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Article

Johnston Atoll: Reef Fish Hybrid Zone between Hawaii and the Equatorial Pacific

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Abstract: Johnston Atoll is isolated in the Central Pacific Ocean (16°45' N 169°31' W) about 1287 km (800 miles) southwest of Honolulu, Hawaii and 1440 km (900 miles) north of the equatorial Line Islands, Kiribati. The labrid species, *Thalassoma lutescens*, has a wide range of distribution in the equatorial Pacific. The related species, *Thalassoma duperrey*, is endemic to the Hawaiian Islands. The pelagic larvae of both species dispersed to Johnston Atoll, where we found a mix of adult phenotypes representing a range of hybridization events over generations. A hybrid acanthurid was also documented. In addition, the arrival and colonization of two pomacentrid (damsel fish) species to the atoll was observed in 1999. These pomacentrid sister-species, *Abudefduf abdominalis* and *A. vaigiensis*, have become established populations with subsequent hybridization. The biogeography of the Johnston Atoll coral reef fish population shows some degree of local population retention. It is also evident that this biogeographic isolation is periodically compromised by large ocean current oscillations in the equatorial and central Pacific Ocean that bring larval fishes from either Hawaii or the Line Islands, and may distribute Johnston Atoll originating larvae elsewhere as well. The reef fauna and oceanography of this atoll provides the circumstances for improving scientific insight into marine fish speciation and island biogeography.

Keywords: biological invasion; *Thalassoma*; *Abudefduf*; Labridae; Pomacentridae; Pacific biogeography; coral reef; invasive species; fish colonization; species definition

1. Introduction

Finding a hybrid fish in nature was once thought to be a rare occurrence as it was generally believed that the “lines between fish species are almost never crossed” [1]. Carl Hubbs challenged this notion when he first presented early evidence that hybridizing fish species were occurring in the wild [1]. Today, finding natural hybrids of fish species is common, especially on coral reefs, with over 75 species documented that hybridize both in oceans [2–4] and in freshwater [5]. The low abundance of one of the parent species combined with a high niche overlap promotes hybridization [6]. Documentation of hybrid fishes is routine, using color photography to preserve the living coloration matched with DNA samples when possible. As a result, a few coral reef locations have been defined as “marine hybrid hotspots”, such as in the Indian Ocean with 15 hybrids [7] and the Arabian Sea with 7 hybrids [8]. This study documents 5 hybrids at Johnston Atoll.

The Johnston Atoll fish fauna (327spp) is dominated by Hawaiian species. There are only 17 (5.2% of 327spp) non-Hawaiian fish species at Johnston Atoll compared to 53 (16.2% of 327spp) endemic Hawaiian species, but these endemics do not range farther south to the Line Islands. Twelve other species are indigenous to Johnston Atoll and the Line Islands but are not found farther

north in Hawaii [9–12]. Overall, Johnston Atoll shares 94.8% of its fish species in common with the Hawaiian Islands.

Comparatively, the marine fauna of this atoll is low in species diversity (327 species of fishes and 28 species of corals) most likely due to the atoll's limited size, low habitat diversity, and isolation [9–11,13,14]. Johnston Atoll contains approximately 39,000 acres (158 km²) of reef habitat and is separated from the closest reefs of French Frigate Shoals, found in the northwest Hawaiian Islands, by 804 km (500 miles). The closest reef habitats to the south are found in the Line Islands of Kiribati, about 1440 km (900 miles) away; to the southwest, the Marshall Islands are about 2560 km (1600 miles) away. The shallow lagoon, containing a limited number of habitat types, is dominated by the tabletop coral *Acropora cytherea*. The stepping stone role of Johnston Atoll for reef fish larvae that originate from the equatorial Line Islands and disperse to the Hawaiian Archipelago was first described by Gosline [15] and later corroborated by an extensive survey of fishes by Randall et al. [9]. Additionally, an ocean model of larval dispersal by Kobayashi [16] suggests two pathways of flow between Hawaii and Johnston Atoll. The capability of far distance larval dispersal was shown for several reef fishes that dispersed across the Eastern Pacific Barrier [17].

The labrid *Thalassoma duperrey* is endemic to the Hawaiian Islands. Its sister species, *Thalassoma lutescens*, is found everywhere else in the tropical Pacific Ocean. These two species both occur at Johnston Atoll, and are very closely related but differ significantly in color pattern [18]. By analyzing the appearance of many individual fish with intermediate and mixed color patterns, we surmised that these species have been freely hybridizing for several generations. Both species have been recorded at Johnston Atoll throughout the history of ichthyological studies that have been conducted there [9,11].

A second phenomenon observed at Johnston Atoll was the colonization of the atoll by two sister species of Pomacentridae (damsel fish). The species *Abudefduf vaigiensis* occurs in the tropical Pacific Ocean (along with *T. lutescens*). Its sister species, *Abudefduf abdominalis*, is found in Hawaii. Neither species were seen in surveys [9] until 1986 when a few individual *A. abdominalis* were observed during reef fish surveys [14,19]. These particular fish disappeared, and no others were noted anywhere in the atoll. Another population of both species was then discovered in 1999. These fish appeared at reef locations where many fish surveys had taken place previously (beginning in 1983), but these two species were not observed during those earlier surveys. These two *Abudefduf* species populations persisted and the individual numbers increased around the atoll. By 2001, these two species became numerous and their populations appear to be well established at Johnston Atoll currently.

In this paper, we show evidence of hybridization events in three genera of reef fishes. We also show evidence that some reef fishes can succeed in long-distance dispersal and colonization from both Hawaii (north) and the Line Islands (south) to Johnston Atoll, and that other reef fishes can maintain locally replenishing populations.

2. Materials and Methods

2.1. Study Location

This study was conducted at Johnston Atoll (JA), an unincorporated territory of the United States of America (US), located about 1287 km (800 miles) southwest of Honolulu, Hawaii in the Central Pacific Ocean (16°45' N 169°31' W). The atoll is a shallow platform of approximately 39,000 acres (158 km²) of reef habitat. The 80 million year old atoll is considered atypical, due to its tilted platform resulting in an emergent reef along the northern border of the atoll only. There were two original islands, Johnston Island and Sand Island (approx. 0.18 km² and 0.04 km²), that consisted of coral sand with little vegetation. There are no natural sources of freshwater and there is no evidence that indigenous Polynesians inhabited or made long-term visits to the atoll. Dredge and fill operations in the 1960s enlarged Johnston Atoll and Sand Island to about 2.58 and 0.09 km² respectively. In addition to this, two new islands were created: North (0.10 km²) and East Island (0.07 km²). Today, Johnston Atoll is a part of the Pacific Remote Islands Marine National Monument and

is managed by the US Fish and Wildlife Service (USFWS), primarily for the protection of twelve species of migratory seabirds. Additional site information and history are available in Lobel and Lobel [11,20,21].

2.2. Underwater Surveys

Underwater surveys were conducted by scientific divers using the basic “roving diver” technique (divers used OC scuba or Rebreathers). Our underwater research at Johnston Atoll (aka JA) was focused on other topics and these observations were incidental [11,20,21]. Any sightings of unusual fishes were noted in the field notebook, or documented in photographs or videos. John E. Randall (JER) first began diving at JA in the late 1950s and participated in many collecting expeditions at JA until the late 1990s. P. Lobel’s observations were compiled over a 20-year time span: from September 1983 to October 2003 [11]. L. Lobel’s observations were compiled from 1995 to October 2003. Species records were documented with photography and specimen collection (photos scanned from original 35 mm slides). The diving depths for these observations ranged to 50m but most were in the shallow lagoon with a typical depth of 15 m.

3. Results

3.1. Hybrid *Thalassoma* Species

We found individual fish of both *Thalassoma duperrey* (Figure 1) and *T. lutescens* (Figure 2) at JA that appear to be typical for species of their native geography. The *Thalassoma* hybrids are easily distinguished by their varied degree of coloration (Figure 3). The diversity of their coloration suggests that the hybrid population is locally sustaining. The coloration of an individual fish is not symmetrical (Figure 4). It is likely that these hybrid populations have been interbreeding among other hybrids and parent species. In our surveys, we found that 30% of the *Thalassoma* population consisted of hybrids; 58% were *T. duperrey* and 12% were *T. lutescens* (Figures 5, 6 Table 1). It is also worth noting that we observed one fish that had the appearance of a hybrid between *Thalassoma duperrey* and either *Thalassoma trilobatum* or *T. purpureum* (it was not clear which one of these was the second parent species).

3.2. Hybrid *Abudefduf* Species

When Randall et al. [9] conducted the first comprehensive underwater fish surveys at Johnston Atoll in 1983–1984, no individuals of either *Abudefduf abdominalis* or *A. vagiensis* were recorded. A subsequent survey by Irons et al. [19] documented a small group of *Abudefduf abdominalis* at one location (a lagoon north of North Island) that persisted over a 4-year period. In 1986, the initial group was about five to six individual fish but by 1989 only one individual was seen, without any apparent subsequent recruitment. Kosaki et al. [14] suggested that this 1986–1989 observation represented a single chance colonization event that was not sufficient for the successful establishment of this species at JA.

The next occurrence was our sighting of two *A. abdominalis* in 1991, and then one lone fish in 1995. The observation of a notable colonization event occurred in the summer of 1999 when numerous *A. abdominalis* and *A. vagiensis* (Figure 7) were found at several locations in the atoll. We observed these fishes spawning as single and mixed species pairs. By 2001, both species had well-established populations at multiple reef sites throughout the atoll (Table 2, Figure 8).

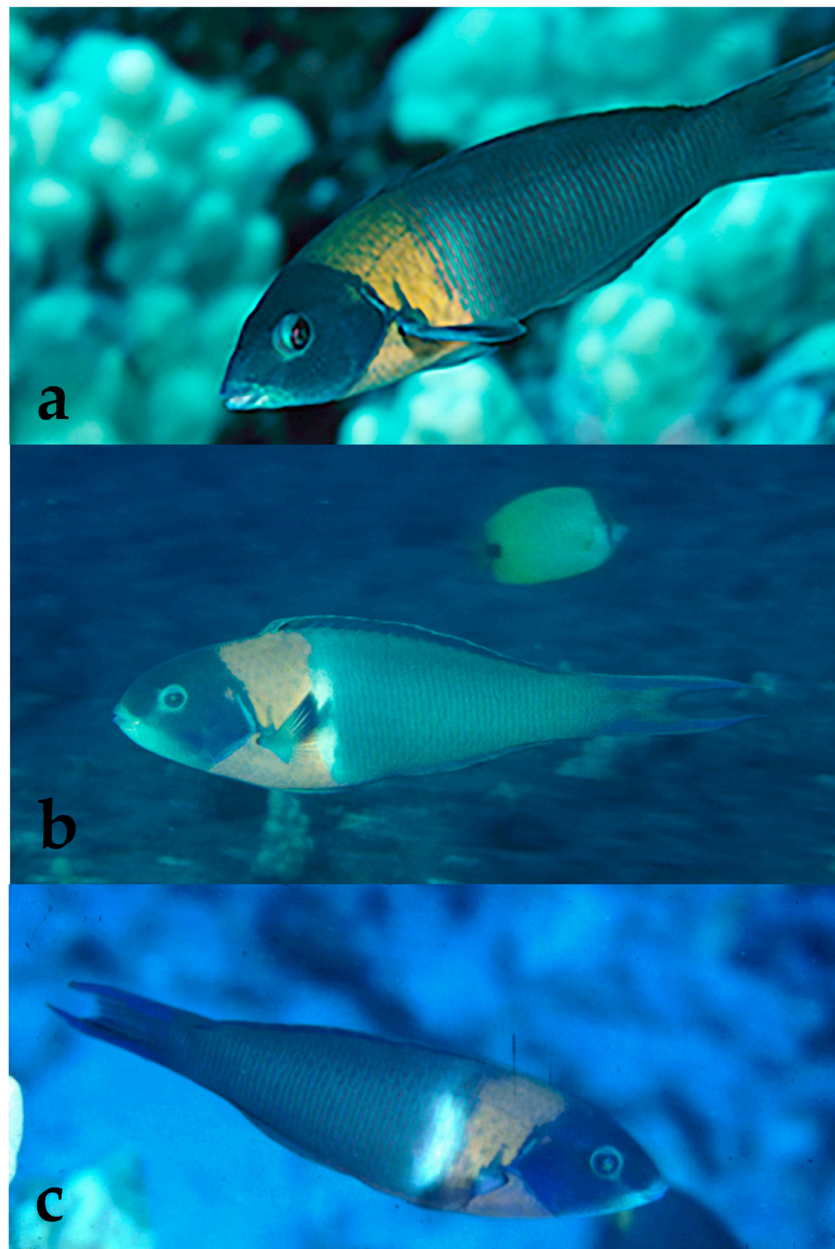


Figure 1. *Thalassoma duperrey* native to the main Hawaiian Islands (a,b) compared to an individual from Johnston Atoll (c).

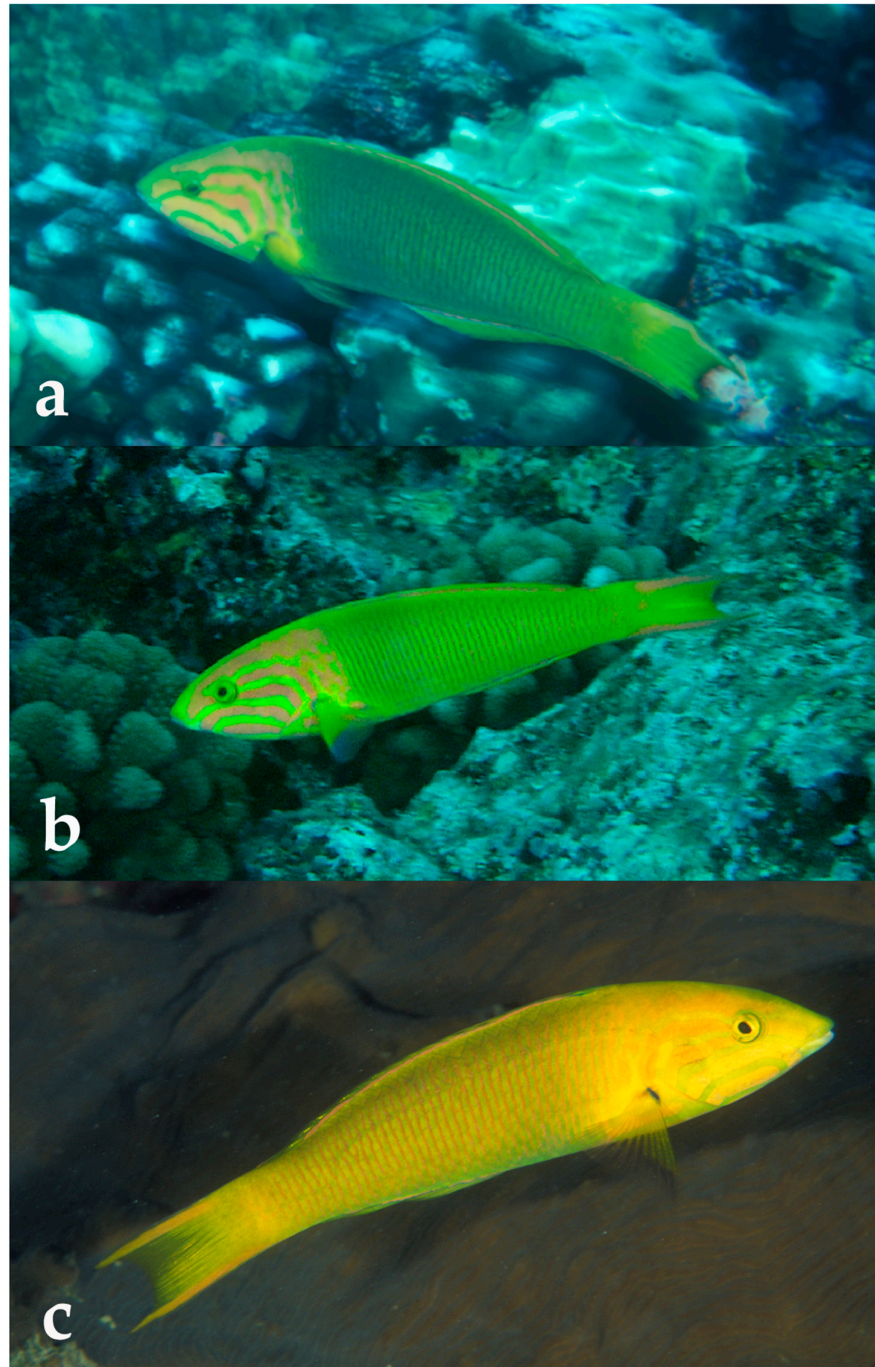


Figure 2. *Thalassoma lutescens* native variations, (a) Fanning Atoll, Line Islands, (b) Palau, Micronesia and (c) Taiwan.



Figure 3. Hybrid *Thalassoma duperrey* X *lutescens* variations at Johnston Atoll.

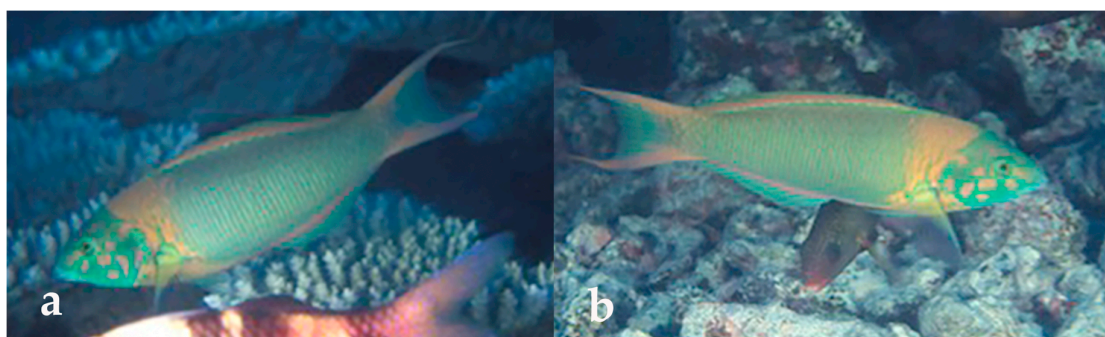


Figure 4. A single *Thalassoma duperrey* X *lutescens* hybrid showing it's left (a) and right (b) sides.

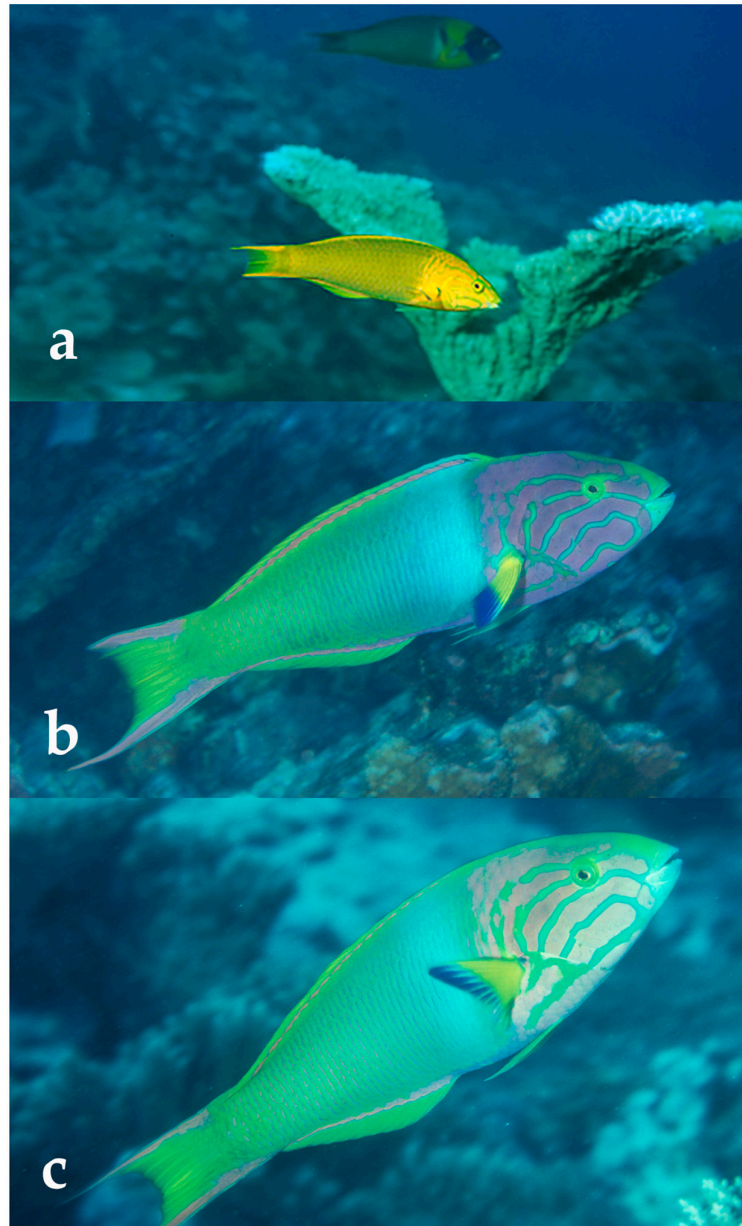


Figure 5. *Thalassoma lutescens* at Johnston Atoll: (a) initial phase with a *T. duperrey* in the background and (b,c) variation in terminal male coloration.

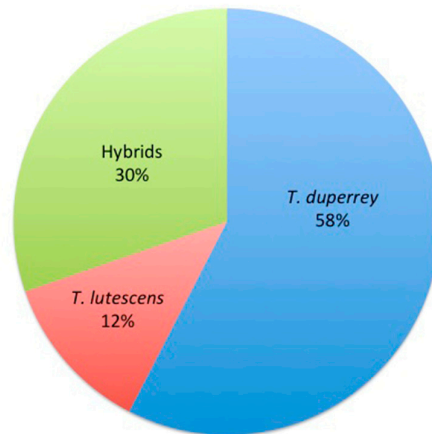


Figure 6. The proportion of individual fish identified as *Thalassoma duperrey* X *lutescens* hybrid, as *Thalassoma duperrey* or as *Thalassoma lutescens*. Data shown in Table 1.

Table 1. Surveys of *Thalassoma* species.

Date	Location	Depth (m)	<i>T. Duppery</i>	<i>T. Lutescens</i>	Hybrid
15 Dec 91	HO Site	1–7	3	2	3
10 May 92	North Is. Channel	3–7	8	1	0
1 Jun 95	Sand Is. Wharf	1–7	1	0	3
12 Sep 97	Outside Munsen’s Gap	4–10	3	1	1
13 Sep 97	West Camera Stand	5–7	18	2	4 ¹
13 Sep 97	Outside Munsen’s Gap	5–10	5	2	9
Total number			38	8	20
% Total			58	12	30

¹ One individual hybrid of *T. duperrey* and *T. trilobatum* or *purpureum* also observed.

3.3. Hybrid *Acanthurus* Species

A single hybrid of *Acanthurus achilles* x *nigricans* was photographed (Figure 9). Both parent species are well established at JA. This was the only hybrid of this type that we observed and was photographed at Donovan’s reef, October 1996.

4. Discussion

Hybrids among marine fishes are now well documented among many families such as the Chaetodontidae, Serranidae, Pomacanthidae, Labidae, Scaridae, Acanthuridae and others [e.g., 3,4,22–25]. While occasional hybridization events happen on most reefs, some locations have been recognized as marine hybrid "hotspots" with multiple species having hybrids [7,26–28]. JA is not as "hot" in terms of numbers of species hybridizing but is distinctive in having a significant and persistent population of hybrid labrid species. Hybrid populations of reef fishes elsewhere have been sometimes historically misidentified as distinct species, especially when their color patterns are used as the main defining characteristic, which has led to confusion in the taxonomy [29]. In one well-known case in the Atlantic, a hybrid of two serranid genera, *Cephalopholis* and *Paranthias* was first described as a distinct genus and species until this taxonomic mystery was solved [30].

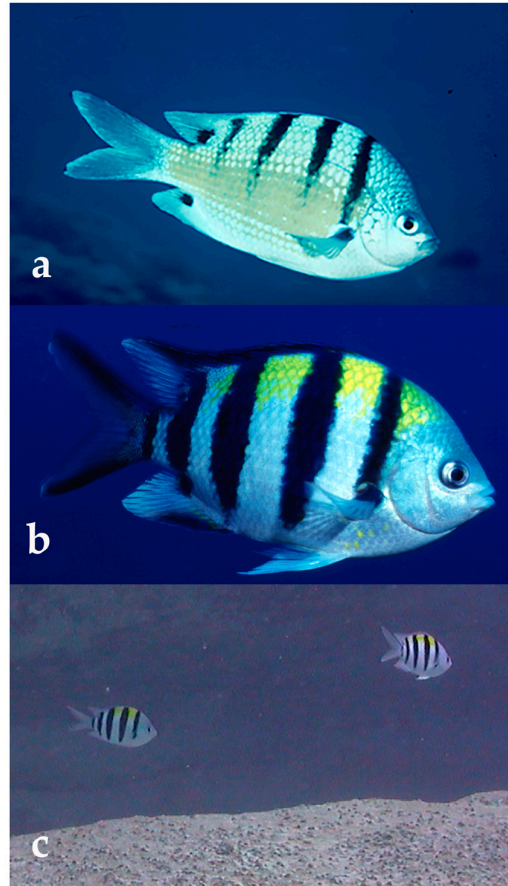


Figure 7. The pomacentrids at Johnston Atoll, *Abudedefduf abdominalis* (a), *A. vaigiensis* (b) and (c) presumptive hybrids (Buoy 14, March 2001).

Table 2. *Abudedefduf* species colonization chronology.

Date	Location	# Fish Observed	
		<i>A. Abdominalis</i>	<i>A. Vaigiensis</i>
15 Dec 91	HO Site	2	0
5 Jun 95	Munsen's Gap	1	0
20 Feb 99	Navy Pier	1	0
19 Apr 99	Munsen's Gap	0	1
3 Jun 99	Navy Pier	1	0
3 Jun 99	Donovan's Reef	0	2
28 Aug 99	Buoy 6	0	12 ¹
28 Aug 99	Buoy 14	0	0
29 Aug 99	North Is. Back Reef	7-10	50 ²
18 Aug 00	North Is. Back Reef	10	50 ³
13 Mar 01	Buoy 14	0	3
17 Apr 01	Buoy 13	0	2
13 May 01	North Island	3	0
23 Jan 03	Tugboat	0	1
20 Feb 03	Tugboat	0	1
24 Feb 03	Boat Ramp	0	2

¹ Four nests observed and one pair spawning (1030 am). ² Both species observed with nests. ³ Both species observed with nests and hybrid spawning observed.



Figure 8. Locations within Johnston Atoll referred to in Tables 1 and 2 (1) HO site, (2) Munsen's gap, (3) west camera stand, (4) Navy pier, (5) boat ramp, (6) Sand Island wharf, (7) North Island channel, (8) North Island back reef, (9) tugboat shipwreck, (10) buoy 6, (11) buoy 13, (12) buoy 14, (13) Donovan's reef.

The labrid species in the genus *Thalassoma* are very similar morphologically, with color patterns being the main feature used to distinguish species [18]. Wrasses in the genus *Thalassoma* ($n = 27$ species worldwide) are well known to hybridize at other locations [2,18,31–33]. *T. duperrey* and *T. lutescens* are sister-species which likely diverged around 8 to 13 million years ago [18], and their hybridization is an indication of their close genetic similarity. Other hybrid *Thalassoma* populations elsewhere are shown to be fertile and able to reproduce successfully, including backcrossing to parental species [2]. Hybrid butterflyfishes (Chaetodontidae) have also been shown to be fertile [3]. The JA population of hybrids appears to be breeding and crisscross mating with other hybrids and parental species. Forthcoming research into the population genetics will be revealing and interesting (I. Fernandez Silva pers. comm.).

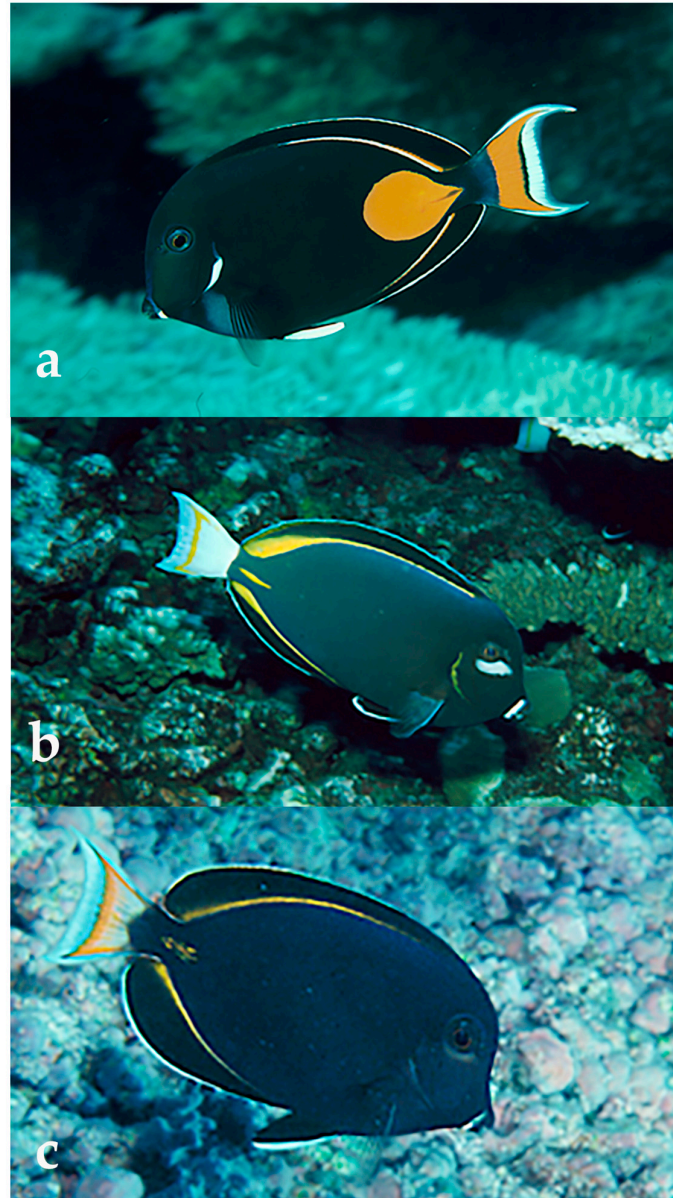


Figure 9. The acanthurids at Johnston Atoll, (a) *Acanthurus achilles*, (b) *A. nigricans* and (c) the presumptive hybrid (October, 1996).

The colonization of *Abudefduf abdominalis* and *A. vaigiensis* was remarkable as both species appeared in large numbers over the span of several months, mainly during 1999. Colonization was successful and both species and their hybrids became well established within the atoll by 2003. During this same time period, *A. vaigiensis* also became established in the main Hawaiian Islands [34,35]. This peak recruitment event of *Abudefduf* to Johnston atoll coincided with the cold El Niño–Southern Oscillation (ENSO) event (La Niña) that lasted 2 years. This La Niña period took place in 1998–2000 [36]. Coincidentally, we found a record number of glass fishing floats drifting onto the shore during this time (Lobel pers obs). Larval *Abudefduf* are well known to gather beneath drifting ocean debris, logs, and buoys [37,38]. This hypothesis could explain how invasive *A. vaigiensis* colonized the main Hawaiian Islands in the early 1990s [35]. By 2009, *A. vaigiensis* co-occurred with *A. abdominalis* throughout the Hawaiian Archipelago [35]. Hybridization between *A. abdominalis* and *A. vaigiensis* in Hawaii is well documented [34,35]. Our example from Johnston Atoll is part of this biogeographic phenomenon of *A. vaigiensis* dispersal from the equatorial Pacific to the Hawaiian

Islands. *A. vaigiensis* is a vigorous species which also recently invaded the Mediterranean Sea [39] and will hybridize with congeners elsewhere [40].

Hybrid surgeonfishes (Acanthuridae) are not rare and have been reported occurring between several species, especially among the four species that comprise the *Acanthurus achilles* complex [23,26]. Our observation of the hybrid *A. achilles* x *A. nigricans* at JA is consistent with these previous findings. It is also worth noting that a single hybrid *Chaetodon* was observed at JA by the USFWS in March 2016 (USFWS email pers comm).

Early evidence from a study of larval recruitment of the damselfish *Plectroglyphidodon imparipennis* suggested that JA had some degree of local retention of pelagic larvae [41]. Several recent genetic studies of damselfish including *A. abdominalis* [42–44], the surgeonfish *Acanthurus nigroris* [8] plus an invertebrate (a sea cucumber), [45] indicate limited connectivity between the Hawaiian archipelago and Johnston Atoll. Limited connectivity does not mean that dispersal events do not occur; these events do happen. The successful dispersal event has to have sufficient numbers in order to establish a population. This is what was observed at Johnston Atoll in 1999, associated with the La Niña oceanographic phenomena and a coincident increase in drifting debris (notably some nets, large logs, and numerous glass balls and fishing floats).

The biogeographic pattern shows that Johnston's fish fauna is dominated by Hawaiian species, but includes a mix of species from the Line Islands to the south. Twenty-five percent (153 of total 612 species) of the Hawaiian shore fishes (up to 200 m) are taxonomically recognized as endemic species [46]. A third of these Hawaiian endemics are also found on JA [9–11]. Many of these species have planktonic larval phases lasting up to three months and therefore have the potential for long-range dispersal. This includes the larvae of *T. duperrey*, with a mean larval duration of 89 ± 11 days ($n = 10$ larvae, [47]). Other hybrid hotspots are notable for the number of different species found with occasional hybrid individuals rather than a large abundance of any particular type of hybrid. Johnston Atoll is distinctive in having a significant number of individuals of one hybrid labrid that appears to have established a locally replenishing population that has existed over time. Johnston Atoll's status as a "hotspot" can then be interpreted as a place where two adjacent regional faunas overlap at a unique location in the middle.

The hypothesis that at least several fish species on Johnston Atoll are comprised of local populations with limited larval connectivity to Hawaii or the Line Islands is supported by the occurrence of one endemic species, as well as some "sub-species" or color variants, and genetic evidence from other species. Several Johnston Atoll fish species exhibit color patterns that are subtle variants from their sister-species in Hawaii [9]. The JA fish species that appear to have a different variation in coloration from their sibling populations in Hawaii include: surgeonfish (*Ctenochaetus strigosus*), parrotfish (*Scarus perspicillatus*), wrasse (*Labroides phthirophagus*), and two populations of butterflyfishes (*Chaetodon multicinctus* and *C. tinkeri*) [9,11]. Only one species of fish, the pygmy angelfish, *Centropyge nahackyi*, is recognized as endemic to the atoll [10]. Nonetheless, exotic species periodically appear at JA as single individuals, which could only be the result of larvae drifting in from the equatorial Pacific. A recent example is from a USFWS researcher who photographed a longfin batfish (*Platax teira*) in the lagoon nearby the Sand Island seaplane ramp, in March 2016 (Johnston Atoll National Wildlife Refuge US Fish and Wildlife Service, email pers comm). It is highly unlikely that this fish arrived any other way than as a stray larva.

5. Conclusions

These observations suggest that Johnston Atoll has some degree of local retention of its coral reef fish populations, but this geographic isolation is periodically compromised by large ocean current oscillations in the equatorial and central Pacific Ocean. These ocean current oscillations are highly variable and inter-annual, and can bring larvae from either the Line Islands (south) or the Hawaiian Islands (north). Although there is some long-distance mixing of populations the evidence so far suggests that JA has a significant degree of local larval retention, which results in a mostly self-replenishing reef population over the long term. To further contribute to our understanding of island biogeography and species conservation in the Pacific, these evolutionary patterns of

colonization and ecological dynamics of local population maintenance are important to define. This is a good justification for the continued study of the Johnston Atoll reef fauna and flora.

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Conflicts of Interest: The authors declare no conflict of interest.

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