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Genomic assessment of larval odyssey: self-recruitment and biased settlement in the Hawaiian surgeonfish *Acanthurus triostegus sandvicensis*

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Abstract

The gap between spawning and settlement location of marine fishes, where the larvae occupy an oceanic phase, is a great mystery in both natural history and conservation. Recent genomic approaches provide some resolution, especially in linking parent to offspring with assays of nucleotide polymorphisms. Here, the authors applied this method to the endemic Hawaiian convict tang (*Acanthurus triostegus sandvicensis*), a surgeonfish with a long pelagic larval stage of *c*. 54–77 days. They collected 606 adults and 607 juveniles from 23 locations around the island of O'ahu, Hawai'i. Based on 399 single nucleotide polymorphisms, the authors assigned 68 of these juveniles back to a parent (11.2% assignment rate). Each side of the island showed significant population differentiation, with higher levels in the west and north. The west and north sides of the island also had little evidence of recruitment, which may be due to westerly currents in the region or an artefact of uneven sampling. In contrast, the majority of juveniles (94%) sampled along the eastern shore originated on that side of the island, primarily within semi-enclosed Kāne'ohe Bay. Nearly half of the juveniles assigned to parents were found in the southern part of Kāne'ohe Bay, with local settlement likely facilitated by extended water residence time. Several instances of self-recruitment, when juveniles return to their natal location, were observed along the eastern and southern shores. Cumulatively, these findings indicate that most dispersal is between adjacent regions on the eastern and southern shores. Regional management efforts for *Acanthurus triostegus* and possibly other reef fishes will be effective only with collaboration among adjacent coastal communities, consistent with the traditional *moku* system of native Hawaiian resource management.

KEYWORDS
connectivity, dispersal, fisheries, marine fishes, parentage, RADseq

1 | INTRODUCTION

Long-range dispersal in reef fishes is limited to the pelagic larval stage, as most coral reef organisms maintain confined home ranges as juveniles and adults (Hellberg, 2009; Leis, 1991; Leis & McCormick, 2002). Furthermore, some species show site fidelity (Meyer *et al*., 2000), and even in highly mobile species, movement can be limited to a few kilometres as demonstrated in the bluefin trevally, *Caranx melampygus* (Holland *et al*., 1996), and coral trout, *Plectropomus leopardus* (Zeller, 1997). In contrast, the pelagic larval phase lasts from weeks to months, providing high dispersal potential and making it difficult to determine the scale of dispersal and population connectivity (Selkoe & Toonen, 2011). Understanding the extent of connectivity between sites on a local scale is essential for proper stewardship if coastal resources require management throughout their life cycles (Johnson *et al*., 2018).

Several methods can be used to identify connectivity and dispersal patterns among reef fishes (Jones, 2015). Traditional population genetic approaches are effective at characterizing connectivity across distances of hundreds and thousands of kilometres; though, they are usually ineffective when applied at smaller spatial scales, such as individual islands or archipelagos, where it is difficult to detect signals of isolation within the existing pool of genetic diversity (Saenz-Agudelo *et al*., 2009). Otolith microchemistry has successfully been applied to reef fishes, in some cases revealing self-recruitment, when juveniles return to their natal location (Patterson & Swearer, 2008; Swearer *et al*., 1999). However, the efficacy of this method is dependent on the distinctness of chemical signatures in the environment to discriminate between regions. Chemical tagging has proven to be an effective tool, but it is labour intensive, expensive, and has been successfully implemented only in demersal egg-laying species (Jones *et al*., 1999). Hydrodynamic and biophysical models have the potential to identify general patterns of larval dispersal (Jones, 2015; Kobayashi, 2006). This computational approach simulates the movement and dispersal of virtual particles and incorporates physical characteristics of the surrounding environment as well as complex biological components to make predictions of larval dispersal. Ideally these models are grounded with empirical data (Bowen, 2016; Galindo *et al*., 2010; Leray *et al*., 2010; White *et al*., 2010), particularly by matching genetic connectivity to oceanic circulation models (Counsell *et al*., 2022). Despite some success, model predictions often fail to match what is observed in nature (Selkoe *et al*., 2016), possibly due to unknown behavioural and life-history traits, along with ever-changing environmental conditions.

An alternative method to describe connectivity and dispersal patterns uses parentage analyses. Genetic parentage analysis is commonly used to inform aquaculture (Houston *et al*., 2020; Liu *et al*., 2016) but has also proven useful for identifying fine-scale connectivity (*e.g*., Abesamis *et al*., 2017; Planes *et al*., 2009; Pusack *et al*., 2014). However, these analyses are limited because they may explain less than a quarter of the variation in true connectivity within a population (Christie *et al*., 2017). Nonetheless, parentage analyses have been successfully applied to a variety of marine fishes, including butterflyfishes (Abesamis *et al*., 2017), clownfishes (Jones *et al*., 1999; Saenz-Agudelo *et al*., 2012), gobies (D'aloia *et al*., 2013), groupers (Almany *et al*., 2013; Williamson *et al*., 2016), snappers (Harrison *et al*., 2012) and surgeonfish (Christie *et al*., 2010). In the case of the yellow tang, *Zebrasoma flavescens* (Bennet 1828), Christie *et al*. (2010) provided direct evidence of connectivity within an existing network of marine-protected areas (MPAs) around Hawai'i Island. In the clownfish *Amphiprion percula* (Lacepède 1802), Planes *et al*. (2009) found high levels of local recruitment to natal reefs in Kimbe Bay, Papua New Guinea, as well as recruitment to adjacent locations within a network of MPAs. These studies show the efficacy of parentage analyses as a tool for characterizing dispersal patterns across small spatial scales pertinent to conservation.

With advances in genomic technology, single nucleotide polymorphisms (SNPs) are becoming increasingly popular for parentage analyses (Andrews *et al*., 2018; Flanagan & Jones, 2018; Hauser *et al*., 2011; Thrasher *et al*., 2018), with as little as 100 SNPs being sufficient to resolve parentage (Flanagan & Jones, 2018; Zhao *et al*., 2018). Here, the authors use a SNP-based parentage analysis to describe dispersal and connectivity patterns of the convict surgeonfish, *Acanthurus triostegus sandvicensis*, known locally in Hawai'i as manini (Randall, 2010). *Acanthurus triostegus* is heavily targeted by sport, leisure, and subsistence fisheries and is described as an exploited species by Hawai'i's Division of Aquatic Resources (Longenecker *et al*., 2008). At the outset of this project, *A. triostegus* was identified by Native Hawaiian community leaders as a species of concern, making it an ideal candidate to understand connectivity patterns around O'ahu, with a focus on Kāne'ohe Bay on the eastern side of the island. This is the largest semi-enclosed bay in the main Hawaiian Islands with an area of 45 km^2 and a popular fishing spot with well-described oceanographic properties and biotic communities (Bahr *et al*., 2015). Authors' results are intended to inform community-based management efforts by identifying propagule sources and sinks for *A. triostegus*, so that resource managers can identify areas that are particularly vulnerable to excessive fishing pressure.

2 | MATERIALS AND METHODS

2.1 | Study species

A. triostegus is a herbivorous surgeonfish found throughout the Indo-Pacific that specializes on benthic algae. In Hawai'i and adjacent Johnston Atoll, *A. triostegus* is recognized as an endemic sub-species (*A. triostegus sandvicensis*), due to morphological and genetic differences when compared to the rest of the range (Otwoma *et al*., 2018; Randall, 1956). This species often occurs in large schools along reef flats and the outer reef of lagoon habitats. Schemmel and Friedlander (2017) recently described aspects of the reproductive biology of *A. triostegus* across the Hawaiian Islands: on O'ahu, group spawning occurs before dusk where aggregations of 25–800 individuals form a few days before the new and full moon. Spawning takes place at

TABLE 1 Locations where *Acanthurus triostegus* was collected around O'ahu, Hawai'i

Sampling location	Site code	Number of adults	Number of juveniles	Number assigned to location	Number self-recruiting
North					
Mokulē'ia	MOK	3	9		
Hale'iwa	HAL	38	16		
Chuns	CHUN	36	16		
East					
Lā'ie	LAIE	30	17	2	
Hau'ula	HAU	10	44	5	
Ka'a'awa	KAA	50	50	7	
Mouth of Kāne'ohe Bay	KBM	15	0		
Kāne'ohe Bay, North	KBN	24	95	1	1
Kāne'ohe Bay, South	KBS	22	130	35	2
Kailua	KAI	88	20	6	1
Waimānalo	WAI	37	80	2	
Rabbit Island	RAB	34	0		
South					
China Walls	CW	34	1		1
Maunalua Bay	MB	45	10		
Shangri La	SL	15	21		
Ala Moana	AM	5	23		
Kewalo	KEW	11	14		
Sand Island	SAN	14	19		
Ewa	EWA	10	8		
West					
Kahe	KAH	32	5	3	
Kalanianaole	KAL	13	7		
Mākaha	MAK	22	10		
Yokohama Bay	YB	18	12		
Total		606	607	61	5

Note: Collection numbers are separated by adults and juveniles. The locations and number of assigned juveniles that were collected at each location, as well as the number of self-recruiting events, are noted.

depths from 7 to 30 m and peaks during February–June. Nonetheless, spawning occurs throughout the year and is likely to be highly variable across the Hawaiian Islands. The pelagic larval duration (PLD) is estimated to range from 54 days (Longenecker *et al*., 2008) to *c*. 77 days (Randall, 2005), a longer interval than most surgeonfishes (Eble *et al*., 2009; Leis & McCormick, 2002).

2.2 | Sampling and DNA extraction

Between May 2015 and July 2017, 1213 fin clips (606 adults and 607 juveniles) were collected from 23 locations around the island of O'ahu, Hawai'i, using pole spears with scuba or snorkelling (Table 1; Figure 1). Individuals <121 mm, aged *c*. 6 months, were classified as juveniles (*i.e*., reproductively immature) based on the average size at maturity for males and females (Longenecker *et al*., 2008; Randall, 1961; Schemmel & Friedlander, 2017). Tissues were transferred to 95% ethanol and stored at room temperature. Genomic DNA was extracted using the E-Z 96 Tissue DNA Kit (Omega Bio-Tek, Norcross, GA, USA) and following the manufacturer's protocol. Genomic DNA was resuspended in nanopure water. High-molecular-weight DNA was confirmed by visualizing on a 1.5% agarose gel stained with GelRed (Biotium, Inc., Fremont, CA, USA).

2.3 | Library preparation and sequencing

Restriction-site associated DNA (RAD) library preparation and sequencing was conducted by the Texas A&M core lab, starting with 150 ng of high-molecular-weight genomic DNA per sample and following the double-digest RAD (ddRAD) protocol (Peterson *et al*., 2012). Briefly, this process included digesting each sample with *Msp*I and *Eco*RI (New England Biolabs, Ipswich, MA, USA) followed by cleaning each sample with polyethylene glycol solution using retained beads. The samples were then normalized to equimolar concentration

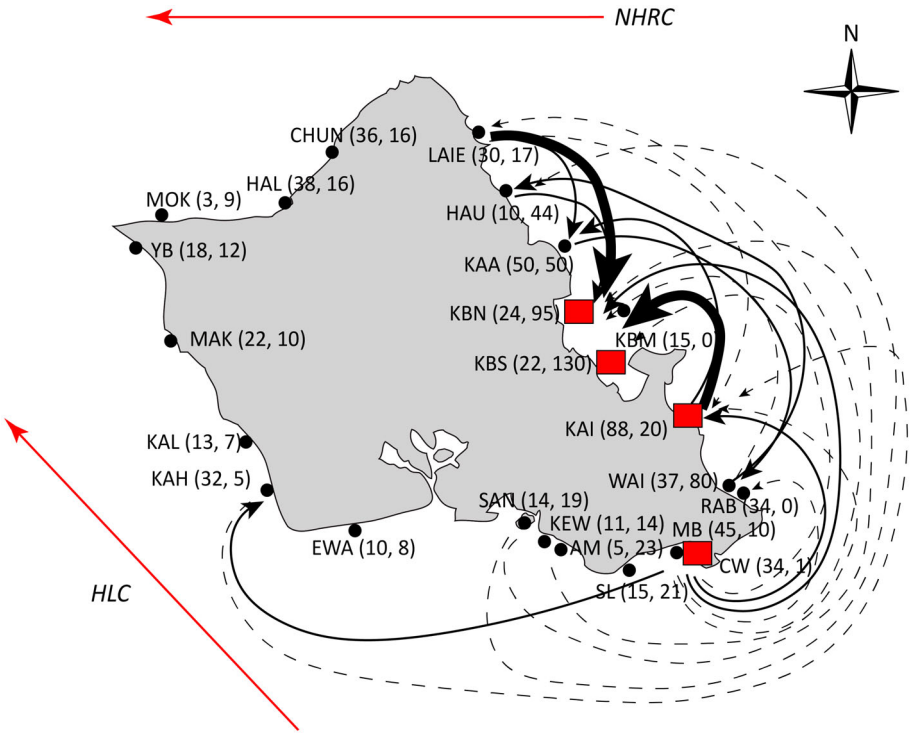

FIGURE 1 Map of O'ahu collection sites and dispersal pathways for O'ahu samples of the Hawaiian surgeonfish *Acanthurus triostegus sandvicensis*. Numbers in brackets indicate the sample size of adults and juveniles, respectively. Lines and arrows indicate the pathway of dispersal from parent to offspring. Dashed lines are a single dispersal event. Thin solid lines indicate dispersal paths shared by two or three larvae, and thick solid lines are >14 dispersal events from a given area. Black dots indicate collection locations. Red squares indicate collection locations where self-recruitment events were observed. Red line denotes the direction of the major currents. Abbreviations: NHRC, North Hawaiian Ridge Current; HLC, Hawaii Lee Current; collection site codes are provided in Table 1

followed by ligation of sequencing adapters. After digestion and ligation, a PCR was performed using dual-indexed primers. Fragments between 325 and 400 bp were selected using BluePippin (Sage Science, Beverley, MA, USA), and Fragment Analyzer was run to visualize library size range followed by quantitative PCR to determine library concentration. The resulting 24 libraries were sequenced on an Illumina HiSeq 4000 (150 bp paired-end reads, performed by NYU Langone Health Genome Technology Center). Sequence data were demultiplexed based on barcodes using *process_radtags* in STACKS 2.41 (Catchen *et al*., 2011, 2013). Each library was randomly sequenced across two or three independent runs to increase coverage per sample and to mitigate potential sequence bias (Ross *et al*., 2013). After sequencing, the authors organized reads into two data sets: a concatenated data set containing all the reads for each individual, allowing for increased coverage, and a second data set where sequences originating from independent runs for each individual were treated separately. That is, each individual had two or three replicates, depending on the number of individual runs that were conducted. Having multiple representation for each individual allowed for two or three opportunities for confirmation of downstream analysis, in particular the genetic parentage analysis.

2.4 | Genotyping and *de novo* assembly of RADseq libraries

Raw reads obtained from Illumina runs were assessed for sequence quality using FastQC 0.10.1 (Andrews, 2010) to remove low-quality bases (Phred quality score threshold of 30). As a reference genome is not available for *A. triostegus*, a *de novo* pseudo-reference catalogue was assembled using Rainbow 2.0.4 (Chong *et al*., 2012) as performed in the dDocent pipeline (Puritz, Hollenbeck, & Gold, 2014; Puritz, Matz, *et al*., 2014) using a minimum depth of 15 and a maximum of 8 mismatches to form reference contigs. The reference contigs were clustered based on a 75% similarity threshold. After generating the reference catalogue, reads were mapped using bwa 0.7.17 (Li & Durbin, 2009), and SNP detection was performed using FreeBayes 1.10.54 (Garrison & Marth, 2012). Variant calls were subjected to several filtering steps to reduce false positives. The data set was filtered to remove all genotypes with fewer than five reads per individual. SNPs were retained if they were genotyped in 95% of individuals and had a minor allele count of 3 or higher, an average depth of greater than 20 and a minor allele frequency greater than 0.05. Using vcftools 0.1.12a (Danecek *et al*., 2011) the authors removed SNPs that were not in Hardy–Weinberg equilibrium. SNPs below the threshold value ($P = 0.01$) were excluded from the data set.

2.5 | Population structure analysis

GenoDive 3.04 was used to generate genetic diversity indices for all coastlines and Kāne'ohe Bay, as well as to test for population structure (populations include adults and juveniles). Pair-wise F_{ST} statistics were generated to assess genetic structure between locations. Deviations from null distributions were tested using non-parametric permutation procedures ($N = 9999$). False discovery rates were controlled for and maintained at $\alpha = 0.05$ among all pair-wise tests (Benjamini & Yekutieli, 2001; Narum, 2006). The authors used STRUCTURE 2.3.2 (Pritchard *et al*., 2000), a Bayesian method that estimates ancestry and categorizes individuals into discrete populations, to determine if

discrete genetic partitions existed. The simulation was run for 1 million generations, with the first 100,000 discarded as burn-in. Five replicates of each simulation from $K = 1$–5 genetic clusters were run. They determined the most likely number of genetic clusters (K) using the Evanno method (Evanno *et al*., 2005) which calculates the probability of the data [LnP(D); Pritchard *et al*., 2000], the corresponding S.D. and selecting the clusters inferred from Evanno's delta K *vs.* K (Evanno *et al*., 2005) in STRUCTURE HARVESTER 0.6.93 (Earl & VonHoldt, 2012). STRUCTURE results were analysed and visualized using the online tool Clumpak (http://clumpak.tau.ac.il/index.html) (Kopelman *et al*., 2015), which integrates the programme CLUMPP 1.1.2 (Jakobsson & Rosenberg, 2007) and minimizes the variance across all iterations.

2.6 | Genetic parentage analysis

The authors conducted a parentage analysis using Cervus 3.0.7 (Kalinowski *et al*., 2007; Marshall *et al*., 1998). This programme calculates the likelihood that each candidate is the parent, considering population allele frequencies and genotype errors. An allele frequency analysis was conducted to determine the suitability of loci for downstream assessment. Cervus requires a parentage analysis simulation to determine the feasibility of the analysis given the set of loci and to calculate the critical likelihood ratios [LOD (limit of detection)] to provide confidence in parent–offspring assignments. For the simulation to determine the critical LOD scores, the authors used 100,000 offspring (as recommended by the authors of Cervus), an estimated genotyping error rate of 0.01 and a proportion of loci typed across all individuals of 0.6868, and a conservative estimate of 0.01 was used for the proportion of candidate parents sampled. The number of typed loci was 200, which was determined after the final number of SNPs was resolved. The genotype of each offspring was then compared to each candidate parent and a random individual in the population to calculate a likelihood ratio. This ratio is presented as an LOD score, the natural logarithm of calculated likelihood ratio. A positive LOD score indicates that a candidate parent is more likely to be the true parent, whereas a negative LOD score indicates the candidate parent is unlikely to be the true parent. Parent–offspring assignments were accepted at a 95% confidence level. The final output presents two candidate parents with an LOD score and a confidence score, which identifies both parents if they happen to be included in the parent candidate pool. Three replicate parentage analyses were conducted after which parent–offspring assignments were congruent across all three replicates indicating the robustness of assignments. Dispersal distances were estimated using the distance calculator tool from sea-seek.com (https://www.sea-seek.com/tools/tools.php).

3 | RESULTS

3.1 | Genotyping/filtering

For the individual data set, after initial trimming, filtering and demultiplexing, the authors retained 80,955 loci. After additional filtering which accounted for coverage, minimum allele frequency and presence among the individuals included in the data set, they identified 399 loci for 2198 individuals (recall that there are multiple sequencing replicates per individual) that met all the criteria for downstream analyses. The step that was mostly responsible for the reduced data set was filtering for mean average depth, which reduced the number of loci to 413. Although this filtering step greatly reduced the number of loci, the authors opted to proceed with the reduced data set for the analysis because previous studies have shown that 100 loci are sufficient to resolve parentage in most cases (Flanagan & Jones, 2018; Zhao *et al*., 2018). When individual libraries were analysed, they showed patterns consistent with the analyses of the concatenated data set. That is, parent–offspring assignments were the same when analysed as individual libraries and when using the concatenated data set. Nonetheless, due to a combination of QC filtering, missing data and low depth coverage among concatenated individuals, the concatenated data set included fewer individuals after filtering ($N = 1127$: 591 adults and 536 juveniles); therefore, the results presented here are only for the individual library analyses ($N = 1213$: 606 adults and 607 juveniles).

3.2 | Population structuring analysis

Molecular diversity indices are summarized in Table 2. The average number of alleles was 2.007. The effective number of alleles was highest in the southern population ($N_{eff} = 1.385$) and lowest in Kāneʻohe Bay ($N_{eff} = 1.374$). Inbreeding coefficients revealed that the influence of inbreeding is negligible across all populations.

Population structure was observed among all coastal and Kāneʻohe Bay populations (Table 3). Genetic differentiation was highest between the western coast of Oʻahu and all other populations ($F_{ST} = 0.0009$–0.013, $P = <0.001$) and was weaker, though still significant, among all other populations ($F_{ST} = 0.002$–0.006, $P = <0.001$). The STRUCTURE HARVESTER analysis resolved two clusters ($K = 2$) (delta $K = 2$, 76.37; Table S1; Figure S1); nonetheless, Evanno is not informative if $K = 1$, and further assessment of the STRUCTURE plot revealed no discernible genetic partitioning across the island of Oʻahu at $K = 2$ (Figure S2). Based on the STRUCTURE plot, there is some indication of genetic partitioning for the northern and western populations, though this is not supported by the Evanno analysis (delta $K = 3$, 30.46; Table S1; Figure S1).

3.3 | Parent–offspring assignment

Overall sampling was biased towards the southern and eastern coasts of Oʻahu, particularly within Kāneʻohe Bay, which was also biased towards juveniles based on the availability of specimens (Figure 1). Of the 607 juveniles screened for DNA parentage analysis, the authors assigned 68 juveniles back to a parent (Table 4; Figure 1), and the geographic distribution of assignments was highly uneven. No assignments were detected on the north shore of Oʻahu. Along the western

TABLE 2 Molecular diversity indices for O'ahu populations of *Acanthurus triostegus sandvicensis* based on 399 SNPs

	n	N_a	N_{eff}	H_O	H_S	H_T	G_{IS}
East	460	2.007	1.375	0.272	0.248	–	−0.098
Kāneohe	286	2.007	1.374	0.270	0.246	–	−0.094
North	118	2.007	1.378	0.269	0.248	–	−0.088
West	119	2.007	1.379	0.285	0.248	–	−0.146
South	230	2.007	1.385	0.285	0.253	–	−0.125
Total	1213	2.007	1.375	0.276	0.249	0.250	−0.110

Note: Number of individuals sequenced (*n*), average number of alleles per locus (N_a), effective number of alleles (N_{eff}), observed heterozygosity (H_O), heterozygosity between populations (H_S), total heterozygosity (H_T) and inbreeding coefficient (G_{IS}) are presented. SNP, single nucleotide polymorphism.

TABLE 3 Matrix of pair-wise F_{ST} statistics for coastal O'ahu and Kāne'ohe Bay populations of *Acanthurus triostegus* based on 399 SNPs

	East	East-Kāne'ohe	North	West	South
East	–				
East – Kāne'ohe	0.002	–			
North	0.006	0.005	–		
West	0.013	0.013	0.012	–	
South	0.002	0.002	0.004	0.009	–

Note: All pair-wise comparisons are significant at $P < 0.001$. SNP, single nucleotide polymorphism.

side only one location, Kahe, had parent–offspring assignments (KAH in Figure 1). Here, the offspring was assigned to an adult in Maunalua Bay (MB in Figure 1). Along the south shore, the only assigned juvenile was a case of self-recruitment at China Walls (CW in Figure 1). The largest concentration of assigned individuals was found along the eastern side, particularly within Kāne'ohe Bay, accounting for 94% of the assignments in this study (Figure 2). The juveniles recovered along the eastern shore mostly originated from locations on the east side of the island, with a few individuals originating from the south shore and one instance of dispersal from Kahe on the west side. There were several instances of self-recruitment in addition to the one at China Walls, one at Kailua (KAI in Figure 1) and three within Kāne'ohe Bay (Table 1; Figure 1).

Distance between parent and detected offspring averaged 27.3 ± 18.4 km and ranged from 0.25 km between Reef 14 and 16 in South Kāne'ohe Bay to 78 km between Kahe and Kailua (Figure 3). The highest proportions of juveniles were found to have dispersed 10–15 km (27%) and between 25 and 30 km (23%). These trends can be attributed to the exportation of juveniles from Lā'ie and Kailua into Kāne'ohe Bay.

4 | DISCUSSION

This study assigned 68 (11.2%) juveniles back to a parent. This is a remarkably high recovery rate considering this species has the potential to remain in the planktonic phase for nearly 2 months. Many factors need to be considered regarding the potential success in assigning juveniles to parents, including the size of the population being sampled, the dispersal potential of the species and the geographic scale of sampling. A study of the yellow tang (*Z. flavescens*) along the western coast of Hawai'i Island recovered four parent–offspring pairs out of 1100 sampled adults and juveniles. Despite *Z. flavescens* having a similar PLD to *A. triostegus* (Claisse *et al*., 2009), the low assignment in that study may be attributed to sampling a small proportion of the adult population. The population of *Z. flavescens* around Hawai'i Island is also estimated to be 4.2 million individuals, four times the estimated population size of *A. triostegus* around O'ahu (Ivor Williams, NOAA, pers. comm.). In studies where the population sizes are much lower, a higher assignment rate is expected (Christie *et al*., 2017). For example, parentage analyses conducted on clownfishes (*Amphiprion polymnus*, *A. percula*) in Papua New Guinea assigned *c*. 20% and 64% of sampled juveniles back to their parents (Berumen *et al*., 2012; Saenz-Agudelo *et al*., 2009). Clownfish are low dispersers with a relatively short planktonic larval phase of *c*. 11 days in addition to having specialized habitat in which collection efforts can be more focused, factors that would favour a high assignment rate (Almany *et al*., 2007). Species in the same region of Papua New Guinea with wider home ranges, a longer planktonic larval phase, and less specialized habitat, such as butterflyfish (*Chaetodon vagabundus*) and groupers (*Plectropomus areolatus*), had a much lower recovery rate of 8% and 10%, respectively (Almany *et al*., 2013; Berumen *et al*., 2012). Notably, when comparing authors' results to studies of similar geographic scale, they find that they share similar and even higher assignment rates. Along 1000 km^2 of the Great Barrier Reef of Australia, Harrison *et al*. (2012) had an assignment rate of 12% for a grouper (*Plectropomus maculatus*) and 16% for a snapper (*Lutjanus carponotatus*). Although the assignment rate of authors' study is on par with previous studies, they caution that a complex interplay of population size, dispersal

TABLE 4 Pathways and distances of dispersal between collection sites.

Location of parent–offspring pairs			
Parent	**Offspring**	**Number of occurrences**	**Dispersal distance (km)**
Lā'ie	Ka'a'awa	3	12.5
Lā'ie	KBN, Reef 42	1	23.0
Lā'ie	KBS Reef S2	1	30.0
Lā'ie	KBS, Reef B25	6	26.7
Lā'ie	KBS, Reef 11	2	25.6
Lā'ie	KBS, Reef 14	3	25.9
Lā'ie	KBS, Reef 15	1	25.9
Lā'ie	Kailua	1	35.2
Ka'a'awa	KBS, Reef 14	1	14.2
Ka'a'awa	Waimānalo	2	30.6
KBN, Reef D1	KBS Reef S2	1	10.2
KBN, Reef D1	KBS, Reef 5	1	6.8
KBN, Reef D1	Hau'ula	2	13.4
KBN, Reef 42	KBS, Reef S3	1	6.1
KBN, Reef 51	KBN, Reef 42	1	1.9*
KBN, Reef 51	Lā'ie	1	23.0
KBS, Reef 14	KBS, Reef 5	1	1.4*
KBS, Reef 14	KBS, Reef 16	1	0.2*
Kailua	Kailua	1	*
Kailua	Ka'a'awa	3	23.2
Kailua	KBS	1	16.8
Kailua	KBS, Reef S3	1	17.9
Kailua	KBS, Reef 10	1	15.0
Kailua	KBS, Reef 14	4	14.0
Kailua	KBS, Reef 15	8	14.3
Waimānalo	KBS, Reef 15	1	23.0
Waimānalo	Hau'ula	2	35.6
Rabbit Island	Ka'a'awa	1	33.2
China Walls	Lā'ie	1	58.3
China Walls	KBS Reef 2	1	40.4
China Walls	KBS, Reef 5	1	38.9
China Walls	Kailua	2	25.6
China Walls	China Walls	1	*
Maunalua Bay	KBS, Reef 10	1	38.7
Maunalua Bay	Kailua	1	26.5
Maunalua Bay	Kahe	3	51.9
Ala Moana	Kailua	1	42.8
Sand Island	Hau'ula	1	70.9
Sand Island	KBS Reef 2	1	59.6
Kahe	Kailua	1	78.0

Note: KBS, Kāne'ohe Bay, South; KBN, Kāne'ohe Bay, North; *, denotes self-recruitment.

potential, geographic sampling and oceanographic patterns likely influence the ability to recover parent–offspring pairs.

The distance between spawning and settlement of juvenile *A. triostegus*, as estimated by assigning juveniles back to their parent, was highly variable. On Hawai'i Island, Christie *et al.* (2010) detected dispersal distances of *Z. flavescens* as high as 184 km, which was attributed to a combination of passive transport and active behavioural mechanisms. No evidence of self-recruitment was observed in

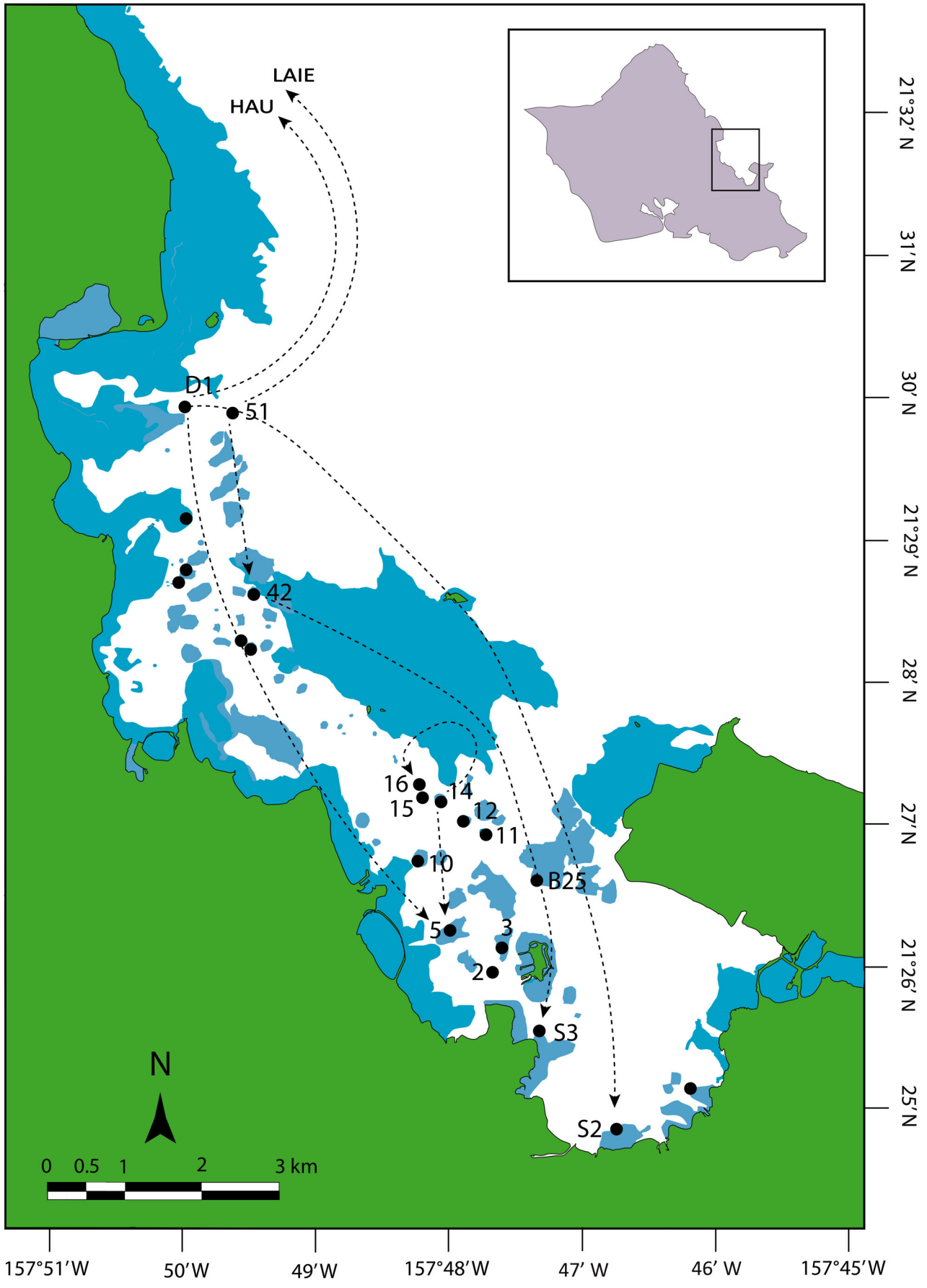

FIGURE 2 Legend on next page.

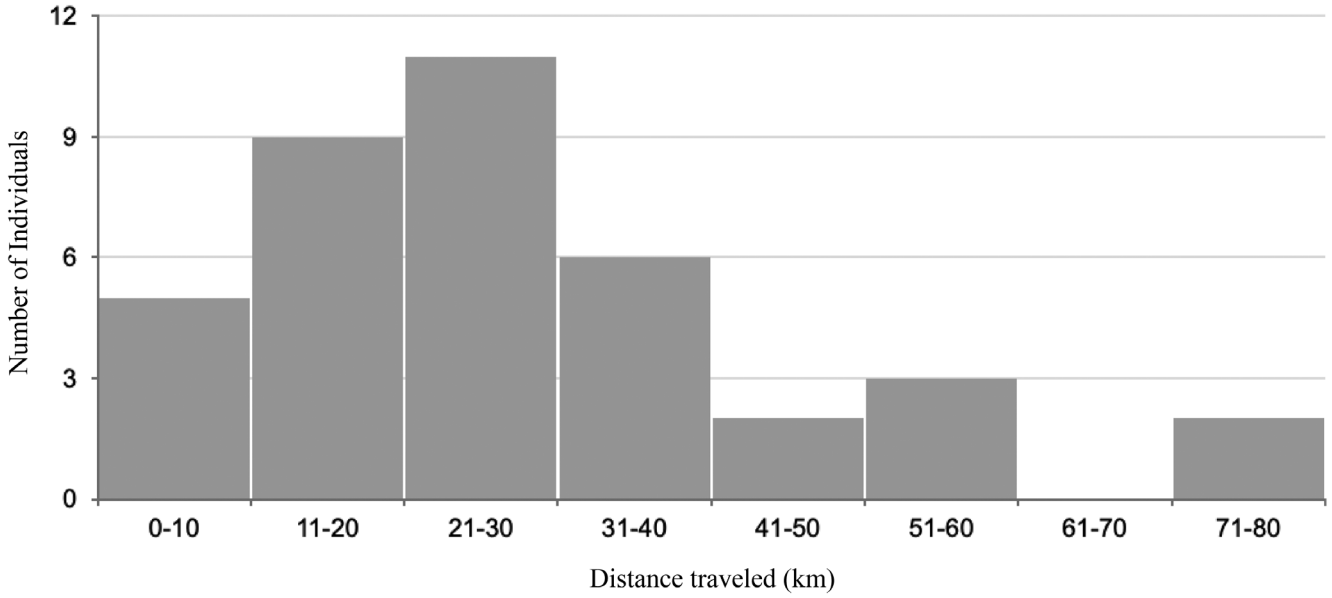

FIGURE 3 Histogram showing the distance between the collections of parent–offspring pairs for O'ahu samples of the Hawaiian surgeonfish *Acanthurus triostegus sandvicensis*

that study. In contrast, clownfish exhibit high levels of self-recruitment as well as shorter maximum dispersal (35 km; Planes *et al*., 2009). In the current study, the authors detected dispersal distances based on parent–offspring assignments that varied from as little as *c*. 0.25 km to as far as 78 km (Kahe to Kailua; Table 4). However, the majority of offspring were recovered within 30 km of their spawning location. The general patterns of limited dispersal observed in *A. triostegus* are similar to many dispersal kernels obtained for marine fishes, which show a high proportion of recruitment close to the spawning site that tapers down as distance increases (Jones, 2015). In one of the most thorough dispersal kernel studies, D'Aloia *et al*. (2015) detected a mean dispersal of only 1.7 km in Belizean linesnout gobies (*Elacatinus lori*), with no dispersal event detected >16.4 km.

Bernardi *et al*. (2012) demonstrated that planktonic larval fish from a single spawning event may remain in close proximity, perhaps using shared sensory and behavioural mechanisms (Dixson *et al*., 2008). Estimating the date of spawning by backcalculating the size of the specimen with the rate of growth (Longenecker *et al*., 2008), the authors found that the three juveniles from Kahe assigned to parents from Kailua appear to have been born about the same time, suggesting they may have originated from the same spawning event and providing tentative evidence of *A. triostegus* cohorts travelling together during the planktonic phase. Despite the potential for these behaviours, authors' initial screen revealed that no two individuals shared the same parent, providing no evidence of siblings at any of their 23 sample sites. The inability to recover individuals who share a parent may simply be due to the low sample size relative to the population of *A. triostegus*.

The dispersal patterns of *A. triostegus* around O'ahu are quite complex and cannot be explained by any single factor. This fish is known to spawn in pairs as well as large groups (Robertson, 1983). Subtidal habitat and marine physical processes vary around the island, both of which may influence dispersal patterns. In addition, larval behaviour will influence settlement, and larval *A. triostegus* can delay metamorphosis as needed to recruit to appropriate habitat (Randall, 1961; McCormick, 1999).

Four caveats are pertinent to these results. First, the simulation analysis in Cervus, which allows the confidence of real parentage assignments to be assessed, is not a formal power analysis and is dependent upon assumptions about the fraction of sampled parents, which, here, is an estimation suggested by NOAAs Coral Reef Ecosystem Program (Ivor Williams, NOAA, pers. comm.). Second, the dispersal patterns the authors described may be influenced by sampling effort biased towards the regions of O'ahu where conditions allowed collections to be conducted year-round and where *A. triostegus* populations were more abundant in areas that were accessible to collectors. The biased sampling happened to also coincide with regions

FIGURE 2 Map of Kāne'ohe Bay collection sites for the Hawaiian surgeonfish *Acanthurus triostegus sandvicensis*. Black dots indicate sampled reefs. Numbers represent the established ID numbers for each patch reef based on nomenclature of Roy (1970). Blue colour represents shallow reef. Only reefs where parents or offspring were recovered are listed; nonetheless, dots denote the location where collections occurred. Lines and arrows indicate the pathway of dispersal from parent to offspring. Lines with no connections heading north (*i.e*., Reef D1, Reef 51) represent dispersal outside of Kāne'ohe Bay. 28° N delineates between reefs that are found in Kāne'ohe Bay, North (KBN), and Kāne'ohe Bay, South (KBS)

where physical oceanographic processes would promote dispersal and settlement, which are discussed in detail. Third, the presence of the sub-population structure around O'ahu will bias assignments, and therefore dispersal patterns, against regions that are genetically differentiated. The presence of the genetic structure is indicative of mechanisms limiting dispersal between regions and can lead to lower assignments between populations that are not genetically differentiated, which is supported by the signal observed in the northern and western sides of the island where less assignments are observed and is also where the highest population differentiation is observed among all regions. Finally, there was sampling bias towards juveniles along the eastern coast and within Kāne'ohe Bay, where local conditions promote larval retention. Considering this, the authors discuss the general patterns of dispersal along each coast of O'ahu and the potential mechanisms that may influence them.

4.1 | North, west and south O'ahu

The assignment of parent–offspring pairs on the north and western sides of O'ahu is strikingly low when compared to other areas of the island. There is only one instance of dispersal from Kahe, located on the south-western side of O'ahu, to Kailua, and another instance from Maunalua Bay to Kahe. No additional parent–offspring assignments were detected along the entire western and northern coasts. There are several possible reasons for this trend. First, although significant genetic differentiation was observed between all populations, it was highest between the western and northern coast populations and all other populations (Table 2; F_{ST} = 0.009–0.013, $P < 0.001$). The STRUCTURE results reveal some indication of genetic partitioning for the western and northern populations, which coupled with the genetic differentiation results indicate that larval input from other areas of the island is restricted. Note, however, that the authors do observe dispersal events between the western and the southern sides as well as the western and eastern sides of the island, which indicates that the mechanisms that reduce larval exchange are weak or not static between these regions.

Second, the low detection within this region may be an artefact of lower sampling effort along the western and northern sides of the island compared to other regions (Table 1). Collection efforts along the northern coast were constrained by higher wave energy, with winter swells often exceeding 7 m in height (Fletcher *et al*., 2008), making many sites inaccessible. When collecting was possible, few juveniles were located. The number of juveniles collected from both western and northern coasts accounts for only 12% of the total juvenile collection. As an effort was made to collect both adults and juveniles at each collection location, the ratio of adults to juveniles may reflect the biological reality of the abundance of each size class. However, to confirm this, a more systematic survey of *A. triostegus* adults and juveniles would be required.

Finally, the low recovery on the northern and western sides may also be attributed to the currents surrounding O'ahu that drive dispersal in a westerly direction. The North Hawaiian Ridge Current flows in a west-northwesterly direction adjacent to the northern coast of O'ahu (Firing, 1996). On the southern coast of O'ahu, the Hawaii Lee Current (HLC) flows north-west following the Hawaiian Ridge from Maui to Kaua'i (Lumpkin, 1998). Therefore, *A. triostegus* propagules originating on the west or north coast may be carried west towards the island of Kaua'i. Notably, planktonic species that are typically found within 1 km of the shore on the eastern side of O'ahu are more common offshore along the western coast of O'ahu (Hassett & Boehlert, 1999). If that pattern holds for *A. triostegus*, larvae may be more common along the western coast of O'ahu. If offshore propagules do in fact make it to Kaua'i, that would greatly increase the dispersal capabilities of *A. triostegus* larvae beyond the distances observed on the scale of O'ahu. However, a recent study assessing connectivity of *A. triostegus* across the Hawaiian Archipelago challenges the ability of propagules to successfully disperse between O'ahu and the neighbouring islands. Coleman and Bowen (2022) found a population structure between O'ahu and the neighbouring islands of Maui (F_{ST} = 0.043) and Kaua'i (F_{ST} = 0.051), indicating that dispersal between islands is limited.

The dispersal observed from Maunalua Bay to Kahe is consistent with the flow of the HLC. However, the dispersal from Kahe, and all locations along the south shore, to the eastern side of O'ahu is against the HLC. The maximum flow of the HLC reaches 20 cm s^{-1}, although there is some interannual fluctuation in the strength of the current (Lumpkin, 1998). Nonetheless, the authors would predict the HLC to be a major barrier to dispersal to an easterly direction, which would suggest that other unknown physical or biological mechanisms are facilitating dispersal towards the eastern side of O'ahu.

4.2 | East O'ahu and Kāne'ohe Bay

On the eastern side of O'ahu, the tide floods to the south-east and ebbs to the north-west. Smaller-scale circulation features are also established by headlands. Therefore, some of the fine-scale coastal processes support the dispersal of juveniles in both a northerly and southerly direction and may facilitate importation of larva into Kāne'ohe Bay. The parent–offspring pairs in this study are overwhelmingly concentrated on the eastern side of O'ahu, primarily into Kāne'ohe Bay, accounting for 94% of successful assignments. Although significant, genetic differentiation was lowest between the eastern, Kāne'ohe Bay, and southern populations (Table 3; F_{ST} = 0.002, $P < 0.001$).

Kāne'ohe Bay, located on the north-east coast of O'ahu, is a semi-enclosed estuarine system characterized by shallow patch reefs and an average depth of 10 m (Jokiel, 1991). It is bounded by a barrier reef on the seaward (north-eastern) side, with two major channels out to the ocean. The bay has an extensive history of anthropogenic modifications, including dredging, sewage outflow and increased sedimentation from runoff, all which have severely altered the natural configuration, bathymetry and even the currents in the bay (Bahr *et al*., 2015).

In a partner study, Counsell *et al*. (2022) modelled *A. triostegus* larval settlement along the eastern coast and within Kāne'ohe Bay. The

overall patterns of simulated connectivity were dominated by settlement and retention within Kāneʻohe Bay. Propagules that originated within the bay or entered the bay had a high chance of being retained. This pattern is consistent with the highest assignment of juveniles occurring within Kāneʻohe Bay. Counsell *et al.* (2022) concluded that the overall pattern of retention and settlement was influenced mostly by oceanography and less by life-history traits. A more comprehensive study that includes the entire island would indicate whether this pattern holds in regions that are more influenced by oceanic conditions.

The circulation patterns are highly variable between the northern and southern reaches of Kāneʻohe Bay (Bathen, 1968; Lowe *et al.*, 2009), with water residence times ranging from <1 day on the outer reef to >1 month at the semi-enclosed southern part of the bay (Bathen, 1968; Lowe *et al.*, 2009; Ostrander *et al.*, 2008). The northern half of the bay has a much more active circulation pattern, with high levels of exchange between the bay and offshore waters. The southern part of the bay is characterized by reduced circulation due to flow restrictions which are absent in the northern part of the bay. Therefore, Kāneʻohe Bay, South, has been previously identified as a potential hotspot for retention and self-recruitment due to the high-water residence time (Lowe *et al.*, 2009). Indeed, Kāneʻohe Bay, South, had the highest rates of parental assignments, accounting for more than 50% of all the recovered offspring matches found in this study. In addition, the highest rates of self-recruitment were found in Kāneʻohe Bay, South. These patterns are consistent with the model predictions of Counsell *et al.* (2022).

There are two instances of dispersal from inside to outside of the bay, both of which followed a northern trajectory towards Hauʻula and Lāʻie (HAU and LAIE in Figure 1). These individuals originated at the northernmost collection site within Kāneʻohe Bay, which is subjected to more oceanic conditions and where water residence time can be <1 day (Lowe *et al.*, 2009). Unlike the southern part of the bay, physical processes in this northernmost part of the bay appear to reduce larval retention, a finding which is also consistent with Counsell *et al.* (2022).

4.3 | Patterns observed elsewhere for *A. triostegus*

Acanthurus triostegus are a ubiquitous feature of reefs from the East Pacific to the Western Indian Ocean, and several previous studies have provided genetic assessments of dispersal. Lessios and Robertson (2006) reported very limited genetic connectivity on the scale of eastern versus central Pacific (mtDNA $\Phi_{ST} = 0.355$). Planes *et al.* (1996) reported a pattern of isolation by distance between proximal islands in French Polynesia. These authors concluded that most dispersal is between adjacent regions and that long-distance dispersal is rare or sporadic. More directly pertinent to this study is the allozyme analysis of *A. triostegus* within the lagoon at New Caledonia, which revealed significant population structure ($F_{ST} = 0.049$) on a scale of a few hundred kilometres, unusual for a reef fish (Planes, Parroni, & Chauvet, 1998). Planes, Romans, and Lecomte-Finiger (1998) reached a similar finding in Taiaro Lagoon in French Polynesia ($F_{ST} = 0.055$ between lagoon and ocean), concluding that *A. triostegus* could close their life cycle within the lagoon, an area of 6 km^2 with no regular connection to the ocean. These results agree with authors' finding of limited larval dispersal on the scale of eastern and southern Oʻahu. Collectively, these studies reinforce the conclusion that a long PLD does not invariably translate into extensive dispersal (Selkoe & Toonen, 2011; Weersing & Toonen, 2009).

4.4 | Conclusions

One of the motivations for this study is to inform management efforts at the community level and to ensure that subsistence fisheries for *A. triostegus* persist sustainably into the future. The Western Pacific Regional Fishery Management Council currently assesses the vulnerability of *A. triostegus* as low based on commercial fishery data (WPFMC, 2016). However, the dominant fisheries in Hawaii are non-commercial (*e.g.*, subsistence, leisure, sport) with an estimated 84% of the total catch of all nearshore coral reef-associated species, five times the catch of commercial fisheries (McCoy *et al.*, 2018). Although the fishing effort specific for *A. triostegus* for non-commercial fisheries has not been assessed, it is the third-highest commercial catch among all acanthurids (WPRFMC, 2021), indicating a heavy fishing pressure and a pre-emptive need to ensure long-term sustainability of these coastal resources. Inherent in this motivation is knowing which areas are connected by larvae (Counsell *et al.*, 2022). Understanding the early life history, ecology and dynamics of *A. triostegus* is critical to projecting the success of adult populations and thus strategizing a method to ensure their sustainability in an integrated fishery management framework (*e.g.*, Hixon *et al.*, 2022). In addition, it would be valuable to reassess the patterns observed here at some future point to resolve how shifting currents and climate influence larval dispersal. The authors hope that by illuminating some of the pathways of dispersal and settlement around Oʻahu, they have provided one of the necessary components to properly inform conservation and management strategies.

Coleman and Bowen (2022) previously documented genetic connectivity in the middle of the Hawaiian Archipelago and population structure within the region of the Main Hawaiian Islands (*i.e.*, Kauaʻi, Oʻahu, Maui, Hawaiʻi Island). The contrasting patterns highlight the need for research focusing on the local region to properly characterize dispersal pathways and identify fine-scale processes (*e.g.*, dispersal potential) that are relevant to the area and organism of interest. This study identified within-island population structure and indicates that local recruitment is low along the northern and western shores of Oʻahu, which are subject to westerly currents, but is much higher in the sheltered waters of Kāneʻohe Bay on the eastern side. Although there were a few instances of self-recruitment inside Kāneʻohe Bay, the major source of recruitment originates outside the bay as far as 60 km. Nonetheless, Kāneʻohe Bay is also a source of recruitment to other regions along the eastern shore. These findings provide a geographic scale at which both communities and agencies may cooperate, depending on individual community needs, to promote sustainability

in subsistence and recreational fisheries. Community-based subsistence fishing areas, a return to *moku* traditional Hawaiian management strategies, which divided the island into socio-ecological regions with community governance (Winter *et al*., 2018), would be most effective on the eastern and southern coasts of O'ahu. Historically, the *moku* system maintained an abundance of resources and sustained a large population. In addition, there has been a recent cultural renaissance among Native Hawaiian cultural practitioners to revisit these agro-ecological systems. Indeed, given the scale of *A. triostegus* dispersal observed in previous studies, *moku*-based management seems a good fit to *A. triostegus* fisheries in general. The possible exceptions are the *A. triostegus* on the western and northern shores, where currents may disperse propagules beyond the coastal waters of O'ahu and outside the realm of the local *moku*.

Finally, the authors note that when demographic composition was skewed towards adults in their study sites, they found very low larval retention. When juveniles were more abundant, the authors found very high larval retention. A low number of adults relative to juveniles may be an artefact of fishing pressure but may also provide a simple observational test that can indicate areas of productivity (in terms of high recruitment) without lethal sampling and expensive lab work.

AUTHOR CONTRIBUTIONS

R.R.C., B.W.B. and R.J.T. designed the research project. R.R.C. generated molecular data. R.R.C., D.W.K. and M.L.H. collected specimens and participated in the analyses and interpretation of data. All authors participated in the writing of the manuscript.

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CONFLICT OF INTEREST

We declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

RADseq sequence files are available at NCBI's Sequence Read Archive (accession numbers: SAMN32605256-32605290, SAMN326211400-32622104, SAMN32625058-32625851) and associated metadata (*i.e.*, sample ID, corresponding collection locations, collection date and categorized as adult or juvenile) are available at the Genomic Observatories MetaDatabase (GeOMe). These sequences were demultiplexed (separated by barcode into individuals) and quality filtered using process_radtags in STACKS. For each individual, forward and reverse reads are provided. For individuals that were sequenced more than once, sequence data from each replicate are provided separately (*i.e.*, replicates are not merged).

ETHICS STATEMENT

We declare that all sample collections were permitted by the State of Hawai'i Board of Land and Natural Resources through its Department of Land and Natural Resources under Special Activities Permit No. 2016-03, 2017-03, issued to Ruth Gates, director of the Hawai'i Institute of Marine Biology. We also declare that all individuals were sampled following guidelines set forth by the University of Hawai'i's Institutional Animal Care and Use Committee under permit no. IACUC 15-2271 issued to B.W.B.

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SUPPORTING INFORMATION

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

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