST + kelp + photo + TL + (1 TagID)	21190.2	0	37.78
PA ~ SST + kelp + TL + (1 TagID)	21192.6	2.4	37.73
PA ~ SST + kelp + TL + moon + (1 TagID)	21192.9	2.7	37.73
PA ~ SST + kelp + photo + moon + (1 TagID)	21194.8	4.6	37.72
PA ~ SST + kelp + (1 TagID)	21196.6	6.4	37.71
PA ~ kelp + (1 TagID)	22099	908.8	35.02

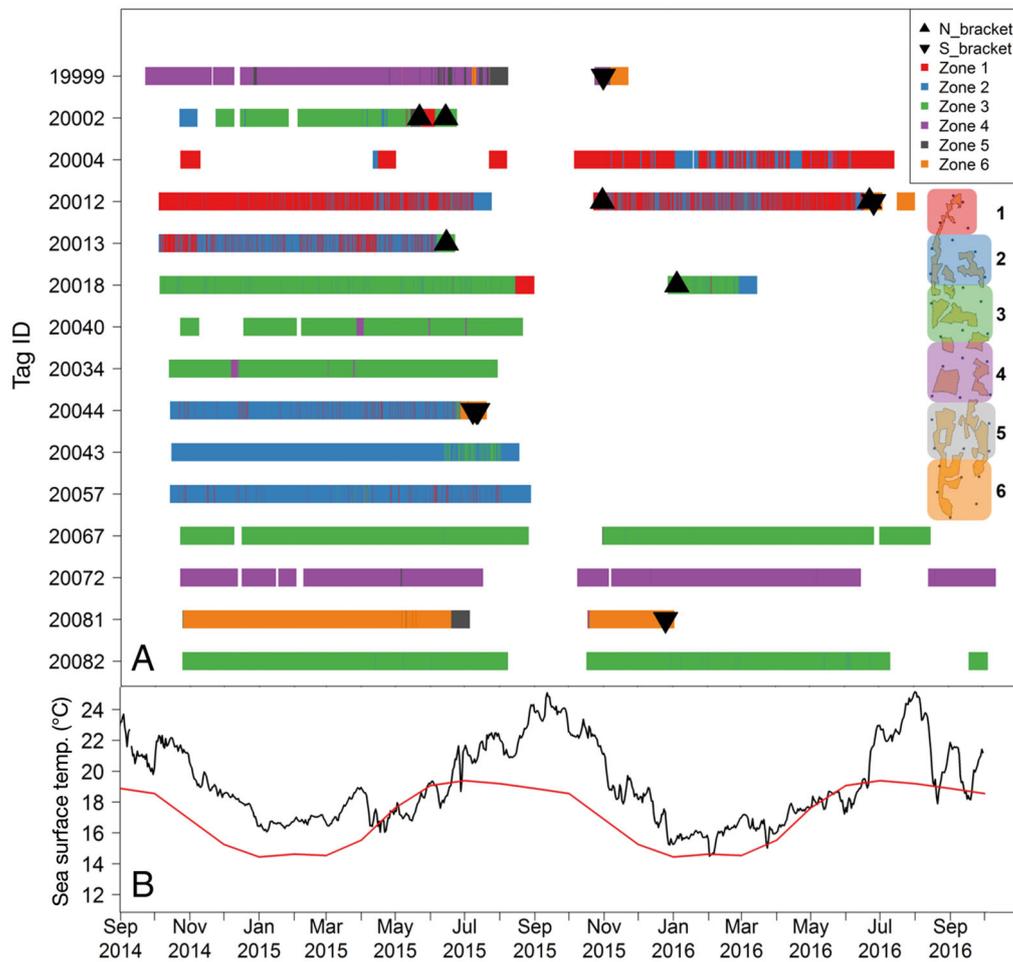
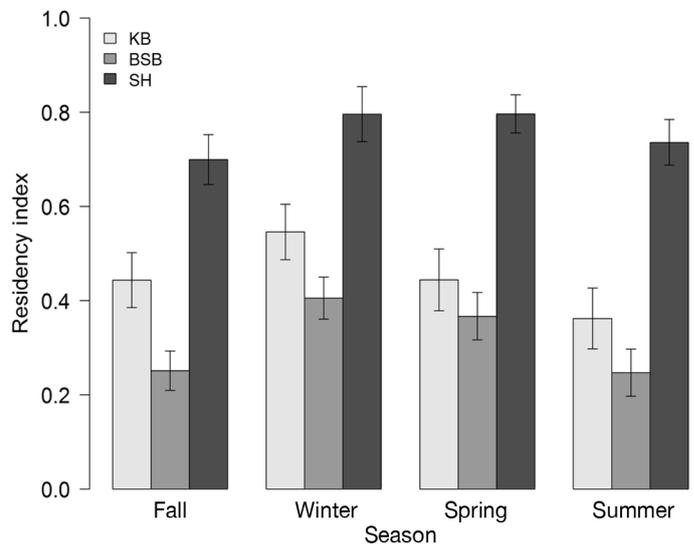


Fig. 3. (A) Presence of individual barred sand bass *P. nebulifer* in different zones of the Wheeler North Artificial Reef (WNAR) (see color-coded inset map) between September 2014 and September 2016, displaying detection patterns characteristic of seasonal spawning migrations. Black triangles depict detections by bracket receivers installed to the north (upward pointed) and south (downward pointed) of WNAR. (B) Daily sea surface temperature over the course of the study period (black line) calculated from NOAA buoy data (www.ndbc.noaa.gov), compared with 2010–2013 monthly average values (red line)

were detected at TR, and only 1 was detected at SMK and SOK.

The majority of KB detected at TR (72%) were only detected there for hours or one day at a time, usually moving back and forth between TR and WNAR within the same day. Only 3 KB spent any appreciable amount of time at TR without returning to WNAR, with an average stay of 73.5 ± 47.6 d among the 3 individuals. Transition networks (Fig. 5A,D) and

Fig. 4. Seasonal residency of tagged kelp bass *Paralabrax clathratus* (KB), barred sand bass *P. nebulifer* (BSB) and California sheephead *Semicossyphus pulcher* (SH) at the Wheeler North Artificial Reef (WNAR) off San Clemente, CA over the monitoring period (September 2014 to September 2016). Data are overall mean (\pm SE) seasonal residency index values, calculated as number of days detected divided by number of days in the season



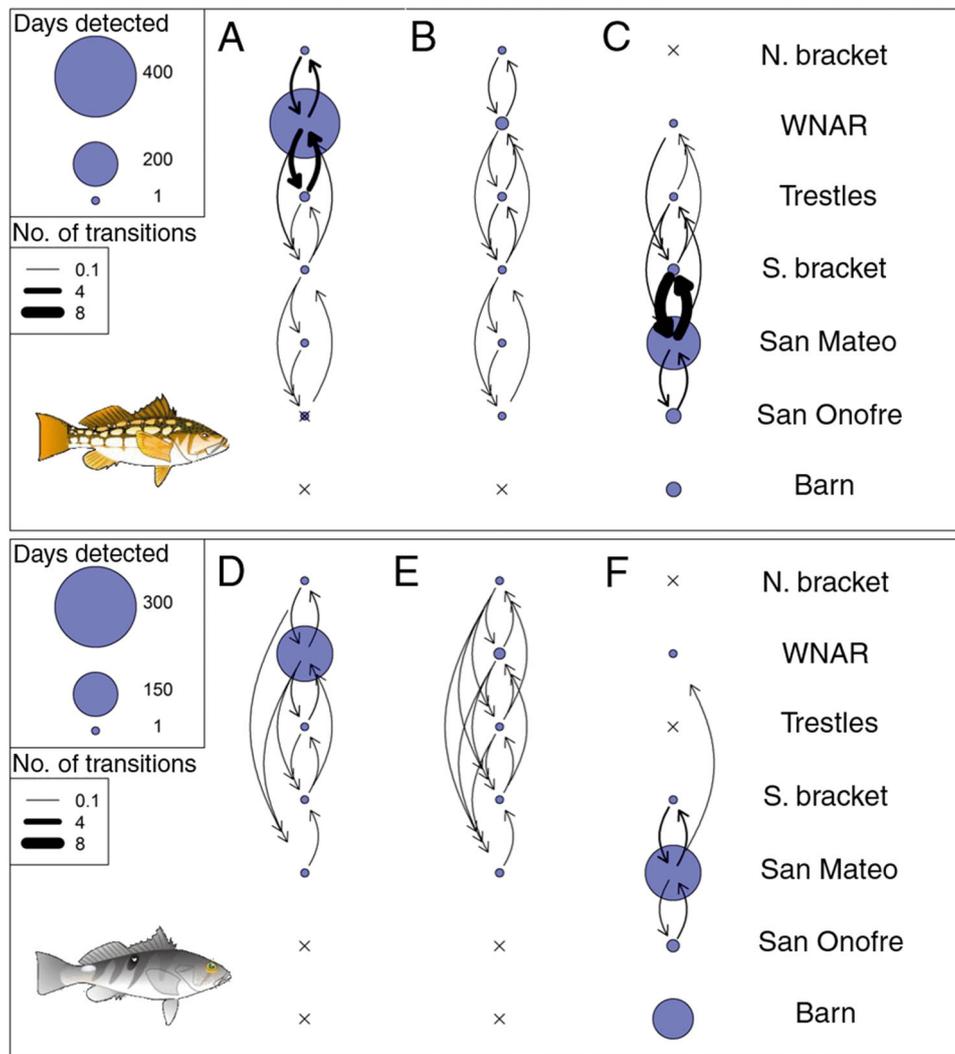


Fig. 5. Transition plots for (A–C) kelp bass *Paralabrax clathratus* and (D–F) barred sand bass *P. nebulifer* tagged on Wheeler North Artificial Reef (WNAR) and nearby natural reefs BK, SOK and SMK (see Table 1 legend for abbreviations). Plots also show presence of fish at Trestles Reef and south and north brackets (rows of receivers placed NW and SE of WNAR), although no fish were tagged in these locations. Panels (A) and (D) show results for 1 random fish (see 'Materials and methods: Dispersal and attraction' for further details) based on pooled data from all 32 receivers on WNAR. Panels (B) and (E) show results for 1 random fish based on results from 1 randomly chosen receiver in the WNAR array. Panels (C) and (F) show results for fish tagged at natural reefs. Node size corresponds to the number of days detected, and line thickness of the arrows shows relative number of transitions made between pairs of reefs. (×) indicates that no fish were detected moving to or from the location. Note that California sheephead *Semicossyphus pulcher* were excluded from analysis because they exhibited very little movement between reef sites

transition probability matrices (Tables S1 to S6 in the Supplement) show that KB tagged at WNAR were detected visiting one more node than BSB. This was driven by 1 KB, which was detected moving to the SOK receiver during the summer months of both years of the study period. Seven out of the 9 (78%) BSB that were detected on a natural reef were detected on TR, and 3 (33%) were detected on SMK. The circular nature of the KB and BSB networks reveal the homing behavior of these species (Fig. 5A,D),

where if a fish was detected leaving WNAR, it was often detected returning after a short period of time.

After normalizing for the number of fish tagged and the number of receivers present between WNAR and the natural reefs, the average number of days that fish were detected on the natural reefs was greater than the average number of days that fish were detected on WNAR. However, this was not a fair representation of the average number of days that fish were detected at WNAR (see Table 1,

Tables S1 & S3). Consequently, using data from all 32 receivers (rather than just one) on WNAR gave a more accurate representation of average fish presence on WNAR versus the presence on natural reefs (panels A vs. C and D vs. F in Fig. 5), and was therefore used in making transition probabilities and stable state distribution estimations.

KB tagged on WNAR had the highest probability of moving to TR based on the probability of transition (0.008) and the stable state distribution (0.02) (Table 3, Table S1). The stable state distribution for BSB suggests that after WNAR, fish would spend the next greatest of proportion of time on SMK and TR (0.02 and 0.003, respectively).

Dispersal and attraction: natural reef fish

Of the 60 fish tagged at the natural reef sites, only 4 fish (6.6%; 2 KB, 1 BSB and 1 SH) were detected on WNAR, and all 4 of these fish were initially tagged at SMK. The 2 KB were detected on the southernmost WNAR receivers for 9 and 21 h, respectively, before returning to SMK. The BSB and SH detected on

WNAR both displayed high residency to the SMK receiver prior to detection on WNAR, then rapidly moved to WNAR, at which point all detections ceased. From this pattern, it is presumed these fish were either preyed upon at SMK, or moved to WNAR and were immediately fished out. The latter seems unlikely, however, given the rapid nature of the movement and immediate loss of detections.

Transition networks and matrices for natural reef fish (Fig. 5C,F, Tables S5 & S6) again reveal the higher likelihood of movement within the receiver network for KB compared to BSB. KB tagged at SMK showed the greatest average number of transitions between reefs of any fish in this study, averaging 8 transitions between the SMK receiver and the southern bracket. However, there was a propensity for fish to return to SMK (Fig. 5C). BSB tagged at natural reefs showed very little movement between reefs, with an average of 1 transition per fish between SMK and the south bracket and 0.1 transitions per fish between SMK and SOK (Fig. 5F). Based on the stable state distribution for all natural reefs, KB and BSB can be expected to spend the majority of their time at SMK (0.82 and 0.92, for KB and BSB respectively).

Table 3. Stable state distribution for kelp bass *Paralabrax clathratus* and barred sand bass *P. nebulifer* tagged on Wheeler North Artificial Reef (WNAR) and nearby natural reefs BK, SOK and SMK (see Table 1 legend for abbreviations), based on records from acoustic receivers. Results for Trestles Reef (TR) and south and north brackets (rows of receivers placed NW and SE of WNAR) are included to display directionality of movement and the importance of nearby habitat, even though no fish were tagged in these locations. These proportions only apply to fish that remained within the receiver array over the course of the study (September 2014 to September 2016), and do not include fish that were no longer being detected by the end of the study due to mortality (fishing and natural), tag failure or complete emigration from the study area. Columns are where the fish were tagged (WNAR or natural reef), and rows are locations where fish were detected. Values show the proportion of time (on average) that individuals from each tagging location are expected to spend their time at each detection location. California sheephead *Semicossyphus pulcher* were excluded from network analysis because only 1 individual was detected on a reef other than the reef on which they were tagged

Detection location	Kelp bass tagging location		Barred sand bass tagging location	
	WNAR	Natural reef	WNAR	Natural reef
BK	0	0	0	0
SOK	0.004	0.11	0	0.06
SMK	0.0002	0.82	0.02	0.93
South bracket	0.004	0.06	0.003	0.007
TR	0.02	0.006	0.003	0
WNAR	0.96	0.002	0.97	0.0007
North bracket	0.003	0	0.002	0

DISCUSSION

Site fidelity and seasonal patterns

Overall, SH, KB and BSB exhibited high, moderate and low site fidelity (proportion of days detected) and long term residency (number of fish remaining at the end of the study) to WNAR, respectively. (Fig. 2, Table 1). Similar patterns of declining presence of other reef-associated fishes have been observed in other natural and AR telemetry studies over similar time periods (Topping & Szedlmayer 2011, TinHan et al. 2014). Sudden loss of detections could be attributed to a number of factors, with fishing mortality as the most likely possibility. WNAR is heavily fished by recreational and commercial fisheries, and is located roughly 9 km south of a major sport fishing port from which multiple CPFV trips are made daily to WNAR and the surrounding natural reefs. Given that only 13% of KB and 22% of BSB tagged were ≥ 35.5 cm TL (the legal minimum size limit), the majority of individuals, if recaptured, should have been released. While no fish were known to have died from

tagging procedures (characterized by constant and regular detections at a single receiver), 4 KB and 5 BSB were either never detected following tagging or detected for <1 d, suggesting possible post-release mortality away from the tagging reef, predation, immediate emigration or tag failure. If fishers were catching and releasing tagged fish shorter than the minimum size limit, this could have resulted in increased levels of mortality or emigration from the study site than would be expected. Cooke et al. (2006) found that mortality rates of recreationally caught-and-released bonefish *Albula* spp. varied extensively (between zero and near 100%), which was influenced by a number of factors including fishing gear, angler behavior, environmental conditions and species-specific characteristics. In contrast, 82% of tagged SH were >30.5 cm TL (the legal minimum size limit), and likely would have been kept if caught. We received 5 reports of recaptured fish (2 SH, 2 BSB and 1 KB) from the local CPFVs. In all 5 of these instances, the fishers reportedly caught and released the fish on WNAR, but in 1 case (a SH) the fish was never detected again, indicating a possible fishing mortality or emigration. Only 1 KB was reported recaptured by a private vessel recreational angler, who also reportedly caught and released the fish at WNAR.

Another plausible explanation for the decrease in KB and BSB detections over time could be attributed to the strong El Niño event that occurred over the course of the study period (i.e. in 2015 to 2016; www.cpc.ncep.noaa.gov). This event was one of the strongest recorded, and resulted in a prolonged increase in sea surface temperature (Fig. 3B), resulting in a concurrent decrease in the abundance of giant kelp, a well-known consequence of El Niño events (Dayton 1985, Tegner & Dayton 1987, Schiel & Foster 2015). Kelp canopy cover on WNAR was estimated to be 1.23 km² in April 2014, 0.164 km² in April 2015, and 0.0 km² by April 2016. In addition, Reed et al. (2015) found that the number of fronds per *Macrocystis* plant on WNAR decreased from a 2009–2014 average of ~6 fronds m⁻², to ~3 fronds m⁻² in 2015. The disappearance and thinning of kelp eliminates refuge from predators for midwater associated fish species, food derived from enhanced secondary productivity, foraging habitat, and physical orientation (Coyer 1979, Bodkin 1988, Holbrook et al. 1990). KB tracked on natural reefs were found to be in kelp-dominated habitat 55% of the time over the course of a 4 mo tracking period on Catalina Island (Lowe et al. 2003), and BSB shows a positive association to sand-rock ecotone habitat with dense kelp coverage (Mason & Lowe 2010, McKinzie et al. 2014). The benefits of

being in close proximity to 2 habitat types (e.g. rocky reef and dense kelp canopy) include having access to higher prey abundance and diversity, while being near resting areas and refuge from predators (Ries et al. 2004). Because WNAR is made up exclusively of low-relief rock with low rugosity, the loss of kelp may have eliminated some of the advantages of being resident to WNAR, and fish in this study may have emigrated in an attempt to find more suitable habitat. Thus, it is possible that KB and BSB may have emigrated away from other low relief natural reefs that also lost kelp beds during this strong El Niño event.

The difference in the residency indices between KB and BSB observed in this study are potentially explained by the different foraging strategies and diet preferences of these 2 species. While adult KB are largely known to be ambush piscivores in kelp-dominated habitats (Love 2011), Johnson et al. (1994) found that KB ≥23 cm TL, similar to fish tagged in our study, consumed a larger variety of prey than BSB of the same size class from a smaller artificial reef where *Macrocystis* does not grow. KB diet consisted of roughly 50% fish, 30% algae and 10% of both crustaceans and molluscs. In contrast, 93% of BSB diet was benthic and epibenthic reef associated fishes, while only 7% was made up of crustaceans and infaunal species. These findings indicate that KB may be more plastic in its ability to prey switch in the event of a climatic disturbance, such as an El Niño, whereas BSB may need to increase their area use in order to satisfy their intake requirements. However, the fact that BSB would leave and return to WNAR after periods of long absences (> 30 d in some cases; Fig. 3A) outside of the spawning season, could indicate that BSB are regionally dependent on WNAR to fulfill energetic demands. Repeated use of an area is a commonly observed behavior in fish and vertebrate species, and has many potential advantages including familiarity with both shelter and prey locations, which is likely to increase the overall fitness of an individual (Zeller 1997, Teesdale et al. 2015).

BSB presence at WNAR was best explained by a combination of several environmental factors, but kelp canopy cover was the single most influential parameter in the model (Table 2). While there was a decrease in BSB abundance due to spawning migrations (Figs. 2 & 3), not all fish migrated, and the timing of these migrations are not consistent with observed departures in previous studies and historical fisheries catch data (Jarvis et al. 2010, Teesdale et al. 2015). The median departure dates for BSB in 2 consecutive La Niña years were 10 July 2011 and 6 June 2012, when departures were highly correlated

with the development of a thermocline (Teesdale et al. 2015). The mean departure date of BSB in this study was much later, i.e. 6 August 2015. This is believed to be due in part to El Niño, where a decrease in upwelling and the warmer than average surface waters prevented or delayed the formation of a strong thermocline, in addition to the peak in the sea surface temperature occurring later in the year than on average (Fig. 3B). In temperate regions, the timing of migration in a number of marine fishes is highly correlated with temperature and seasonal photoperiod (Jonsson & Ruud-Hansen 1985, Quinn and Adams 1996, Lowe and Bray 2006, Teesdale et al. 2015); however, given the timing observed in this study, it is believed that temperature, more than photoperiod, may drive the timing of BSB migration. Given that all tagged BSB were sexually mature, the fact that the BSB that migrated were, on average, larger than the BSB that did not migrate might indicate that older BSB continue to migrate, while younger mature BSB may not. This finding could also provide insight into the recent declines in BSB abundance at known spawning aggregation sites as the larger individuals continue to be fished out (Jarvis et al. 2014). It is important to note that BSB spawning behavior has been observed on WNAR during the peak spawning season (M. A. Steele and M. Adreani unpubl. data), suggesting this population of BSB may consist of migratory and resident spawning subpopulations.

Space use on WNAR

Based on the ZFIs within and among species, while fish were present at WNAR, they exhibited very high site attachment to a small portion of the available habitat. These results indicate that all zones of the reef are likely of similar habitat quality, and suggest that no one zone on the reef is more profitable habitat than any other for the species examined. These findings are corroborated by a recent report on the physical and biological characteristics of WNAR (Reed et al. 2015) where important prey species for KB and BSB (e.g. kelp perch *Brachyistius frenatus*, seniorita *Oxyjulis californica*, blackeye goby *Rhinogobiops nicholsii*, blacksmith *Chromis punctipinnis*, and mobile invertebrates) were found in similar densities throughout all reef modules of WNAR (Johnson et al. 1994, Steele 1999, Reed et al. 2015). While the total density of all mobile invertebrates was down from the 2009–2014 average, numbers of larger species, such as California spiny lobster *Panulirus interruptus*,

giant keyhole limpet *Megathura crenulata* and red sea urchin *Mesocentrotus franciscanus* have remained relatively constant, or in the case of the spiny lobster, have increased 4-fold since 2013 (Reed et al. 2015). These findings may help explain why the SH remained highly resident to WNAR, and selected habitat in the interior of the reef where the encounter rate of preferred benthic invertebrate prey is highest.

Dispersal and attraction

Transition probability matrices indicated that all 3 fish species tagged at WNAR, to the extent that they were consistently detected at any reef in the array, have a high probability of remaining on WNAR (0.997) and, on average, showed a lower probability of moving to any of the neighboring natural reef sites (~0.001). Fish that were detected moving away from WNAR traveled to natural reefs in close proximity, such as TR, with a high probability of returning to WNAR (Tables S1 and S3). For example, the probability of a BSB transitioning from WNAR to TR or the south bracket is 0.001, while the probability of transitioning from TR or the south bracket back to WNAR is 0.44 and 0.23, respectively. Because only 1 fish was detected moving to or away from SOK, and no fish were detected moving to or away from BK, these reefs are essentially ignored in the stable state distribution (Fig. 5, Table 3, Tables S5 & S6). In contrast, because SMK is in close proximity to reefs in both directions, it 'gives' and 'receives' tagged fish to and from multiple adjacent areas (south bracket and TR), and is therefore heavily weighted in the stable state distribution.

The amount of movement observed between WNAR, TR and SMK is not surprising, given the amount of rocky reef habitat spread between these sites making this area nearly contiguous habitat (Fig. 1). However, given the length of the study and the number of fish tagged in the area, the amount of movement observed between these sites was small. Similar findings of AR site fidelity were observed by Lowry et al. (2017), where yellowfin bream *Acanthopagrus australis* were observed to remain resident to the reef they were tagged on, and were highly resident to AR habitat. In contrast, Keller et al. (2017) noted significant connectivity (>5 km) between natural and ARs where individuals of 3 species of benthic fish and elasmobranch were often detected at up to 6 separate reef sites. The differences in life history strategies and homing behavior of the species examined in Keller et al. (2017) and the current study are

likely responsible for the difference in inter-reef connectivity observed between the 2 studies. It is also important to note that the lack of receiver coverage at the natural reef sites likely impacted our ability to detect all movements to the natural reef sites.

While there was a net loss of tagged fish from the AR (Fig. 2), there were few cases of confirmed emigration to the surrounding reef habitats (Table 2). In addition, there was little evidence of attraction to the AR from the surrounding natural reef fish, similar to Lowry et al. (2017). Because fish are clearly attracted to ARs almost immediately upon construction when fish densities are low (Lindberg 1997, Bolding et al. 2004, Reed et al. 2015), it is hypothesized here that immigration to ARs may be density dependent, where if the density of fish becomes too high on the AR it becomes less attractive to potential immigrants. In this study, if fish were detected moving to an adjacent reef, natural or artificial where fish densities have been shown to be similar (Reed et al. 2015), they were highly likely to return to the reef from which they came (Fig. 5, Tables S1–S6).

Management implications

Over 30 permitted ARs have been constructed in Southern California since the 1950s, consisting of over 100 rock-pile modules, with the goal of producing fish biomass, particularly of popular sportfish (Bedford et al. 2000). Central to the problem of establishing reef productivity for mobile species is knowing when and for how long a variety of species are resident to a reef, which has been largely overlooked in many AR studies (Bedford et al. 2000, Brickhill et al. 2005, Smith et al. 2016). This study suggests that when conditions were favorable, fish were highly resident to WNAR, and for those that were not highly resident, repeated presence suggests WNAR is needed to fulfill reproductive and energetic demands. Immediately following construction of WNAR, Reed et al. (2015) noted the large sizes and high abundance of fish on WNAR, indicating initial attraction. This was followed by a large decrease in fish abundance the following year which the authors attribute to a tenfold decrease in blackeye goby *Rhinogobios nicholsii* abundance; since then, abundance and biomass estimates have fluctuated, but show an overall increasing trend (Reed et al. 2015). Residency indices and network analyses presented here reveal fish are resident to a single reef and it does not appear fish are redistributing throughout the area over an inter-annual period.

Results herein suggest that future AR management plans in California may be best served by implementing low relief modules ideal for giant kelp attachment (Reed et al. 2006), supplemented with modules of high vertical relief. Although habitat associations to vertical relief could not be explicitly tested here, kelp cover (used as a proxy for vertical structure) was shown to be the most significant predictor of BSB presence to WNAR. Artificial structures with high vertical relief have been shown to provide important habitat qualities for certain species and can result in an increase in species diversity and abundance (Martin & Lowe 2010, Claisse et al. 2014). The mix of different relief modules may make the proposed AR more appealing to a wider variety of species than only low or high relief reefs, while serving as a natural buffer for climatic disturbances (e.g. El Niño events) by providing high relief habitat to vertical structure-oriented species when natural kelp cover is reduced. Regardless of relief type, Reed et al. (2016) found that many fish of various trophic levels occur in similar densities, recruit and reproduce at WNAR and neighboring natural reefs. Additionally, results of this study suggest that fish remain resident to a single reef, and are not consistently attracted to WNAR. Therefore, in its current community state, WNAR is functioning and producing fish similarly to surrounding natural reef habitat.

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