

Research Article

Widespread Dispersal of the Crown-of-Thorns Sea Star, *Acanthaster planci*, across the Hawaiian Archipelago and Johnston Atoll

Molly A. Timmers,¹ Kimberly R. Andrews,² Chris E. Bird,² Marta J. deMaintenton,³ Russell E. Brainard,⁴ and Robert J. Toonen²

¹Joint Institute for Marine and Atmospheric Research, University of Hawai'i, 1000 Pope Road, Honolulu, HI 96822, USA

²Hawaii Institute of Marine Biology, University of Hawaii, P.O. Box 1346, Kaneohe, HI 96744, USA

³University of Hawaii at Hilo, 200 W. Kawili Street, Hilo, HI 96720, USA

⁴NOAA Pacific Island Fisheries Science Center Coral Reef Ecosystem Division, 1125 B Ala Moana Boulevard, Honolulu, HI 96814, USA

Correspondence should be addressed to Molly A. Timmers, molly.timmers@noaa.gov

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The population structure of marine species is variable along the Hawaiian Archipelago; thus, it is important to understand dispersal and recruitment patterns for economically and ecologically important taxa to inform Ecosystem-based Management. Connectivity of the coral-eating crown-of-thorns sea star, *Acanthaster planci*, was examined from Johnston Atoll and 12 locations across the Hawaiian Archipelago. Sequences of mitochondrial DNA from 383 individuals were analyzed to infer patterns of gene flow among the Northwestern Hawaiian Islands (NWHIs), the main Hawaiian Islands, and Johnston Atoll. Population samples were genetically similar across the Hawaiian Archipelago with the exception of the west side of the Big Island of Hawaii, which was significantly differentiated from the majority of Hawaiian samples (pairwise $\Phi_{ST} = 0.0607-0.1068$, $P < .05$). Although differentiated, Hawai'i West shares haplotypes with every other site across the Hawaiian Archipelago. Johnston Atoll was genetically distinct from every location (pairwise $\Phi_{ST} = 0.064-0.13$, $P < .05$) except French Frigate Shoals ($\Phi_{ST} = 0.03$, $P = .10$), supporting connectivity between the central NWHIs and Johnston Atoll. Taken together with the lack of geographic population structure and haplotypes shared among all populations, these results indicate widespread larval dispersal with few restrictions to gene flow along the archipelago.

1. Introduction

The most geographically isolated island group in the world, the Hawaiian Archipelago, spans 2500 km and is composed of eighteen primary islands, reefs, and atolls separated into the remote Northwestern Hawaiian Islands (NWHIs) and the inhabited main Hawaiian Islands (MHIs). The NWHIs and MHIs are distinguishable by human habitation, geomorphology, and geological age; the MHIs are heavily populated high islands and geologically young, while the NWHIs are geologically older and predominantly uninhabitable low coral islands and atolls. The reefs of the MHIs are anthropogenically impacted from sewage outflow [1–3],

alien invasive algae [4–6], overfishing [2, 7], and nutrient discharge [8], whereas the NWHIs have remained relatively pristine [7]. Fish communities and biomass in the NWHIs are unparalleled to the MHIs [7], and in terms of ranking overall “health”, the NWHIs have retained their biological richness and value compared to the MHIs [9–11].

Currently under protection as the Papahānaumokuākea Marine National Monument, the NWHIs remain shielded from most direct threats induced by human activities such as commercial fishing, military use, and tourism [11]. To inform ecosystem-based management in both the Monument and the reefs in the MHIs, it is necessary to know the direction and magnitude of connectivity across

the archipelago. Ascertaining whether the NWHIs serve as a recruitment source to the MHI or whether the MHI serve as a recruitment source to the NWHIs should be investigated to better support implementation of ecosystem-based approaches to management.

The genetic structure and degree of differentiation among populations of surveyed marine species are highly variable along the Hawaiian Archipelago. Marine species are thought to diverge from their Pacific roots but maintain species cohesion and not diversify in the Hawaiian Archipelago [12–14]. Thus, marine species in Hawai'i were historically expected to be generally well mixed because the spectacular species radiations seen in terrestrial species are not mirrored in the sea, and there is limited evidence to suggest divergence and diversification of marine taxa [12, 14]. Several studies supported this lack of genetic structure for the damselfish, *Stegastes fasciolatus* [15], the soldierfish, *Myripristis berndti* [16], the spiny lobster, *Panulirus marginatus* [17], and the snapper, *Pristipomoides filamentosus* [18]. In contrast to these examples, however, several marine species have also shown significant genetic differentiation within the Hawaiian Archipelago. For example, the Hawaiian grouper, *Epinephelus quernus*, exhibits genetic subdivision along the middle of the archipelago [19]. Similarly, subpopulations of the Hawaiian spinner dolphin exist between the MHI and the NWHIs and within each region [20]. Furthermore, two genetically distinct populations of the endemic bobtail squid, *Euprymna scolopes*, have been discovered on the island of O'ahu [21]. Finally, major restrictions to gene flow were found within the Hawaiian Archipelago for the subtidal Hawaiian limpet, *Cellana talcosa* [22], as well as for vermetid gastropods [23]. Research thus far dictates that the levels of connectivity and gene flow between the NWHIs and MHI and among all Hawaiian islands are highly variable among species [22]. Thus, population structure must be investigated species by species to understand the dispersal and recruitment patterns for economically and ecologically important taxa until sufficient data emerge to make meaningful generalizations.

Here, we investigate the population structure of the ecologically influential, corallivorous crown-of-thorns sea star, *Acanthaster planci*. Large aggregations of the crown-of-thorns, termed outbreaks, are among the most significant biological disturbances that occur on a tropical reef [24]. Outbreaks can destroy a coral reef [24], change coral community structure [25–27], promote algal colonization [24, 28], and affect fish population dynamics [29–31]. What specifically drives outbreak formation is still unknown, and whether recent outbreaks are more of a human-induced phenomenon as a result of sedimentation and urbanization [32], run-off [32–34], or overfishing [35, 36] rather than a naturally occurring phenomenon remains under debate. Regardless of the mechanism, infestations are detrimental not only ecologically, but also economically by reducing the aesthetic value of coral reefs in locations where the economy is driven by tourism.

Coral reef tourism is a multibillion dollar industry for island nations. Net benefits from Hawaiian coral reefs alone were estimated to be USD \$360 million per year [37] with 50

to 60 million a year in revenue from the dive industry [38]. Control and eradication programs have been established in several countries to manage *Acanthaster* reef impacts for ecological and economical reasons [26, 39]. Knowledge on the dispersal and connectivity patterns of this corallivore along the Hawaiian Archipelago would provide managers with information regarding potential larval pathways enabling them to monitor reef areas that may be at risk to *A. planci* aggregations and act proactively to control outbreaks and prevent spread.

This paper uses genetic markers (mtDNA) to investigate gene flow and connectivity of *A. planci* across the Hawaiian Archipelago and Johnston Atoll. Located 865 km to the south-southwest of French Frigate Shoals in the NWHIs, Johnston Atoll is the closest Indo-West Pacific source of marine species that could have potentially populated the Hawaiian Islands and has alternately been proposed as a gateway into Hawai'i and an outpost of Hawaiian diversity. In this study, we ask the following questions. (1) Do populations of *A. planci* show evidence of genetic subdivision between and within the NWHIs and the MHI? (2) Is there gene flow among Johnston Atoll, the NWHIs, the MHI, or all three? (3) Do *A. planci* populations conform to a genetic isolation by geographic distance (IBD) model along the Hawaiian Archipelago?

2. Materials and Methods

2.1. Sampling. Adult *Acanthaster planci* were collected between 2005 and 2007 from Johnston Atoll and 11 sites along the 2500 km long Hawaiian Archipelago (Figure 1). Of those 11 sites, two were in the NWHIs (Pearl and Hermes Atoll and French Frigate Shoals) and nine within the MHI (Ni'ihau, Kaua'i, O'ahu, Maui, Moloka'i, Lana'i, Hawai'i East, Hawai'i West, and Hawai'i South). Sites, Oahu and Hawai'i East, were outbreak populations having greater than 1500 sea stars/km² [40]. Live stars were sampled nonlethally by snipping off an arm tip in the field by means of both free diving and SCUBA [41]. Tube feet tissue was preserved in 95% ethanol and stored at –20°C. In addition, 44 samples collected in 1982 from an unknown location of the Big Island of Hawai'i were used in this study. For these historical samples, whole animals were collected and pyloric caeca were preserved in 95% ethanol before being stored at –20°C.

2.2. DNA Extraction and PCR. Two different procedures were used for DNA extraction and amplification based on the tissue type and age of the samples. DNA extractions mirrored the protocols described in Jessop [42] or the Hotshot boiling protocol [43].

Approximately 530 base pairs of the noncoding mitochondrial DNA control region were amplified using polymerase chain reaction (PCR) with the following primers: COTS-ctrl-fwd 5'CAAAAGCTGACGGGTAAGCAA3' and COTS-ctrl-rvs 5'TAAGGAAGTTTGCGACCTCGAT3' (Volger et al., unpublished). 100 µl PCR reactions were performed for tube feet samples using 30 µl of dH₂O, 10 µl of template, 10 µl of each primer (5 µM), and 50 µl of Promega

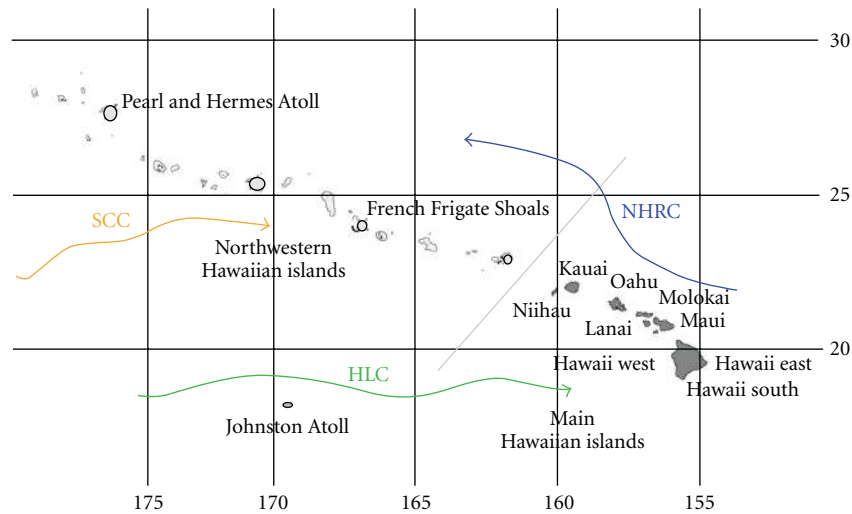


FIGURE 1: Scaled map of island and atoll collections of *Acanthaster planci* along the Hawaiian Archipelago and Johnston Atoll. High islands are represented in dark gray. Submerged reef area to a 30 meter isobath is outlined in light gray. The blue line represents the North Hawaiian Ridge Current (NHRC), the green line represents the eastward Hawaiian Lee Countercurrent (HLC), and the orange line presents the Subtropical Countercurrent (SCC).

MasterMix. The PCR for historical samples occurred in 25 μ l reactions with 2.5 μ l of 10X buffer, 5 μ l of dNTPs (2 μ M), 1 μ l of $MgCl_2$ (1.5 mM), 0.5 μ l of each primer (0.2 μ M), 0.5 μ l of template, and 1.5 U of Bionline's Immolase Taq polymerase. Thermocycling for all samples was performed with an initial denaturation at 94°C for 5 min, 34 cycles (94°C for 30 s, 55°C for 1 min, and 72°C for 1 min), and a final extension for 10 min at 72°C. PCR products from tube feet samples were cleaned using UltraClean PCR kit (MO BIO Laboratories). PCR products from 1982 samples were treated with 1.5 μ l of exonuclease I and 1.5 μ l of calf intestinal alkaline phosphatase (Exo-CIAP), incubated at 37°C for 60 minutes, and then deactivated at 85°C for 15 minutes.

Amplified DNA fragments were sequenced in the reverse direction, and all unique or questionable sequences were repeated using an alternate reverse primer on an ABI 3130XL automated sequencer (Applied Biosystems Incorporated).

2.3. Data Analysis. Sequences were compared, and assembled using SEQUENCHER (v4.52b; Gene Codes Corporation, Ann Arbor, MI, USA). Sequences were aligned using MANGO (multiple alignment with *N* gapped oligos) because this program uses a novel orthogonal multiple sequence alignment method that processes information of all sequences as a whole and builds the alignment vertically, avoiding the “once a gap, always a gap” alignment phenomenon [44]. Gap placement was then double checked by eye using Bioedit [45], and haplotypes were determined based on sequence identity.

A median joining haplotype network with the default weight of 10 applied to each character was created using NETWORK ver 4.5 (Fluxus Technology Ltd., Suffolk England) to illustrate haplotype variability and clustering. An

analysis of molecular variance (AMOVA) was conducted using ARLEQUIN 3.1 [46]. A Kimura 2P model [47] was determined to be the most appropriate model for these data as determined by MODELTEST 3.7 [48]; therefore, all AMOVA analyses assumed this base substitution model. Haplotype diversity (h), nucleotide diversity (π), and population pairwise Φ_{ST} values were calculated in ARLEQUIN. A partial mantel test as implemented in IBDWS [49] was used to determine if genetic distance was correlated with geographic distance between islands.

3. Results

A total of 383 specimens of *A. planci* were sampled. There were 308 haplotypes, of which 125 were singletons (Table 1). Haplotype diversity was high both overall ($h = 0.98$ or 50 effective haplotypes) and within sample locations ($h = 0.968\text{--}0.997$; Table 1). The overall nucleotide diversity was $\pi = 0.027$, and within sample locations $\pi = 0.019\text{--}0.041$.

The median joining network revealed no obvious association between haplotype and geographic location (Figure 2). Haplotypes were not clustered in distinguishable groups. When haplotypes of the 1982 samples were added, there was no distinction between the older samples and the newer ones (Figure 2).

Excluding Johnston Atoll, an AMOVA to test the separation of the NWHIs and the MHIs detected no significant difference among regions ($\Phi_{CT} = 0.003$, $P = .38$), but significant differences were detected among populations within regions ($\Phi_{SC} = 0.052$, $P = .01$). Including all populations, there was an indication of population partitioning between Johnston Atoll and all sites within the Hawaiian Archipelago ($\Phi_{CT} = 0.052$, $P = .075$), with 5.24% of the genetic variation explained by these groups.

TABLE 1: Sample size and descriptive statistics for control region data of *Acanthaster planci* collected along the Hawaiian Archipelago and at Johnston Atoll. The “*” indicates the Northwestern Hawaiian Islands.

Location	<i>N</i>	No. of haplotypes	No. of unique haplotypes	Averaged haplotype diversity (<i>h</i>)	Averaged nucleotide diversity (π)
Hawai'i 1982 Samples	44	32	11	0.978	0.023
Hawai'i East	29	25	6	0.991	0.023
Hawai'i South	34	29	12	0.989	0.029
Hawai'i West	42	26	8	0.969	0.024
Maui	26	20	7	0.982	0.033
Moloka'i	25	23	11	0.993	0.034
Lana'i	30	25	10	0.982	0.032
O'ahu	25	23	10	0.993	0.03
Kaua'i	24	24	6	0.996	0.033
Ni'ihau	30	21	7	0.975	0.023
* French Frigate Shoals	13	11	5	0.974	0.019
* Pearl and Hermes Atoll	27	26	17	0.997	0.041
Johnston Atoll	33	23	15	0.968	0.013
Total	382	308	125	0.984	0.027

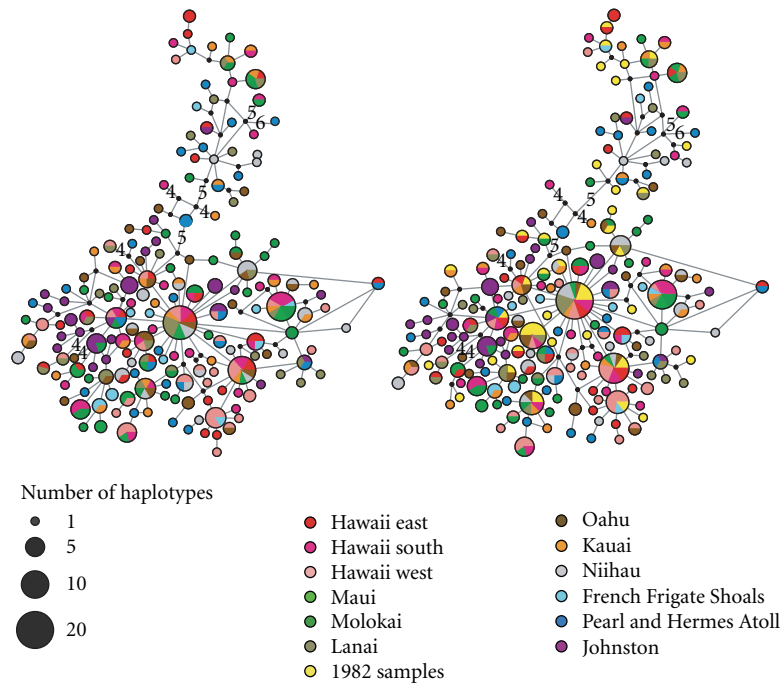


FIGURE 2: Median joining haplotype network of *Acanthaster planci* samples from Johnston Atoll and the Hawaiian Archipelago. The network to the right includes the samples from 1982 and the network to the left does not. Each circle represents a unique haplotype connected by a line to those that differ by one or more base pairs. Those lines that represent >4 bp differences were labeled, but lines are not to scale. Nodes on the lines indicate missing haplotypes. Each haplotype is color coded by region and size of the pie chart is proportional to frequency. The smallest colored circles represent a singleton haplotype and the largest circle represents 20 individuals who share that haplotype.

Pairwise population fixation (Φ_{ST}) values revealed two locations significantly differentiated from the rest of the archipelago: Johnston Atoll and Hawai'i West (Table 3). Given these results, a post hoc AMOVA was conducted to look for regional differences between Johnston Atoll, Hawai'i West, and the rest of the archipelago. Significant differences

were found among regions, explaining 5.71% of the genetic variation ($\Phi_{CT} = 0.057$, $P < .05$, Table 2).

Pairwise Φ_{ST} values were used to assess whether genetic and geographic distances conformed to the Isolation by Distance model. Only 8% of the relationship was explained ($R^2 = 0.078$) by the IBDWS model, and the associated

TABLE 2: Analysis of molecular variance results for *Acanthaster planci* populations along the Hawaiian Archipelago and from Johnston Atoll. The regional variance component relative to the total variance is Φ_{CT} . The between-site within region variance component divided by the sum of itself and the within-site variance is Φ_{SC} . Statistical significance ($P < .05$) is indicated by the bold font.

Statistic	df	SS	Var Comp	% Var	Φ_{CT} Φ_{SC}	Significance
NWHIs and MHIs						
Region	1	6.65	0.001	0.03	0.0003	0.38
Sites within regions	10	70.08	0.079	1.66	0.0167	0.01
Total	5348	1656.05				
Archipelago and Johnston						
Region	1	22.72	0.255	5.24	0.052	0.075
Sites within regions	11	76.74	0.084	1.73	0.018	0.000
Total	381	1773.88				
Archipelago, Johnston, and Hawai'i West						
Region	2	46.44	0.276	5.71	0.057	0.013
Sites within regions	10	53.01	0.027	0.58	0.006	0.000
Total	381	1773.88				

Mantel test indicated no significant correlation between genetic and geographic distances ($P = .997$, $r = -0.28$, $n = 78$). When log transformed, the results remained similar ($R^2 = 0.067$, $P = .98$, $r = -0.26$).

4. Discussion

4.1. Connectivity along the Hawaiian Archipelago. *Acanthaster planci* larvae are planktotrophic and, based on laboratory rearing, have an estimated pelagic larval duration (PLD) of 42 days [50]. Their resilience to temperature and salinity changes [51], and adaptation to limited nutrients [50] enable *A. planci* larvae to survive in a broad range of conditions which is thought to facilitate long-distance dispersal [50–53]. In addition to having resilient larvae, adults are fecund broadcast spawners. Females release up to 10^8 eggs during one spawning season and can spawn for up to 4 years of their approximated 8-year lifespan [26, 54]. The use of PLD as a reliable proxy for dispersal potential has been questioned in several recent meta-analyses of the existing literature [55–58]. In this case, however, the data support the expectations based on life-history traits. The haplotype network (Figure 2), the nonsignificant AMOVA Φ_{CT} between the NWHIs and the MHIs populations ($\Phi_{CT} = 0.003$, $P = .38$), and the lack of significant isolation by distance ($P = .997$) indicate that, with the exception of the Hawai'i West population, *A. planci* in the Hawaiian Archipelago experience few barriers to gene flow. Furthermore, the shared haplotypes between the 1982 samples with locations throughout the archipelago today suggest long-term mixing of the populations.

The distance traveled during pelagic development is obviously a function of both PLD and of the oceanic currents in which those larvae find themselves [59–62]. Thus, the mechanism for this widespread dispersal is likely the

variable currents that flow along the 2500 km archipelago. The prevailing oceanic currents that run along the Hawaiian Archipelago—the west/northwestward flowing North Hawaiian Ridge Current (NHRC), the eastward Hawaiian Lee Countercurrent (HLC), and the Subtropical Countercurrent (SCC)—are conducive to the widespread dispersal of species with long-lived larvae that leave the coastal realm [63, 64]. With the NHRC, recruitment is more likely to move from the MHIs to the NWHIs [65]. However, the SCC has been found, in part, to drive recruitment of spiny lobsters from the NWHIs atolls down the chain [66]. In addition to the prevailing currents, there are wind-driven southwesterly flowing currents moving through the channels of the MHIs [67], and all currents within the archipelago are dominated by eddies and are unstable because of mesoscale and seasonal variability [64, 67, 68].

The temporal and spatial dynamics of all these currents along and within the archipelago provide the mechanism for *A. planci* larvae to disperse widely and haphazardly up and down the chain thereby facilitating mixing. Thus, the isolation of the Hawai'i West population from the rest of the Hawaiian Archipelago samples, with the exception of Ni'ihau ($\Phi_{ST} = 0.020$, $P = .064$), is surprising. However, this pattern of isolation has also been seen with anchialine shrimp [69], yellow tang [70], and multiple species of vermetid gastropods [23], where the populations on the west side of Hawai'i Island were strongly subdivided from the rest of the Big Island, and the other MHIs [71, 72].

The west leeward side of Hawai'i island is an active area for eddy formation [73]. Two to three times a year anticyclonic eddies form, propagate to the southwest, and approach the westward flowing North Equatorial Current moving away from the Hawaiian Archipelago [74]. These eddies may be limiting larval dispersal from the leeward side of Hawai'i island to the rest of the chain and from the chain to the west side. Mesoscale and submesoscale circulation may

TABLE 3: Population pairwise Φ_{ST} values (below diagonal) and statistical significance (above diagonal) for *Acanthaster planci* populations along the Hawaiian Archipelago. Bold text indicates significant values: * $P \leq .05$, ** $P \leq .01$, and *** $P \leq .001$.

FFSS	HE	HS	HW	JOH	KAU	LAN	MAI	MOL	NII	OAH	1982	PHR
FFSS												
HE	0.297	0.771	0.002**	0.104	0.391	0.492	0.429	0.651	0.041*	0.258	0.231	0.147
HS	0.009	0.423	0.002**	0.002**	0.546	0.685	0.108	0.227	0.161	0.173	0.894	0.407
HW	-0.022	-0.002	0.001***	0.016*	0.746	0.860	0.733	0.915	0.101	0.522	0.365	0.208
JOH	0.107**	0.070**	0.064***	0.000***	0.001***	0.002**	0.000***	0.001***	0.064	0.040*	0.001***	0.000***
KAU	0.030	0.093**	0.046*	0.005**	0.005**	0.004**	0.005**	0.028*	0.000***	0.005**	0.001***	0.000***
LAN	-0.002	-0.010	-0.015	0.077**	0.926	0.926	0.486	0.544	0.079	0.181	0.736	0.818
MAI	-0.007	-0.013	-0.016	0.068**	-0.022	-0.002	0.411	0.654	0.184	0.318	0.671	0.655
MOL	-0.006	-0.013	0.078***	0.064**	-0.006	-0.002	0.697	0.697	0.043*	0.254	0.134	0.184
NII	-0.020	-0.019	0.061***	0.042*	-0.009	-0.012	-0.014	0.183	0.183	0.803	0.225	0.123
OAH	0.051*	0.021	0.021	0.126***	0.033	0.012	0.040*	0.013	-0.012	0.776	0.118	0.038*
1982	0.011	-0.005	0.023*	0.066**	0.014	0.004	0.008	-0.014	-0.012	0.018	0.122	0.048*
PHR	0.013	0.000	0.085***	0.102***	-0.014	-0.010	0.019	0.009	0.020	0.018	-0.004	0.449
	0.030	0.010	0.105***	0.127***	-0.018	-0.012	0.014	0.023	0.047*	0.039*	-0.004	

FFSS: French Frigate Shoals, JOH: Johnston Atoll, MOL: Molokai, OAH: Oahu, HE: Hawaii East, KAU: Kauai, NII: Niihau, HS: Hawaii South, LAN: Lana'i, PHR: Pearl and Hermes Atoll, HW: Hawaii West, MAI: Maui, and HAW 1982: Hawaii'i.

minimize long-distance dispersal of larvae [75]. Eddies and gyres have caused larval retention in some reefs along the Great Barrier Reef [76] and in Guam [77]. Eddy systems capture larvae and advect them to deep oceanic waters where they have a higher likelihood of perishing [75]. The eddies occurring along the west side of Hawai'i island seem a likely candidate driving the isolation of this population. Despite the significant genetic differentiation, however, gene flow does exist because Hawai'i West shares haplotypes with every island, including Johnston Atoll, and thus is not completely isolated or self-sustaining.

4.2. Connectivity between Johnston Atoll and the Hawaiian Archipelago. Johnston Atoll is the most geographically isolated population in this study and the closest Indo-West Pacific source of marine species that could have potentially populated the Hawaiian Islands. It has long been postulated that species disperse readily from Johnston Atoll to French Frigate Shoals (FFSs) in the NWHIs. The first indirect evidence came from coral surveys comparing species at Johnston Atoll with the Hawaiian Islands. These surveys found that the most abundant coral at Johnston Atoll, *Acropora cythera*, was prevalent at FFSs but extremely rare elsewhere in the Hawaiian Archipelago [78, 79]. The next indirect evidence was demonstrated using computer simulations that revealed FFSs as being oceanographically connected to Johnston Atoll via the SCC and HLC for larvae with a PLD > 40 days [63]; *A. planci* fit this model. The FFSs population in this study was the only one that was not significantly different from Johnston Atoll ($\Phi_{ST} = 0.029$, $P = .10$). The genetic similarity between FFSs and Johnston Atoll to the exclusion of all other Hawaiian islands supports the FFSs and Johnston Atoll connection. In contrast, gene flow between Johnston Atoll and the remaining Hawaiian Islands is clearly limited (pairwise $\Phi_{ST} = 0.064$ – 0.13 , $P < .05$).

5. Conclusion

Although some genetic structuring was found between Hawai'i West and the rest of the Hawaiian Archipelago, the absence of *A. planci* genetic population structure along 2500 km of the Hawaiian Archipelago indicates that the dispersal potential of this coral-eating sea star is vast. High dispersal is generally associated with a lack of genetic population structure [80, 81]. The genetic pattern found is driven by the dynamic nature and seasonality of the variable currents and eddies that stretch across the chain. The numerous islands and reefs along the chain provide stepping stones for population expansion. It is likely the larvae released in the MHIs will eventually have progeny in the NWHIs and vice versa.

Understanding *A. planci* dispersal and recruitment mechanisms has become important for reef managers in order to mitigate their populations and monitor their impacts on reef communities. Ecosystem-based management is attractive in this case because in addition to the possible role of anthropogenic activities in initiating outbreaks, these

coral-eating sea stars impact more than just the habitat-forming corals on which they prey and can alter entire coral reef ecosystems [26, 82–84]. With coral reef tourism being a multibillion dollar industry, *A. planci* outbreaks could severely impact the economics of island nations. For example, outbreaks on the Great Barrier Reef (GBR), Guam, American Samoa, and Japan have resulted in up to 90% coral mortality in localized areas [85–88]. In the GBR recruitment pathways from mass spawning events have been predicted based on the flow of the East Australian Current [89, 90], and eradication programs have been established to remove *A. planci* populations upstream in order to limit population expansion downstream [91]. The same is true in Japan along the Kuroshio Current [92]. Unlike the GBR and Japan, it will be more difficult to predict potential recruitment pathways in the Hawaiian Archipelago due to the variable currents and high population mixing along the chain.

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