

Assessing environmental correlates of fish movement on a coral reef

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Abstract Variation in dispersal and movement patterns of coral reef fishes is likely linked to changes in environmental conditions. Monitoring in situ environmental parameters on coral reefs in conjunction with the movements of fishes can help explain the relationship between exploited populations and their environment. Sixty adult *Lethrinus miniatus* were acoustically tagged and monitored along a coral reef slope for up to 1 yr. Individuals occurred more often on the reef slope during days of cooler temperatures, suggesting a thermal tolerance threshold may exist. Results indicate that individuals responded to elevated temperatures by moving away from the reef slope to deeper adjacent habitats, thus shifting their position in the water column to remain at a preferred temperature. Space use within the water column (vertical activity space) was not influenced by environmental parameters or fish size, but this result was possibly influenced by use of deeper habitat outside the acoustic array that was not monitored. With elevation of ocean temperature, *L. miniatus* may need to adapt to warmer waters or disperse into cooler habitats, by either shifting their distribution deeper or towards

higher latitudes. Identifying key environmental drivers that affect the distribution of reef fishes is important, and may allow managers to predict the effect of these changes on exploited species.

Keywords Acoustic telemetry · Fisheries management · Ocean temperature · Changing climate · Lethrinidae

Introduction

Changes that occur in the environment cause a variety of biological and ecological responses in fishes across spatial and temporal scales (Brill and Lutcavage 2001; Elmqvist et al. 2003). Large-scale processes such as acidification and temperature of the oceans, as well as localised changes in environmental conditions, can directly affect reef fish abundance and distribution (Munday et al. 2008b). The specific environmental factors that influence movement patterns of coral reef fishes at specific scales are not well understood for many species, and this information is essential for species-specific spatial ecology, particularly for exploited populations (Roessig et al. 2004).

The majority of research that links the environment to coral reef fishes has focused on large differences in measured parameters. For example, large increases in water temperature have been related to biological and behavioural changes in reef species. Reduced reproductive performance (Donelson et al. 2010), decreased growth potential (Munday et al. 2008a), and riskier behaviour in the presence of predators (Lienart et al. 2014) have been reported for small, relatively sedentary species. For larger-bodied species of commercial importance, recent studies have revealed that elevation in water temperature can cause reductions in swimming speed (Pratchett et al. 2013;

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Johansen et al. 2014) and modification of reproductive scope (Potts et al. 2014). In addition to these experimental studies, movement of fishes has been related to large changes in the natural environment. Extreme storm events can alter the distribution of fish populations and severely impact their associated fisheries (Tobin et al. 2010; Udyawer et al. 2013; Henderson et al. 2014). Tropical Cyclone Justin, which impacted the Great Barrier Reef in 1997 caused advection of cold water up onto the continental shelf into shallow reef areas resulting in increased catches of *Lethrinus miniatus* and decreased catches of *Plectropomus leopardus* (Tobin et al. 2010). It was suggested that reduced catch rates of *P. leopardus* likely reflected a reduction in metabolism caused by a drop in water temperature to 2 °C cooler than the long-term seasonal average. In contrast, *L. miniatus* from deeper shelf and shoal habitats were hypothesised to move into shallow reef areas with colder water (Tobin et al. 2010). Higher catch rates of *L. miniatus* and *Lutjanus sebae* were also reported in the northern Great Barrier Reef (the northern extremity of *L. miniatus* species distribution) directly following a number of other cyclones (A. Tobin personal communication). Although empirical evidence is lacking, catch rates suggest that movement of these species occurs during or after extreme storm events. Further research is required to identify which environmental parameters are responsible for changes in movement patterns, as well as the influence of less-extreme changes on daily activity of individuals.

More subtle, daily fluctuations in environmental conditions are also likely to influence the movement patterns of reef fishes. It is necessary to identify the specific environmental parameters that are responsible for changes in the daily activity and movement patterns of individuals, since localised dispersal and activity of reef fishes are highly variable (Kaunda-Arara and Rose 2004; O'Toole et al. 2011; Currey et al. 2014a). In situ monitoring can provide a greater understanding of the environmental conditions that shape the movement ecology of reef fishes. For example, underwater visual surveys and temperature loggers used in a 2-yr study in Japan identified range shifts in the distribution of tropical and subtropical reef fishes into temperate reef and rocky habitat (Nakamura et al. 2013). In addition to water temperature, Richards et al. (2012) found that depth and distance to deep water were among the factors important to the distribution of large-bodied reef fish. Fulton and Bellwood (2004) determined that the distribution and abundance of labrids was related to wave exposure, and Noble et al. (2014) found that the majority of butterflyfishes increased their selectivity towards live hard coral prey on reefs with high wave energy. Since higher winds generate greater wave energy, Noble et al. (2014)

suggested that there are direct impacts on the foraging success of butterflyfishes due to increased wave activity with changes in climate. In addition to these parameters, rainfall can alter fish abundance (Travers et al. 2006), and moon phase has been linked to reproductive movements of wrasses (Chateau and Wantiez 2007). Since water temperature, wind, rainfall, and moon phase can all influence fish movement, identifying which parameters drive the presence and space use of fish at localised scales allows the influence of less-extreme environmental changes on fish populations to be predicted.

The family Lethrinidae includes a number of emperor species that constitute a large proportion of commercial, recreational, subsistence, and artisanal catch in coral reef fisheries throughout the Western Pacific and Indian Oceans (Carpenter 2001). Only recently has research investigated the spatial ecology of emperors and identified movement patterns among species and individuals that may be related to changes in environmental conditions (Taylor and Mills 2013; Currey et al. 2014a; Pillans et al. 2014). The aim of this study was to identify which environmental variables explained the movement patterns of lethrinids at the reef scale, by assessing whether the presence and vertical space use of adult *L. miniatus* along reef slopes was related to water temperature, air pressure, wind speed, wind direction, rainfall, or moon phase. Acoustic telemetry of tagged individuals monitored for periods of up to 12 months was paired with in situ monitoring of environmental variables to provide insight into the parameters responsible for the occurrence and space use of this commercially important reef fish. The ability to specify the effects of environmental conditions and drivers of reef fish movement is important for predicting how fish distribution and activity space will change under future environmental scenarios.

Materials and methods

Study site

Movements of *L. miniatus* were investigated at Heron Island Reef (23.4500°S, 151.9167°E; Fig. 1a), in the Capricorn-Bunker group of the southern Great Barrier Reef (GBR; Fig. 1b). Heron Island Reef is approximately 10 km long and 5 km wide and consists of a large lagoon and emergent cay. The reef crest is exposed at the lowest tidal levels (tidal range \approx 3 m). The reef slope has complex coral cover and coral bommies with sand patches, sloping into sandy habitat that descends into two channels surrounding the reef approximately 40 m in depth. Deep access points into the lagoon are limited with the lagoon isolated at low tide.

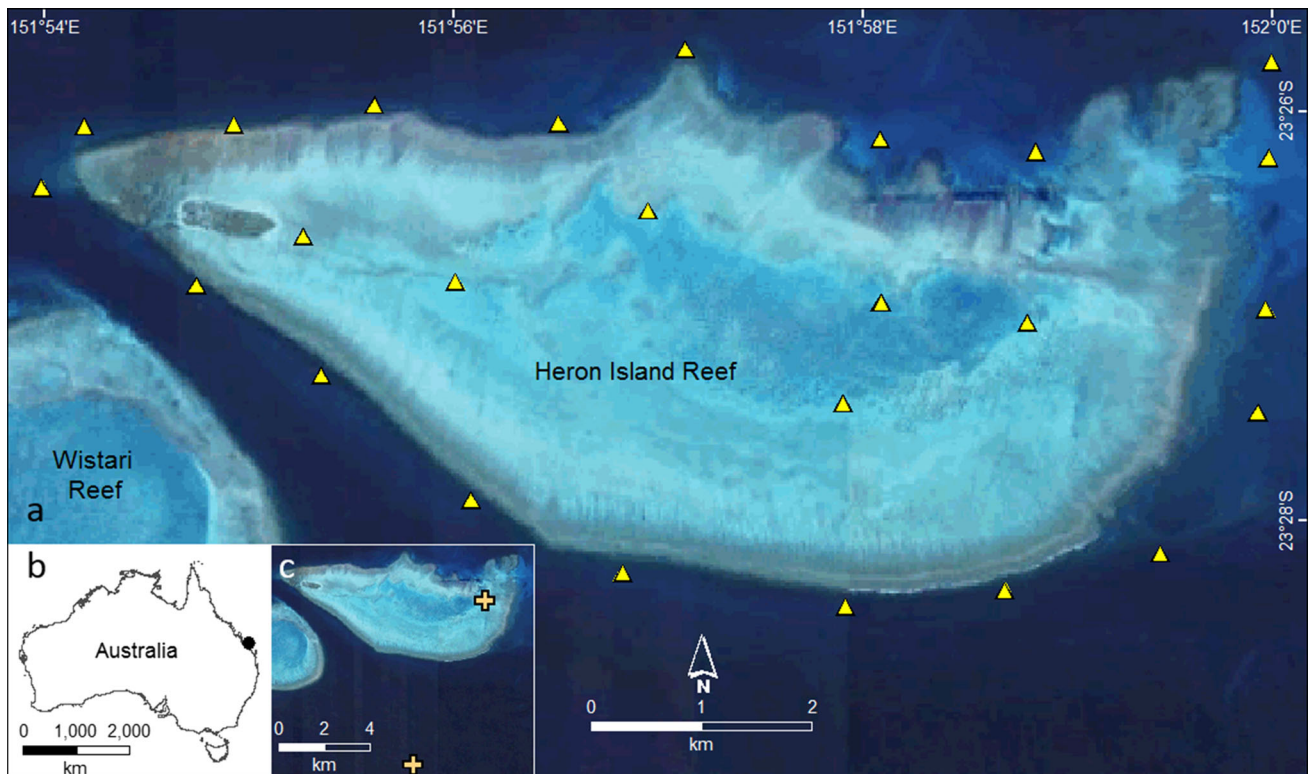


Fig. 1 Positions of acoustic receivers (*triangles*) at Heron Island Reef (**a**) in the southern Great Barrier Reef, Queensland, Australia (**b**). Crosses on *inset* (**c**) indicate the location of the weather station on Heron Island Reef flat, and the GBRHIS mooring in channel

Fish tagging and acoustic array

Individual *L. miniatus* were captured by line fishing on the reef slope using rod and reel (13.6-kg line and 27.2-kg leader) with barbless 8/0 hooks baited with pilchard or squid. Fish were vented to release excess gases from the swim bladder on capture, and then anaesthetised with Aqui-S. A V13P transmitter with pressure (depth) sensor (Vemco Ltd., Canada, 364 day battery life) was surgically implanted into the abdominal cavity via a small incision made longitudinally between the pectoral and ventral fins on the left side. Acoustic transmitters emitted a unique identification code for each individual and depth in the water column (maximum depth 50 m). Two simple, interrupted stitches using absorbable sutures closed the incision. Fork length (FL, in mm) was recorded and a dart tag (PDS; Hallprint©) was fitted externally for identification by insertion into the dorsal musculature. After recovery in fresh sea water, fish were released at the site of capture, with the tagging and measuring procedure conducted in less than 8 min. Adult individuals were tagged in three deployments: (1) in April 2011 ($n = 20$), (2) February 2012 ($n = 20$), and (3) September 2012 ($n = 20$).

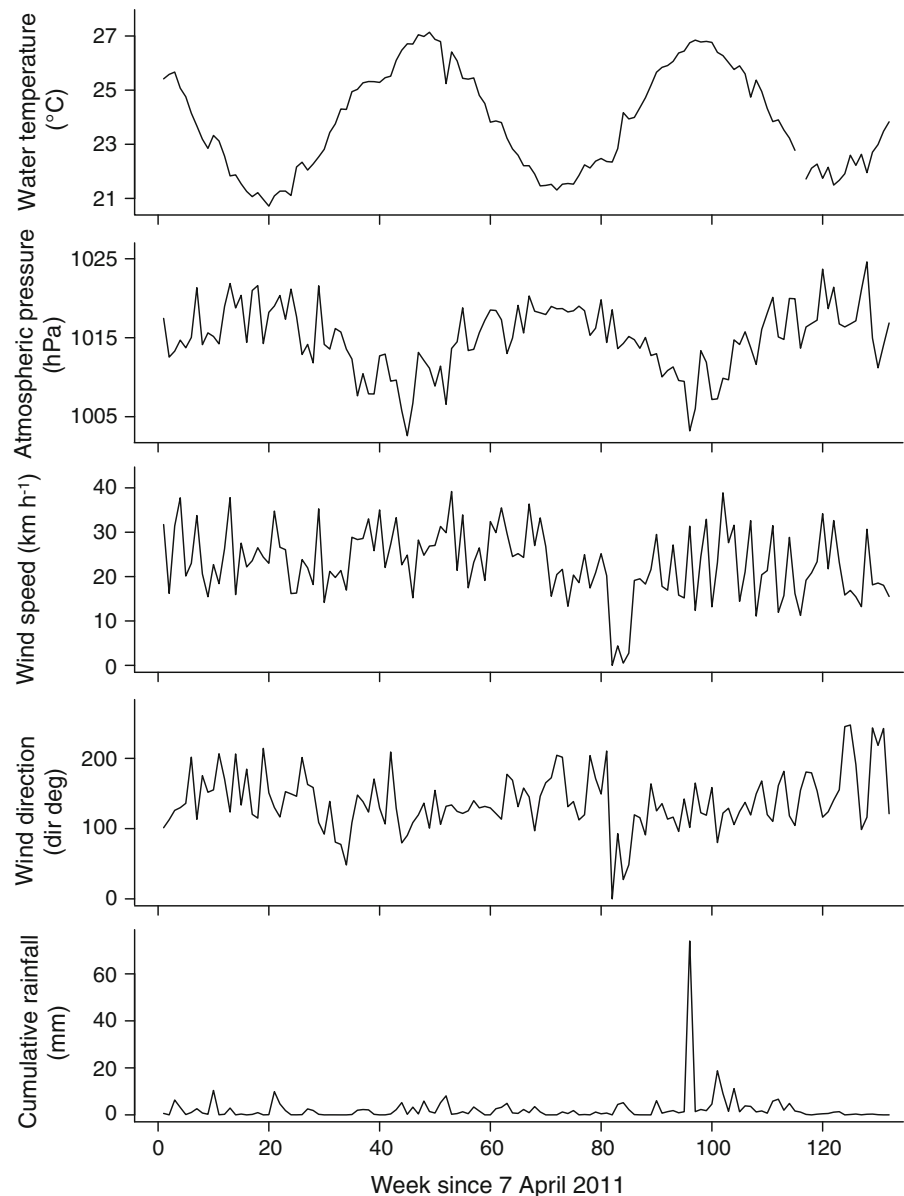
Long-term monitoring of the presence and movements of individuals was enabled by 25 VR2 W[®] acoustic

receivers (Vemco Ltd., Canada) deployed in an array on the reef slope adjacent to the reef crest (19 receivers) and within the lagoon (6 receivers). This array was designed to investigate reef-scale movements of individuals for periods of up to 12 months (duration of transmitters: 365 days). Receivers were fastened to star pickets embedded in the substrate at 10 to 20 m depth along the reef slope and in <10 m in the lagoon. Range testing was conducted via six permanent sentinel tags deployed at varying distances from receivers (70 to 270 m) in representative substrates, and monitored during the course of the study (Currey et al. 2014a). Receivers detected transmitters within 270 and to 25 m in depth (depth of the substrate away from the reef crest). Data from acoustic receivers were downloaded twice each year.

Environmental data

Environmental data for the period April 2011 to September 2013 were obtained from in situ monitoring by the Facility for Automated Intelligent Monitoring of Marine Species sensor network and Great Barrier Reef Ocean Observing System mooring (www.imos.org.au; Figs. 1c, 2). Water temperature was measured at a mooring off the southern side of Heron Island (GBRHIS); atmospheric pressure,

Fig. 2 Weekly environmental measurements for Heron Island Reef from April 2011 to September 2013



wind speed, wind direction, and rainfall were measured from a weather station on Heron Island; and moon phase was calculated in the *phenology* package in R version 3.1.0 (R Core Team 2013). Mean daily and weekly values of each parameter were calculated, since data were recorded at intervals ranging from 5 min (e.g., temperature) to 30 min (e.g., wind speed). Daily environmental parameters were compared to daily detectability of the sentinel tag positioned closest to a receiver (70 m distance) to ensure detectability was not linked to environmental conditions.

Environmental factors including water temperature, wind speed, rainfall (\log_{10} transformed), and moon phase were examined as potential drivers of presence and vertical space use of *L. miniatus*. The biological parameter FL was also included to assess the influence of fish size.

Atmospheric pressure and wind direction were excluded from the analyses because atmospheric pressure was highly correlated with water temperature ($R^2 = 0.67$), and data for wind direction were unbalanced since winds typically originate from the south-east.

Data analysis

Data were analysed to identify presence on the reef slope and vertical space use of *L. miniatus* at Heron Island Reef relative to environmental parameters. Individual fish were included in analyses when detected for ≥ 5 days, and when more than two detections were recorded by a given receiver on a given day. Vertical activity space was estimated by vertical kernel utilisation distributions (vKUD) following

methods by Currey et al. (2014a) and Heupel and Simpfendorfer (2014). In short, average hourly positions of individuals were calculated in two-dimensional space to estimate mean depth and distance along the reef. Receivers positioned along the reef slope were represented as a linear system, calculated as the distance from the north-west point of the Heron Island Reef crest in a clockwise direction. Individual fish positions were calculated as the distance (m) from the receiver on which a detection occurred to the north-west point (in an anticlockwise direction around the reef; Currey et al. 2014a; Heupel and Simpfendorfer 2014). Weekly vertical activity areas of core use (50 % vKUD) and extent (95 % vKUD) were calculated by mean depth (m) and reef distance (m) for each individual.

Mixed-effects models (restricted maximum likelihood estimation) were used to determine whether daily presence was influenced by environmental or biological (i.e., FL) parameters using a logistic regression approach. Models were analysed using the *lme4* package in R (Bates et al. 2014) with an information theoretic model selection process and model averaging. Daily presence or absence of each individual on the reef slope (PA) was coded as a binary variable and analysed using the *glmer* function (Bates et al. 2014) for data with a binomial distribution. PA was treated as the response variable, and water temperature, wind speed, rainfall, moon phase, and FL were modelled as fixed factors. Individual fish were treated as a random-effects term to account for the lack of temporal and spatial independence among individuals (Bolker et al. 2008). Since the study period involved three deployments of acoustically tagged individuals, days since deployment (days) with deployment number (1–3) were also treated as a random-effects term to account for temporal bias in detections with time on fish presence (Fig. 3). All fixed effects were standardised to be comparable on the same

scale by centring. First, the dredge function in the *MuMIn* package (Barton 2013) allowed computerised selection of the best-fitting models according to the Akaike information criterion corrected for small-sample bias (AIC_c). Second, the model averaging process ranked the sub-models ($AIC_c < 10$) by AIC_c and weighted parameters with respect to AIC_c weight using the zero method (Burnham and Anderson 2002; Grueber et al. 2011). Zero was substituted into models where the parameter was absent, then parameter estimates (and error) were averaged over all sub-models, which is a robust process that allows incorporation of model uncertainty (Burnham and Anderson 2002; Grueber et al. 2011). The most significant drivers of presence were determined as the factors with the greatest relative importance across the averaged sub-models.

Effects on weekly vertical activity space were also examined using mixed-effects models using the *nlme* package in R (Pinheiro et al. 2013) with an information theoretic model selection process. In these analyses, 50 and 95 % vKUD estimates for each individual per week were \log_{10} transformed (to normalise data) and treated as the response variables. Fixed factors, the single random-effects term (individual) and model selection followed the PA analysis, calculated by week. Residual spread increased with FL, so the *varExp* variance structure was used in the *nlme* package (Pinheiro et al. 2013) to weight the 95 % vKUD models by FL and achieve homogeneous variances (Zuur et al. 2009).

Results

The influence of environmental parameters on presence and vertical activity space was examined for 26 adult *L. miniatus* at Heron Island Reef, between April 2011 and

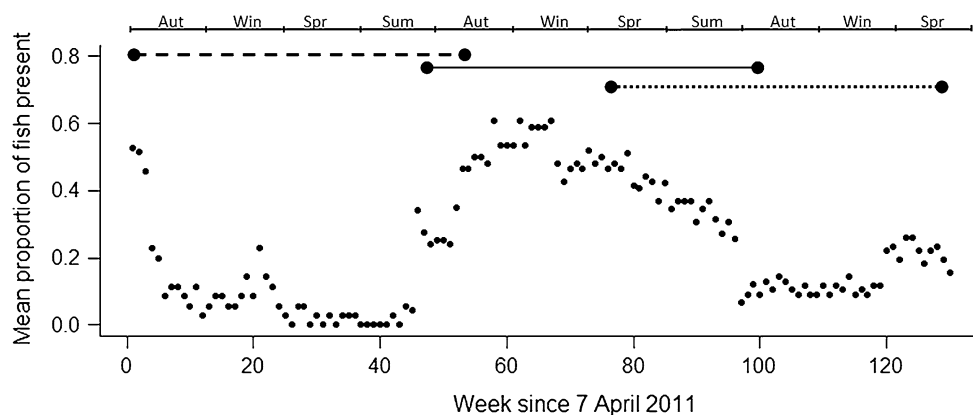


Fig. 3 Mean proportion of acoustically tagged *Lethrinus miniatus* present over time, illustrating the confounding effect of time since deployment on the presence and absence of tagged individuals. The three deployments and associated monitoring periods (battery life of

transmitters) are represented by *dashed*, *solid*, and *dotted* lines, and the seasons of autumn (Aut), winter (Win), spring (Spr), and summer (Sum) are indicated

September 2013. All other individuals were detected for <5 days and excluded from analyses. Individuals ranged in size from 372 to 493 mm FL and were detected from 2 to 52 weeks on receivers located on the reef slope only (Table 1). Lack of detections on lagoon receivers indicates individuals were not present in this area. Daily detectability of transmitters was not influenced by environmental parameters based on detection of a sentinel tag for 212 consecutive days, during 215 d of the total monitoring period of 222 d (97 % detectability, 20 August 2011 to 28 March 2012).

Presence

Sixteen sub-models (with $\Delta AIC_c < 10$) were used to analyse the effects on presence of *L. miniatus*, from which three models strongly supported the data ($\Delta AIC_c < 2$; Table 2). Temperature, rainfall, and wind were present in these three sub-models, with only temperature as a parameter in the best-fitting model (M1). Model averaging results summarising relative effects of each parameter on PA indicated that water temperature was the most important and significant predictor, with increased probability of fish presence associated with lower water temperature (Table 3; Fig. 4). Predictions from model M1 indicate that a 50 % chance of individuals being present occurs at a daily mean water temperature of approximately 24 °C (Fig. 4). During days warmer than 24 °C, individuals were less likely to be detected on the reef slope, compared to days below 24 °C. Although water temperature followed a seasonal trend, presence of individuals was not limited to cooler months (June–September). All other parameters had less than a third of the importance relative to temperature, highlighting the relevance of water temperature to occurrence of *L. miniatus* on the reef slope (Table 3).

Vertical activity space (vKUDs)

Weekly activity space of *L. miniatus* was not strongly related to environmental parameters (temperature, wind speed, rainfall, or moon phase). The null model for 50 and 95 % vKUDs fitted the data best, with a model including FL and 50 % vKUD also strongly supported ($\Delta AIC_c < 2$; Table 4). Relative importance of parameters produced by model averaging indicated that FL was most important, with a weak relationship (related to adult size range) of a smaller 50 % vKUD observed with increased fish size (model averaging results: estimate = -0.360 , $p > 0.05$, relative importance with shrinkage = 0.28). Although rainfall, temperature, and wind speed were present in the top sub-models, all environmental parameters had low relative importance on vertical activity space, suggesting

individual variability and deployment period played a greater role than environmental factors.

Discussion

The results of this research provide useful information on the correlation between environmental factors and the presence of an important reef fish. Water temperature was found to be an important driver of *L. miniatus* presence on the reef slope, which provides insight into their movement relative to environmental conditions over periods of up to 12 months. Greater probability of presence on the reef slope was observed during days of lower mean water temperature. With ocean temperatures predicted to rise (Poloczanska et al. 2007; IPCC 2013), it is uncertain how fish distribution and movement patterns will be affected. Research into the effects of warmer water temperature on reef fishes has focussed on fish metabolism, growth, and reproduction (e.g., Munday et al. 2008a; Donelson et al. 2010), with few reports of environmental influences on dispersal and distribution (but see: Henderson et al. 2014). However, the correlation between temperature and fish presence from data indicated here suggests that *L. miniatus* may need to alter their distribution or depth use to remain in a preferred water temperature, or avoid sub-optimally warm conditions in the longer term. Vertical activity space of *L. miniatus* was not related to environmental conditions, likely due to use of deeper areas outside receiver range, and suggests that movement patterns are highly variable when individuals use reef slope habitats. The ability to specify the effects of environmental conditions and drivers of reef fish movement at the reef scale can aid in predicting how fish distribution and activity space will change under future environmental scenarios.

Acoustically tagged individuals likely sought deeper (cooler) waters on warmer days. This is proposed since *L. miniatus* (a) were not detected or sighted in the lagoon, (b) were not observed sheltering down within coral that would result in the obstruction of signal transmission for periods of 24 h or more, and (c) are thought to utilise deeper habitats seaward from the reef slope (Currey et al. 2014a). Absence from the reef slope during days of elevated temperature suggests a thermal preference may exist for this species. Temperature influences physiological processes and optimal aerobic performance of teleosts (Rummer et al. 2014), and thermal tolerance ranges have been investigated widely for temperate fishes (e.g., Pörtner 2002; Farrell et al. 2008; Crozier and Hutchings 2013). Inferences of thermal tolerance can be gained by interspecific comparisons of the critical thermal maxima, which is an approximation of the maximum non-lethal temperature fishes can endure in the short term (Elliot and Elliot

Table 1 Details of acoustically tagged individuals (transmitter number), with fork length (FL; mm), release date, number of days detected (with proportion of days monitored/days detected in parentheses), and number of receivers visited

Transmitter number	FL (mm)	Release date	Days at liberty	Days detected	Receivers visited	50 % hKUD	95 % hKUD	50 % vKUD	95 % vKUD
4022	381	08/04/2011	6	5 (83 %)	2	0.19	1.08	0.003	0.027
4024	399	08/04/2011	25	21 (84 %)	4	0.32	1.27	0.004	0.036
4026	454	09/04/2011	7	7*	1				
4027	369	09/04/2011	297	121 (41 %)	2	0.35	1.51	0.002	0.023
4029	323	10/04/2011	6	6*	1				
4032	486	13/04/2011	352	57 (16 %)	1				
4034	412	13/04/2011	20	13 (65 %)	3	0.23	2.09	0.002	0.017
6702	436	08/02/2012	158	114 (72 %)	1				
6706	474	09/02/2012	12	8 (67 %)	5	0.62	3.72	0.010	0.025
6707	493	09/02/2012	351	264 (75 %)	3	0.18	0.85	0.001	0.013
6710	450	09/02/2012	353	20 (6 %)	4	0.40	–	0.006	0.033
6712	390	10/02/2012	370	318 (86 %)	1				
6713	480	10/02/2012	351	323 (92 %)	2	0.17	0.77	0.001	0.007
6714	455	11/02/2012	339	332 (98 %)	1				
6721	440	11/02/2012	38	37 (97 %)	4	0.54	2.72	0.006	0.038
7030	415	13/09/2012	212	7 (3 %)	2	0.23	1.35	0.001	0.007
7036	395	14/09/2012	296	125 (42 %)	1				
7037	449	14/09/2012	294	71 (24 %)	1				
7038	405	14/09/2012	127	80 (63 %)	1				
7039	419	14/09/2012	296	34 (11 %)	1				
7040	469	14/09/2012	134	126 (94 %)	1				
7041	461	15/09/2012	134	124 (93 %)	1				
7045	372	15/09/2012	7	6 (86 %)	3	0.30	1.90	0.004	0.019
7046	410	16/09/2012	10	9 (90 %)	4	0.64	2.94	0.004	0.013
7047	391	16/09/2012	28	11 (39 %)	6	0.52	2.99	0.008	0.039
7048	427	16/09/2012	15	8 (53 %)	1				

The 50 % KUD and 95 % KUD estimates (km²) in horizontal (hKUD) and vertical (vKUD) space were calculated for individuals where possible. Two individuals (indicated by*) appeared dead (displayed depth profiles consistent with the tidal signature) after a number of days, thus detections received after these individuals were deceased were removed from analysis

1995). A preliminary study reported a critical thermal maximum of 38 °C for *Lethrinus reticulatus* and suggested that this species had a low capacity to withstand direct exposure to elevated temperature compared to other large reef fishes (Pratchett et al. 2013). Sensitivity to small increases in water temperature (e.g., Nilsson et al. 2009; Gardiner et al. 2010) and limited thermal ranges can affect spatial ecology and distribution of populations. Larger-bodied species such as *P. leopardus* and *Paralichthys dentatus* displayed reduced mobility and swimming performance at higher water temperature (Henderson et al. 2014; Johansen et al. 2014), which could consequently impact the frequency of encountering and capturing prey (Blake 2004). For *L. miniatus*, movement to cooler nearby habitats (absence from the monitored array) during warmer periods may provide a physiological benefit, since this species is thought to prefer temperatures below 28 °C

(Williams et al. 2007; Munday et al. 2008b). A recent study observed individuals utilising deeper areas away from the reef slope (Currey et al. 2015), which could support this hypothesis. The thermal preference of *L. miniatus* is highlighted by their fragmented distribution, separated at the equatorial zone, with populations not occurring in similar habitat at the warmest latitudes between approximately 15°N–15°S (Munday et al. 2008b). Temperature (and thus thermal optima) is clearly a major driver of the distribution and habitat use of *L. miniatus*. Yet, further research is required to define the thermal maxima of this species, to confirm whether *L. miniatus* currently experiences water temperatures close to the limit of thermal tolerance, and to evaluate how this will impact this species in the longer term.

Importantly, the observed correlation between water temperature and fish presence was not based on seasonal

trends in water temperature. Cooler temperatures were recorded in winter during the middle of the year, while warmer temperatures occurred in summer towards the end and beginning of each year. Neither season nor month could be incorporated as fixed factors into the models because the presence of fish from each of the three deployments was influenced by time since deployment (which is not uncommon; Pillans et al. 2014), so these factors were incorporated as random effects. Despite this bias, individuals were detected on the monitored reef slope in all months of the year, at all temperatures, regardless of season. Thus, the fact that fish were more frequently present on the reef slope during days of lower temperatures was not indicative of a seasonal trend. The lower probability of presence during days of warm temperatures was not directly related to particular months, rather warmer days within each season through the year. Overall, this can

be interpreted as individuals were more frequently absent from the reef slope during days of elevated temperatures.

Vertical activity space of *L. miniatus* was not influenced by water temperature, which is likely a result of sampling design. Acoustic receivers were placed only in depths of 10–20 m on the reef slope, not in the adjacent deeper waters. Therefore, vertical activity space could only be estimated when individuals were within the receiver detection range (i.e., to depths of 25, ≈300 m from a receiver) and shifts to depths beyond 25 m were unlikely to be recorded. Detection data indicated that individuals likely optimise their position in the water column according to temperature and depth. However, they avoided increases in temperature (absence of individuals during warmer periods) by moving to deeper areas outside the receiver detection range. Timescale must also be considered when interpreting the results of activity space, as

Table 2 Top mixed-effects sub-models examining the effects of water temperature (temp), rainfall (log₁₀rain), wind speed (wind), moon phase (moon), and fork length (FL) on presence (PA) of *Lethrinus miniatus* at Heron Island Reef

Model	df	AIC _c	ΔAIC _c	w
M1 PA ~ temp	6	4791.88	0	0.32
M2 PA ~ temp + lograin	7	4793.81	1.93	0.12
M3 PA ~ temp + wind	7	4793.86	1.99	0.12
M4 PA ~ temp + FL	7	4793.88	2.00	0.12
M5 PA ~ temp + moon	9	4794.93	3.05	0.07
M6 PA ~ temp + lograin + wind	8	4795.74	3.86	0.05
M7 PA ~ temp + lograin + FL	8	4795.74	3.86	0.05
M8 PA ~ temp + wind + FL	8	4795.87	3.99	0.04

All models included a random effect for individual fish and day of deployment by deployment number. AIC_c is the small-sample bias-corrected form of Akaike information criterion, ΔAIC_c is the Akaike difference, and w is the Akaike weight. Models with ΔAIC_c < 2 (in bold) were the best-fitting models

Table 3 Model averaging results summarising effects of each parameter on *Lethrinus miniatus* presence at Heron Island Reef

Parameter	Estimate	SE	p	Coefficients	Relative importance
Intercept	0	0			
Temp	-1.187	0.093	<0.001*	-1.187	1.00
Lograin	-0.031	0.090	0.726	-0.009	0.28
Wind	-0.008	0.089	0.925	-0.002	0.27
FL	-0.005	1.303	0.997	-0.001	0.27
Moon (full)	-0.048	0.112	0.669	-0.008	0.18
Moon (last)	-0.067	0.109	0.537	0.012	
Moon (new)	-0.102	0.109	0.347	-0.018	

Parameters of water temperature (temp), rainfall (log₁₀rain), wind speed (wind), fork length (FL), and moon phase (moon) were standardised to allow comparison. Coefficients were calculated with shrinkage. Asterisks indicate significant parameters (p < 0.05)

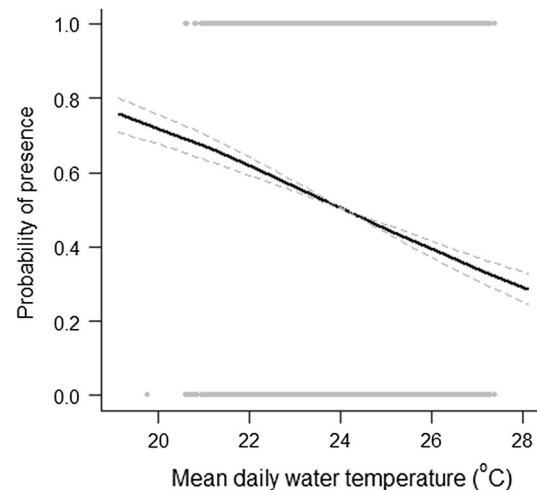


Fig. 4 Predicted probability (solid line) of *Lethrinus miniatus* daily presence on the reef slope with the most influential parameter, mean water temperature, from the model M1. Dashed lines indicate 95 % confidence intervals and points are raw data

Table 4 Top mixed-effects sub-models examining the effects of fork length (FL), moon phase (moon), rainfall (\log_{10} rain), wind speed (wind), and water temperature (temp) on *Lethrinus miniatus* vertical activity space (50 and 95 % vKUDs) at Heron Island Reef

Model		df	AIC _c	Δ AIC _c	w
MA	50 % vKUD ~ 1	6	470.59	0	0.66
MB	50 % vKUD ~ FL	7	472.44	1.86	0.26
MC	50 % vKUD ~ lograin	7	477.38	6.79	0.02
MD	50 % vKUD ~ wind	7	477.83	7.25	0.02
ME	50 % vKUD ~ temp	8	477.88	7.29	0.02
MF	50 % vKUD ~ FL + lograin	8	479.26	8.67	0.01
MG	50 % vKUD ~ FL + wind	8	479.71	9.12	0.01
MH	50 % vKUD ~ FL + temp	8	479.75	9.16	0.01
M1	95 % vKUD ~ 1	4	345.78	0	0.72
M2	95 % vKUD ~ FL	5	348.61	2.83	0.17
M3	95 % vKUD ~ temp	5	350.73	4.95	0.06
M4	95 % vKUD ~ wind	5	353.40	7.62	0.02
M5	95 % vKUD ~ lograin	5	353.46	7.68	0.02
M6	95 % vKUD ~ FL + temp	6	353.49	7.71	0.02

All models included a random effect for individual fish, and parameters were standardised. AIC_c is the small-sample bias-corrected form of Akaike information criterion, Δ AIC_c is the Akaike difference, and *w* is the Akaike weight. Models with Δ AIC_c < 2 (in bold) represent the best-fitting models. Models for 95 % vKUD were weighted by FL using the *varExp* variance structure

space use might vary in response to temperature at a shorter timescale (e.g., days), than at the weekly timescale used here. Since the constraints of the experimental design of this study were the likely cause for no influence of temperature on vertical activity space, future studies should endeavour to provide greater spatial coverage and include deeper areas adjacent to the reef slope to test this hypothesis. Likewise, more information is required at longer timescales (greater than 12 months) to better understand effects of water temperature on fish dispersal. For many other reef fishes with a latitudinal range that encompasses a broad gradient in temperature, it is likely that individuals are adapted or acclimatised to their local latitudinal region (Munday et al. 2008b). Broad distribution over a wide area and localised adaptation to a variety of temperatures may mean that some species have a greater capacity to adapt to and withstand increased water temperature associated with longer-term climatic changes. However, the restricted distribution of *L. miniatus* suggests this species may already be excluded from warmer equatorial waters, indicating less resilience compared to others. Thus, long-term monitoring is required, because distributions of species can also shift at different rates and directions corresponding to local climates (Pinsky et al. 2013).

Other environmental parameters incorporated in this study were not correlated with fish presence or vertical space use. Inclusion of wind speed, rainfall, and moon

phase as parameters in the models did not explain movement patterns of *L. miniatus* over the monitored time periods. Atmospheric pressure, although not incorporated into the model analysis, was highly correlated with water temperature and therefore could be a factor influencing the presence of *L. miniatus*. The opposite trend in atmospheric pressure to water temperature occurred on a weekly and monthly (seasonal) timescale, so it is uncertain whether daily absence of fish could be associated with days of lower atmospheric pressure. Declines in atmospheric pressure during extreme storm events has caused movements of sharks (Heupel et al. 2003; Udyawer et al. 2013), and was thought to be responsible for the movement of individuals away from detection range for the congener *Lethrinus nebulosus* (Pillans et al. 2014) and flounder *P. dentatus* (Henderson et al. 2014). However, no tropical cyclone was encountered during the monitoring period of this study, and previous movements in response to extreme weather were assumed to be associated with water temperature (Tobin et al. 2010). Thus, further research is required to determine how atmospheric pressure might influence *L. miniatus* and how individuals will respond to predictions of increased storm activity.

These findings suggest that in the face of environmental change, *L. miniatus* may be able to utilise their mobility to adapt to changing conditions. With elevation in sea surface temperatures and increased frequency of storms, individuals can potentially move to alternative habitats and incorporate optimal environmental parameters within their areas of activity. The density of individuals could possibly diminish along the shallow coral reef slopes as they seek cooler waters, potentially frequenting deeper shelf and shoal habitats. Previous research has reported *L. miniatus* in shoal habitats at depths beyond 160 m (M. Cappo pers. comm.), yet it is uncertain whether these individuals remain at depth for long periods, or if they use these habitats and depths for specific activities such as reproduction or feeding over a short timeframe. Further information on the residency of *L. miniatus* at depths >80 m would help define their distribution and potentially add to the evidence supporting their broad-scale dispersal (Williams et al. 2010; Currey et al. 2014b). Alternatively, individuals may adapt to increased temperatures with time, but this is considered to be more difficult for populations further from the equator (Rummer et al. 2014), such as the individuals sampled here from the southern GBR. It will be important to further investigate these hypotheses at broader spatial and temporal scales, especially if fishing effort shifts from shallow reef slopes to deeper shoal areas to target this important fishery species.

Water temperature was an important predictor of *L. miniatus* movement, suggesting elevated temperatures could reduce the occurrence of this species along shallow

coral reef slopes. While space use in deeper habitats with in situ monitoring of environmental conditions and physiological research is required to confirm the thermal tolerance of this species, this study can be built upon to identify the response of *L. miniatus* to longer-term changes in climate. Gaining insight into the movement ecology of coral reef fishes will allow managers to understand how species movements are influenced by extreme and subtle changes in the environment and to predict future impacts on fishery species as the climate changes.

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