

Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus*

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Summary

1. In studies of an organism's functional ecology, key behavioural traits such as foraging periodicity are assumed to be uniform across the species. In particular, the fundamental division between diurnal and nocturnal activity patterns is usually assumed to be a fixed one, with organisms demonstrating physiological traits optimised for a particular diel rhythm.

2. In this study, we explore the activity rhythm of a tropical reef fish, the golden-lined rabbitfish, *Siganus lineatus*. We make use of acoustic telemetry (manual tracking), combined with underwater observations of feeding behaviour to investigate the diel foraging patterns of *S. lineatus*, at three sites around the lagoon of Lizard Island, Great Barrier Reef.

3. We found significant differences in the activity patterns of shoreline and reef-based populations of *S. lineatus*. Individuals inhabiting the boulder-shoreline site foraged during the day and remained stationary in rest holes during the night, whereas individuals from the two reef populations foraged only during nocturnal hours, remaining stationary at the edge of favoured coral bommies during the day. To our knowledge, this represents the first example of a wholesale intraspecific shift in diel activity rhythm for a tropical marine fish.

4. We suggest that *S. lineatus* is a diurnal nominal herbivore whose biological rhythm has developed the flexibility to be nocturnal. This development may simply represent the masking effects of predation, competition or ontogeny, or it may represent entrainment over an evolutionary time-scale necessary to enable the species to expand its range into the coral reef environment.

5. Either way, the results identify *S. lineatus* as a potential subject for research into the relative importance of the various biological forces driving divisions along the temporal niche axis and suggest that the species has the potential to provide insights into the impact of biological rhythm plasticity on ecosystem functioning at the ecological and evolutionary level.

Key-words: acoustic telemetry, adaptive foraging, biological rhythm, chronoecology, coral reef, facultative nocturnal herbivore, rabbitfish, temporal niche partitioning

Introduction

The behavioural traits of an organism are governed by three factors: its endogenous circadian rhythm, environmental influences that entrain the endogenous clock and any masking environmental stimuli that interfere with the endogenous rhythm (Kronfeld-Schor & Dayan 2003, 2008). Because the day/night cycle is the most predictable environmental cue to which organisms are exposed, entrainment of biological rhythms to the cycle of light intensity is one of the most significant drivers of the internal circadian clock and associated activity pattern (Kronfeld-Schor & Dayan 2003). It is this

presumed fundamental division between diurnal and nocturnal activity that lies at the heart of behavioural and evolutionary ecology. The nocturnal–diurnal dichotomy provides a temporal axis of niche segregation that has facilitated coexistence between competitors (Pianka 1969; Kunz 1973; O'Farrell 1974; Ziv *et al.* 1993; Brännäs & Alanärä 1997), defined partitioning between predators and prey (Culp & Scrimgeour 1993; Fenn & MacDonald 1995) and brought about the evolution of whole lineages such as mammals (Kronfeld-Schor & Dayan 2008). Yet despite its ubiquity, the temporal niche axis and its impact on the structure and functioning of individual ecosystems have received relatively little attention in studies of behavioural ecology (Curtis & Rasmussen 2006; Kronfeld-Schor & Dayan 2008).

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This may, in part, be a result of the fact that diel activity patterns are usually assumed to be inflexible (effectively constrained by evolution) and consistent across individual species, with organisms demonstrating specific physiological traits optimised for one activity pattern that would, in theory, render its performance sub-optimal during the opposing diel period (Metcalf, Fraser & Burns 1998; Kronfeld-Schor *et al.* 2001; Halle 2006). The assumption of intraspecific rigid diel rhythms essentially underpins all generalisations about the structure and functioning of individual ecosystems and observations on the interactions between species within those ecosystems. But how stable are these rhythms and the activity patterns they generate? Certainly, ecological theory suggests that temporal shifts in activity patterns should be rare (Schoener 1974a,b) and wholesale shifts in diel rhythm have not generally been commonly acknowledged (Lima & Dill 1990; Kronfeld-Schor *et al.* 2001; Kronfeld-Schor & Dayan 2003). However, a growing body of literature is now challenging the intraspecific fixed rhythm paradigm for vertebrates, including mammals (Blanchong *et al.* 1999; Kramer & Birney 2001; examples in Curtis & Rasmussen 2006; Halle 2006; Refinetti 2006, 2008), primates (Tattersall 1978; Curtis, Zaramody & Martin 1999; Fernandez-Duque 2003) and birds (Craig & Douglas 1984; Helm & Visser 2010).

Fishes, like other vertebrates, are currently assumed to be fixed to a particular diurnal rhythm. Species have tended to be classified as either nocturnal or diurnal (Hobson 1965; Munz & McFarland 1973; Helfman 1981, 1993; McFarland 1991) and described as having specific physiological adaptations for operating in either high- or low-light levels, most of which are related to visual sensory ability (Pankhurst 1989; McFarland 1991; Warrant 2004; Karpestam *et al.* 2007). Research is providing increasing evidence of plasticity in the activity patterns of fishes (see Reeb 2002), but the overwhelming majority of these examples come from temperate freshwater (Heggenes *et al.* 1993; Alanärä & Brännäs 1997; Alanärä, Burns & Metcalfe 2001; Metcalfe & Steele 2001) or diadromous (Godin 1981; Fraser, Metcalfe & Thorpe 1993) species. A small number of cases of diel plasticity in foraging behaviour for tropical marine fish have been anecdotally documented, for example, Hobson (1974) reported some evidence of diurnal and nocturnal feeding in nine of the 102 species he examined on Hawaiian coral reefs. Overall, however, the extent of our knowledge of variation in diel activity patterns in aquatic vertebrates and the causes of this variation undoubtedly lags behind the research on terrestrial taxa.

Part of the reason for this lag must certainly be attributed to the observational challenges posed by the aquatic environment. Many of the documented cases of plasticity of activity patterns in the terrestrial environment have been brought to notice by accident through casual behavioural observation, rather than direct study of activity cycles (Curtis & Rasmussen 2006). The comparative inaccessibility of the aquatic environment, particularly at night, means that little research is carried out in these ecosystems during nocturnal periods. Field studies of activity rhythms for aquatic organisms are further complicated by limitations on the researcher's ability

to directly observe activity over periods longer than that allowed for under scientific SCUBA (Self-Contained Underwater Breathing Apparatus) diving limits. Previous field measurements of activity have been based on inference from trapping in fishing gear (Reeb *et al.* 1995), direct observation (Hobson 1965, 1974; Hobson, McFarland & Chess 1980; Helfman 1981) or radiotracking for freshwater taxa (Clark & Green 1990; Bunnell *et al.* 1998; David & Closs 2001). For the marine environment, the advent of acoustic telemetry has now provided a means to obtain direct and continuous information on the movement of organisms, and over the last decade and a half, increasing use has been made of the technology to track the movement patterns of marine fishes (see Holland *et al.* 1993; Holland, Lowe & Wetherbee 1996; Zeller 1997; Lowry & Suthers 1998; Eristhee & Oxenford 2001; Lowe *et al.* 2003; Topping, Lowe & Caselle 2005; Afonso *et al.* 2008). With advances in technology allowing for the manufacture of smaller and smaller acoustic transmitters, the technology has now opened up to be applied to a wider range of species, including the smaller species of herbivorous fishes that inhabit coral reefs.

One of the four main families of herbivorous fishes on coral reefs is the rabbitfish (F: Siganidae). Rabbitfishes are common to coral reefs of the Indo-Pacific where they are collectively defined as diurnal herbivores (Woodland 1990; Randall, Allen & Steene 1997). The largest species of rabbitfish present on reefs is the golden-lined spinefoot, *Siganus lineatus* (Valenciennes, 1835) (Fig. 1a). Previous work on the Great Barrier Reef examining the behaviour of *S. lineatus* had suggested that individuals may be foraging during crepuscular or nocturnal periods (Fox *et al.* 2009), in contrast to most other reef herbivores that feed during daylight hours. The daily activity pattern of this species therefore remained unclear. The aim of this study was to establish the foraging periodicity and diel activity pattern of *S. lineatus* to determine whether the species could be defined as nocturnal or diurnal. Making use of acoustic telemetry (active tracking), combined with direct behavioural observations and indirect sampling, we investigated the foraging patterns (timing and spatial extent) of *S. lineatus* in coral reef and neighbouring shoreline habitats, with the goal of establishing the chronoecology (Halle & Stensteth 2000) of this species.

Materials and methods

STUDY SITE

The study was conducted at Lizard Island, a 7-km² granitic island located 30 km off the Australian mainland in the northern section of the Great Barrier Reef. To the south of the main island lies Palfrey Island and South Island which, together with Lizard, form a shallow (max. 10 m) lagoon surrounded on two sides by well-developed reef systems extending down to c. 20 m depth (Fig. 1b). Many locations around the lagoon support reef-based populations of *S. lineatus*, while a sandy shoreline of the main island with associated beach-rock boulder outcrops and small area of mangroves supports a separate population of *S. lineatus* (Fig. 1b). The boulder-shoreline area is

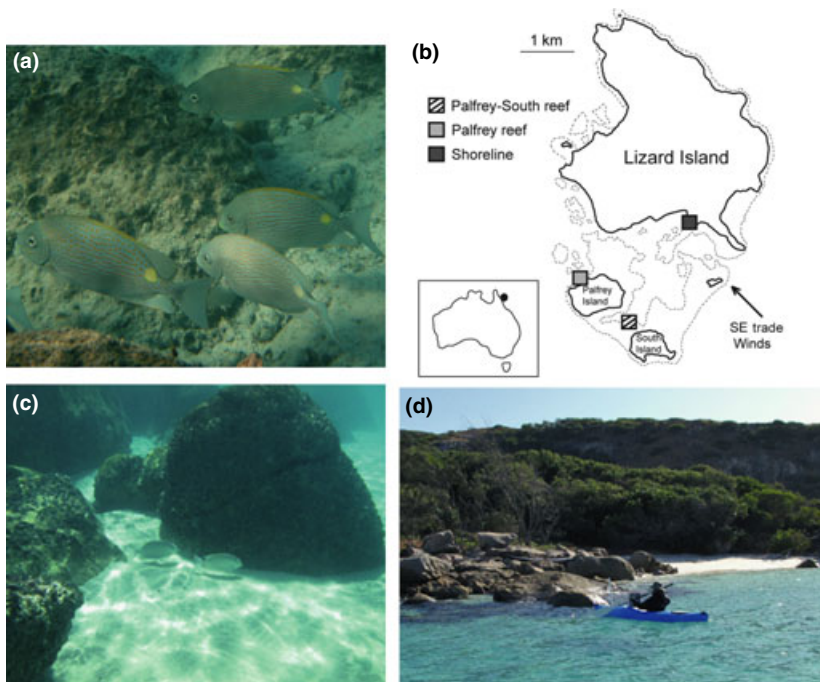


Fig. 1. (a) Golden-lined rabbitfish, *Siganus lineatus*, (b) Map of Lizard Island showing location of populations of *S. lineatus* tracked and sampled in this study, (c) *S. lineatus* at boulder-shoreline site and (d) view of shoreline site from above water showing tracking in progress from 3-m kayak outfitted with directional acoustic hydrophone and acoustic receiver. Photographs reproduced by kind permission of K Brooks (a) and J Donelson (c,d).

separated from reef habitat typically utilised by *S. lineatus* (large stands of branching *Porites cylindrica* and large mounds of *Porites* sp. with neighbouring sand aprons) by a 50-m expanse of sand and coral rubble. But shoreline-based individuals do not move between the shore and this reefal area, even at low tide and appear tied to the sand-boulder habitat (Fig 1c,d).

DIEL ACTIVITY PATTERNS

Between August and November 2009, individual *S. lineatus* were collected from reef and shoreline sites around the Lizard Island lagoon, returned immediately to the research station and transferred to a 10 000-L aquarium of running seawater. Fish were then placed in a 30-L tub containing MS-222 (Tricaine, 0.1 g L^{-1}) until a total loss of equilibrium was reached. Individuals were weighed and measured and a small (2–3 cm) incision made on the left-hand side of the body, c. 2 cm behind the base of the pectoral fin. An acoustic transmitter (Vemco, V9-1L, $24 \times 9 \text{ mm}$, 1000 or 2000 ms repeat rate, 20 or 37-day battery life, respectively) coated in antiseptic was inserted into the peritoneal cavity. The incision was closed using three non-overlapping, non-absorbable nylon sutures (Ethilon 3/0 24 mm 45 cm). Fish were returned to the aquaria, where their gills were flooded with running seawater until they regained equilibrium. The procedure (from the onset of anaesthesia to recovery) took c. 7 min. Fish were kept in aquaria overnight to permit recovery from anaesthesia and were released at the point of capture at least 3 h after dawn (to minimise the chance of crepuscular predation). The total time from capture to release was < 24 h. A total of 11 fish were tagged and released, but four reef-based individuals were omitted from the study. These individuals exhibited atypically large and rapid movement patterns followed, within an hour, by disappearance from the area. They appeared to be the victims of shark predation (*Triaenodon obesus* were seen hunting in the immediate vicinity of released fishes).

Seven *S. lineatus* were actively tracked during the course of the study, with a total of over 550 h of data collected on the movement patterns of these individuals (Table 1). Tracking was conducted from a 3-m kayak equipped with a directional hydrophone (Vemco, V110)

and acoustic receiver (Vemco, VR100), following the method pioneered by Meyer & Holland (2001, 2005) (Fig. 1d). Each fish was tracked for continuous periods of between 12 and 24 h on up to five occasions. Every 15 min, the kayak was manoeuvred to within 5–10 m of the individual and its position recorded via GPS, resulting in a minimum of 185 positional fixes for each individual across diurnal and nocturnal time periods (average number of fixes per fish was 354, Table 1). Fish were not tracked until at least 3 day post-release to minimise the chance of recording abnormal movement patterns associated with capture and surgery. At the start of each track, the individual was sighted to confirm its identity. In all these sightings, it was noted that tagged individuals were within a school of conspecifics, substantiating the fact that the fish had recovered from handling and was exhibiting behaviour typical of the populations in question.

The overall size of individual home ranges and core areas of usage for *S. lineatus* were calculated through nonparametric kernel density estimation using Home Range Tools (HRT) (Rogers *et al.* 2005) for ArcGIS® (ESRI, Redlands, CA, USA). A biased cross-validation (BCVh) bandwidth smoothing factor was selected for the kernel analysis (Horne & Garton 2006) as the least squares cross-validation (LSCVh) parameter was found to undersmooth the data. Because data were characterised by outlying regions of low density resulting in a multimodal data set, utilisation distributions were calculated based on adaptive, rather than fixed, kernels (Worton 1989). For each individual, an overall home range (defined as the 95% volume isopleth) and core areas of usage (defined as the 50% volume isopleth) were calculated. Comparisons between mean home range sizes of reef and shoreline populations were made via Student's *t*-test. To assess the diel activity patterns of individual populations, separate nocturnal and diurnal home ranges [defined as 95% kernel utilisation distribution (KUD)] were calculated for each fish based on fixes recorded between 07:00–19:00 h (diurnal) and 19:01–06:59 h (nocturnal). Comparisons between mean nocturnal and diurnal home range sizes for reef and shoreline sites were made via Student's *t*-tests (Bonferroni correction applied to account for multiple comparisons). To obtain a pictorial reference of these home ranges, the polygon shape files generated in HRT were projected onto a satellite image of the study site

Table 1. Summary of acoustic tracking data from seven individuals of the species *Siganus lineatus* at Lizard Island, GBR

Fish	Size (SL cm)	Site	Tracking period (no of tracks)	Tracking hours	No of Fixes	Home range estimations (10^3 m^2)		Partial activity estimates (10^3 m^2)		Diel activity estimates (10^3 m^2)	
						KUD ₅₀	KUD ₉₅	No of core areas	First track (KUD ₉₅)	Final track (KUD ₉₅)	Diurnal (07:00–19:00)
SL1	26.2	Reef	02/09/09–21/09/09 (5)	106.5	426	45.860	7.649	12.553	12.010	14.455	43.325
SL2	24.6	Reef	04/11/09–22/11/09 (4)	82	332	17.273	2.575	15.553	6.546	6.802	17.258
SL3	25.4	Reef	06/11/09–20/11/09 (4)	94	386	35.787	3.916	17.441	17.658	8.743	33.495
SL4	26.1	Reef	06/11/09–20/11/09 (3)	53	185	29.561	4.189	21.911	22.506	10.931	21.826
SL5	24.6	Shoreline	04/09/09–14/09/09 (5)	76.5	429	37.648	1.739	16.806	27.810	38.740	4.581
SL6	26.1	Shoreline	07/09/09–20/09/09 (4)	71	332	28.044	3.679	9.510	14.273	28.857	4.846
SL7	25.6	Shoreline	08/09/09–22/09/09 (4)	72.5	392	26.389	3.539	12.013	11.800	24.408	5.251

Home range characteristics are presented here as kernel utilisation distribution areas (KUDs) where KUD₅₀ represents the area (10^3 m^2) in which animal spends 50% of its time. Core area defined as KUD₅₀, where animal spends 50% of its time. Partial activity estimates represent total area (KUD₉₅, 10^3 m^2) covered by animal during first and final tracks. Diel activity estimates represent total area covered by animal during diurnal (07:00–19:00 h) and nocturnal (19:00–07:00 h) periods, as defined by the KUD₉₅.

using the Export to KML extension to ARCMAP 9.x (Export to KML version 2.5.4, 2009; Bureau of Planning and Sustainability, City of Portland, Oregon, USA; <http://www.esri.com>) (see Supporting information).

DIEL FORAGING PERIODICITY

To determine whether differences in diel activity patterns could be attributed to differences in foraging behaviour, diurnal feeding rates of both reef- and shoreline-based *S. lineatus* were recorded from dawn to dusk (06:00–18:00 h) via underwater focal individual censuses on SCUBA. This was undertaken after the completion of acoustic tracking studies to minimise disturbance within the area. An adult individual was followed for 2–5 min and the number of bites recorded (converted to bites min^{-1}). In addition, data on the passage of digesta through the guts of individuals from the shoreline population ($n = 16$) were collected to compare with the pattern previously described for reef-based *S. lineatus* (Fox *et al.* 2009). Fish were sampled using speargun at three times of day: morning (06.00–07.30 h), midday (11.30–13.00 h) and evening (16.30–18.00 h). Individuals were kept on ice and dissected within 1 h of capture. The gut was dissected out, weighed and the total alimentary tract length measured. The tract was then divided into five sections. The stomach section (S) (up to and including the pyloric caecum) was removed, and the remaining tract divided into four sections of equal length (Choat, Robbins & Clements 2004). The first three segments were designated intestine (I1, I2 and I3) and the posterior segment hindgut (H). For each section, the wet weight of contents was recorded and expressed as a proportion of total gut weight. Averages for the five sections in each of the three time periods were then calculated.

ONTOGENY

The population age structure within each of the two habitats studied was investigated by examining the ages of a sample of individuals collected from reef ($n = 12$) and shoreline ($n = 16$) populations. Sample sizes were restricted by the overall population densities of *S. lineatus* at the respective study sites. Age determination was carried out by examining transverse sections of the sagittal otoliths of fish collected from all three study sites. Sectioned otoliths were examined under a compound microscope and the number of opaque bands counted. The deposition of annual opaque bands within the otoliths of siganids has been validated for *S. canaliculatus* by Grandcourt *et al.* (2007), and here, we assume the annual pattern of deposition to be valid for *S. lineatus*. Counts of annual bands were made on three separate occasions to ensure consistency of readings.

BODY CONDITION

The body condition of *S. lineatus* within the reef and shoreline populations was investigated via the calculation of two condition indices for each of the individuals collected in the ageing study: (i) Fulton's condition factor (K) = $W*100/SL^3$, where W = gutted wet weight of the individual (g) and SL = standard length (mm), giving an index of relative fish weight for a given length, and (ii) relative liver weight or hepato-somatic index (HSI) was calculated as $HSI = WL*100/W$, where WL = liver weight (g). Comparisons of the two measures of body condition for reef and shoreline population samples were made using *t*-tests. Differences in the mean size at age between habitats were also examined using analysis of covariance (ANCOVA) with $\ln(\text{age})$ as the covariate, $\ln(\text{size})$ the dependent variable and habitat the fixed factor.

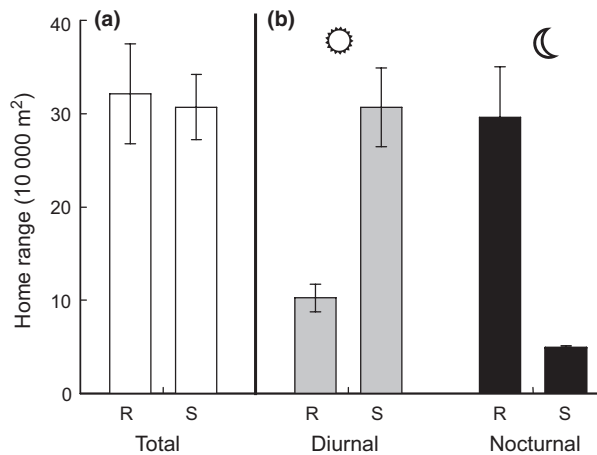


Fig. 2. (a) Overall home range size (mean \pm SE) of *Siganus lineatus* within reef (R) and shoreline (S) populations (white bars) based on manual acoustic tracking of individuals over multiple 12- to 24-h periods. Home range is defined here by the 95% volume isopleth (kernel density analysis). For both populations, home range size is also presented as estimated by (b) diurnal (grey) and nocturnal (black) observations only.

Results

DIEL ACTIVITY PATTERNS

Home range areas for individual *S. lineatus* varied from 1.7–4.6 ha (Table 1). However, the average home range size of *S. lineatus* did not differ significantly between reef and shoreline sites ($t_5 = 0.1862$, $P = 0.8596$) (Fig. 2a). Within this total area, activity was highly concentrated around core areas of use, usually individual coral bommies in the reef environment or specific boulders along the shoreline habitat. On any given day, individuals would spend large portions of time resting in a single spot, meaning that *S. lineatus* spent 50% of its time in an area covering just 12% of the total home range and up to 80% of the time of these fish was spent in an area covering just 40% of the overall home range. In terms of core habitat usage (KUD₅₀), the average home range of *S. lineatus* was just 0.39 ha (Table 1).

Remarkably, the overall similarity in home range size for the two populations of *S. lineatus* obscured an important difference: the temporal distribution of activity patterns at reef and shoreline sites was diametrically opposed (Figs 2b and 3). Diurnal (07:00–19:00 h) observations alone on *S. lineatus* from the reef sites yielded an average home range of just 1.02 ha \pm 0.15 SE, less than a third of the true home range of these individuals (Fig. 2b, Table 1). However, the average nocturnal home range of *S. lineatus* in these reef environments was 2.96 ha \pm 0.54 SE, representing more than 92% of the total measured home range (Fig. 2b). Reef-based *S. lineatus* would typically spend daylight hours in a stationary position at the edge of a particular coral bommie with the only diurnal movement being a change to an alternate 'resting bommie'. Between 19:00 and 19:30 h, fish would start to move off the edge of the reef, and there followed a period of sustained and wide-ranging movement, lasting

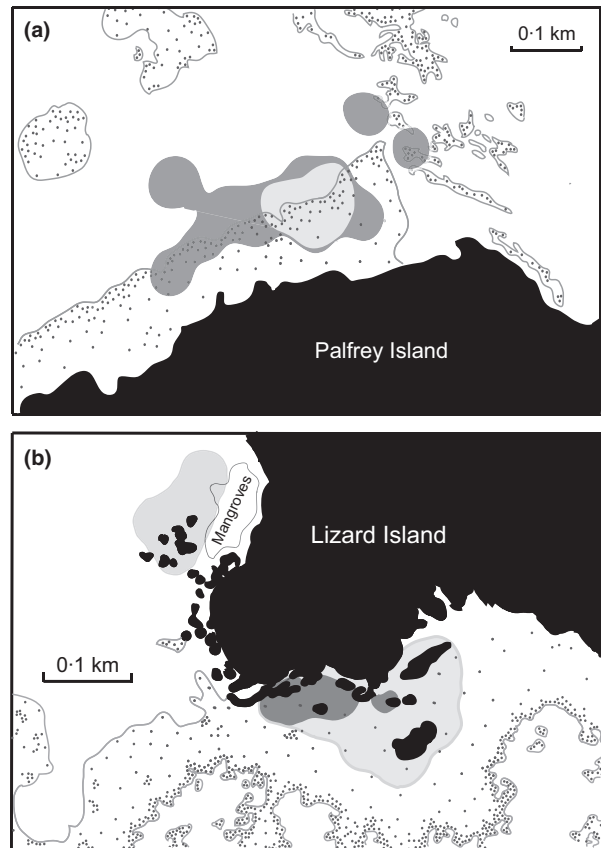


Fig. 3. Home ranges of *Siganus lineatus* individuals (a) SL3 captured and tracked in a reef habitat and (b) SL6 captured and tracked in a sandy shoreline habitat surrounding Lizard Island lagoon, GBR. Home range is defined here by 95% volume isopleth. Light grey-shaded areas represent the home range of these individuals as measured by diurnal observations only, and dark grey areas represent the home range of the same individual as measured by nocturnal observations. Areas of grey stippling indicate patches of reef surrounding the islands.

until c. 21:30 h when individuals would return to a resting spot and remain stationary for an extended period (Fig. 3). This pattern was repeated through the remainder of the night, with individuals generally undertaking between 2 and 3 forays of movement, punctuated by periods of stationary behaviour.

By contrast, *S. lineatus* inhabiting the shoreline site exhibited the overwhelming majority of their movement during daylight hours. These individuals had a measured nocturnal home range of just 0.49 ha \pm 0.02 SE, representing just 16% of the total measured home range, and significantly smaller than the nocturnal home range of reef individuals ($t_5 = 3.4405$, $P < 0.025$) (Fig. 2b, Table 1). The diurnal home range of shoreline individuals was more than 6 times greater than their nocturnal range and significantly greater than the diurnal range of reef individuals ($t_5 = 5.0578$, $P < 0.025$) (Fig. 2b, Table 1). Movement generally commenced shortly before 06:00 h and would continue throughout the day in bursts punctuated by periods of motionless. These 'resting' periods usually took place along the perimeter of boulder outcrops, and individuals had favourite spots to which they would repeatedly return over the tracking period. Around 18:00 h,

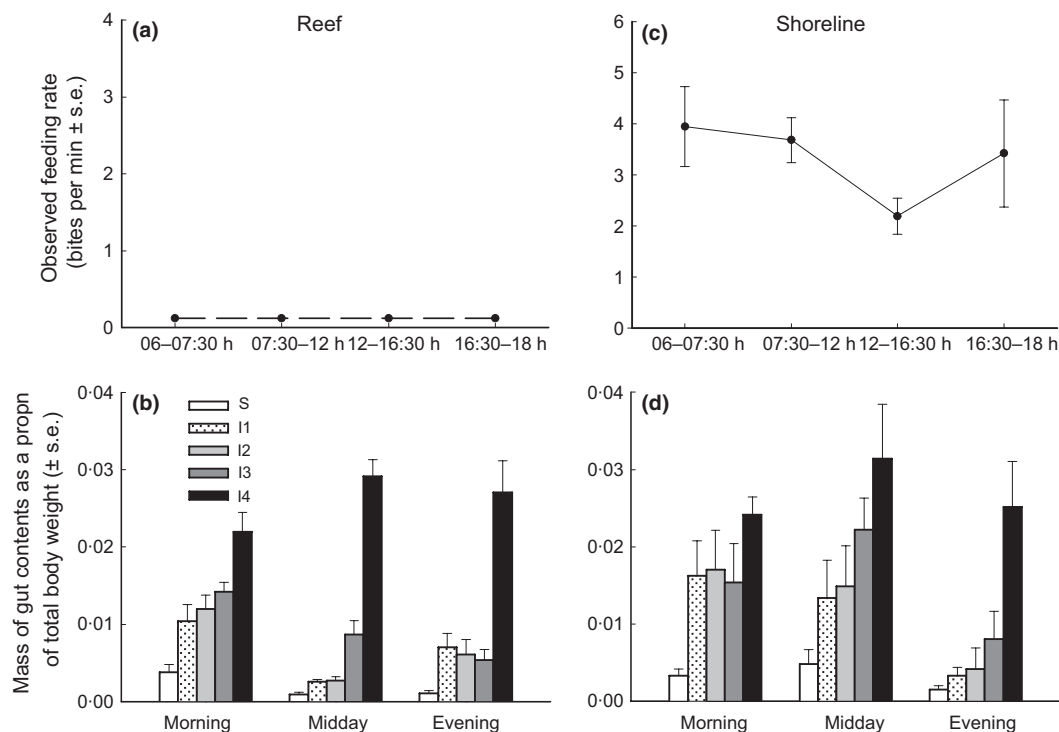


Fig. 4. Timing of foraging activity in (a,c) reef and (b,d) shoreline populations of *Siganus lineatus* as evidenced by (a,b) direct underwater observations of feeding rates (bites min^{-1}) over the diurnal period 06:00–18:00 h and (c,d) measurement of passage of digesta through the gut of individuals collected from both populations. Feeding rates for reef-based *S. lineatus* (Fig. 4a) had a mean value of zero and no variation about this mean; however, data have been offset from zero for presentation purposes. Wet weights of digesta (mean \pm SE) in five regions of the alimentary tract [stomach (S), first intestinal segment (I1), second intestinal segment (I2), third intestinal segment (I3) and hindgut (H)] are expressed as a proportion of the total body mass of the animal for individuals collected from (c) reef and (d) shoreline populations at three times of day, morning (06:00–07:30 h), midday (11:30–13:00 h) and evening (16:30–18:00 h). Data in Fig. 4c. from published data (Fox *et al.* 2009).

while it was still daylight, fish would move into positions deep in the shoreline rock crevices, occasionally switching to a nearby shoreline crevice position during the night (Fig. 3).

DIET FORAGING PERIODICITY

Underwater observations of feeding behaviour carried out at coral reef sites during diurnal hours discovered no evidence of any feeding activity by *S. lineatus* (Fig. 4a). Of the 484 observations taken between 06:00 and 18:00 h for reef-based *S. lineatus*, not a single fish was seen feeding, and therefore, zero bites were recorded during diurnal hours. These direct observations were corroborated by examination of the passage of digesta through the intestine of fishes collected from reef habitats. Individuals collected early in the morning (06:00–07:30 h) displayed the maximum volume of stomach and intestinal contents, with digesta passing progressively through to the posterior segments of the alimentary tract through the course of the day (Fig. 4b). By contrast, individuals at the shoreline site were observed feeding throughout the course of the day (Fig. 4c). Feeding rates were relatively uniform through daylight hours, and this was reflected in the build-up of digesta in the stomach and anterior portion of the intestine through to early afternoon, after which time the feeding rate decreased and individuals began the process of emptying their gut (Fig. 4c,d). The rate of defecation

observed in shoreline-based fishes actually peaked during the 12:00–16:30-h period (0.2 defecations fish^{-1}), explaining the decrease in gut contents observed in individuals collected in the evening period (16:30–18:00 h) (Fig. 4d).

ONTOGENY

The average size (SL) of individuals collected from reef sites was $25.3 \text{ cm} \pm 5.2 \text{ SE}$, compared to an average of $24.3 \text{ cm} \pm 5.8$ for those collected from the shoreline site. The samples taken therefore revealed no significant difference in overall body length ($t_{26} = 1.145$, $P = 0.263$) between the two populations. Individuals collected from the reef spanned an age range from 1 to 7 year, while individuals collected from the shoreline site spanned a 1–11 year range (Fig. 5). In terms of an ontogenetic basis for the shift in diel activity patterns, the age distributions of samples from the reef and shoreline populations were not significantly different (Kolmogorov–Smirnov test, $P > 0.1$), although this result could have been an artefact of low sample sizes.

BODY CONDITION

Individuals within the shoreline population displayed a significantly bulkier frame for a given size than their reef counterparts, with a significantly higher value of Fulton's K

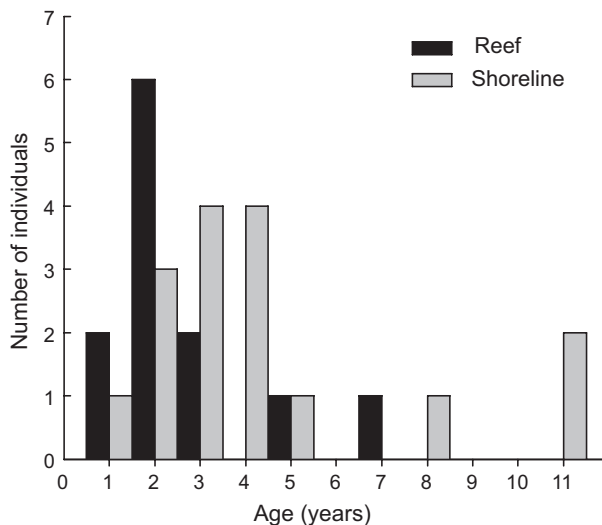


Fig. 5. Age structure of *Siganus lineatus* populations within reef and shoreline sites. Age frequency distributions are derived from examination of sectioned sagittal otoliths of individuals collected from reef ($n = 12$) and shoreline ($n = 16$) populations.

index (t -test, $t_{26} = 2.273$, $P = 0.032$). However, the relative liver size (hepatosomatic index) of individuals within the two populations did not differ significantly (t -test, $t_{26} = 0.254$, $P = 0.802$). In terms of their size at a given age, the results of the ANCOVA suggested that, on average, the reef individuals sampled grew to a significantly greater size at age than shoreline individuals (ANCOVA, $F_1 = 15.24$, $P = 0.001$).

Discussion

The plasticity of diel activity patterns of *S. lineatus* observed in this study was striking, with the species exhibiting diurnal foraging in shoreline populations and nocturnal foraging on coral reefs. Within reef habitats, *S. lineatus* remained stationary during the day and was active only during nocturnal hours, particularly in the early period of complete darkness, when foraging took place just off the reef in surrounding sand aprons. In contrast, at the shoreline site, individuals commence foraging at the first signs of dawn and continued with periodic bouts of movement during the day. Lack of replication of independent sites within the two habitat types means that some caution must be exercised in ascribing the differences in activity pattern to specific habitat features; however, it is undoubtedly the case that, within a range of habitats, the species is capable of exhibiting a wholesale shift in diel activity pattern. Such a wholesale intraspecific shift in activity pattern is particularly surprising because herbivorous and nominally herbivorous fishes such as *S. lineatus* are usually recognised as being only diurnally active (Hobson 1965; Zemke-White, Choat & Clements 2002) (but see Rooker *et al.* 1997; Hammerschlag, Heithaus & Serafy 2010; and anecdotal evidence in the case of *S. guttatus* Woodland 1990). The results provide one of the first examples of adaptive foraging behaviour (Dill 1983; Loeuille 2010) from coral reef ecosystems and highlight a useful model species with which to tease

apart the selective forces that determine activity patterns within organisms (Metcalf, Fraser & Burns 1999; Kronfeld-Schor & Dayan 2003).

The results of the present study inevitably raise questions of how and why *S. lineatus* exhibits this wholesale inversion in diel activity. To answer both, we must first settle the more fundamental issue of what the natural rhythm for this species is. One way of answering this is to examine whether those individuals operating at the opposite part of the diel cycle are incurring a cost in terms of their fitness. Evidence from mammals, including human shift workers, suggests that whatever the proximate cues or ultimate drivers of the inversion, organisms that invert their activity pattern do pay a price in terms of reduced health or performance (Moore-Ede & Richardson 1985; Knutsson *et al.* 1986). In this study, the comparison of average ages of individuals within the reef and shoreline populations, together with the measurements of body condition, hints at the fact that diurnally active individuals within the shoreline population are smaller in length but bulkier for a given age. These preliminary results would suggest that diurnal activity is the natural rhythm for *S. lineatus* and that reef individuals, constrained in their rhythm biology to their legacy as diurnal herbivores, may be paying a price for being active nocturnally in terms of poorer overall condition.

If we accept the premise that diurnal activity is the natural rhythm for this species, we are left with two questions: (i) Why does *S. lineatus* exhibit such a wholesale activity shift? and (ii) What aspect of the species' physiology enables the shift? Diel divergences in behavioural patterns within the marine environment are considered to be largely dependent on vision (McFarland 1991), with distinct differences in eye morphology between nocturnal and diurnal species (Myrberg & Fuiman 2002). Switches to nocturnal feeding such as those exhibited by *S. lineatus* inhabiting reef sites should therefore be associated with a reduction in feeding efficiency (Beers & Culp 1990; Fraser & Metcalfe 1997). The tracking results of this study demonstrated that *S. lineatus* from reef habitats moved off the reef into neighbouring deep and shallow sand aprons to feed. It is possible that these excursions are targeting the nocturnal exodus of sand-dwelling invertebrates, thereby adding an extra source of protein to a diet otherwise characterised by detritus and filamentous algal material (Fox *et al.* 2009), which would otherwise have its highest nutritional content during late afternoon (Zoufal & Taborsky 1991; Zemke-White, Choat & Clements 2002). The increased incidence of epifaunal crustacea in the bacterial film covering the reefal sand aprons may result in a qualitative difference in the nutritional intake of *S. lineatus* feeding nocturnally that can compensate for the quantitative decrease because of inefficiencies associated with feeding in the dark. However, it is conceivable that the reduction in feeding efficiency experienced by a nocturnal detritivorous-herbivorous benthic forager such as *S. lineatus* may be less extreme than in the case of a zooplanktivorous or piscivorous species targeting specific prey items (Thetmeyer 1997). In this case, the switch from diurnal to nocturnal feeding would not represent so great a trade-off in efficiency terms. The fact that benthic

herbivory–detritivory is not target specific may facilitate the adaptability in diel rhythm for *S. lineatus* observed here.

Siganus lineatus may also possess ocular adaptations for feeding in reduced light levels that make nocturnal feeding possible (cf. Fraser, Metcalfe & Thorpe 1993). Potential structural distinctions in the eye of *S. lineatus* have yet to be fully investigated. Certainly, the relative eye diameter of *S. lineatus* is significantly larger than that of *Siganus argenteus* (a shallow-water species that diverged early from the remainder of the family), but is comparable to that of its more closely related reef-based family members (see Supporting information). Regardless of relative eye size, the larger body size in *S. lineatus* and correspondingly larger absolute eye diameter may facilitate facultative nocturnal feeding. It is noteworthy that juvenile *S. lineatus* and its sister species *S. guttatus* are often reported from mangroves, a characteristically low-light environment. Indeed, it may be that this species is physiologically adapted to low-light coastal waters and that the reef habitat represents a more recent habitat shift. Diet and physiology may therefore explain the ability of *S. lineatus* to feed at night, but does not explain why this is only observed for the reef individuals.

In fishes, the majority of documented shifts in diel rhythm to date have been in response either to ontogenetic transitions between life stages (Reebs *et al.* 1995; Annese & Kingsford 2005; Verweij *et al.* 2006) or to environmental ‘zeitgebers’ such as light intensity (or daylight length) (Beers & Culp 1990; Heggenes *et al.* 1993; Greenwood & Metcalfe 1998) or water temperature (Fraser, Metcalfe & Thorpe 1993; Fraser *et al.* 1995). Given the greater relative stability of environmental parameters within tropical ecosystems, such physical factors are unlikely to play a significant role in driving diel plasticity within tropical marine fishes. Similarly, it would appear that ontogeny is not the proximate cause of the shift in diel rhythm described here for *S. lineatus*. The body size of individuals tracked at the shoreline site (294–300 mm fork length), compared to those tracked in the reef habitat (281–308 mm FL), was almost identical and would represent mature fish of an age of *c.* 3 year (R.J.F. unpublished data). In addition, examination of the population structures at the reef and shoreline sites revealed no statistically significant ontogenetic basis for the plasticity in foraging behaviour of *S. lineatus*. It is possible that the lack of a significant result could have been because of the necessarily small sample sizes and ontogenetic transitions between life stages cannot be completely ruled out as a proximate determinant of the wholesale shift in biological rhythm observed in *S. lineatus*. However, it would appear that what we are seeing here is variation in diel activity within a single life stage, most likely driven by biological factors.

In terms of the potential biological drivers of plasticity in diel rhythms, optimal foraging theory (MacArthur & Pianka 1966) would suggest that any reduction in feeding efficiency experienced by reef-based *S. lineatus* from feeding nocturnally must be more than compensated for in either (i) a reduced risk of predation compared to diurnal feeding or (ii) a reduction in interference competition. On the first of these,

evidence from the current study suggests that overall predation pressures are higher in the reef environment than along the shoreline. Of the tagged fish released at the boulder-shoreline site all survived, compared to just four of the eight released back onto the reef. The losses of tagged reef fish cannot be definitively attributed to predation; however, the fact that none of the tags belonging to these individuals could be recovered does make predation the most likely explanation. The reef sites studied are frequented by several species of shark, and daytime observations of *Triaenodon obesus* were common during the tracking period. The higher level of predation pressure in the reef environment may therefore be a factor driving the alternate behavioural strategies observed for *S. lineatus* at Lizard Island. Certainly, the pattern of nocturnal foraging would allow *S. lineatus* to exploit a temporal niche untapped by other reef detritivores such as *Ctenochaetus* sp. and members of the family Gobiidae and Blenniidae, all of whom forage diurnally (Randall, Allen & Steene 1997), although these detritivores forage over the reef matrix, whereas *S. lineatus* was found to exploit neighbouring sand aprons as its source of detritus and algae, suggesting that the food resource is already divided up spatially.

In our study, the ultimate factors driving selection on diel activity patterns for *S. lineatus* are still unclear, and further work will be required to distinguish between the competing hypotheses of predation and competition. Nevertheless, the findings represent an important first step in the process of identifying species that are capable of providing insights into the properties of circadian rhythms in vertebrates. Most species demonstrate either nocturnal or diurnal activity patterns, and so identifying the factors that have selected for particular patterns can be difficult. Taxa that can be either nocturnal or diurnal are invaluable as subjects for research into the relative importance of the various physical and biological forces driving divisions along the temporal niche axis (Kronfeld-Schor & Dayan 2003). In addition, an examination of whether the change in foraging behaviour exhibited by *S. lineatus* represents a real shift in endogenous rhythm or whether it is merely a ‘masking’ (Mrosovsky 1999) effect of one or more of the biological drivers mentioned earlier has the potential to provide insights into the level of flexibility of circadian clocks through time (Helm & Visser 2010). In preliminary results from the current study, individual SL3 from the Palfrey reef population was recaptured at the end of the tracking period and ‘transplanted’ over to the shoreline population, where it was monitored for a 4-day period. Over this time, SL3 remained at the shoreline location and continued to display the diel rhythm of a ‘reef’ *S. lineatus*, remaining stationary during diurnal hours at the edge of a rocky outcrop and showing no tendency to forage during the daytime with the school of resident shoreline *S. lineatus*. Further replication of the transplant experiment over a longer time-scale is required to make any inferences from this observation; however, the fact that there was no immediate inversion of activity pattern for this individual hints that, for *S. lineatus*, nocturnal foraging may represent a true case of entrainment of the endogenous rhythm that has allowed the species to adapt over an

evolutionary time-scale to reef environments, rather than just a masking effect.

Much of the research into biological rhythms over the last two decades has focussed on the activity patterns of mammals, in particular rodents (see Kronfeld-Schor & Dayan 2003 and references therein), and there is now a call to extend the study of activity patterns to other lineages and species. Here, we identify an ectothermic teleost, *S. lineatus*, as an example of one of the relatively few species currently known to undertake a wholesale inversion of its activity pattern under natural field conditions. Our results suggest that *S. lineatus* has the potential to provide insights into biological rhythms and how those rhythms relate to behavioural traits and ultimately to evolutionary ecology.

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Supporting Information

Additional Supporting information may be found in the online version of this article.

Figure S1. Home ranges of *Siganus lineatus* individuals SL1–SL4 captured and tracked within coral reef sites surrounding Lizard Island lagoon, GBR.

Figure S2. Home ranges of *Siganus lineatus* individuals SL5–SL7 captured and tracked within a sandy shoreline site surrounding Lizard Island lagoon, GBR.

Figure S3. Average relative eye diameter of four species of rabbitfish (family Siganidae), *Siganus argenteus*, *Siganus lineatus*, *Siganus doliatus* and *Siganus coralinus*.

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