

# Integration of a social cluster of Atlantic spotted dolphins (*Stenella frontalis*) after a large immigration event in 2013

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## Abstract

Demographic changes can result in alterations of social structure and behavior which in turn may affect survival, reproduction, or movement and may influence how populations respond to changes in the environment. In 2013, 52 Atlantic spotted dolphins (*Stenella frontalis*) left Little Bahama Bank (LBB) and immigrated into a resident group of spotted dolphins on Great Bahama Bank (GBB). Initially there was little interaction and two distinct social clusters delineated by residency status. Here we describe the social structure of the dolphins on GBB between 2015–2020. Analyses were conducted with SOCPROG 2.9 and coefficients of association were nonrandom. The number of associations between LBB and GBB individuals increased, and standardized lagged association rates indicated continued associations over time. Modularity analysis showed one community without clear social clusters, although there were preferential associations within the original communities. Multiple Regression Quadratic Assignment Procedure indicated that sex, age, and residency status were good predictor variables that explained the patterns of the association indices. Male alliances were present between LBB, GBB, and LBB/GBB males. New and old relationships are influencing the social restructuring of this community. This

study furthers our understanding of how demographic changes can shape the social structure of a population.

#### KEYWORDS

alliance, coefficients of association, dispersal, immigration, integration, social structure, Socprog, spotted dolphins, standardized lagged association rates

## 1 | INTRODUCTION

Social structure is interconnected with ecological specializations, community structure, and influences how populations respond to changes in the environment (Chabanne et al., 2021; Louis et al., 2018; Snijders et al., 2017). Processes that disrupt social patterns and stability can be detrimental to a population (Banks et al., 2007) and influence its long-term survival. One way this can happen is through dispersal (Bowler & Benton, 2005; Elliser & Herzing, 2011). Demographic changes have been shown to result in altered behavior and social structure in a variety of social species (Cantor et al., 2017; Elliser & Herzing, 2011, 2014b; Lazaro-Perea et al., 2000; Lehmann & Boesch, 2004; Lusseau & Newman, 2004; Matkin et al., 2008; Sapolsky & Share, 2004). The interplay between demographic processes and social behavior can affect survival, reproduction or movement and have significant impacts on social networks (Shizuka and Johnson, 2020).

The presence of immigrants in a community can induce change in local social organization (Elliser & Herzing, 2011; Lin et al., 2004). However, the long-term effects of emigration/immigration events are not well known and only recently has immigration begun to be quantified in studies of population dynamics (see review by Millon et al., 2019). This is due to the fact that even for well-studied species immigration events are often rare (Kahlenberg et al., 2008), the logistics involved in following individuals are often prohibitory (Bowler & Benton, 2005), and long-term data sets and monitoring are lacking for many populations. However, these events are important in understanding the origin and structure of social groups (Baker & Dietz, 1996; Brockelman et al., 1998) and are needed to understand the ways that immigration interacts with local demographic processes to shape population dynamics (Millon et al., 2019). Variations in social processes underlying how individuals respond to loss and gain of individuals can result in differential responses of social networks to different rates of turnover (Shizuka & Johnson, 2020). How many individuals immigrate and the ability of individuals to assimilate can affect the resulting social structure (Elliser & Herzing, 2011) and can have implications for the long-term health and stability of a community or population.

Immigration events usually involve a single individual or a small group, and the level of assimilation into the community is determined by the association choices of the resident individuals (Baker & Dietz, 1996; Elliser & Herzing, 2011; Kahlenberg et al., 2008). Assimilation of immigrants into a population is even more complex when the number of animals immigrating at the same time is larger, especially if they are a cohesive group. How does such a group, with their established relationships, move into a resident community that has their own social structure and relationships among individuals? How do these new relationships affect the social structure of the population? Understanding how social network structure changes when immigration events occur requires longitudinal studies of the same population (Shizuka & Johnson, 2020).

Large-scale immigration events may become more common as animal distribution, movement, and residency patterns shift in relation to climate change and associated environmental disturbances. Climate variations have been linked to altered habitat use and community changes in marine animals (e.g., Ferguson et al., 2005; Genner et al., 2004; Hamilton et al., 2019; Herzing et al., 2017; Lusseau et al., 2004; MacLeod et al., 2005). Marine mammals are particularly vulnerable to climate-related redistributions and both environmental and anthropogenic

perturbations are increasing (Silber et al., 2017). These environmental changes may cause increasing demographic upheaval and changes in dispersal patterns, which can affect association patterns and community or population structure. Understanding the interplay of demography and social processes can provide insight on variations in social networks and help predict ecological resilience of social systems (Shizuka & Johnson, 2020).

A long-term study in the Bahamas provided a unique opportunity to observe how a large cohesive group assimilates into a resident population. An unprecedented large scale immigration event (over 50% of the long-term residents immigrated), referred to as the immigration event throughout the paper, occurred between September 2012 and May 2013, when 52 Atlantic spotted dolphins (*Stenella frontalis*) from Little Bahama Bank (LBB) immigrated to Great Bahama Bank (GBB), which was already occupied by a resident community of Atlantic spotted dolphins (Herzing et al., 2017). These LBB dolphins previously had a stable community comprised of 3 distinct social clusters, the Northern, Central, and Southern based on social associations (Elliser & Herzing, 2012, 2014a,b), genetics (Green, 2008), and distribution and home ranges (Augliere, 2012). The 52 individuals were mainly from the Central cluster (45) with a few from the Northern (5) and Southern (2) clusters, but when they moved to GBB they became one cohesive group, with homogenous associations (Herzing et al., 2017) strikingly different from their nonrandom associations and distinct social clusters documented from 1991 to 2007 (Elliser & Herzing, 2014a,b). For the first 3 years following the immigration event (2013–2015) there was little integration of the LBB immigrants with the GBB residents and the community was split into two distinct social clusters delineated by residency status (Herzing et al., 2017). This study documented the social structure of this new community on GBB for 6 years after that initial analysis to determine if integration between the LBB and GBB dolphins occurred, described the current social structure, and compared this to their respective previous social structures on LBB and GBB before the immigration event.

## 2 | METHODS

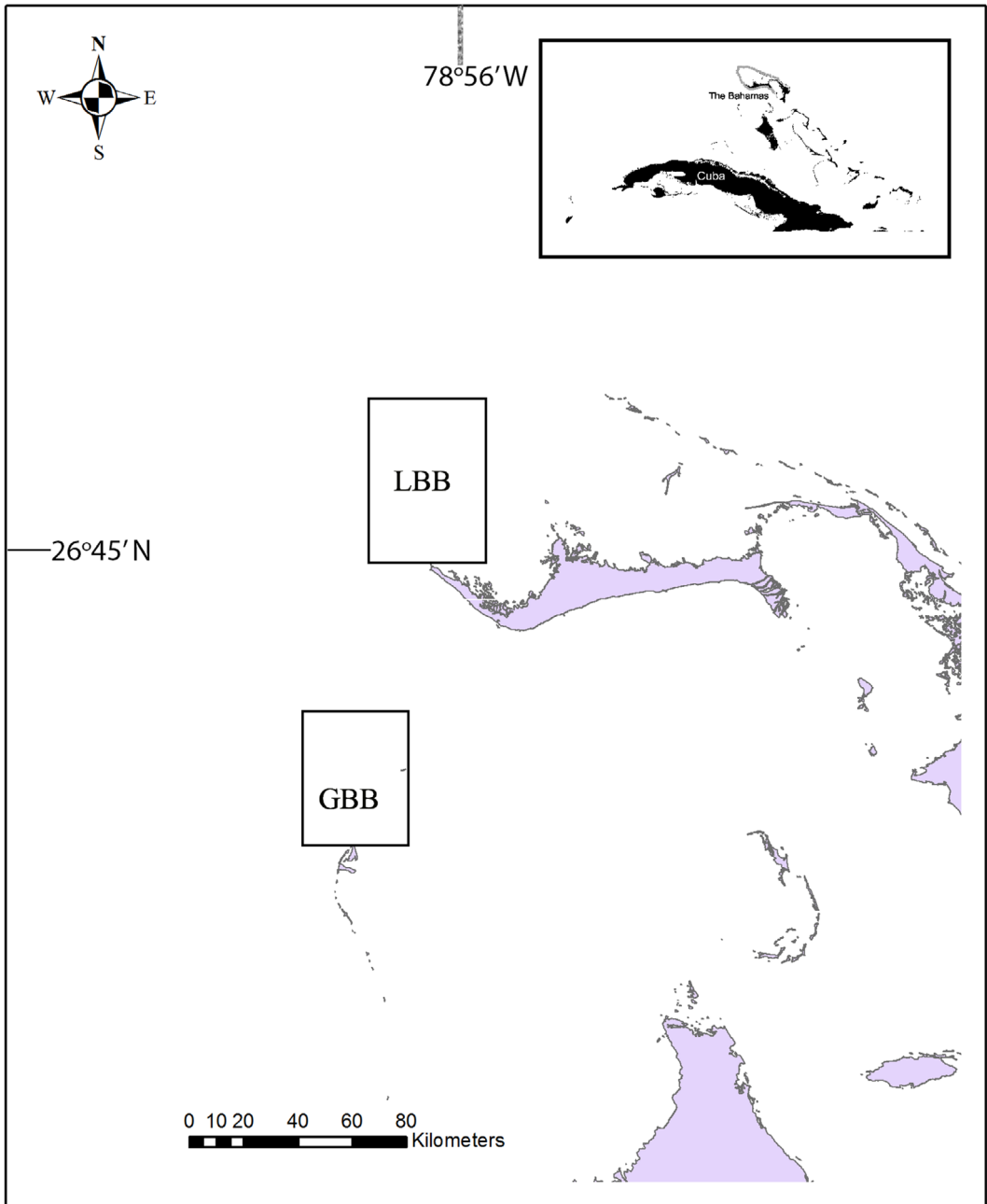
### 2.1 | Study area

GBB is north of Bimini, Bahamas and separated from LBB to the North by deep water. This sandbank is approximately 960 km<sup>2</sup> and is shown in relation to LBB in Figure 1. Similar to LBB, GBB has shallow sandbanks for daytime foraging and protection from East/West tidal flow and the western edge has depths between 6 m and 16 m and provide access to nocturnal foraging opportunities (Herzing & Elliser, 2014) in deep water (to over 500 m). Thus, the LBB immigrants moved into a ecologically similar area when moving to GBB. All data collected in this study were from the dolphins on GBB (including LBB immigrants and GBB residents).

### 2.2 | Data collection

Data were collected on GBB from May to September each year and effort is given in Table 1. Observers scanned an arc of 180° while underway and 360° while anchored in all but rough weather conditions (over Beaufort 3 and/or intense rain squalls) from 0700 to 2000 in 1 hr shifts.

Atlantic spotted dolphins have four developmental color phases (Herzing, 1997) including: two-tones (calves, up to 4 years), speckled (juveniles, 4–9 years), mottled (young adults, 10–16 years), and fused (adults, 16+ years). On average, spotting patterns and age are strongly correlated, with the age of an individual matching the corresponding color phase. However, the degree and timing of acquiring spots can vary by individual such that transitions between color phases may not line up exactly with the age ranges; for example, an individual may be a young adult by age, but still be speckled in coloration. Color phase data were updated each year. Spotting patterns along with additional marks such as nicks and scars on the dorsal fin, flukes, pectoral fins, and marks or scars on the body were used to



**FIGURE 1** Boxes indicate the Little Bahama Bank (LBB) and Great Bahama Bank (GBB) study sites. Land masses (Grand Bahama Island by LBB and Bimini by GBB) are shaded.

identify individuals. Males were sexed by a gap between the genital slit and the anus, or observation of an erection. Females were sexed by observation of mammary slits or observation of nursing by a calf.

A group was defined as all dolphins in sight, moving in the same direction and typically involved in the same activity (Shane, 1990). An encounter was defined as a group of dolphins observable underwater for more than 2–3 min (Elliser & Herzog, 2012). The final group size was a product of visual identification during the encounter

**TABLE 1** Field effort on GBB in number of days, number of encounters, and total duration in minutes.

Year	# Days	# Encounters	Total duration
2015	14	20	855
2016	14	12	438
2017	27	47	1,640
2018	31	46	2,031
2019	30	63	2,052
2020	11	18	736
Total	127	206	7,752

and photo-identification afterwards. We used the same methods for identifying individuals from photographs and determining group size as described in Elliser and Herzing (2012, 2014a).

### 2.3 | Data analysis

Coefficients of association (CoAs) were calculated using the half-weight index (Cairns & Schwager, 1987) with the software program SOCPROG 2.9 (Whitehead, 2009). CoAs were calculated for pooled years 2015–2017 and 2018–2020. We used the same 3-year pooling as in previous work on the LBB and GBB populations (Elliser & Herzing 2014a,b; Herzing et al., 2017) to allow for comparisons of social structure between studies on these populations.

CoAs were calculated for pairs of noncalf individuals of known sex using two sighting criteria: (1) those sighted at least six times per pooled period and (2) at least four sightings per pooled period. Power and precision statistics were very similar for both (six sightings statistics: 2015–2017:  $S = 0.43 \pm 0.10$ ,  $S^2 \times H = 15.9$ ,  $CC = 0.57 \pm 0.05$ ; 2018–2020:  $S = 0.78 \pm 0.04$ ,  $S^2 \times H = 152.1$ ,  $CC = 0.88 \pm 0.03$ , compare with the four sightings statistics in Table 2). The four sightings criteria were used because it included more individuals, and thus would be more representative (similar to Elliser & Herzing, 2014a).

The power and precision of the calculated CoA were determined using social differentiation ( $S$ , which indicates the variability of association indices within a population),  $S^2 \times H$  ( $H$  is the mean number of observed associations per individual) and the correlation coefficient ( $CC$ ) (Whitehead, 2008a,b). Data with intermediate ( $S \sim 0.5$ ) to high ( $S$  close to 1.0 or above) social differentiation will need fewer associations than data with low differentiation to detect preferred companionship (Whitehead, 2008a). The  $CC$  between the true association indices (the proportion of time dyads spend together) and estimated association indices using the likelihood method (Whitehead, 2008a,b) was used to infer the reliability of the results and if the data were a reliable representation of the social system ( $CC = 0.40$  CoA matrix is somewhat representative,  $CC = 0.80$  CoA matrix is a good representation). These metrics help to determine how reliable the results were and if there was enough data to be representative of the true social structure.

SOCPROG was used to conduct permutations to test the null hypothesis of random associations and no preferred/avoided companions (Christal & Whitehead, 2001; Whitehead, 2009). The sampling period was set to day. Permutations were increased until the  $p$ -values stabilized at 10,000 with 1,000 flips per permutation. The “permute groups within samples” test was used because this accounts for cases when not all individuals are present (birth, death, migration, etc.) in each sampling period (day). For this test the elements of the incidence matrix of groups by individuals are permuted for each sampling period, keeping the row and column totals constant, and tests the null hypothesis that there are no preferred or avoided companions given the number of groups each individual was observed in each sampling period (Whitehead, 2009). Significantly higher  $SD$  or  $CV$  of the real association indices

**TABLE 2** The total number of encounters, individuals (by residency status and sex) and CoA statistics (including mean, SD, CV, S, CC, H,  $S^2 \times H$ ) for individuals sighted at least four times per pooled period. *P*-values refer to significantly higher SD and CV of the real data compared to the permuted data.

Year	No. Enc <sup>a</sup>	No. LBB (M/F/U)	No. GBB (M/F)	Mean CoA real/perm	SD real/perm	CV real/perm	S ± SE	H	CC ± SE	$S^2 \times H$	<i>p</i>
2015–2017	74 (18, 10, 46)	10/11/0	24/19	0.17/0.17	0.17/0.16	1.03/0.98	0.60 + 0.06	83.16	0.58 + 0.05	29.9	≤.0001
2018–2020	112 (44, 58, 10)	9/14/1	26/26	0.21/0.21	0.20/0.16	0.95/0.76	0.82 + 0.04	239.89	0.86 + 0.03	161.3	.000

<sup>a</sup>Numbers in parentheses are the number of encounters in 2015, 2016, and 2017 and 2018, 2019, and 2020, respectively.

compared to the permuted data indicates nonrandom associations and long-term preferred companionship (Whitehead, 2009). If the associations were found to be nonrandom, then Mantel tests were conducted to compare matrices and test the hypothesis that associations between and within classes (sex, age, and residency status matrices) were similar (Whitehead, 2009). Positive  $t$ -values indicate that within class associations were higher and the  $p$ -value for a 2-tailed test for analytical approximation was used to determine significance (Whitehead, 2009). Multiple regression quadratic assignment procedure (MRQAP), with 1,000 permutations, were also conducted. MRQAP tests are similar to Mantel tests, but consider whether each of the predictor matrices (sex, age, and residency status) make significant contributions to explaining the association matrix while controlling for the presence of the other predictors (Whitehead, 2009). This procedure helps to determine which of the predictors were useful in explaining the patterns of association observed. The 3-year pooling categories allow most individuals to be included under one age class, however, if an individual changed during that time, then they were classified as the age class they were 2 of the 3 years (Elliser & Herzing, 2014a). Strong associations were defined as greater than twice the mean CoA of the study group (Gero et al., 2005; Whitehead, 2008a). Male alliances were determined by being greater than twice the male–male mean of the population or social cluster (if present).

To investigate social grouping, the community by modularity (gregariousness) test in SOCPROG was conducted. Modularity (difference between the proportion of the total of the association indices within clusters and the expected proportion; Whitehead, 2009) was used to differentiate clusters within the communities, if present, where a modularity greater than about 0.30 is usually considered to indicate useful divisions (Newman, 2004).

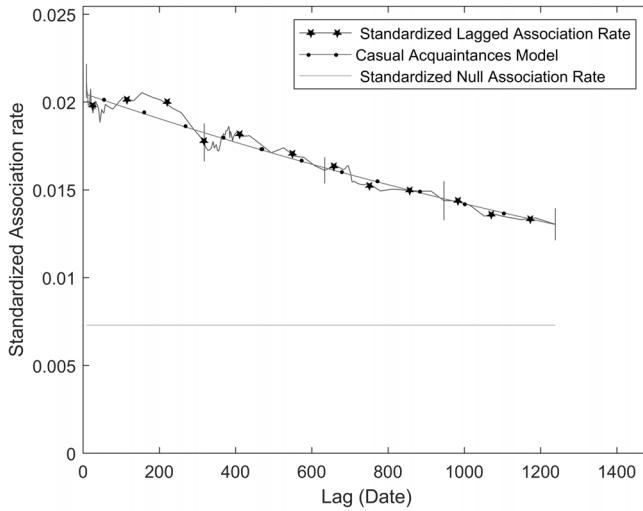
To further investigate the level of integration that occurred, the temporal stability of the associations overall and within and between residency status was measured by calculating the standardized null and lagged associations rates (SLAR). SLAR are used over lagged association rates when a zero in the association data means that a dyad was not observed to associate, not that they did not associate (i.e., the researcher cannot be sure they did not associate, Whitehead, 2008a). SLAR estimates the probability that if two individuals are associated, then after the lag time the second individual is a randomly chosen associate; the standardized null association rate is the expected value if the previous statement is true and associations are completely random over the given time lag (Whitehead, 2009). SLARs were conducted on the data without any restrictions (all years (2015–2020) and all individuals regardless of sightings) for all individuals, and between residency status (i.e., the probability of a GBB individual associating with another GBB or LBB individual vs. random). The jackknifing method, in which the analysis is done many times omitting one or more sampling periods each time, was used to estimate the precision of the SLAR (Whitehead, 2009) and the grouping factor was set to 30 sampling periods (days). Models of association patterns were fit to the overall data and the model with the lowest quasi-Akaike information criterion (QAIC) was chosen as the best fit. Models with  $\leq 2$  change in QAIC were also identified as having substantial support for the model (Whitehead, 2009).

### 3 | RESULTS

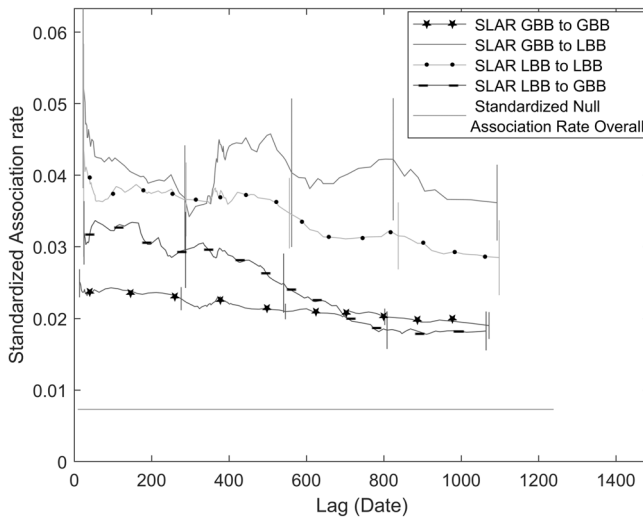
The total number of encounters, individuals (by residency status and sex), and CoA statistics (including mean,  $SD$ ,  $CV$ ,  $S$ ,  $CC$ ,  $H$ ,  $S^2 \times H$ ) are given in Table 2. In 2015–2017 the number of encounters per individual averaged 7.8 and ranged from 4 to 16 and in 2018–2020 averaged 15.4 and ranged from 4 to 28. The statistical power for both data sets to reject the null hypothesis of no preferred companions was good with  $S^2 \times H > 5$  and social differentiation was greater than the 0.50 which denotes a well differentiated society (requiring fewer associations to detect preferred companionship). The  $CC$  were intermediate (0.58 for 2015–2017) and good (0.86 for 2018–2020). The first time period (2015–2017) is between somewhat representative ( $CC = 0.40$ ) and good ( $CC = 0.80$ ), thus there is less confidence in representation of the society during this time period compared to the later (2018–2020). However, the data still provided a good enough representation of the true social system for both data sets and further analysis could be conducted. For both data sets, permutation tests revealed nonrandom associations with significantly higher  $SD$  and  $CV$  compared to the permuted data (all  $p \leq .0001$ ) indicating preferred and/or avoided companions (Table 2).







**FIGURE 2** Standardized lagged association rate (SLAR), null association rate, and the best fit model (casual acquaintances) for all years 2015–2020 for all individuals (no restrictions). Second best fit model was two levels of casual acquaintances (line not shown but is the same as casual acquaintances model). Moving average was set to 500,000 associations, standard errors were calculated by jack-knifing over 30-day periods.



**FIGURE 3** Standardized lagged association rate (SLAR) within and between residency status, for all years 2015–2020 for all individuals (no restrictions) and overall null association rate. Moving average was set to 500,000 associations for the overall null association rate and GBB to GBB, 30,000 associations for GBB to LBB and 60,000 associations for the LBB to LBB and LBB to GBB, standard errors were calculated by jack-knifing over 30-day periods.

(decreasing slope) over all time scales. Mixed residency associations had more variation in their SLAR. GBB to LBB associations decreased and then spiked up at about 400 days, then decreased and had another spike at about 800 days before decreasing again, whereas LBB to GBB continually decreased until about 700 days when it fell below the GBB to GBB rate.

Overall male–male associations had the strongest average CoA ( $0.20 \pm 0.05$  and  $0.33 \pm 0.11$ ) compared to female–female associations ( $0.16 \pm 0.05$  and  $0.19 \pm 0.05$ ) and male–female associations ( $0.16 \pm 0.08$  and  $0.17 \pm 0.07$ ) in 2015–2017 and 2018–2020, respectively. Definition of male alliances is determined by being greater than the male–male mean of the population or cluster. Although the clusters identified approached, but did not reach the modularity threshold for useful delineations, it is possible that the closeness of those individuals could be biologically important in the population. If this is the case and the overall male–male population average is used, this could incorrectly identify male alliances at artificially low association values. Thus, to be conservative, the definition of male alliance is based on being at least twice the average of the clusters which ranged from 0.27 to 0.39 (average 0.32) for 2015–2017 and 0.32 to 0.46 (average 0.40) for 2018–2020. Thus, male alliances were identified as twice the average cluster CoA,  $>0.64$  for 2015–2017 and  $>0.80$  for 2018–2020.

There were nine alliances identified in 2015–2017 each with two or three individuals (mostly mottled and fused, but with some speckled individuals): three LBB, five GBB, and one LBB/GBB (Table 5). There were three previously documented alliances with slight changes in membership after the immigration event: two LBB and one GBB. There was one GBB alliance that remained unchanged since the immigration event. Finally, there was one mixed residency alliance (which had three of the top five CoA), between one LBB male and two GBB males.

In 2018–2020 there were seven definitive alliances (five GBB and two LBB) and three GBB pairs/trio that were linked but definitive structure could not be determined (Table 5). All of these males were also in alliance level associations in 2015–2017, though some membership changes occurred. The majority of males were mottled and fused individuals, the only speckled individuals were in the undefined group of three pairs/trio. There were five previously documented alliances with minor changes from 2015 to 2017, four GBB and one LBB. There were two alliances that remained unchanged, one GBB and one LBB. The final GBB alliance level associations were between three groups (including speckled individuals), making determination of structure difficult.

**TABLE 5** This table shows the alliances per pooled data set. The bold and italicized names are the individual males who were added to alliances and the crossed-out names are males no longer in alliances for the 2018–2020 years. Cobalt, Lhasa, and Kong have not been sighted since 2017 and therefore they were not include in the 2018–2020 data set.

LBB	GBB	LBB/GBB
<b>2015–2017 Alliances</b>		
(1) Cobalt, Legend	(1) Donkey, Kong	(1) Lhasa, Lord, Drogo
(2) Achilles, Bonito	(2) Doublescoop, Latte	
(3) Picasso, Sunami, Finesse	(3) Atlas, Duke, Lamda	
	(4) Pulsar, Toad, Baelish	
	(5) Monkey, Lettice, Trident	
<b>2018–2020 Alliances</b>		
<del>Cobalt</del> , Legend	(1) Donkey, <del>Kong</del> , <b>Baldy</b> , <b>Vox</b>	<del>Lhasa</del> , Lord, <del>Drogo</del>
(1) Achilles, Bonito	(2) Doublescoop, Latte, <b>Mocha</b>	
(2) Picasso, Sunami, <del>Finesse</del>	(3) Atlas, Duke, <del>Lamda</del> <sup>a</sup>	
	(4) Pulsar, Toad, Baelish,	
	(5) Trident, <sup>b</sup> <b>Zeke</b> , <b>Evren</b>	
	(6) Lettice, <sup>b</sup> <b>Jammin</b>	
	(7) Monkey, <sup>b</sup> <b>Zeke</b>	
	(8) Lord, Drogo	

<sup>a</sup>Lamda still associated with Atlas and Duke, but at a lower level.

<sup>b</sup>Monkey, Lettice, and Trident are each a part of new alliances that have strong associations between the three groups making determination of structure difficult.

## 4 | DISCUSSION

The results revealed that the LBB and GBB dolphins are now living as one community, with increased amount of mixed residency associations, mixed residency SLAR remaining above the standardized null association rate, and lack of definitive social clusters. This new community of LBB and GBB dolphins has similar social structure to that seen in their previous communities prior to the immigration event, with associations stronger within age and sex than between (Danaher-Garcia et al., 2020; Elliser & Herzing, 2014a). This seems to be an important part of the social structure in many dolphin populations as interactions can involve many combinations of age and sex, but long-term affiliations are correlated with age, sex, reproductive status, and kinship (Wells et al., 1999).

This new community structure is strikingly different from what was documented directly after the immigration event in 2013–2015, where the new community on GBB was made up of two distinct social clusters: one made up of the resident GBB dolphins the other made up of LBB dolphins that moved to GBB, with very few associations between GBB and LBB individuals (Herzing et al., 2017). Long-term work previous to the immigration event showed that the LBB and GBB dolphins had different community structures, though the size of both communities was relatively similar, with roughly 80–100 individuals identified (Danaher-Garcia et al., 2020; Elliser & Herzing, 2014b). Dolphins on LBB were separated into the Northern, Central, and Southern clusters (Elliser & Herzing, 2012) that remained consistent through demographic changes and environmental disturbances (Elliser & Herzing, 2014b). However, when the 52 LBB dolphins moved to GBB, their social structure changed as they moved as one group with homogenous associations (Herzing et al., 2017). In contrast, long-term work on the resident dolphins on GBB shows that they seem to live in one community, without delineation into separate social clusters (Danaher-Garcia et al., 2020), and this was consistent with what was seen in the first 3 years after the immigration event (Herzing et al., 2017). The GBB and LBB communities are now integrating into one community. This highlights the social plasticity of these dolphins and how important it may be to exploit different habitats (Lusseau et al., 2003) and to survive environmental or demographic changes (Elliser & Herzing, 2011).

The SLAR analysis further emphasizes the integration of these two communities as well as the retaining of relationships from the original communities. The best fit models were the casual acquaintances and two levels of casual acquaintances, both with substantial support with only two points difference in the QAIC. For smaller populations, the casual acquaintance model can indicate that the dolphins may be avoiding previous associates (e.g., not re-associating with individuals of different residency status); whereas the two levels of casual acquaintances model can indicate that the shorter associations are social disaffiliation, but more permanent relationships (within units or preferred associations) eventually decay because of movement between permanent units, shifts in preferred companionship, mortality, emigration, or some combination of these (Whitehead, 2008a). For example, in the modularity analysis there was varied membership in the potential clusters (which were either GBB only or mixed LBB/GBB). Some individuals were grouped in different clusters for each data set, whereas others remained grouped in the same one. This indicates changes in associations/preferred companions within and between residency status, even if the groupings are not true social clusters. All of the SLAR (overall and by residency status) stayed well above the standardized null association rate, indicating that the associations were not random at any time lag. Thus although there were still strong associations within residency status (discussed below), the SLAR fitted models indicate patterns of continued, yet varied, associations between LBB and GBB dolphins that were not previously observed on GBB.

The association patterns and SLAR also show a strong influence of residency status. Although there were more associations between LBB and GBB dolphins, individuals still had stronger associations with others of the same residency status (i.e., LBB with LBB or GBB with GBB) than between. Similarly, in a remote Hawaiian atoll although immigrant and resident spinner dolphins rarely interacted, when they did the original group membership was always restored (Karczmarski et al., 2005). Thus integration or increasing associations between immigrants and residents may not negate the previous relationships they have spent years creating.

The loss and gain of new social connections creates a dynamic process that molds the social structure of a population (Shizuka & Johnson, 2020). After immigration events, the association choices made by resident individuals can

strongly affect the acceptance of the immigrants into the population (Baker & Dietz, 1996; Kahlenberg et al., 2008) and ultimately affect the grouping patterns and social structure (Elliser & Herzog, 2011). This is evident in the fact that residency status had a strong effect on association patterns as seen in the Mantel, MRQAP and SLAR analyses. There was still preference in associating within the original communities (LBB with LBB or GBB with GBB individuals), but also increased associations across residency status (between LBB and GBB individuals), though this differed between GBB and LBB individuals. The SLAR for GBB to LBB individuals had two spikes at around 400 and 800 days, indicating continued reassociations. However, after an initial increase, LBB to GBB associations showed a continual decrease until the rate fell below the GBB to GBB SLAR. This may indicate that some LBB dolphins were less likely to reassociate with GBB dolphins than vice versa and emphasizes that there are differences in association choices between residents and immigrants. Although the clusters were not useful for definitive community divisions, they also reveal variation in association choices, where some GBB individuals were clustered by themselves, whereas others were clustered with LBB individuals. In group composition analysis LBB individuals were found to be in mixed groups more often, while GBB residents were seen more often in GBB only groups (Hill, 2021). These results indicate that the relationships are complex and variable in the choice of associations between LBB and GBB individuals, particularly in relation to residency status. The association choices of both the residents and immigrants are influencing the structure of this new community and supports the idea that changes in composition of a population will influence social structure through the loss and creation of social connections (Shizuka & Johnson, 2020).

These changes in grouping and association patterns may be influenced by both foraging and social needs as the choices in group membership are related to the costs and benefits of group living (Krause & Ruxton, 2002). Potential costs of emigration/immigration include aggression, decreased foraging and energetic travel costs, while benefits can include increased mating opportunities (Kahlenberg et al., 2008). Associations being made by the dolphins on GBB are likely related to reducing competition (social and foraging), but also meeting the social needs of the individuals. Although LBB dolphins were more frequently encountered in mixed residency groups, they foraged less and had more aggressive behaviors in these groups compared to other group compositions (Hill, 2021), and these costs may explain why associations were still stronger within residency status than between. The reduced foraging time means that LBB dolphins had to find prey elsewhere. They had significantly larger home ranges and spent more time in northern areas closer to deep water nocturnal foraging grounds, whereas GBB residents retained their primary sandy bottom foraging habitat (Hill, 2021). Similarly, in a common bottlenose dolphin (*T. truncatus*) population, social clusters had relatively distinct ecological niches, and this resource partitioning among clusters is thought to reduce competition, allowing for a larger population to inhabit the area (Louis et al., 2018). These choices in habitat use/distribution can affect associations and social cluster formation as an individual's movements, which are influenced by sex, age, ontogenetic status, and social surroundings may affect, or be affected by others (Brandt, 1992) and a shared use of space/habitat preferences may create opportunities for individuals to interact (Louis et al., 2018). LBB immigrants may have less time to interact with GBB residents (indicated by the decreasing trend in the LBB to GBB SLAR) and have more time with other LBB individuals if they need to spend more time traveling and/or foraging. Thus, an individual's home range will influence the association and grouping choices available.

However, there are benefits to interacting with other community members or outside individuals, including increased courtship opportunities. If mating between LBB and GBB individuals occurs, then immigration can increase gene flow between these two previously isolated (from each other by deep water and long distance) communities and can increase genetic diversity, which can be beneficial to the population both short-term and in an evolutionary perspective (Ellstrand & Rieseberg, 2016). Indeed, in these mixed residency groups there was increased courtship behavior (Hill, 2021). In a social context, the costs (aggression) and benefits (mating) of being in mixed groups are different for males vs. females. In Indo-Pacific bottlenose dolphins (*T. aduncus*), repeatable social traits that are stable across decades have been shown to constitute a social behavioral syndrome, and that structure varies by sex (Evans et al., 2021). Male and female sociality are driven by different factors (e.g., females - social and foraging behavior and males - mating strategies) (Evans et al., 2021), and this may influence the social structure and acceptance of immigrant individuals.

There is often a conflict of interest between males and females and whether they should accept or fight off new individuals, and this is widespread in polygynous mating systems (Davies, 1989). Depending on the mating strategies and social structure of the population, this may mean that female immigrants may find more resistance from residents than male immigrants (Baker & Dietz, 1996; Schaffner & French, 1997). Female immigrants may compete for physical resources and mating opportunities with males. This may negatively impact resident female fitness and reproductive success and thus female immigrants may be aggressively chased away by resident females (Baker & Dietz, 1996; Kahlenberg et al. 2008; Lin et al., 2004; Pusey et al., 2008; Schaffner & French, 1997), and in some populations by resident males as well (Baker & Dietz, 1996). Female associations may also depend on social familiarity (Möller & Harcourt 2008), meaning resident females may not form relationships with immigrant females, as seen in LBB common bottlenose dolphins following demographic upheaval after hurricanes (Elliser & Herzing, 2011). Male dolphins often have larger home ranges (e.g., Gubbins, 2002; Quintana-Rizzo & Wells, 2001; Rogers et al., 2004; Wells et al., 1987) and it may not be uncommon for males and females to interact with immigrant or visiting males, and thus immigrant males may find less resistance than females. This was also observed in LBB common bottlenose dolphins following the hurricanes (Elliser & Herzing, 2011). There is limited evidence of this also from Herzing et al. (2017) and the current study. Just after the immigration event there were three GBB residents that seemed to be creating a link between the immigrant and resident communities, two of which were male (Herzing et al., 2017). Further, in 2015–2017 there was a mixed residency alliance between those two males and a third male from LBB. Limited support also comes from the associations within the potential social clusters that showed similar association trends. For example, in the mixed clusters with mainly GBB individuals, most of the LBB individuals were males. Even if they are not true social clusters, the closer associations between those animals are still relevant and may be important in the overall community structure. Males in many dolphin populations have larger home ranges (e.g., Gubbins, 2002; Rogers et al., 2004; Wells et al., 1987), and thus make it much more common for residents to interact with various unknown males, making integration easier for males than females as suggested for common bottlenose dolphins on LBB (Elliser & Herzing, 2011). It is possible that these males played an important role in the development of connections between the residents and immigrants, similar to individuals termed “centralized brokers” in a common bottlenose dolphin population in New Zealand (Lusseau & Newman, 2004). Further research is needed to understand if males may have a stronger influence than females on the development of the integrated social structure of this new community.

Male alliance formation is an important part of the social structure of LBB dolphins. Long-term research since 1991 showed the presence of both first order (strong associations between two or three individuals) and second order alliances (strong associations between two first order alliances) (Elliser & Herzing, 2014a). In contrast, long-term work (2003–2016) on GBB dolphins showed no evidence of male alliance formation despite the fact that males had higher CoAs (including a group of five males that had the highest CoAs of the population), and higher mean network statistics for all measures calculated in the network analysis (Danaher-Garcia et al., 2020). However, it is unclear how the lack of alliances was determined as there were no details about the distribution of the CoAs, what level of CoA would be considered as alliance level, what CoAs individual males had, or how that related to the population average. It is possible they utilized a different definition for alliances, such as Harcourt and de Waal (1992) that defines a coalition or alliance as two individuals acting together in an aggressive or competitive context against a third party. If this type of interaction was not observed, then even male pairs with high CoA may not be considered an alliance. In contrast to that study, male alliances in GBB residents were observed during the initial immigration event between 2013 and 2015 (Herzing et al., 2017), and the current study based on strong CoA values. Additionally, satisfying the alternative definition, alliances have been observed in aggressive or competitive contexts with conspecifics as well as interspecies interactions with common bottlenose dolphins on GBB (D.L.H., unpublished data). Similarly, these types of interactions have also been documented on LBB (Cusick & Herzing, 2014; Volker & Herzing, 2021). Due to the lack of details on the CoA analyses for the Danaher-Garcia et al. (2020) study, it is difficult to determine why the results were so different, however, it is clear that male alliances are present in the GBB community, at least since the immigration event occurred in 2013.

First order alliances between pairs or trios, as seen in other populations (Connor et al., 1992; Elliser & Herzing, 2014a; Wells et al., 1987), were present throughout the study, with all of the 2015–2017 alliances also seen in the

2018–2020 data set, though some had changes to membership. There is also evidence for possible second order alliances in this community. There were a couple cases where strong associations linked two alliances that might indicate a second order alliance, but they did not last through both data sets, and it was not as clear cut as those seen in LBB dolphins long-term (Elliser & Herzing, 2014a). It is possible that the disturbance of the immigration event has shifted alliance formation towards primarily first order alliances, as seen on LBB after demographic upheaval (Elliser & Herzing, 2014b). In 2018–2020 there were also some alliance level associations where the structure was unclear in relation to first/second order status. The changes observed in alliance membership between data sets may be a function of the disturbance caused by the immigration event, where social relationships may still be in flux. It may take years for individuals to adapt to new conditions; for example, it took more than 5 years for “normal” aggressive behaviors to occur during interspecies encounters between spotted dolphins and common bottlenose dolphins on LBB after the demographic upheaval after the hurricanes in 2004 (Elliser & Herzing, 2016). Additionally, male alliance formation may be impacted by population density, but also by ranging patterns and the distances where individuals can detect each other (Whitehead & Connor, 2005). In Shark Bay, variation in alliance structure and behavior was observed along a spatial axis, revealing that alliance complexity has an ecological component (Connor et al., 2017). The varied ranging patterns and differential habitat use of LBB and GBB dolphins, or another unknown ecological factor, may be affecting the development and structure of male alliances on GBB. Continued monitoring of this community will shed light on the structure, stability, and longevity of the alliances seen in this study.

## 4.1 | Conclusion

This new community of residents and immigrants on GBB has shown that merging two different, stable communities is complicated, and takes time. This study was a unique opportunity to observe changes in social structure and level of integration after a large-scale immigration event in a highly social species. The results presented here emphasize how demographic processes (the turnover of individuals) change composition of a population and influence the social structure through changes in social connections (Shizuka & Johnson, 2020) and further shows that social variability is a common response to environmental variability (Karczmarski et al., 2005; Lusseau et al., 2003). Residency status, sex, and age classes influenced association patterns. It is evident that the social structure of the LBB and GBB communities prior to the immigration event influenced the resulting social structure and ability for the communities to integrate, supporting the idea that differences in social structures play an important role in the survival of the community through environmental and/or demographic changes (Elliser & Herzing, 2014b). These changes can also affect gene flow, where previous barriers (like the distance between LBB and GBB), may no longer restrict movement. These demographic, social and related genetic dynamics, are important to understand for the conservation of many species and/or populations as climate change and associated environmental disturbances begin to alter delphinid distribution, movement and residency patterns possibly causing more, large scale, permanent shifts like that seen here. These demographic changes can alter social interactions that can affect survival, reproduction, or movement (Shizuka & Johnson, 2020) and are thus vital to understand for the conservation of species in a changing environment.

### AUTHOR CONTRIBUTIONS

**Cindy R. Elliser:** Conceptualization; formal analysis; visualization; writing – original draft; writing – review and editing. **Denise L. Herzing:** Conceptualization; data curation; writing – review and editing. **Cassandra L. Volker:** Conceptualization; data curation; writing – review and editing.

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