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Keep your friends close and your anemones closer – ecology of the endemic wideband anemonefish, *Amphiprion latezonatus*

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Abstract Endemic marine species often exist as metapopulations distributed across several discrete locations, such that their extinction risk is dependent upon population dynamics and persistence at each location. The anemonefish *Amphiprion latezonatus* is a habitat specialist, endemic to two oceanic islands (Lord Howe and Norfolk) and the adjacent eastern Australian coast from the Sunshine Coast to Southwest Rocks. To determine how extinction risk varies across the limited number of locations where *A. latezonatus* occurs, we quantified ecological, biological, and behavioural characteristics at six locations and four reef zones. The abundance of *A. latezonatus* and its host anemones varied considerably throughout its range, with *A. latezonatus* abundance being very low at Sunshine Coast and Elizabeth Reef, low at Lord Howe Island and Norfolk Island, and moderate at North Solitary Island. This species was not detected at Middleton Reef, despite local abundance of their host anemones. Abundance of *A. latezonatus* was generally correlated with depth and host anemone abundance, from which we infer that extirpation risk is directly proportional to their host anemone population's size. Consistent with this, *A. latezonatus* social group size was positively correlated with the number of anemones inhabited. *A. latezonatus* may be impacted by interactions and competition with other anemonefish species in shallow (< 10 m) waters, but competition has little effect in deeper water where population abundances are highest. Significant differences in population characteristics demonstrate a need for location-specific conservation strategies and identify the Sunshine Coast population as most vulnerable.

Keywords Anemone bleaching · Endemic · Climate change · Clownfish · Conservation · Reef

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Introduction

Endemic species are inherently vulnerable to extinction, though extinction risk may be further compounded by other ecological, biological, and behavioural traits (Lawton 1993; Gaston 1998; Frankham 1998; Dowding and Murphy 2001; Munday 2004). Due to the discontinuities of benthic habitats in many marine systems, many endemic marine species exist as isolated metapopulations (Kritzer and Sale 2004), such that species persistence depends on the viability of each discrete population (Wiens 1989). For example, coral reefs species occur on discrete reef patches separated by deep oceans. Despite the propensity for marine species to form metapopulations, the majority of research on metapopulation persistence and variability of traits among populations has focused on terrestrial ecosystems (Hanski et al. 1997). The need to understand trait variability and persistence in populations of marine species is particularly pertinent given escalating human impacts.

Marine ecosystems are increasingly threatened by environmental change, diseases, overharvesting, and invasive species (Goldberg and Wilkinson 2004). On coral reefs, rising sea temperatures have caused bleaching events resulting in mass mortality of corals and anemones (Wilkinson 1998; Hoegh-Guldberg 1999; Hattori 2002; Hobbs et al. 2013; Hughes et al. 2017). The subsequent habitat loss has had negative flow-on effects, particularly for ecological specialists (Pratchett et al. 2008). Among the most specialised of reef fishes are anemonefishes, which have an obligate association with specific host anemones (Jones et al. 2002; Pratchett et al. 2016). The close relationship between anemones and anemonefishes means that characteristics (e.g., size, number, quality) of anemones influence the size and replenishment of anemonefish populations (Hattori 2002; Saenz-Agudelo et al. 2011; Hobbs et al. 2013; Frisch et al. 2019). Local extinction of anemonefishes has also occurred following mass bleaching of host anemones (Hattori 2002). Overharvesting of anemonefishes and their host anemones also threatens population persistence (Shuman et al. 2005; Frisch et al. 2016, 2019).

Habitat patches within a species range are often environmentally heterogeneous, leading to differences in abundance, distribution, and resource use across locations. On coral reefs, for example, the abundance and habitat use of fishes varies with reef structure, habitat size and quality (Noonan et al. 2012; Nadler et al. 2013), competition with congenerics (Ormond et al. 1996; Robertson 1996; Bonin et al. 2015), and microhabitat selectivity (Fulton et al. 2016; Pratchett et al. 2016). Due to this variability, a thorough assessment of vulnerability in marine species requires understanding how traits vary across the entire geographic range, rather than assuming a single population represents the whole.

The Lord Howe Island – Norfolk Island region (29.04–31.55°S) in the south-west Pacific Ocean is a hotspot for endemic coral reef species, where many endemics are distributed across four isolated reefs and islands (Randall 1976, 1998; van der Meer et al. 2013, 2014; Steinberg et al. 2016). Some endemics also occur on the adjacent Australian mainland coast to the west of the hotspot. This is one of the most rapidly warming ocean regions due to climate change effects on the East Australian Current (Ridgway 2007; Hobday and Pecl 2013; Robinson et al. 2015) and has already caused at least three bleaching events at Lord Howe Island which affected corals and anemones (Harrison et al. 2011; Moriarty et al. 2019).

The purpose of this study was to determine spatial variation in ecological, biological, and behavioural traits for the wideband anemonefish, *Amphiprion latezonatus*. This was achieved by surveying at two spatial scales (reef zone and location) at six discreet locations across its geographic range. Existing knowledge of the biology and ecology of this study species comes from research conducted at one location on mainland Australia – North Solitary Island (Richardson 1999; Scott et al. 2011). Little is known about the other populations at oceanic locations, where environmental conditions differ considerably to those experienced by mainland populations. The specific aims of this study were to determine variability among locations and across reef zones within locations in: 1) host anemone abundance and reef zone distribution; 2) *A. latezonatus* abundance and reef zone distribution*;* 3) *A. latezonatus* social group size and composition; 4) *A. latezonatus* host anemone species use and occupancy rates; and 5), life history of *A. latezonatus* (age and pelagic larval duration). Insufficient samples limited inferences for the fifth aim.

Methods

Study species

Amphiprion latezonatus occurs on rocky and coral reefs at oceanic locations (Lord Howe and Norfolk Islands) and along the subtropical east Australian coast from the Sunshine Coast to South West Rocks (Fautin and Allen 1997; Fig. 1). Along the east Australian coast, populations of *A. latezonatus* are extremely small, except at North Solitary Island (Richardson 1996). *A. latezonatus* is a habitat specialist, originally reported to inhabit only one species of anemone, *Heteractis crispa* (Fautin and Allen 1997; Santini and Polacco 2006). Along the Australian coastline *A. latezonatus* also inhabits the anemone *Entacmaea quadricolor* and was once recorded occupying *Stichodactyla gigantea* (Richardson 1999; Scott et al. 2011, 2016; Malcolm and Scott 2017).

Survey design

To build on previous research undertaken at North Solitary Island, this study surveyed all three other locations known to sustain populations of *A. latezonatus* – Norfolk Island, Lord Howe Island, and Sunshine Coast. Two adjacent oceanic locations (Middleton Reef and Elizabeth Reef) where *A. latezonatus* populations have not been recorded were also surveyed because many other Lord Howe Island-Norfolk Island endemics occur at these remote reefs, as do the host anemones *H. crispa* and *E. quadricolor* (van der Meer et al. 2012, 2013, 2014). To determine variation in the distribution and abundance of *A. latezonatus* and its host anemones, underwater visual surveys (belt transects and timed swims) were undertaken in four distinct reef zones at all five surveyed locations: lagoon (1–3 m), outer reef crest (~5 m), outer reef slope (~15 m), and deep outer reef (~30 m). By swimming at constant speed, surveying a constant width (5 m) and recording survey duration (mins), timed swims were converted to reef area. Timed swims were used instead of belt transects in the deep outer reef to increase survey efficiency given time constraints associated with deep diving. Variability in survey area was due to differences in dive duration. Sites were randomly selected. Details of survey methods are provided in Supplement 1 and Table 1. All abundance data were standardized to abundance per 250 m^{-2}.

Host anemone species were identified using the description by Fautin and Allen (1997). Host anemone species inhabited and occupancy rate (whether the anemone was inhabited) were recorded for every host anemone encountered in surveys. To determine social group size and composition, the size and number of *A. latezonatus* in each social group and the number of anemones inhabited were recorded. A social group was defined as the number of anemonefish per anemone or cluster of anemones within 1 m of each other. *A. latezonatus* individuals were categorised into three size classes: adult size >50 mm total length (TL), juveniles 25–50 mm TL, and new recruits <25 mm TL. Total length of each fish was either visually estimated to the nearest 5 mm or measured underwater after capture using a hand net.

Life history

All adult pairs found in anemone clusters were assumed to be breeding pairs, and surfaces within 1 m of the anemone were searched for egg clutches to determine breeding season. Egg clutches were expected during all surveys because *A. latezonatus* breed year-round at North Solitary Island, with a peak in the Austral summer (Richardson et al. 1997). To estimate age and pelagic larval duration (PLD), five adult individuals were captured and euthanized using a clove oil anaesthetic solution. Age was estimated by removing and transversely sectioning sagittal otoliths (ear bones) following Wilson and McCormick 1999, using the equipment and approach outlined in Hobbs et al. 2014. Increments at the otolith core were assumed to represent daily rings up to the settlement mark, which is characterized by an abrupt decrease in increment width (Wilson and McCormick 1999). Broad bands after the settlement event were assumed to be annual rings. For both PLD and age, otolith rings were counted on three different days, by the same reader. There were no differences between otoliths counts of any sampled individuals.

Statistical analyses

Distribution and abundance

All statistical analyses were performed in R version 3.6.1 (R Core Team 2016). Differences in abundances of both *A. latezonatus* and host anemones between reef zones (deep outer reef, outer reef slope, reef crest, and lagoon) both within and between all five study locations, were examined using a Scheirer-Ray-Hare test as data were non-normal. Pairwise comparisons were examined using the Welch two sample t-test (two tailed), as it allows for unequal sample sizes. Though the t-test assumes unequal variance and normal distribution, it is still robust for skewed distributions and recommended above non-parametric tests for large datasets (Fagerland 2012). α-

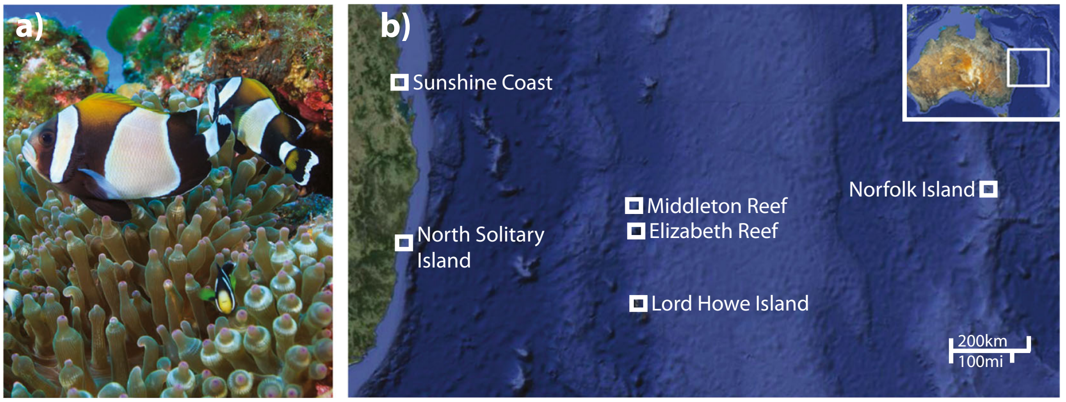

Fig. 1 Study species and sampling locations. a) A social group of *Amphiprion latezonatus* (two adults and one juvenile) in *Entacmaea quadricolor* at Lord Howe Island, photograph by Tane Sinclair-Taylor. b) Google Earth image of Eastern Australia and Tasman Sea showing *Amphiprion latezonatus* inhabited locations and study sites: Sunshine Coast (26.6500°S, 153.0667°E), North Solitary Island (29.9294°S, 153.3915°E), Middleton Reef (29.4722°S, 159.1194°E), Elizabeth Reef (29.9417°S, 159.0625°E), Lord Howe Island (31.5553°S, 159.0821°E), and Norfolk Island (29.0408°S, 167.9547°E). All sites were surveyed except North Solitary Island, where data from Scott et al. (2011), and Richardson (1996, 1999) were used

values were Bonferroni corrected to account for multiple comparisons. The relationship between the abundance of *A. latezonatus* and its host anemones was examined at Norfolk Island using a linear model that incorporated reef zone, because this was the only site where *A. latezonatus* inhabited multiple reef zones. Due to a lack of individuals in shallow water at Lord Howe Island, reef zone was not included in the analysis at this location.

Host use and social group size

The relationship between number of anemones inhabited and social group size was examined using a linear model with location initially included as an interaction. Any interactions that were not significant were subsequently removed from final analyses.

Results

Distribution and abundance of host anemones

A total of 3858 potential host anemones (*E. quadricolor* and *H. crispa*) were recorded in surveys across all reef zones and locations. Mean host anemone abundance differed significantly between locations and reef zones (Sheirer-Ray-Hare, $p < 0.05$, Table 2). Across locations, abundance was highest at Lord Howe Island (23.56 ± 7.9 SE 250 m^{-2}) and Norfolk Island (15.5 ± 3.4 SE 250 m^{-2}) and 19- to 76-fold lower at remaining locations: Elizabeth Reef (0.81 ± 0.63 SE 250 m^{-2}), Middleton Reef (0.7 ± 0.3 SE 250 m^{-2}) and Sunshine Coast (0.31 ± 0.17 SE 250 m^{-2}) (Table S1, Fig. 2a).

At Norfolk Island, 942 host anemones (*E. quadricolor* only) were recorded in surveys. Anemone abundance differed significantly between reef zones and was highest in the lagoon (47.83 ± 3.79 SE 250 m^{-2}) and lowest at the outer reef crest (1.46 ± 0.65 SE 250 m^{-2}) (Table S2, Fig. 3a). Outside of surveys, one individual of another host anemone, *Stichodactyla haddoni,* was recorded, however it was not inhabited by any anemonefish.

At Lord Howe Island, 2776 host anemones were recorded in surveys (Fig. 2a) and included two species: *E. quadricolor* (90.2% of all surveyed anemones) and *H. crispa,* with *A. latezonatus* inhabiting both species. Anemone abundance differed considerably across reef zones and was highest in the lagoon (101.48 ± 30.39 SE 250 m^{-2}), and lowest at the outer reef crest (0.05 ± 0.03 SE 250 m^{-2}) (Table S3, Fig. 3c).

When comparing within reef zones between locations, anemone abundances were significantly greater at Norfolk than Lord Howe Island at the deep outer reef and outer reef slope, but were not significantly different at the outer reef crest and lagoon (Table S4, Fig. 3e).

At Elizabeth Reef and Middleton Reef, 48 and 62 host anemones (*E. quadricolor* only) were recorded, respectively (Fig. 2a). Despite surveying all reef zones, anemones were only recorded in the lagoon. Outside of surveys, one *H. crispa* was observed on the outer reef slope at Elizabeth Reef and was inhabited by one pair of *A. latezonatus*. At Sunshine Coast only one reef zone

Table 1 Transect design at all study sites. Details of transects conducted at Norfolk Island, Lord Howe Island, Sunshine Coast, and Elizabeth and Middleton Reefs. All transect data were normalized to abundance 250 m^{-2}

	Norfolk Island	Lord Howe Island	Sunshine Coast	Elizabeth Reef	Middleton Reef
Lagoon transects					
Depth (m)	2	1–5	–	2–7	2–7
Sites	2	9	–	4	8
Transect type	Belt	Belt	–	Belt	Belt
Transect size (m)	50 × 5	50 × 5	–	30 × 10 50 × 5	30 × 4 30 × 10
Total number of transects	6	27	–	8 16	40 4
Outer reef crest transects					
Depth (m)	5	5	–	2	2
Sites	8	14	–	4	6
Transect type	Belt	Belt	–	Belt	Belt
Transect size (m)	50 × 5	50 × 5	–	30 × 10 50 × 5	30 × 4 50 × 5
Total number of transects	24	42	–	6 4	15 12
Outer reef slope transects					
Depth (m)	15	15	–	7	7
Sites	8	13	–	5	14
Transect type	Belt	Belt	–	Belt	Belt
Transect size (m)	50 × 5	50 × 5	–	30 × 4 30 × 10 50 × 5	30 × 4 50 × 5
Total number of transects	24	39	–	15 4 4	65 12
Deep outer reef transects					
Depth (m)	15–30	15–30	13–25	15–30	15–30
Sites	8	10	6	7	3
Transect type	Belt	Timed swim	Timed swim	Timed swim	Timed swim
Transect size (m)	300 × 5	~840 × 5	~840 × 5	~840 × 5	~840 × 5
Total number of transects	8	10	6	8	22
Dates	March 2012	April 2009, March 2011, November 2011	June 2011	February 2006, February 2007, March 2011	February 2006, February 2007, March 2011

(deep outer reef) was present and 30 host anemones (all *E. quadricolor*) were recorded.

A. latezonatus distribution and abundance

A total of 355 *A. latezonatus* individuals were recorded during surveys. The mean abundance of *A. latezonatus* differed significantly between locations and reef zones (Sheirer-Ray-Hare, $p < 0.05$, Table 2). Across locations, abundance was highest at Norfolk Island (4.83 ± 1.07 SE 250 m^{-2}) and Lord Howe Island (0.26 ± 0.06 SE 250 m^{-2}) and lowest at Elizabeth Reef, Middleton Reef, and Sunshine Coast (0250 m^{-2}) (Table S5, Fig. 2b).

At Norfolk Island, 314 *A. latezonatus* individuals were recorded in surveys. The abundance of *A. latezonatus* was considerably higher on the deep

Table 2 Sheirer-Ray-Hare results of anemone and Amphiprion latezonatus abundance, social group size, and number of anemones inhabited by each A. latezonatus social group across location and reef zones, with interaction. Significant values are indicated in bold face

Group tested	Df	Sum Sq	H	*p* value
Anemone abundance				
Location	**4**	**1,247,849**	**129.730**	**< 0.001**
Reef zone	**3**	**946,999**	**98.452**	**< 0.001**
Location x reef zone	**8**	**504,514**	**52.451**	**< 0.001**
Residuals	409	1,379,031		
A. latezonatus abundance				
Location	**4**	**530,035**	**118.517**	**< 0.001**
Reef zone	**3**	**437,437**	**97.812**	**< 0.001**
Location x reef zone	**8**	**573,765**	**128.295**	**< 0.001**
Residuals	409	354,992		
A. latezonatus social group size				
Location	1	3964	1.915	> 0.08
Reef zone	2	4487	2.167	> 0.87
Location x reef zone	177	364,255	175.918	> 0.49
Residuals				
Number of anemones inhabited by each *A. latezonatus* social group				
Location	1	7731	3.093	> 0.17
Reef zone	2	675	0.270	> 0.34
Location x reef zone	177	441,424	176.636	> 0.51
Residuals				

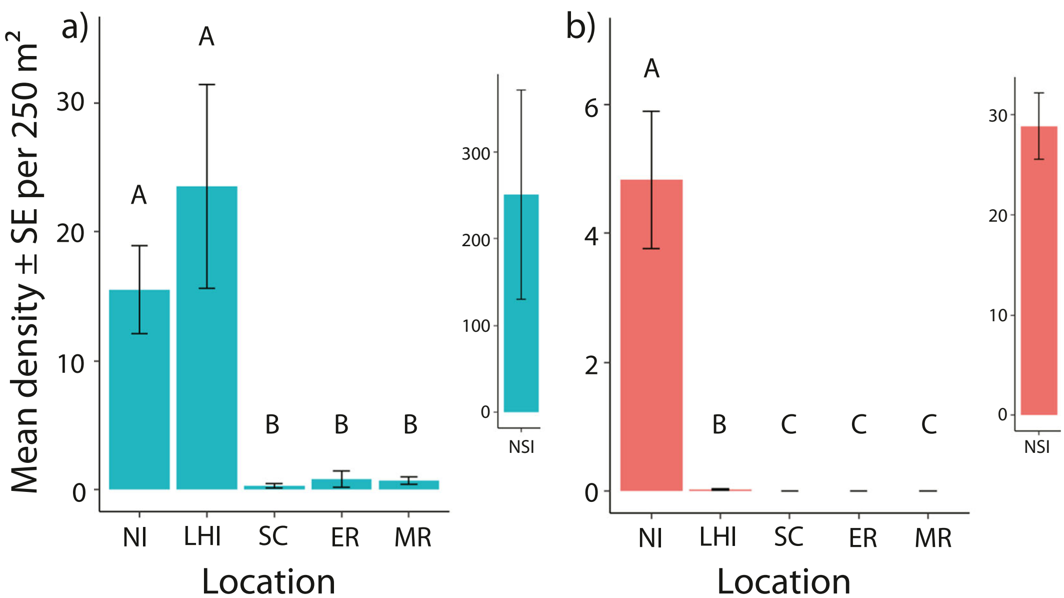

Fig. 2 Mean abundance (± SE 250 m^{-2}) of anemone and *Amphiprion latezonatus* at each sampled location. a) Host anemones at all sampled locations - Norfolk Island (NI), Lord Howe Island (LHI), Sunshine Coast (SC), Elizabeth Reef (ER), and Middleton Reef (MR). North Solitary Island (NSI) data (from Scott et al. 2011 and Richardson 1996) provided as insets for comparative purposes (since mean anemonefish densities at NSI are an order of magnitude greater than at the other study sites). Statistical comparisons with North Solitary Island were not performed because raw data was not available for all samples. b) *A. latezonatus* at all sampled locations and North Solitary Island (inset). Locations with the same letter group are not significantly different. For *p* values, see Tables S1 and S5

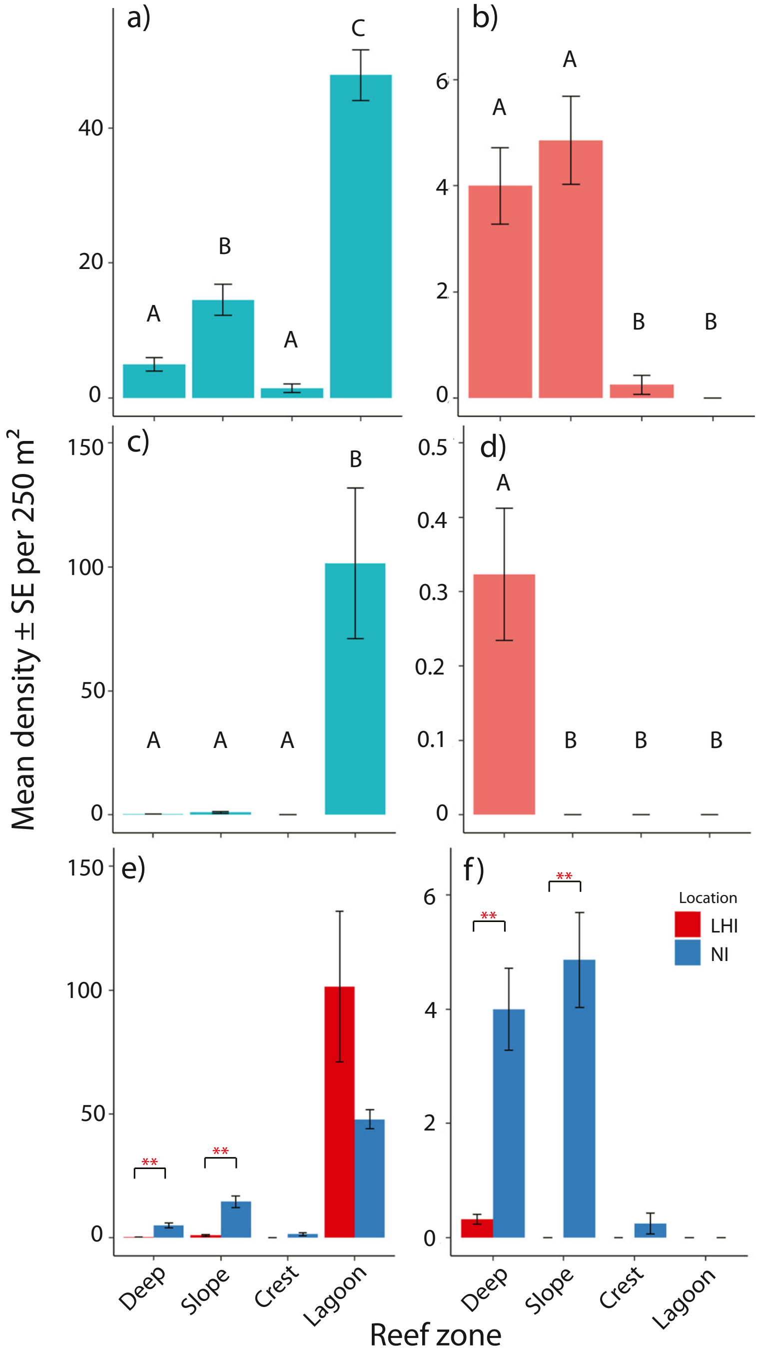

Fig. 3 Mean abundance (± SE 250 m^{-2}) of host anemone and *Amphiprion latezonatus* in each reef zone. Note the scale difference of 1–2 orders of magnitude in mean densities of anemones and anemonefish. Reef zones are denoted as follows: Deep outer reef (deep), outer reef slope (slope), outer reef crest (crest), and lagoon. a) host anemones in different reef zones at Norfolk Island. b) *A. latezonatus* in different reef zones at Norfolk Island. c) host anemones in different reef zones at Lord Howe Island. d) *A. latezonatus* in different reef zones at Lord Howe Island. e) host anemones in each reef zone at Norfolk (NI) and Lord Howe (LHI) Islands. f) *A. latezonatus* in each reef zone at Norfolk and Lord Howe Islands. In a) through d), groups with the same letter group are not significantly different. In e) and f), significant differences between habitats are illustrated with horizontal bars, values are denoted as * for $p < 0.05$, ** for $p < 0.005$, and *** for $p < 0.0005$

outer reef (5 ± 1.02 SE 250 m^{-2}) and outer reef slope (4.86 ± 0.83 SE 250 m^{-2}), compared to the lagoon (0250 m^{-2}) and outer reef crest (0.25 ± 0.18 SE 250 m^{-2}; Table S6, Fig. 3b). No other anemonefish species were recorded.

At Lord Howe Island, all 41 *A. latezonatus* recorded in transects were on the deep outer reef (15–30 m), where the mean abundance was 0.32 (± 0.09 SE) individuals per 250 m^{-2} (Table S7, Fig. 3d). Another anemonefish species, *A. mccullochi,* was abundant at Lord Howe Island, particularly in shallow waters (< 15 m).

Comparing within reef zones between locations, *A. latezonatus* abundance was significantly greater at

Norfolk than Lord Howe Island at the deep outer reef and outer reef slope, but was not significantly different at the outer reef crest or lagoon (Fig. 3f, Table S8).

At the Sunshine Coast, Elizabeth Reef, and Middleton Reef, *A. latezonatus* were not recorded in surveys (Fig. 2b). However, two and four adults were found outside transects at Elizabeth Reef and Sunshine Coast, respectively. Two other anemonefishes (*A. melanopus* and *A. akindynos*) were present at Sunshine Coast, whilst *A. mccullochi* was found at Elizabeth and Middleton Reefs.

Social group size and composition

Social group size was similar at Norfolk ($N = 161$ groups, mean = 1.94 ± 0.06 SE, range 1 to 6 individuals) and Lord Howe Islands ($N = 18$ groups, mean = 2.28 ± 0.25 SE, range = 1 to 4 individuals) and across reef zones (Sheirer-Ray-Hare, $p > 0.05$, Table 2). 53.6% of all social groups consisted of two adults (96 of 179, Fig. 4). The number of anemones inhabited by social groups between locations or between reef zones were not significantly different (Sheirer-Ray-Hare, $p > 0.05$, Table 2).

Of the 355 *A. latezonatus* encountered in surveys at Norfolk and Lord Howe Islands, eight (2.25%) were classified as new recruits (< 25 mm TL), 104 (29.3%) as juveniles (25–50 mm TL), and 243 (68.45%) as adults (>50 mm TL). The new recruits:juveniles:adults ratio was 6:88:220 at Norfolk Island and 2:16:23 at Lord Howe Island. At Sunshine Coast and Elizabeth Reef, the social groups observed outside of surveys each contained two adults ($N = 3$ groups).

Host use

Two species of host anemone were recorded at Lord Howe Island, with 13 *A. latezonatus* social groups occupying *E. quadricolor,* two social groups occupying *H. crispa,* and three social groups using both host anemone species when the anemones were side by side. Adults and juveniles inhabited both *E. quadricolor* and *H. crispa,* with 17 adults and nine juveniles inhabiting only *E. quadricolor,* two adults and three juveniles inhabiting only *H. crispa,* and four adults and four juveniles inhabiting mixed species microhabitat. All new recruits inhabited only *E. quadricolor*. Notably, seven of the 18 *A. latezonatus* groups cohabitated with *A. mccullochi*, five of which only contained one juvenile *A. mccullochi,* whilst the remaining two groups contained a single adult-sized *A. mccullochi.* Five cohabiting groups were on *E. quadricolor* and two cohabiting groups were on the mixed *E. quadricolor-H. crispa* microhabitat.

At Norfolk Island, all surveyed *A. latezonatus* inhabited *E. quadricolor*. At Sunshine Coast, *E. quadricolor* was the only anemone recorded in surveys and these were mainly occupied by *A. akindynos* (28 individuals) and rarely by *A. melanopus* (2 individuals). Outside of the transects, *A. latezonatus* occupied *E. quadricolor*, with two adults in one anemone at 18 m depth, and two adults in three anemones at 20 m depth. At Elizabeth and Middleton Reefs, all anemones were recorded in the lagoon and were inhabited by *A. mccullochi,* despite surveying across reef zones. No *A. latezonatus* were recorded in surveys, but outside of transects, one adult *A. latezonatus* pair occupied a single *H. crispa* at 12 m depth on the outer reef slope at Elizabeth Reef.

A. latezonatus abundance was positively correlated with host anemone abundance across locations ($R^2 = 0.96$, $p < 0.001$, $n = 18$, Table 3) and reef zones ($R^2 = 0.84$, $p < 0.001$, $n = 38$, Table 4). Overall social group size was also positively correlated with the number of anemones inhabited by each social group ($R^2 = 0.21$, $p < 0.001$, $n = 181$, Fig. 5).

Despite the positive relationship between host anemone abundance and *A. latezonatus* abundance across locations and reef zones, no *A. latezonatus* were recorded in the lagoons at either Norfolk or Lord Howe Islands, where host anemone abundances were highest (Fig. 3a–e). The relationship between host anemone abundance and *A. latezonatus* abundance was also different between reef zones at Norfolk and Lord Howe Islands (Table 4), where the increase in *A. latezonatus* abundance with increasing anemone abundance was much greater at deep outer reefs compared to outer reef crests and slopes.

Biological traits

The smallest new recruit observed in surveys measured 15 mm TL and the largest adult measured 165 mm TL. Examination of sectioned sagittal otoliths revealed that pelagic larval duration varied between 14 and 17 days, with a mean of 15.2 days ($n = 5$). Age estimates from otoliths of five adults were 6 (95 mm TL), 8 (109 mm TL), 9 (113 mm

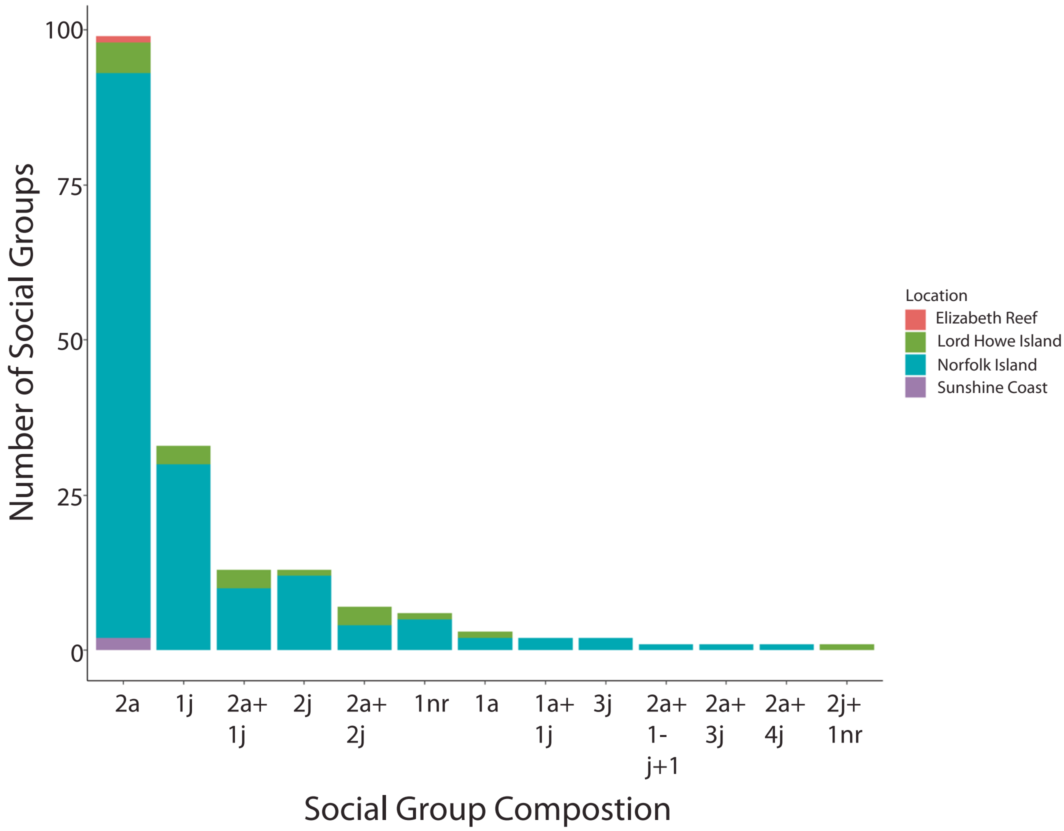

Fig. 4 Histogram of *Amphiprion latezonatus* social group composition. Size class is denoted as follows: a – adult, j – juvenile, nr – new recruit. Adult *A. latezonatus* were defined as having total length greater than 50 mm, juveniles as having total length between 25 and 50 mm, and new recruits as having total length less than 25 mm

TL), 11 (110 mm TL), and 13 years (125 mm TL). No egg clutches were recorded at Norfolk Island in March or at Lord Howe Island in April, but in November egg clutches were observed at 2 of 18 Lord Howe Island social groups. In one social group (two adults and two juveniles occupying two *H. crispa*), the breeding pair consisted of a 93 mm TL male and a 100 mm TL female. The second

Table 3 ANOVA of linear regression and linear regression results table of mean *Amphiprion latezonatus* abundance by mean anemone abundance (± SE 250 m^{-2}) per reef site at Norfolk and Lord Howe Islands. Linear regression results combine Norfolk and Lord Howe Island as there are no significant differences between sites. Significant factors are indicated in bold face

ANOVA of linear regression				
	Sum Sq	DF	*F* value	*p* value
Mean anemone abundance	**26.3712**	**1**	**132.0982**	**<0.001**
Location	0.6317	1	3.1645	0.097
Mean anemone abundance x location	0.125	1	0.0628	0.81
Residuals	2.79	14		
Linear regression table $R^2 = 0.9623$ ($p = 8.152e-13$)				
	Estimate	Standard error	*t* value	*p* value
Intercept	0.12455	0.14097	0.884	0.39
Mean anemone abundance	**0.74933**	**0.03708**	**29.209**	**<0.001**

Table 4 ANOVA of linear regression and linear regression results table of *Amphiprion latezonatus* abundance by anemone abundance (± SE 250 m^{-2}) per transect with interaction with reef zone at Norfolk and Lord Howe Islands. The lagoon was not included in analysis for Norfolk or Lord Howe Islands as no *A. latezonatus* were present. Regression analysis was performed only at the deep outer reef at Lord Howe Island, as no *A. latezonatus* individuals were present at either the outer reef crest or outer reef slope. Significant values are indicated in bold face

ANOVA of linear regression Norfolk Island				
	Sum sq	DF	*F* value	*p* value
Anemone abundance	**50.458**	**1**	**22.6592**	**0.0025**
Depth	**28.834**	**2**	**6.4742**	**0.0094**
Anemone abundance x depth	11.728	2	2.6333	0.10
Residuals	33.403	15		
Linear regression table Norfolk Island $R^2 = 0.791$ ($p = 0.0001141$)				
	Estimate	Standard error	*t* value	*p* value
Intercept	0.6524	1.1103	0.588	0.5655
Anemone abundance	**0.6695**	**0.1954**	**3.427**	**0.00375**
Outer reef crest	−0.9477	1.4281	−0.664	0.51698
Outer reef slope	0.9074	1.4943	0.607	0.55297
Anemones x outer reef crest	−0.3715	0.3233	−0.149	0.26853
Anemones x outer reef slope	**−0.4628**	**0.2026**	**−2.284**	**0.03736**
ANOVA of linear regression Lord Howe Island				
	Sum sq	DF	*F* value	*p* value
Anemone abundance	**0.09013**	**1**	**6.6533**	**0.0418**
Residuals	0.08128	6		
Linear regression table Lord Howe Island $R^2 = 0.5258$ ($p = 0.0418$)				
	Estimate	Standard error	*t* value	*p* value
Intercept	0.16386	0.07631	2.147	0.0754
Anemone abundance	**0.41027**	**0.15906**	**2.579**	**0.0418**

group occupied two *E. quadricolor* and comprised a breeding pair – a 147 TL male and a 165 mm TL female.

Discussion

Host anemone distribution and abundance

The distribution and abundance of host anemone species (*E. quadricolor* and *H. crispa*) varies greatly between locations and reef zones, representing varying constraints on habitat availability for *A. latezonatus*. Host anemone abundance (both species combined) was greatest at North Solitary Island and Norfolk Island and lowest at Elizabeth Reef, Middleton Reef, and Sunshine Coast (Scott et al. 2011; this study). Across the *A. latezonatus* range, *E. quadricolor* was much more abundant than *H. crispa* (Scott et al. 2011; this study). Throughout the *A. latezonatus* range, host anemone abundance was greatest in shallow waters.

A. latezonatus distribution and abundance

Amphiprion latezonatus occurred at low to moderate abundances at North Solitary, Norfolk, and Lord Howe Islands, while abundances at the Sunshine Coast and along the Australian coastline (except North Solitary Island) were extremely low (Richardson 1996; this study), increasing their risk of extirpation. Additionally, the presence of one *A. latezonatus* pair at Elizabeth Reef, and of host anemones at Middleton Reef, indicate that *A. latezonatus* could potentially establish populations at these locations in the future. Genetic studies reveal that *A. latezonatus* populations (Steinberg et al. 2016) and populations of other fishes endemic to the

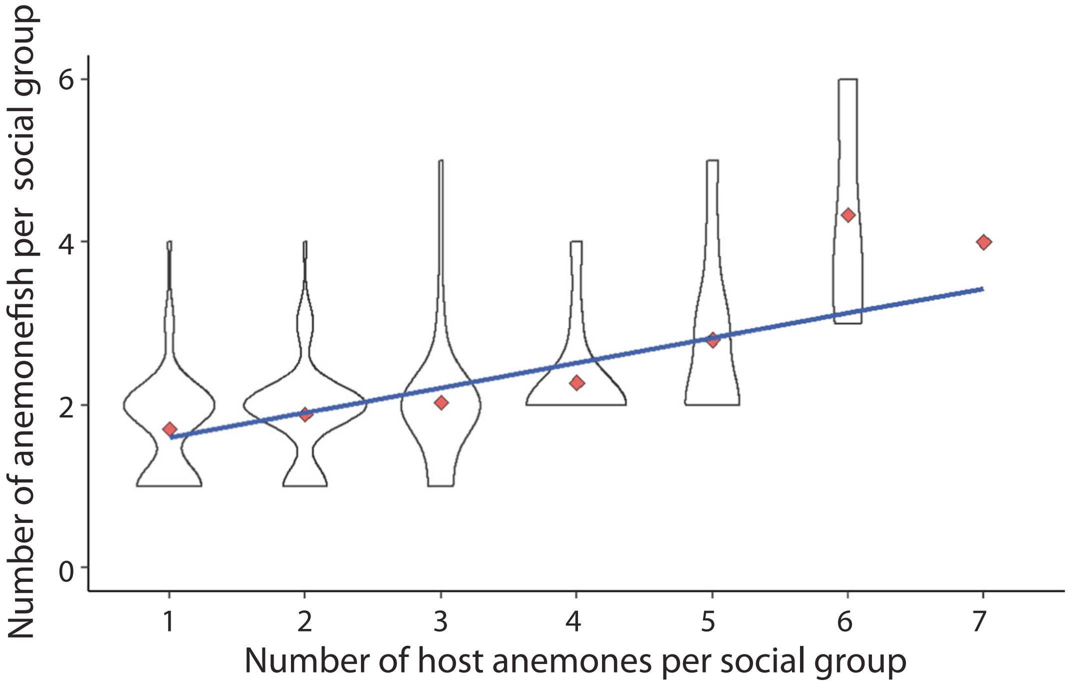

Fig. 5 Correlation between number of *Amphiprion latezonatus* in a social group and number of anemones inhabited by that group. Number of *A. latezonatus* per social group increased significantly with number of anemones in an inhabited cluster. Mean number of *A. latezonatus* per social group is indicated by the red diamond, the height of each shape represents the interquartile range, and the width of each shape indicates the probability abundance of the data points

Lord Howe Island-Norfolk Island region (van der Meer et al. 2012, 2013, 2014) are genetically isolated and contribute little to other populations in contemporary time frames. Thus, recolonization or population recovery following disturbances, or colonization of new reefs, will likely take considerable time.

Across all locations, *A. latezonatus* abundance increases with depth. Although some individuals were observed at 5 m depth, *A. latezonatus* is rare or absent in water less than 10 m deep across its range (Richardson 1996, 1999; Scott et al. 2011). This is interesting because our surveys revealed that host anemones are most abundant in shallow (< 5 m) lagoons at most locations. These shallow water anemones are occupied by other anemonefishes (*A. mccullochi*, *A. akindynos*, *A. melanopus*) that may outcompete *A. latezonatus*.

The abundance of many anemonefish species is positively correlated with their host anemone abundances (Fautin 1992; Richardson 1999; Elliott and Mariscal 2001; Mitchell and Dill 2005; Jones et al. 2008; Scott et al. 2011; Frisch et al. 2016; Howell et al. 2016). Indeed, monitoring studies reveal anemonefish abundance tracks changes in host anemone abundance (Shuman et al. 2005; Scott et al. 2011; Frisch et al. 2016; Scott and Hoey 2017) and large declines in host anemone abundance result in local anemonefish extinctions (Hattori 2002; Thomas et al. 2015). For *A. latezonatus*, this positive relationship also holds and implies that abundance will be negatively affected by mass bleaching or other impacts that affect host anemone abundance.

A. latezonatus social group size and composition

The average social group size for *A. latezonatus* was two individuals (maximum = 6) and this may be a major factor limiting its abundance and total reproductive output. At North Solitary Island, social group size was smaller, with only one to three individuals per group (Richardson 1999; Scott et al. 2011). The relative abundance of different host anemone species varies across the *A. latezonatus* range and this will affect the number of breeding pairs because adult fish tend to prefer *E. quadricolor* over *H. crispa* (Richardson 1996; Scott et al. 2016). Therefore, conserving *E. quadricolor* as fish breeding habitat is important.

A. latezonatus host use

Hecteractis crispa was considered the primary host anemone used by *A. latezonatus* (Fautin and Allen 1997; Santini and Polacco 2006; Ollerton et al. 2007), but this study identified *E. quadricolor* as the primary host at Lord Howe Island, Norfolk Island, and Sunshine Coast. At North Solitary Island, *A. latezonatus* occupied both *H. crispa* and *E. quadricolor* (Richardson 1996, 1999; Scott et al. 2016). The use of multiple host species decreases extinction risk associated with specialisation. Several anemonefish species alter host use across their range due to competition (Camp et al. 2016) and *A. latezonatus* may compete with other anemonefishes (*A. mccullochi*, *A. akindynos*, *A. melanopus*). Thus, the observed anemone abundance differences and the presence of potential competitors across the *A. latezonatus* range could contribute to differences in its host use, distribution, and abundance.

Multiple host use can also affect social group size and reproduction (Fautin and Allen 1997). For *A. latezonatus*, breeding pairs occupied both host anemone species, whilst group size and social group composition appeared similar. At North Solitary Island, *A. latezonatus* formed breeding pairs only on *E. quadricolor*, with *H. crispa* supporting juveniles (Richardson 1996; Scott et al. 2016). While this suggests that juvenile *A. latezonatus* may prefer *H. crispa* hosts, in another anemonefish species that also occupies *E. quadricolor* and *H. crispa,* all sizes of anemonefish preferred *E. quadricolor* as their host, but only adults occupied *E. quadricolor* (Huebner et al. 2012). Ontogenetic changes in host use have been reported in other anemonefishes (Fautin and Allen 1997; Chadwick and Arvedlund 2005; Huebner et al. 2012; Howell et al. 2016). For *A. latezonatus*, the number of host anemone species supporting breeding pairs differs across its range, likely contributing to range-wide differences in maximum potential reproductive population sizes, which in turn will alter local extinction risk.

Conclusions

Ecological and behavioural traits that influence extirpation risk differed between locations and emphasise the need for range-wide studies. These traits can also act synergistically to increase extinction risk. Based on these vulnerable traits we conclude that *A. latezonatus* is most at risk of extirpation at Sunshine Coast, less so at Lord Howe Island, and least at Norfolk and North Solitary Islands. Given the positive relationship between population size and host abundance, and the increasing severity and frequency of bleaching events (Hughes et al. 2017) - conserving host anemones, especially in deep outer reefs where host anemone abundance is relatively low and *A. latezonatus* abundance is greatest - should be a management priority to prevent *A. latezonatus* extirpation or extinction.

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Compliance with ethical standards

Conflicts of interest/competing interests No authors have any conflicts of interest to disclose.

Ethics approval All applicable national and institutional guidelines for sampling, care, and experimental use of organisms were followed and all necessary approvals were obtained. Permits obtained are Australian Government Department of Sustainability, Environment, Water, Population and Communities Permit for Activity in a Commonwealth Reserve number 003-RRRWN-110211-02, New South Wales Marine Parks Permit numbers LHIMP/R/2011/004 and LHIMP/R/2011/004b, and James Cook University Australia Animal Ethics Committee Approval Application ID A1605.

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