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Mesophotic surveys of the flora and fauna at Johnston Atoll, Central Pacific Ocean

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Despite its extreme geographical isolation, numerous expeditions have surveyed the marine flora and fauna of Johnston Atoll. However, historical information about the marine biodiversity of Johnston is mostly limited to SCUBA surveys in shallow-waters (<30 m), and submersible observations in deeper waters (100–500 m). Extensive coral reefs, known as mesophotic coral ecosystems, exist between these two depth ranges at Johnston, but have remained largely unexplored. We used closed-circuit rebreathers to survey eleven sites at mesophotic depths (32–78 m) surrounding Johnston Atoll. A total of 130 species were recorded, including 99 species of fish, 15 species of corals, nine species of macroalgae, three species of echinoderms, three species of sponges and one species of squat lobster. Most species recorded during our mesophotic surveys have previously been recorded on shallow-water (<30 m) reefs at Johnston, with the exception of one black coral, one zoanthid, one squat lobster, two macroalgae, three sponges, and 22 fish, which represent new records for the atoll. As noted in previous studies, our surveys found a near absence of endemism, and recorded high proportions of species that are also known from the Hawaiian Archipelago. The similarity between the mesophotic biodiversity of Johnston Atoll and Hawai'i provides further support for the strong connectivity between these two locations highlighted in previous studies.

Keywords: closed-circuit rebreathers, mesophotic coral ecosystems, range expansion, technical diving

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INTRODUCTION

Located in the Central Pacific over 800 km from the Hawaiian Islands, 1,450 km from the Line Islands, and 2,500 km from the Marshall Islands, Johnston Atoll is the most remote atoll on Earth. Despite its remoteness, numerous expeditions have targeted the atoll in order to explore and characterize its marine biodiversity (reviewed by Amerson & Shelton, 1976; Lobel & Lobel, 2008). In 1880, a vessel of the North Pacific Guano Company collected 27 fish species from Johnston, including five undescribed species, which were subsequently described by scientists at the United States National Museum (Smith & Swain, 1882). In 1923, a partnership between the US Navy, the Bishop Museum and the Bureau of the Biological Survey (now US Fish and Wildlife Service) led to a series of expeditions to the north-western Hawaiian Islands, Wake Atoll and Johnston Atoll. As part of these expeditions, several scientists visited Johnston Atoll in 1923 aboard the US Navy minesweepers 'Tanager' and 'Whippoorwill' (Amerson & Shelton, 1976; Olson, 1996). These two minesweepers returned to the atoll in 1924 along with other US navy ships. Although no scientific personnel joined that expedition, biological specimens were collected for the Bishop Museum (Amerson & Shelton, 1976). Descriptions of the biota of Johnston Atoll, obtained as part of these efforts by the Bishop Museum to study the biodiversity throughout the Central Pacific, were later published in separate papers focusing on invertebrates (Edmondson *et al.*, 1925; Clark, 1949), fish (Fowler & Ball, 1925), insects (Bryan, 1926; Chilson, 1953) and birds (Olson, 1996).

In the 1960s and 1970s, the Smithsonian Institution led the Pacific Ocean Biological Survey Program, a research programme that aimed to increase the knowledge about various islands throughout the Central Pacific. As part of the programme, several biologists visited Johnston Atoll between 1963 and 1973, and although the major focus was on seabirds, other biota were also studied and inventoried (Amerson & Shelton, 1976). Throughout the 1960s, the University of Hawai'i conducted a series of studies to measure the effects of dredging on the reef ecosystems of Johnston Atoll, and in particular on the prevalence of ciguatera around the atoll (Brock *et al.*, 1965, 1966; Buggeln & Tsuda, 1969).

In 1983, the Hawai'i Undersea Research Laboratory brought its manned submersible 'Makali'i' to Johnston in order to study the deep waters surrounding the atoll. A total of 35 submersible dives were performed to maximum depths of 500 m, four of which were dedicated to geological studies (Keating, 1985), and the remainder centred on biological investigations (Randall & Ralston, 1984; Agegian &

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Abbott, 1985; Randall *et al.*, 1985; Ralston *et al.*, 1986; Chave & Mundy, 1994; Chave & Malahoff, 1998). In 2000, the Bishop Museum coordinated a major effort to inventory the shallow-water (<30 m) marine biota of Johnston as part of a survey of non-indigenous marine species of the atoll (Coles *et al.*, 2001). Following these efforts, the US National Oceanic and Atmospheric Administration (NOAA) has regularly visited Johnston since 2004, in order to further characterize and monitor the shallow-water (<30 m) algae, fish, corals and other invertebrates of the atoll (Brainard *et al.*, 2005; NOAA, 2006; Lobel & Lobel, 2008; Tsuda *et al.*, 2010).

As a result of the multitude of scientific expeditions that have surveyed Johnston, there is ample information available on the marine biodiversity found in the shallow waters (<30 m) of the atoll (reviewed by Coles *et al.*, 2001; Lobel & Lobel, 2008). Additionally, numerous records exist on the flora and fauna found in the deeper waters (100–500 m) surrounding Johnston Atoll (Randall & Ralston, 1984; Agegian & Abbott, 1985; Randall *et al.*, 1985; Ralston *et al.*, 1986; Chave & Mundy, 1994; Chave & Malahoff, 1998). However, as in many regions around the world, little is known about the marine biodiversity found between these two depth ranges. This intermediate depth range hosts mesophotic coral ecosystems (MCEs), which are light-dependent coral reefs found below the depth limits of conventional SCUBA diving (>30 m) that extend to the deepest portion of the euphotic zone, which may be over 150 m in some oceanic regions with high water clarity like Johnston (Maragos & Jokiel, 1986; Kahng & Maragos, 2006; Kahng *et al.*, 2010). The fixed upper depth limit of MCEs (30 m) corresponds to the depth limits of conventional SCUBA diving and does not represent a static ecological boundary (Kahng *et al.*, 2014). As a result, shallow-water (<30 m) and mesophotic reefs (>30 m) can be quite similar in the distributions of their flora and fauna, particularly close to the depth boundary between these two ecosystems.

The only information on the mesophotic biodiversity of Johnston Atoll is derived from a limited number of surveys for reef fish at depths between 25 and 75 m (Kosaki, 1989; Kosaki *et al.*, 1991). The purpose of this study was to survey this historically under-surveyed depth range at Johnston, in order to characterize and quantify the mesophotic flora and fauna of the atoll. Additionally, this study sought to compare the mesophotic biodiversity between Johnston Atoll and the Hawaiian Archipelago, because numerous previous studies have noted strong faunal and floral similarities between these two geographical areas (Gosline, 1955; Buggeln & Tsuda, 1969; Bailey-Brock, 1976; Grigg, 1981; Grigg *et al.*, 1981; Randall *et al.*, 1985; Maragos & Jokiel, 1986; Kosaki *et al.*, 1991; Coles *et al.*, 2001; Maragos *et al.*, 2004; Tsuda *et al.*, 2010). Due to these similarities, Johnston Atoll has been considered an important stepping stone for marine organisms reaching the Hawaiian Archipelago (Grigg, 1981; Grigg *et al.*, 1981), an interpretation that is supported by both genetic (Rivera *et al.*, 2004, 2011; Timmers *et al.*, 2011) and oceanographic studies (Kobayashi, 2006) that demonstrate strong connectivity between these two regions.

MATERIALS AND METHODS

All dive surveys were performed using closed-circuit rebreathers on a research expedition to Johnston Atoll aboard the NOAA ship 'Hi'ialakai' in the summer of 2013 (HA-13-01). Dive sites were chosen using historical charts, as well as new multibeam data collected by the NOAA ship 'Hi'ialakai'. Chosen areas contained steep vertical drop-offs and hard substrate at depths between 32 and 78 m. A total of eleven dive sites were surveyed around Johnston Atoll (Figure 1). During each survey, one diver identified and counted all large, conspicuous, diurnally-active fish to the lowest possible taxonomic level along a 25 × 2 m belt transect

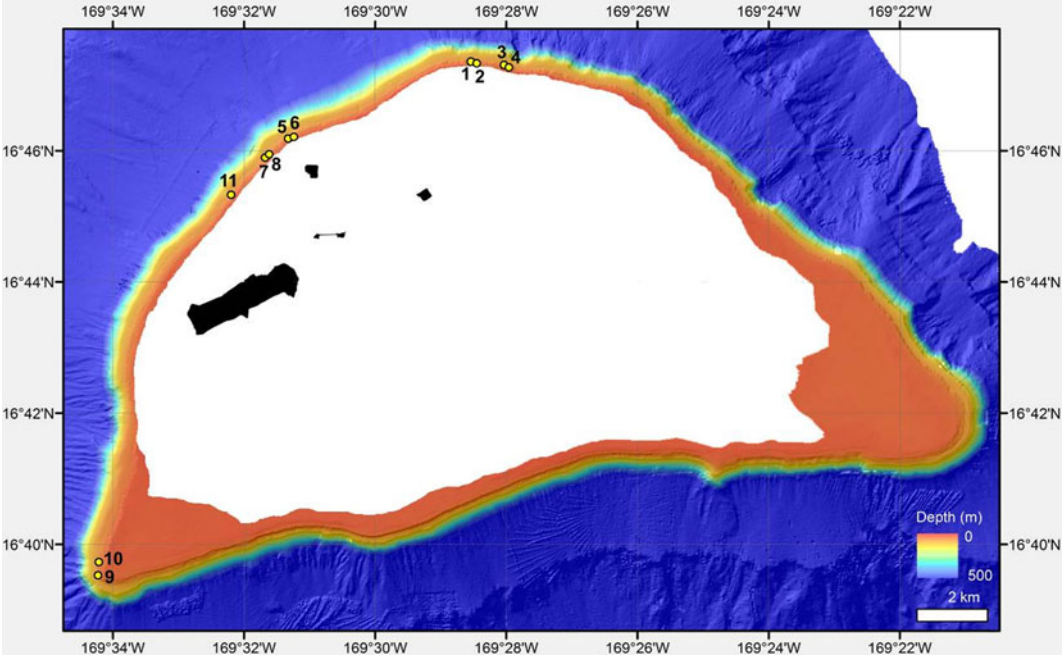

Fig. 1. Map showing the location of the eleven sites that were surveyed at mesophotic depths (32–78 m) as part of surveys of the flora and fauna off Johnston Atoll. Areas in black show the four emergent land features of Johnston Atoll.

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(Kane *et al.*, 2014). A second diver took photographs of the benthos at 25 randomly selected points along the transect using a 0.5 m^2 photoquadrat. Upon transect completion, both divers collected macroalgae, sponges and corals that could not be identified *in situ* as time permitted. No crustose coralline algae or turf algae were collected due to time constraints. Collected samples were photographed *in situ*, placed into separate bags and preserved for later identification by taxonomy experts. Additionally, both divers recorded the presence of fish and macrobenthic species that were not captured during the transect itself, and documented observations with video vouchers. Benthic cover was determined from photoquadrat images with the aid of Coral Point Count with Excel extensions software (CPCe) using 100 random points per image (Kohler & Gill, 2006). For this purpose, all macrobenthic organisms were identified to the lowest possible taxonomic level from photoquadrat images, using identifications of collected specimens by taxonomy experts where available. All species of the calcifying green alga *Halimeda* that were identified from collected specimens were grouped during the photoquadrat analysis, due to difficulties of differentiating individual species in photographs. Additionally, all identified organisms were classified *post hoc* based on their geographical distribution as being restricted to: (1) circumtropical or circumtemperate waters; (2) the Indo-Pacific; (3) the Indo-Pacific but not found in Hawai'i; or (4) Johnston Atoll and Hawai'i (Gosline, 1955; Randall *et al.*, 1985; Kosaki *et al.*, 1991).

RESULTS

Macrobenthos

A total of 31 macrobenthic species in seven phyla, 15 orders and 21 families were identified from mesophotic depths, including one antipatharian coral (*Stichopathes* sp.), one zoanthid (*Palythoa caesia*), three sponges (*Dragmacidon* sp., *Prosuberites* sp. and unidentified niphatid), two macroalgae (*Neomeris vanbosseae* and *Halimeda distorta*) and one squat lobster (*Babamunida debrae*) which were not previously recorded from Johnston Atoll (Table 1). Macrobenthic species identified to species level included 15 species of cnidarians, nine species of macroalgae, three species of echinoderms and one species of squat lobster (Table 1). With the exception of site 10, which was mostly covered by crustose coralline algae (58.0% ± 22.7%), sponges (25.5% ± 15.9%) and corals (16.5% ± 20.6%), all other sites were dominated by sand, turf algae and crustose coralline algae, which collectively accounted for 68.8–93.4% of the substrate (Figure 2). Macroalgae were generally the next most abundant macrobenthic group, and covered between 4.0 and 25.3% of the substrate, with the exception of site 10 where no macroalgae were recorded (Figure 2). Coral cover was generally low (0.56–4.56%), with the exception of sites 4 and 10, which had coral covers of 13.36% (±27.6%) and 16.50% (±20.6%), respectively (Figure 2). The most abundant macrobenthic species were the sponge *Prosubirites* sp. at site 10 (17.19% ± 14.1%), the green macroalga *Caulerpa bikinensis* at site 9 (13.72% ± 18.0), and the scleractinian corals *Acropora cytherea* (10.72% ± 28.5%) and *Montipora capitata* (9.07% ± 16.7%) at site 4 and 10, respectively (Table 1). Of the 31 macrobenthic species that were identified, 17 (54.8%) are also found throughout other Indo-Pacific locations including Hawai'i; five (16.1%) have widespread circumtropical or circumtemperate distributions, three (9.7%) are found throughout the Indo-Pacific but not in Hawai'i, three (9.7%) have unknown distributions, two (6.5%) have a distribution restricted to Hawai'i and Johnston Atoll, and one (3.2%; *Caulerpa bikinensis*) has a distribution restricted to Micronesia, French Polynesia and Johnston Atoll (Table 1).

Fish

A total of 99 fish species in 29 families were identified during mesophotic surveys, including 22 species which had not

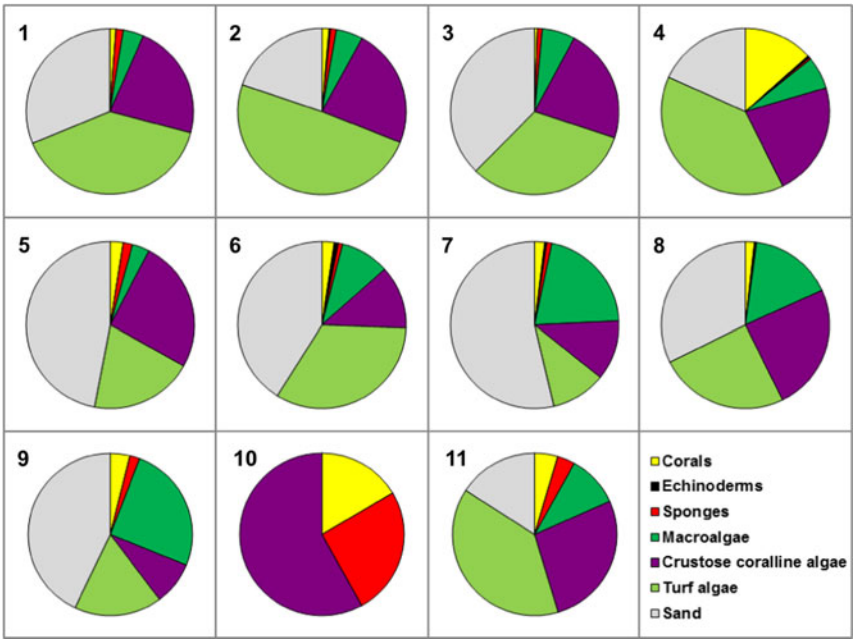

Fig. 2. Relative cover by macrobenthic group at the eleven sites that were surveyed at mesophotic depths (32–78 m) off Johnston Atoll.

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Table 1. Species of macrobenthic organisms recorded during mesophotic surveys off Johnston Atoll. *, new record for Johnston Atoll; off transect, species recorded outside of transect and therefore benthic cover data were not collected; †, percentage cover at transect with the highest value; ‡, mean percentage cover of all transects ± standard deviation.

Phylum	Order	Family	Species	Authority	Depth (m)	Identification type	Maximum cover† (%)	Mean cover‡ (%)	Geographical distribution
Arthropoda	Decapoda	Munididae	*Babamunida debrae**	Baba, 2011	61	Visual	Off transect	Off transect	Johnston and Hawai'i
Cnidaria	Anthothecata	Milleporidae	*Millepora tenera*	Boschma, 1949	46–64	Visual	1.25	0.12 (±0.38)	Indo-Pacific not Hawai'i
	Anthothecata	Stylasteridae	*Distichopora violacea*	(Pallas, 1766)	64–70	Visual	6.70	0.66 (±2.00)	Indo-Pacific not Hawai'i
	Antipatharia	Antipathidae	*Antipathes griggi*	Opresko, 2009	76	Specimen	Off transect	Off transect	Johnston and Hawai'i
	Antipatharia	Antipathidae	*Cirrhipathes* cf. *anguina*	(Dana, 1846)	47	Specimen	0.30	0.03 (±0.09)	Indo-Pacific
	Antipatharia	Antipathidae	*Stichopathes* sp.*	N/A	61	Specimen	Off transect	Off transect	Indo-Pacific
	Antipatharia	Myriopathidae	*Myriopathes* cf. *ulex*	(Ellis & Solander, 1786)	61	Specimen	Off transect	Off transect	Indo-Pacific
	Scleractinia	Acroporidae	*Acropora cytherea*	(Dana, 1846)	46–67	Visual	10.72	1.01 (±3.22)	Widespread
	Scleractinia	Acroporidae	*Montipora capitata*	(Dana, 1846)	46–70	Visual	9.07	2.06 (±2.55	Indo-Pacific
	Scleractinia	Agariciidae	*Leptoseris incrustans*	(Quelch, 1886)	46–67	Visual	0.62	0.08 (±0.18)	Indo-Pacific
	Scleractinia	Agariciidae	*Leptoseris tubulifera*	Vaughan, 1907	64–67	Visual	0.29	0.04 (±0.09	Indo-Pacific
	Scleractinia	Agariciidae	*Leptoseris hawaiiensis*	Vaughan, 1907	46–70	Visual	0.73	0.17 (±0.26)	Indo-Pacific
	Scleractinia	Agariciidae	*Pavona maldivensis*	(Gardiner, 1905)	67	Visual	0.20	0.02 (±0.06)	Indo-Pacific
	Scleractinia	Fungidae	*Cycloseries vaughani*	(Boschma, 1923)	46–66	Visual	0.18	0.03 (±0.09)	Indo-Pacific
	Scleractinia	Poritidae	*Porites lobata*	Dana, 1846	46–67	Visual	0.88	0.30 (±0.27)	Indo-Pacific
	Zoantharia	Sphenopidae	*Palythoa caesia**	Dana, 1846	46	Visual	0.08	0.01 (±0.02)	Indo-Pacific
			Total cnidarians				16.50	4.54 (±5.31)	
Echinodermata	Camarodonta	Toxopneustidae	*Tripneustes gratilla*	(Linnaeus, 1758)	46	Visual	0.13	0.02 (±0.04	Indo-Pacific
	Diadematoida	Diadematidae	*Diadema paucispinum*	Agassiz, 1863	46–47	Visual	0.80	0.13 (±0.25)	Indo-Pacific
	Valvatida	Acanthasteridae	*Acanthaster planci*	(Linnaeus, 1758)	66	Visual	0.38	0.03 (±0.11)	Indo-Pacific
			Total echninoderms				0.80	0.18 (±0.26)	
Porifera	Hadromerida	Suberitidae	*Prosuberites* sp.*	N/A	46–70	Specimen	17.19	2.02 (±5.04)	Unknown
	Halichondrida	Axinellidae	*Dragmacidon* sp.*	N/A	64–67	Specimen	0.05	0.02 (±0.02)	Unknown
	Haplosclerida	Niphatidae	Unidentified sp.*	N/A	46	Specimen	0.09	0.01 (±0.03)	Unknown
	N/A	N/A	Unidentified sponges	N/A	46–70	Visual	8.29	1.46 (±2.37)	N/A
			Total sponges				25.48	3.51 (±7.34)	
Chlorophyta	Bryopsidales	Caulerpaceae	*Caulerpa bikinensis*	W.R. Taylor, 1950	46–67	Specimen	13.72	1.34 (±4.11)	Pacific not Hawai'i
	Bryopsidales	Caulerpaceae	*Caulerpa racemosa*	(Forsskål) J. Agardh, 1873	12–61	Specimen	Off transect	Off transect	Widespread
	Bryopsidales	Caulerpaceae	*Caulerpa serrulata*	(Forsskål) J. Agardh, 1837	45–47	Specimen	0.61	0.13 (±0.23)	Widespread
	Bryopsidales	Halimedaceae	*Halimeda discoidea*	Decaisne, 1842	46	Specimen	N/A	N/A	Widespread
	Bryopsidales	Halimedaceae	*Halimeda distorta**	(Yamada) Hillis-Colinvaux, 1968	46	Specimen	N/A	N/A	Indo-Pacific
	Bryopsidales	Halimedaceae	*Halimeda taenicola*	W.R. Taylor, 1950	55–67	Specimen	N/A	N/A	Indo-Pacific not Hawai'i
	Bryopsidales	Halimedaceae	*Halimeda* spp.	N/A	46–67	Visual	20.95	8.13 (±6.02)	N/A
	Dasycladales	Dasycladaceae	*Neomeris vanbosseae**	M. Howe, 1909	46	Visual	0.84	0.08 (±0.25)	Indo-Pacific
Ochrophyta	Dictyotales	Dictyotaceae	*Dictyota ceylanica*	Kützing, 1859	61–67	Specimen	0.72	0.07 (±0.22)	Indo-Pacific
Rhodophyta	Bonnemaisoniales	Bonnemaisoniaceae	*Asparagopsis taxiformis*	(Delile) Trevisan de Saint-Léon, 1845	55	Specimen	Off transect	Off transect	Widespread
			Total macroalgae				25.32	9.74 (±7.89)	
N/A	N/A	N/A	Crustose coralline algae		46–70	Visual	58.02	23.42 (±13.06)	N/A
	N/A	N/A	Turf algae		46–67	Visual	49.17	27.71 (±14.64)	N/A
	N/A	N/A	Sand		46–67	Visual	53.67	30.89 (±15.93)	N/A
7 phyla	15 orders	21 families	31 species (8 new records)						

Table 2. Fish species recorded during mesophotic surveys off Johnston Atoll. *, new species record for Johnston Atoll; off transect, species recorded outside of transect and therefore abundance data were not collected; †, abundance at transect with the highest value; ‡, mean abundance of all transects ± standard deviation; NR, depth not recorded.

Family	Species	Authority	Depth (m)	Maximum abundance† (/m²)	Mean abundance‡ (/m²)	Geographical distribution
Acanthuridae	*Acanthurus achilles*	Shaw, 1803	8–45	Off transect	Off transect	Indo-Pacific
	Acanthurus dussumieri	Valenciennes, 1835	62–70	0.04	0.01 (±0.01)	Indo-Pacific
	*Acanthurus nigrofuscus**	(Forsskål, 1775)	39	Off transect	Off transect	Indo-Pacific
	Acanthurus olivaceus	Bloch & Schneider, 1801	36–67	0.20	0.04 (±0.06)	Indo-Pacific
	Acanthurus thompsoni	(Fowler, 1923)	35–47	0.40	0.04 (±0.12)	Indo-Pacific
	Ctenochaetus hawaiiensis	Randall, 1955	47–66	0.04	0.01 (±0.02)	Indo-Pacific
	Ctenochaetus strigosus	(Bennett, 1828)	47	0.08	0.01 (±0.02)	Johnston and Hawai'i
	*Naso caesius**	Randall & Bell, 1992	46–59	Off transect	Off transect	Indo-Pacific
	Naso hexacanthus	(Bleeker, 1855)	11–66	0.08	0.01 (±0.03)	Indo-Pacific
	Naso lituratus	(Forster, 1801)	33–70	0.08	0.01 (±0.03)	Indo-Pacific
	*Naso thynnoides**	(Cuvier, 1829)	48–70	Off transect	Off transect	Indo-Pacific
	Zebrasoma flavescens	(Bennett, 1828)	9–47	0.04	0.01 (±0.01)	Indo-Pacific
Apogonidae	*Pristiapogon kallopterus*	(Bleeker, 1856)	65–78	Off transect	Off transect	Indo-Pacific
Aulostomidae	*Aulostomus chinensis*	(Linnaeus, 1766)	7–70	0.02	0.00 (±0.01)	Indo-Pacific
Balistidae	*Melichthys vidua*	(Richardson, 1845)	9–70	0.08	0.01 (±0.02)	Indo-Pacific
	Sufflamen bursa	(Bloch & Schneider, 1801)	46–70	0.08	0.02 (±0.03)	Indo-Pacific
	Xanthichthys auromarginatus	(Bennett, 1832)	21–65	0.02	0.00 (±0.01)	Indo-Pacific
	*Xanthichthys caeruleolineatus**	Randall, Matsuura & Zama, 1978	41–63	Off transect	Off transect	Indo-Pacific
Carangidae	*Carangoides orthogrammus*	(Jordan & Gilbert, 1882)	10–66	0.04	0.00 (±0.01)	Indo-Pacific
	Caranx lugubris	Poey, 1860	50–66	0.04	0.01 (±0.02)	Widespread
	Caranx melampygus	Cuvier, 1833	46	0.02	0.00 (±0.01)	Indo-Pacific
	Caranx sexfasciatus	Quoy & Gaimard, 1825	67	Off transect	Off transect	Widespread
	Decapterus macarellus	(Cuvier, 1833)	64	Off transect	Off transect	Widespread
	*Naucrates ductor**	(Linnaeus, 1758)	65	Off transect	Off transect	Widespread
	*Uraspis helvola**	(Forster, 1801)	60–70	Off transect	Off transect	Widespread
Carcharhinidae	*Carcharhinus amblyrhynchos*	(Bleeker, 1856)	46–70	0.06	0.01 (±0.02)	Indo-Pacific
	Triaenodon obesus	(Rüppell, 1837)	50–70	0.02	0.00 (±0.01)	Indo-Pacific
Chaetodontidae	*Chaetodon auriga*	Forsskål, 1775	45–66	0.02	0.00 (±0.01)	Indo-Pacific
	*Chaetodon kleinii**	Bloch, 1790	47	0.02	0.00 (±0.01)	Indo-Pacific
	Chaetodon multicinctus	Garrett, 1863	42	Off transect	Off transect	Johnston and Hawai'i
	Chaetodon tinkeri	Schultz, 1951	47–72	0.04	0.01 (±0.01)	Indo-Pacific
	Chaetodon trifascialis	Quoy & Gaimard, 1825	46	0.04	0.00 (±0.01)	Indo-Pacific
	Forcipiger flavissimus	Jordan & McGregor, 1898	42–46	0.02	0.00 (±0.01)	Indo-Pacific
	*Forcipiger longirostris**	(Broussonet, 1782)	32	Off transect	Off transect	Indo-Pacific
	*Hemitaurichthys polylepis**	(Bleeker, 1857)	31–32	Off transect	Off transect	Indo-Pacific
	Hemitaurichthys thompsoni	Fowler, 1923	32	Off transect	Off transect	Indo-Pacific
Cirrhitidae	*Cirrhitus pinnulatus*	(Forster, 1801)	61–67	Off transect	Off transect	Indo-Pacific
	Paracirrhites arcatus	(Cuvier, 1829)	9–67	Off transect	Off transect	Indo-Pacific
	Paracirrhites forsteri	(Schneider, 1801)	63	Off transect	Off transect	Indo-Pacific
Fistulariidae	*Fistularia commersonii*	Rüppell, 1838	67	Off transect	Off transect	Indo-Pacific
Gobiidae	*Trimma milta**	Winterbottom, 2002	75	Off transect	Off transect	Indo-Pacific

Continued

Table 2. Continued

Family	Species	Authority	Depth (m)	Maximum abundance† (/m²)	Mean abundance‡ (/m²)	Geographical distribution
	*Trimma taylori**	Lobel, 1979	61	Off transect	Off transect	Indo-Pacific
Holocentridae	*Myripristis berndti*	Jordan & Evermann, 1903	35–67	Off transect	Off transect	Indo-Pacific
	Myripristis chryseres	Jordan & Evermann, 1903	58–67	Off transect	Off transect	Indo-Pacific
	Sargocentron spiniferum	(Forsskål, 1775)	32–67	0.02	0.00 (±0.01)	Indo-Pacific
Labridae	*Bodianus albotaeniatus*	(Valenciennes, 1839)	45–67	0.04	0.01 (±0.01)	Johnston and Hawai'i
	Coris ballieui	Vaillant & Sauvage, 1875	65	Off transect	Off transect	Johnston and Hawai'i
	Coris flavovittata	(Bennett, 1828)	47	0.02	0.00 (±0.01)	Johnston and Hawai'i
	Coris gaimard	(Quoy & Gaimard, 1824)	34–46	0.02	0.00 (±0.01)	Indo-Pacific
	Labroides phthirophagus	Randall, 1958	50	Off transect	Off transect	Johnston and Hawai'i
	Iniistius pavo	(Valenciennes, 1840)	65	Off transect	Off transect	Indo-Pacific
	*Oxycirrhitus typus**	Bleeker, 1857	74	Off transect	Off transect	Indo-Pacific
	*Oxycheilinus bimaculatus**	(Valenciennes, 1840)	62	Off transect	Off transect	Indo-Pacific
	Pseudocheilinus evanidus	Jordan & Evermann, 1903	36–70	0.06	0.02 (±0.03)	Indo-Pacific
	*Pseudocheilinus ocellatus**	Randall, 1999	44–65	Off transect	Off transect	Indo-Pacific
	Pseudojuloides cerasinus	(Snyder, 1904)	45–46	0.02	0.00 (±0.01)	Indo-Pacific
	Thalassoma duperrey	(Quoy & Gaimard, 1824)	34–47	0.04	0.00 (±0.01)	Johnston and Hawai'i
Lethrinidae	*Monotaxis grandoculis**	(Forsskål, 1775)	34	Off transect	Off transect	Indo-Pacific
Lutjanidae	*Aprion virescens*	Valenciennes, 1830	46–60	0.02	0.00 (±0.01)	Indo-Pacific
	Aphareus furca	(Lacépède, 1801)	7–75	Off transect	Off transect	Indo-Pacific
Malacanthidae	*Malacanthus brevirostris*	Guichenot, 1848	42–50	0.02	0.00 (±0.01)	Indo-Pacific
Microdesmidae	*Gunnellichthys curiosus**	Dawson, 1968	67–71	Off transect	Off transect	Indo-Pacific
Mullidae	*Mulloidichthys vanicolensis*	(Valenciennes, 1831)	32	Off transect	Off transect	Indo-Pacific
	Parupeneus cyclostomus	(Lacépède, 1801)	8–72	0.06	0.01 (±0.02)	Indo-Pacific
	*Parupeneus insularis**	Randall & Myers, 2002	8–72	0.02	0.00 (±0.01)	Indo-Pacific
	Parupeneus multifasciatus	(Quoy & Gaimard, 1825)	34–67	0.12	0.03 (±0.04)	Indo-Pacific
	Parupeneus pleurostigma	(Bennett, 1831)	47	0.02	0.00 (±0.01)	Indo-Pacific
Muraenidae	*Gymnothorax javanicus*	(Bleeker, 1859)	13–45	Off transect	Off transect	Indo-Pacific
	Gymnothorax meleagris	(Shaw & Nodder, 1795)	45–64	0.02	0.00 (±0.01)	Indo-Pacific
	Gymnothorax undulatus	(Lacépède, 1803)	60	Off transect	Off transect	Indo-Pacific
Ostraciidae	*Ostracion whitleyi*	Fowler, 1931	31–58	Off transect	Off transect	Indo-Pacific
Pinguipedidae	*Parapercis schauinslandii*	(Steindachner, 1900)	46–67	0.03	0.01 (±0.02)	Indo-Pacific
Pomacanthidae	*Centropyge fisheri**	(Snyder, 1904)	59–64	Off transect	Off transect	Indo-Pacific
	Centropyge loricula	(Günther, 1874)	37–70	0.06	0.01 (±0.03)	Indo-Pacific
	Centropyge nahackyi	Kosaki, 1989	41–70	0.12	0.03 (±0.05)	Johnston and Hawai'i
	Centropyge potteri	(Jordan & Metz, 1912)	38	Off transect	Off transect	Johnston and Hawai'i
Pomacentridae	*Apolemichthys arcuatus*	(Gray, 1831)	50–56	Off transect	Off transect	Johnston and Hawai'i
	Chromis acares	Randall & Swerdloff, 1973	47	Off transect	Off transect	Indo-Pacific
	Chromis agilis	Smith, 1960	61–75	Off transect	Off transect	Indo-Pacific
	Chromis verater	Jordan & Metz, 1912	45–78	0.52	0.14 (±0.17)	Johnston and Hawai'i
	Dascyllus albisella	Gill, 1862	50–67	0.02	0.00 (±0.01)	Johnston and Hawai'i
Pterelectridae	*Nemateleotris magnifica*	Fowler, 1938	8–63	Off transect	Off transect	Indo-Pacific
	Ptereleotris heteroptera	(Bleeker, 1855)	62–64	Off transect	Off transect	Indo-Pacific
Scaridae	*Calotomus carolinus*	(Valenciennes, 1840)	7–70	Off transect	Off transect	Indo-Pacific
	Calotomus sp.*	N/A (*C.* cf. *spinidens* or undescribed)	64	Off transect	Off transect	Johnston and Hawai'i

	Chlorurus perspicillatus	(Steindachner, 1879)	67	0.02	0.00 (±0.01)	Johnston and Hawai'i
	Chlorurus sordidus	(Forsskål, 1775)	46	0.02	0.00 (±0.01)	Indo-Pacific
	Scarus dubius	Bennett, 1828	47–50	0.02	0.00 (±0.01)	Johnston and Hawai'i
	Scarus psittacus	Forsskål, 1775	47	0.02	0.00 (±0.01)	Indo-Pacific
Scorpaenidae	*Scorpaenopsis diabolus*	(Cuvier, 1829)	60	Off transect	Off transect	Indo-Pacific
Serranidae	*Caprodon unicolor**	Katayama, 1975	75	Off transect	Off transect	Johnston and Hawai'i
	*Luzonichthys earlei**	Randall, 1981	46	0.12	0.01 (±0.04)	Indo-Pacific
	Pseudanthias randalli	(Lubbock & Allen, 1978)	54–70	0.40	0.01 (±0.01)	Indo-Pacific not Hawai'i
Sphyraenidae	*Sphyraena barracuda*	(Edwards, 1771)	1–40	Off transect	Off transect	Widespread
Tetraodontidae	*Arothron meleagris*	(Lacépède, 1798)	45–50	Off transect	Off transect	Indo-Pacific
	Canthigaster coronata	(Vaillant & Sauvage, 1875)	64	Off transect	Off transect	Johnston and Hawai'i
	Canthigaster jactator	(Jenkins, 1901)	8–75	0.04	0.01 (±0.01)	Johnston and Hawai'i
	*Canthigaster epilampra**	(Jenkins, 1903)	62–67	Off transect	Off transect	Indo-Pacific
Zanclidae	*Zanclus cornutus*	(Linnaeus, 1758)	46–70	0.04	0.01 (±0.02)	Indo-Pacific
29 families	99 species (22 new records)					

previously been recorded from Johnston Atoll (Table 2). Additionally, we recorded *Centropyge fisheri*, a species with an uncertain previous sighting at Johnston Atoll (Randall *et al*., 1985). In terms of number of individuals, *Chromis verater*, *Pseudanthias randalli*, *Acanthurus olivaceus*, *A. thompsoni*, *Centropyge nahackyi*, *Parupeneus multifasciatus*, *Pseudocheilinus evanidus* and *Sufflamen bursa* were most common (Table 2). With the exception of *A. thompsoni*, which was only recorded at one site, this group of fish was also most widespread, being recorded from seven (*Chromis verater*) to three (*Pseudanthias randalli*) of the surveyed sites. Among species that were less abundant, *Canthigaster jactator*, *Parapercis schauinslandii*, *Centropyge loricula*, *Bodianus albotaeniatus*, *Chaetodon tinkeri*, *Ctenochaetus hawaiiensis*, *Zanclus cornutus* and *Acanthurus dussumieri* were widespread on the surveyed mesophotic reefs, being recorded at three or more of the surveyed sites. Of the 99 fish species that were identified, 74 (74.7%) are widely distributed throughout the Indo-Pacific including Hawai'i, 18 (18.2%) are restricted to Johnston Atoll and Hawai'i, six (6.1%) have widespread circumtropical distributions, and one (1.0%; *Pseudanthias randalli*) is found throughout the Pacific but not in Hawai'i (Table 2).

DISCUSSION

In contrast to the shallow (<30 m) and deep-water (100–500 m) marine biodiversity of Johnston, which has been extensively surveyed (reviewed by Coles *et al*., 2001), only limited surveys have been performed at mesophotic depths surrounding the atoll (Kosaki, 1989; Kosaki *et al*., 1991). This study thus represents the first dedicated effort to inventory and quantify the mesophotic flora and fauna at Johnston Atoll. We recorded a total of 130 species from mesophotic depths, most of which (76.4%) have also been found during previous shallow-water (<30 m) surveys off Johnston Atoll (Tables 1 & 2). This indicates that the mesophotic flora and fauna of Johnston is not composed of a specialized group of species, but rather consists of a subset of species that is also found in shallow waters (<30 m). The only species which have not been found in previous surveys off Johnston Atoll include one black coral, one zoanthid, one squat lobster, two macroalgae, three sponges and 22 fish (Tables 1 & 2). With the exception of the three sponges, which have unknown geographical distributions (Table 1), all other species are commonly found in shallow-water reefs throughout the Indo-Pacific (Hoover, 2006; Huisman *et al*., 2007; Randall, 2007). Thus, it is likely that these species have been missed in previous shallow-water surveys at Johnston, and are not restricted to mesophotic depths at the atoll. This interpretation is consistent with most mesophotic surveys in the Hawaiian Islands, which indicate that the mesophotic flora and fauna are composed mainly of the same species, albeit in different proportions, that are also found in shallow waters (Brock & Chamberlain, 1968; Parrish & Boland, 2004; Rooney *et al*., 2010; Kane *et al*., 2014). However, in some Hawaiian locations, the mesophotic benthic flora and fauna appears distinct from shallow-water (<30 m) communities (Kahng & Kelley, 2007; Spalding, 2012).

Our surveys indicate that mesophotic reefs off Johnston are covered mostly by turf algae, crustose coralline algae, macroalgae and sand (Figure 2). These groups were also identified as

being most abundant in previous surveys on many shallow-water (<18.3 m) reefs off Johnston Atoll (Brainard *et al.*, 2005; NOAA, 2006). However, previous shallow-water surveys off Johnston have also noted high coral cover on several reefs of the atoll, particularly inside the lagoon, where coral cover can approach 100% (Maragos & Jokiel, 1986; Jokiel & Tyler, 1992; Brainard *et al.*, 2005; NOAA, 2006). In contrast, coral cover at most of our mesophotic sites was generally low (0.56–4.56%), with the exception of two sites which had 13.36% and 16.50% coral cover (Figure 1). The most commonly recorded corals during our mesophotic surveys were *Acropora cytherea*, *Montipora capitata*, *Distichopora violacea* and *Millepora tenera* (Table 1). With the exception of *Distichopora violacea*, these coral species are also dominant on shallow-water (<18.3 m) reefs of the atoll (Maragos & Jokiel, 1986; NOAA, 2006). Additionally, *Montipora patula*, *Pavona* spp. and *Pocillopora* spp. are also dominant on shallow-water (<18.3 m) reefs of Johnston (Maragos & Jokiel, 1986; NOAA, 2006); all species which we did not record during our mesophotic surveys (Table 1). Among macrobenthic species identified during our mesophotic surveys, only the green alga *Caulerpa bikinensis*, the scleractinian coral *Leptoseries hawaiiensis* and the black corals *Antipathes griggi* and *Myriopathes* cf. *ulex* were recorded during previous deep-water (>100 m) submersible surveys off Johnston Atoll (Agegian & Abbott, 1985; Maragos & Jokiel, 1986; Coles *et al.*, 2001).

The most common reef fish recorded during our mesophotic surveys were *Chromis verater*, *Pseudanthias randalli*, *Acanthurus olivaceus*, *A. thompsoni*, *Centropyge nahackyi*, *Parupeneus multifasciatus*, *Pseudocheilinus evanidus* and *Sufflamen bursa* (Table 2). While all of these species have been recorded during previous shallow-water (<30 m) surveys at Johnston, only *Parupeneus multifasciatus* and *Sufflamen bursa* are also reported as being abundant on shallow-water (<18.3 m) reefs off the atoll (NOAA, 2006). Among species that were abundant at our mesophotic sites (Table 2), only *Parupeneus multifasciatus* was also reported as being abundant during previous deep-water (100–365 m) surveys at Johnston Atoll (Ralston *et al.*, 1986). In contrast, many of the species we recorded at mesophotic depths have also been recorded during previous deep-water (>100 m) submersible surveys off Johnston, including *Carcharhinus amblyrhynchos*, *Myripristis chryseres*, *Parapercis schauinslandi*, *Carangoides orthogrammus*, *Caranx lugubris*, *C. melampygus*, *Chromis verater*, *Parupeneus cyclostomus*, *P. multifasciatus*, *Chaetodon tinkeri*, *Forcipiger flavissimus*, *Bodianus albotaeniatus*, *Acanthurus dussumeri*, *Naso hexacanthus*, *Zanclus cornutus* and *Xanthichthys auromarginatus* (Randall *et al.*, 1985; Ralston *et al.*, 1986; Chave & Mundy, 1994).

Abundances of macrobenthic organisms recorded during our surveys (Table 1), differed from those recorded during mesophotic surveys in the Hawaiian Islands (Rooney *et al.*, 2010). The mesophotic benthos at Johnston consists mostly of crustose coralline algae (8.6–58%), sand (0–54%), turf algae (0–49%) and macroalgae (0–21%), with coral cover being low at most mesophotic locations (0.56–4.56%) (Figure 2). In contrast, at similar depths (40–70 m) Rooney *et al.* (2010) noted that the macrobenthos in the north-western Hawaiian Islands was mostly covered by sand (45–55%), macroalgae (25–40%), crustose coralline algae (~5%), and coral (~2%). While the ultimate drivers for these differences remain unknown, they might be related to differences in the temperature regimes between Johnston Atoll and Hawai'i. Johnston is located much closer to the equator (16°N) than the Hawaiian Archipelago (19–28°N) and as a result experiences elevated water temperatures. Previous studies note that sea surface temperatures show little seasonality at Johnston and range between 25 and 27°C (Ralston *et al.*, 1986; Boehlert *et al.*, 1992). In comparison, sea surface temperatures can dip as low as 16°C in the north-western Hawaiian Islands (Kane *et al.*, 2014). Differences in temperature regime have been related to differences in macrobenthic cover within the Hawaiian Archipelago (Grigg *et al.*, 2008; Rooney *et al.*, 2010; Spalding, 2012), and might also explain why macroalgal cover is reduced at Johnston Atoll (0–21%; Figure 2) compared to the north-western Hawaiian Islands (25–40%; Rooney *et al.*, 2010).

Consistent with previous biogeographical studies (Gosline, 1955; Maragos & Jokiel, 1986; Kosaki *et al.*, 1991; Maragos *et al.*, 2004), our mesophotic surveys recorded a near absence of species that are endemic to Johnston Atoll. The scarcity of endemic species has previously been noted among many different taxa at Johnston Atoll, including fish (Gosline, 1955; Randall *et al.*, 1985; Kosaki *et al.*, 1991), corals (Maragos & Jokiel, 1986), algae (Buggeln & Tsuda, 1969; Agegian & Abbott, 1985; Tsuda *et al.*, 2010) and crustaceans (Edmondson *et al.*, 1925; Amerson & Shelton, 1976). The only potential endemic species from Johnston Atoll are three unidentified reef fish (Randall *et al.*, 1985; Kosaki *et al.*, 1991), the angelfish *Centropyge nahackyi* (Kosaki, 1989), the ostracods *Parasterope pacifica* and *Bruuniella beta* (Kornicker & Harrison-Nelson, 2005), the red alga *Neotenophycus ichthyosteus* (Tsuda *et al.*, 2010), the cyanobacterium *Borzia elongata* (Tsuda *et al.*, 2010), the gammaproteobacterium *Pseudoxanthomonas kalamensis* (Harada *et al.*, 2006) and the three unidentified sponges recorded during this study (Table 1). However, several of these species will likely be found in other locations in the future, either as solitary waifs from Johnston Atoll (Kosaki, 1989), or as species that were originally described from Johnston Atoll (Fowler & Ball, 1925; Bryan, 1926), but were subsequently found to have reproducing populations elsewhere in the Indo-Pacific.

Despite its extreme geographical isolation, the very low level of endemism indicates that Johnston is relatively well connected with other parts of the Pacific, particularly Hawai'i (Grigg, 1981; Grigg *et al.*, 1981; Rivera *et al.*, 2004, 2011; Kobayashi, 2006; Timmers *et al.*, 2011). Kobayashi (2006) used computer simulations and high-resolution current data to identify at least two corridors connecting Johnston Atoll with the Hawaiian Archipelago, an interpretation that is consistent with genetic studies (Rivera *et al.*, 2004, 2011; Timmers *et al.*, 2011). Additionally, many other studies highlight the strong floral and faunal similarities between Johnston Atoll and the Hawaiian Islands (Gosline, 1955; Buggeln & Tsuda, 1969; Bailey-Brock, 1976; Grigg, 1981; Grigg *et al.*, 1981; Randall *et al.*, 1985; Maragos & Jokiel, 1986; Kosaki *et al.*, 1991; Coles *et al.*, 2001; Maragos *et al.*, 2004; Tsuda *et al.*, 2010). These studies report that the flora and fauna of Johnston Atoll are mostly composed of species that are also found in Hawai'i, with 91% of all marine species found at Johnston also occurring in Hawai'i (reviewed by Coles *et al.*, 2001). Our results are consistent with these previous studies, as 96% of species identified during our mesophotic surveys are also known from Hawai'i

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(Tables 1 & 2). Additionally, this pattern was consistent amongst various taxonomic groups identified during our mesophotic surveys, as 100% of echinoderms, 99% of reef fish, 87% of corals and 78% of macroalgae are also known to occur in Hawai'i (Tables 1 & 2). In comparison, previous studies noted that 94% of reef fish species (Randall *et al.*, 1985; Kosaki *et al.*, 1991), 74% of coral species (Maragos *et al.*, 2004) and 94% of algal species (excluding cyanobacteria) of Johnston Atoll are also found in Hawai'i (Roy Tsuda, unpublished data). It is currently unknown whether the three unidentified sponge species recorded during this study also occur in Hawai'i and elsewhere in the Indo-Pacific. Further investigations will be necessary to determine the taxonomic status and geographical affinities of the sponge species recorded during our surveys.

Coral reef ecosystems below the depth limits of conventional SCUBA diving remain scarcely surveyed worldwide, and particularly in remote locations like Johnston Atoll. This study represents the first dedicated effort to characterize the mesophotic flora and fauna at Johnston Atoll. Our results support the strong connectivity between Johnston Atoll and the Hawaiian Archipelago highlighted by previous studies. Finally, this study adds 30 new records to Johnston Atoll, thereby emphasizing the value of deep-diving technologies in surveying the largest portion of the depth range of coral reef ecosystems (30–150 m), which remains largely unexplored.

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