Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers

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ABSTRACT: Fine-scale behaviour such as foraging is difficult to quantify in free-swimming wild fish yet has important basic and applied implications. Here, we used tri-axial accelerometer biologgers to determine accelerometric predictors of bonefish *Albula vulpes* behaviours (resting, swimming, bursting, coasting, and foraging) in a wetland mesocosm in Eleuthera, The Bahamas. We also used a swim flume to estimate the relationship between acceleration and swimming speed for bonefish (n = 9). In the wetland study, 5 bonefish were tagged externally with accelerometer loggers and monitored for a 5 d period during which visual behavioural observations were conducted for 4 h. Classification tree models were used to identify accelerometric criteria for bonefish behaviours, and a classification algorithm was applied to estimate behavioural frequencies for bonefish in the wetland for the 5 d period. Bonefish spent the majority of time resting (57%), followed by swimming (26%) and coasting (17%), and foraged an average of 11 times h^{-1}. Bonefish exhibited primarily slow swimming speeds (average 0.18 m s^{-1}) while in the wetland, with occasional burst swimming events (14 h^{-1}) to maximum swimming speeds ranging from 4.3 to 6.4 m s^{-1} across individuals. Swimming and foraging behaviours varied among individuals and over the diel cycle. Bonefish generally swam most at dawn and foraged most at night. Temperature and tide were also significant predictors of swimming behaviour, and fish were generally most active at lower temperatures (~24°C) and during ebbing tidal periods despite the fact that the wetland was disconnected from the ocean. The ability to estimate fine-scale behaviours such as foraging and activity levels has important implications for understanding energy dynamics, which is fundamental to the fitness of wild fish.

KEY WORDS: Accelerometry · Activity · Behaviour · Foraging · Swim speed · Bonefish

INTRODUCTION

Environmental and ecological factors influence the behaviour and energy dynamics of animals, with direct implications for their fitness (Lima & Zollner 1996, Lind & Cresswell 2005). For example, energetic costs of movement may vary among habitat types (Nathan et al. 2008, Shepard et al. 2013), while the distribution of resources can affect foraging success and behaviour (Pyke et al. 1977). Energy is the currency of life for wild animals, and thus, energy dynamics have the potential to influence its allocation to different activities such as growth and gonadal development, influencing organismal fitness (Kleiber 1975, Callow 1985). Indeed, these energy dynamics can have population-level effects, as has been documented for a variety of taxa (e.g. Tytler & Calow 1985, Lemon 1993, Nagy et al. 1999). While

understanding how environmental conditions and animal behaviour interact is key for both basic biology (i.e. foraging theory; Altmann & Altmann 2003) and applied conservation (Buchholz 2007), measurement of these dynamics *in situ* is challenging. A variety of biologging and biotelemetry tools with various sensors have been developed, and they show much promise for the study of detailed aspects of animal behavior and energetics in natural environments, including aquatic ecosystems (Cooke et al. 2004, Rutz & Hays 2009).

Tri-axial accelerometer loggers have been used to obtain estimates of animal behaviour and energy use in a wide range of species, from invertebrates to sharks (Halsey et al. 2011, Whitney et al. 2010, Robson et al. 2012, Brown et al. 2013), and even have potential to examine very fine-scale behaviour, such as foraging (Suzuki et al. 2009). To date, measurements of foraging behaviour have been restricted mainly to large species, such as seals (Viviant et al. 2010) and sea turtles (Narazaki et al. 2013), although recent studies have used accelerometry to identify foraging behaviour of Atlantic salmon *Salmo salar* L. in aquaculture cages (Føre et al. 2011) and feeding strikes by great sculpin *Myoxocephalus polyacanthoceaphalus* in laboratory tanks (Broell et al. 2013). While accelerometers show promise for measuring foraging behaviour in teleost fishes, to our knowledge, this technique has yet to be applied on wild fish in more natural environments.

Bonefish *Albula* spp. are a group of 8 teleost fish species that occupy shallow tropical and subtropical seas worldwide (Alexander 1961, Colborn et al. 2001), including a wide range of habitats: sand flats, coral reefs, and sea grass beds (Colton & Alevizon 1983a,b, Cooke & Philipp 2004, Danylchuk et al. 2007). Bonefish move into shallow areas with flooding tides to feed and return to adjacent deeper-water habitat with ebbing tides (Colton & Alevizon 1983a, Humston et al. 2005, Murchie et al. 2013). Because of this diurnal feeding migration, bonefish are thought to play an important role in the movement of nutrients offshore in shallow seas (Murchie et al. 2013), including when some species form large aggregations and move offshore to spawn (Danylchuk et al. 2011). Bonefish are not only ecologically important but also generate significant revenue for local economies through recreational angling (Humston 2001, Danylchuk et al. 2008). Therefore, bonefish offer an excellent model for understanding behavioural ecology and energy dynamics to contribute to both basic biology and applied conservation.

Bonefish behaviour has been quantified using accelerometer transmitters (see Murchie et al. 2011); however, this technology does not enable fine-scale measurement of animal movement and posture required for certain behaviours (i.e. foraging). Our objective was to examine fine-scale behaviour (e.g. swimming, resting, and foraging) and swimming speeds of bonefish using tri-axial accelerometer loggers. To this end, we determined accelerometric predictors of these behaviours in an experimental wetland mesocosm and determined swimming speeds in a swim tunnel. We then estimated bonefish behaviours and swim speeds in the mesocosm over a 5 d period. In doing so, we aimed to develop methods for examining fine-scale behaviour and energetics and to gain insight into the behavioural ecology of bonefish.

MATERIALS AND METHODS

Fish capture

Bonefish *Albula vulpes* used in both swim tunnel and wetland experimentation were captured by seine net in Kemps Creek, Eleuthera, The Bahamas (24° 48.9′ N, 76° 18.1′ W) and held in a circular tank (3.7 m diameter × 1.25 m height; 13 180 l) for up to 1 wk prior to experimentation. Tanks were supplied with constant flow (~1800 l h^{-1}) of fresh seawater, and fish were fed daily rations of cut fish.

Swim tunnel

Nine bonefish (41.3 ± 2.9 cm fork length [FL]; 897 ± 162 g) were tagged with tri-axial accelerometer loggers (model X8M-3, 500 mAh battery, 15 g in air, 25 Hz recording frequency; Gulf Coast Data Concepts) externally through the dorsal musculature below the dorsal fin (see Brownscombe et al. 2013 for visual of location). Accelerometers were secured using plastic frontal and backing plates with 36 kg strength braided Dacron line. Once accelerometers were secured, the bonefish were placed in a Blazka-style recirculating swim tunnel (24.1 internal diameter × 116 cm length) capable of generating laminar flows up to 2.1 m s^{-1} (see Thorstad et al. 1997 for additional details on the swim tunnel). Fish were tagged the night prior to their trial and held in the swim tunnel overnight at a water velocity of 1 cm s^{-1}. This velocity allowed for circulation of fresh seawater but was slow enough to allow the fish to escape the

flow and rest on the bottom of the tunnel. Swimming trials were conducted between 07:00 and 10:00 h from 18 to 27 January 2013. Water velocity was increased in increments of 15 cm s^{-1}, and accelerometrics were derived from a 1 min period when fish were visually observed as stationary (moving the same speed as the flow) in the tunnel. The observer's watch was time-synced with the biologgers upon launching the devices, and time drift was quantified upon reconnecting the devices but was negligible (<2 s), ensuring accurate synchronization between observations and swimming speeds. Water velocity was increased until the fish could no longer maintain position in the tunnel.

Wetland mesocosm

Five bonefish (45.6 ± 2.7 cm FL; 1141 ± 173 g) were equipped with accelerometer loggers in the same manner as the swim tunnel study and were released immediately after tagging into an ~2500 m^2 enclosed wetland mesocosm in Eleuthera on 22 February 2012. The wetland is situated adjacent to the sea and receives a constant influx of seawater from a wetlab facility. It is vegetated with red mangrove *Rhizophora mangle*, black mangrove *Avicennia germinans*, and *Halimeda* spp. Tagged bonefish remained in the wetland for 5 d, during which time behavioural observations were conducted by an observer from a raised bridge that runs through the wetland for 2 h in the morning (07:00 to 09:00 h), 1 h in the afternoon (12:00 to 14:00 h), and 2 h in the evening (16:30 to 18:30 h). The observer noted the timing of behaviours including swimming, burst swimming, coasting, resting, and foraging using the same watch-logger synchronization as the swim tunnel study. Individual bonefish were identified by unique colouration of each accelerometer. A temperature logger (Thermochron iButton ver. DS1921G, −40 to 80°C range, Maxim) was placed in the center of the wetland for the course of the study.

Data analysis

Tri-axial accelerometer loggers were programmed to continuously record total acceleration (*g*) at 25 Hz frequency in 3 axes (*x* = heave, *y* = surge and *z* = sway), where *g* was the sum of both static (gravity) and dynamic (animal movement) acceleration with maximum values of ±8 *g*. Device output was calibrated by rotating the device through known angles

to real *g* (9.8 m s^{-2}) prior to deployment (as per Gleiss et al. 2010). Static and dynamic acceleration were separated by weighted smoothing at an interval of 2 s (see Brownscombe et al. 2013). Overall dynamic body acceleration (ODBA) was calculated as the absolute sum of the dynamic acceleration from all 3 axes (see Gleiss et al. 2011). Spectral analysis was used to estimate frequencies and amplitudes in the sway axis, which comprised the dominant signal and, while swimming, indicates tail beat frequency. Spectral data were band-pass filtered to include frequencies of 0.5 to 10 Hz in the analysis. Pitch (°) was calculated from the static values of the surge axis (*g*) using Eq. (1) below, where μ is the mean static value in the surge axis during a 1 min period when each bonefish was observed to be resting level to the substrate. All analysis of accelerometer data was conducted using Igor Pro 6.0 software (WaveMetrics) and Ethographer (see Sakamoto et al. 2009).

$$\text{Pitch} = \arcsine(\text{surge static} - \mu) \times (180 / \pi) \quad (1)$$

For bonefish in the swim tunnel, accelerometer-derived ODBA (*g*) was estimated using a linear mixed effect model with swimming speed (body lengths [BL] s^{-1}) as a predictor and individual fish as a random factor. Swimming speeds were corrected for blocking effect prior to analysis (Jones et al. 1974). Marginal and conditional R^2 values were calculated as outlined by Nakagawa & Schielzeth (2013).

Using acceleration data from visually observed bonefish behaviours, classification trees (Breiman et al. 1984) were used to determine accelerometric criteria to identify bonefish behaviours. First, swimming behaviours (routine and burst swimming) were distinguished from non-swimming behaviours (resting and coasting) using ODBA (*g*), sway amplitude (*g*), sway frequency (Hz), pitch (°), and Δ pitch (°) as predictors. Time post-swimming was used as additional predictor variable to classify coasting and foraging behaviours. A classification criteria algorithm was then used to identify bonefish behaviours for all 5 fish for the 5 d period they inhabited the wetland. During periods identified as swimming behaviour, swimming speeds were also predicted using the linear mixed effects model developed from the swim tunnel data.

Mesocosm data of swimming behaviour (% time spent actively swimming), foraging behaviour (foraging events h^{-1}), and average swimming speed (m s^{-1}) were analyzed with generalized least squares regression using a backwards model-selection procedure and log-ratio tests. The full models included

the predictors: time of day (dawn, day, dusk, and night), tide (low, flooding, high, and ebbing), study hour (continuous from the first hour of the study), temperature (continuous covariate), and fish ID (categorical). To determine how individuals responded to release in the wetland and any changes in behaviour, 2-way interactions included fish ID time of day, fish ID temperature, fish ID tide, and fish ID hour. Single-term deletions resulted in models that only contained significant terms at α = 0.05. A variance structure was used to correct for heterogeneity in the categorical factors (Pinero & Bates 2000). Temporal autocorrelation was accounted for by including a correlation structure in each model (Pinero & Bates 2000, Zuur et al. 2009). We validated each model by following the protocol of Zuur (2009). Due to patterns in the residuals, foraging behaviour and average swimming speed were $\log_{10}$ transformed. All statistical analyses were conducted using RStudio (v. 0.97.314) and R (v. 2.15.3; R Core Development Team 2012).
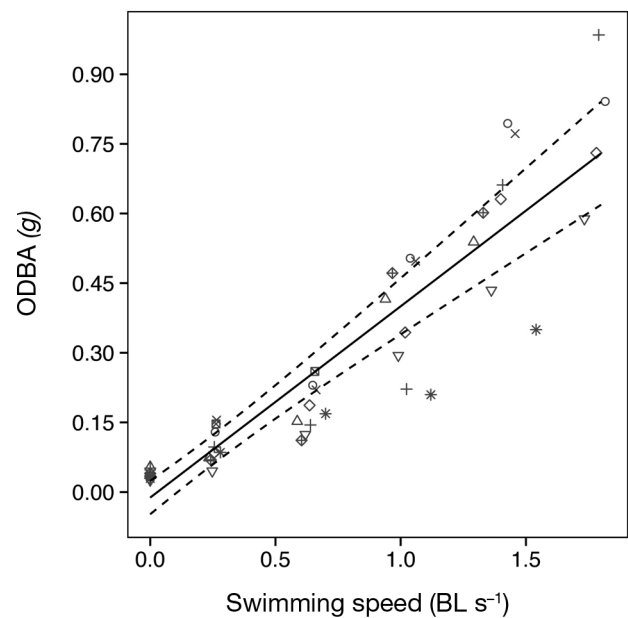

Fig. 1. Relationship between swimming speed (body lengths [BL] s^{-1}) and overall dynamic body acceleration (ODBA, g [total acceleration]) and the fitted linear mixed model (black line) with upper and lower 95% CI (dashed lines). Each symbol type represents individual fish (n = 9)

RESULTS

Acceleration and swim speed

Accelerometer-equipped bonefish *Albula vulpes* in the swim tunnel maintained swimming speeds from 0 to 2.1 BL s^{-1}. A linear mixed model predicted ODBA from swimming speed (Fig. 1; marginal R^2 = 0.82, conditional R^2 = 0.92), which was defined with Eq. (2):

$$ODBA = 0.412 \times BL\ s^{-1} - 0.012 \qquad (2)$$

Acceleration and behaviour

There were minimum of 7 instances of each type of behaviour visually observed for bonefish in the wetland (Table 1). Swimming behaviour consisted of high values of ODBA, sway frequencies, and amplitudes (Table 1, Fig. 2). Swimming behaviour was classified by sway amplitudes ≥0.03 g, while coasting behaviour was classified by z ≥ 0.01 g, ≤5 s post-swimming (Table 1). Otherwise, sway amplitudes <0.03 g were classified as resting (Table 1). Bonefish were considered to be burst swimming when sway amplitudes were ≥0.25 g. Foraging behav-

iour was classified using 3 defining characteristics. The foraging event itself was classified by a sharp decline in pitch (minimum −3° s^{-1}) to minimum pitch values of −4° (Table 1), consistent with the manner in which bonefish feed (i.e. head down and tail up; Fig. 3). Additionally, swimming behaviour always preceded (≤4 s prior) foraging behaviour, which was incorporated into the classification criteria. Using these criteria, an average of 97% of all visually observed behaviours were classified correctly; only 3% were misclassified.
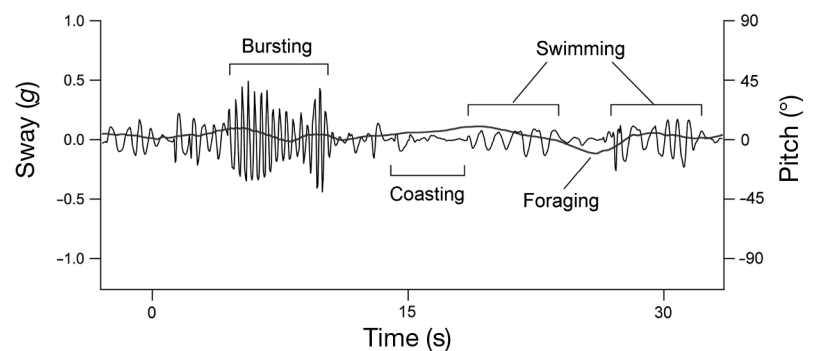

Fig. 2. Example of accelerometric signals from the dynamic sway (tail beat) axis and static surge axis (pitch) during observed bonefish behaviours while in the wetland, excluding resting. g: total acceleration

Table 1. Observed bonefish behaviours, corresponding accelerometrics, criteria, and identification efficiency using tri-axial accelerometer loggers. Under Criteria, Swim refers to time post-swimming; z represents dynamic acceleration in the sway axis. All accelerometrics are presented as mean ± SD (min., max.). ODBA: overall dynamic body acceleration; (−) data not applicable

Measured variable	Rest	Swim	Burst	Coast	Forage
No. of obs. (duration, s)	10 (17 ± 12)	16 (14 ± 17)	7 (4.1 ± 1.1)	9 (4.7 ± 0.7)	10 (10.4 ± 5.2)
ODBA (g)	0.03 ± 0.009 (0.005, 0.10)	0.21 ± 0.08 (0.02, 1.2)	1.0 ± 0.45 (0.14, 3.5)	0.05 ± 0.02 (0.01, 0.14)	0.12 ± 0.05 (0.04, 0.16)
Sway frequency (Hz)	1.1 ± 0.36 (0.56, 11.2)	1.8 ± 0.51 (0.56, 4.0)	4.0 ± 0.96 (0.56, 8.9)	0.89 ± 0.32 (0.56, 2.0)	1.5 ± 0.57 (0.62, 2.3)
Sway amplitude (g)	0.01 ± 0.003 (0.003, 0.03)	0.10 ± 0.04 (0.02, 0.47)	0.41 ± 0.14 (0.12, 0.96)	0.02 ± 0.003 (0.008, 0.03)	0.04 ± 0.02 (0.02, 0.06)
Swim speed (m s^{-1})	−	0.57 ± 0.41 (0.09, 2.5)	2.5 ± 2.1 (0.69, 6.4)	−	−
Pitch (°)	1.4 ± 2.2 (−6.5, 7.7)	4.0 ± 1.5 (−3.4, 11.3)	9.8 ± 4.3 (−1.25, 31.9)	3.4 ± 1.5 (−0.40, 8.8)	−8.7 ± 4.5 (−17.3, −4.3)
Δ Pitch° s^{-1}	0.15 ± 0.32 (−3.3, 5.1)	−0.02 ± 0.40 (−4.9, 6.2)	0.52 ± 0.97 (−15.8, 18.5)	3.1 ± 1.7 (−0.79, 8.8)	−5.5 ± 2.3 (−9.8, -3.1)
Criteria	z < 0.03 g	z ≥ 0.03 g	z ≥ 0.25 g	Swim ≤5 s + z ≥0.01	Swim ≤4 s + Δpitch ≤ −3° + pitch ≤ −4°
% correct ID (% false)	100 (3.2)	96 (2.2)	100.0 (6.2)	91 (3.0)	100 (0.25)

Fig. 3. Untagged bonefish foraging in the wetland meso-cosm. Photo credit: Karen Murchie

Bonefish behaviour in the wetland

During the 5 d period that bonefish inhabited the wetland, they spent the majority of their time resting (57%), followed by swimming (26%) and coasting (17%), while foraging occurred on average 11 times h^{-1} (Fig. 4). While swimming, bonefish maintained primarily slow speeds (mean 0.18 m s^{-1}; Fig. 4) with occasional burst swimming activity (mean 14 h^{-1}) at maximum swimming speeds ranging from 4.2 to 6.4 m s^{-1} across individuals (Table 1).

Individual fish ID and diel period were significant predictors of bonefish swimming behaviour, swimming speeds, and foraging behaviour (Table 2, Fig. 4). The majority of fish were most active at dawn but exhibited the highest mean swimming speeds during the day and at dusk (Fig. 4). Bonefish were also active at night, which is generally when most foraging behaviour occurred. Fishes 44 and 45 (number based on the fish FL in cm) exhibited contrasting behavioural patterns. Fish 45 spent the least time swimming of all tagged fish but exhibited the highest mean swimming speeds (Fig. 4). In contrast, Fish 44 exhibited the highest proportion of time swimming, with low average swimming speeds and was also highly active at night, both swimming and foraging (Fig. 4).

Environmental factors, temperature, and tide were also significant predictors of bonefish swimming behaviour (Table 2). Bonefish were most active at low temperatures (22 to 25°C) and generally became less
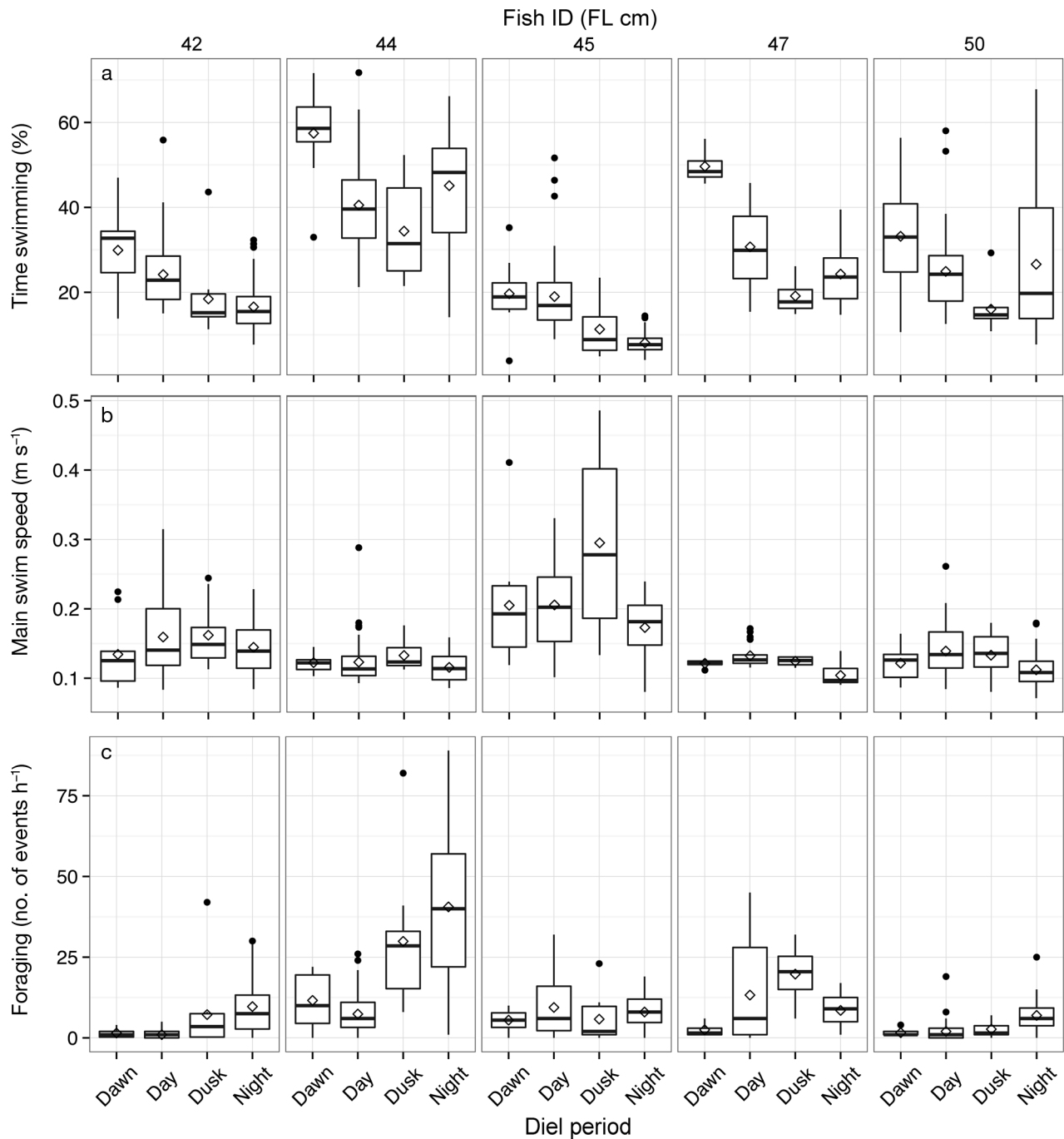
Fig. 4. Individual bonefish (a) swimming behaviour (% time), (b) mean swimming speed (m s^{-1}), and (c) foraging (no. of events h^{-1}) across the diel period (dawn, day, dusk, night) in the wetland mesocosm. Boxes: 1st and 3rd quartiles; horizontal lines: medians; whiskers: 1.5 × inner quartile range; diamonds: means; dots: outliers; FL: fork length

active as temperatures increased (Fig. 5). However, while Fishes 42 and 45 generally followed this pattern, activity peaked again at the highest temperatures observed in the wetland (26 to 30°C; Fig. 5). Across the tidal cycle, bonefish were generally most active during ebbing and low tidal periods and least active during flooding tides (Fig. 5).

DISCUSSION

Tri-axial accelerometers provided an effective means for quantifying bonefish *Albula vulpes* behaviours (resting, swimming, bursting, coasting, and foraging) and swimming speeds. Sway amplitudes provided the best proxy for most behaviours (i.e.

Table 2. Significant factors predicting bonefish swimming behaviour (% time), mean swimming speeds (m s⁻¹), and foraging behaviour (no. of events h⁻¹) in the wetland mesocosm over a 5 d period using generalized least squares models

Variable Factor	df	F-value	p-value
Swim (% time)			
Fish ID	4475	67.8	<0.001
Time of day	3475	21.9	<0.001
Temperature	1475	21.6	<0.001
Tide	3475	4.4	0.005
Hour	1475	7.7	0.006
Hour: Fish ID	4475	5.3	<0.001
Time of day: Fish ID	12475	2.8	0.001
Mean swim speed (m s⁻¹)			
Fish ID	4495	10.4	<0.001
Time of day	3495	5.6	<0.001
Hour	1495	45.8	<0.001
Foraging (no. h⁻¹)			
Fish ID	4474	24.5	<0.001
Time of day	3474	28.3	<0.001
Hour	1474	11.7	<0.001
Time of day: Fish ID	12474	3.3	<0.001
Hour: Fish ID	4474	4.4	0.002
Fish ID: Temperature	5474	2.3	0.04

swimming, resting, and coasting), while pitch metrics allowed for effective measurement of foraging behaviour. Similarly, tail beat metrics were also good measures of whitetip reef shark *Triaenodon obesus* swimming, resting, and even reproductive behaviours (Whitney et al. 2007), while more complex metrics have also been employed to identify a wide range of behaviours, including foraging strikes in great sculpin (Broell et al. 2013). Remote measurement of foraging behaviour is particularly challenging for animals in aquatic environments; however, accelerometers have greatly improved the ability to infer foraging behaviour. Bonefish are benthic feeders, and accordingly, bonefish foraging was characterized by sharp declines in pitch and minimum pitch values preceded by swimming behaviour, which were effectively measured using tri-axial accelerometer loggers. While accelerometers have been used recently to identify foraging of fish in cages or tanks (Føre et al. 2011, Broell et al. 2013), this study was, to our knowledge, the first to measure foraging behaviour of a teleost fish in a more natural environment. The ability to remotely measure foraging behaviour has important applications for understanding behavioural ecology (i.e. foraging locations and their characteristics) and energy dynamics, enabling the measurement of not only energy expenditure but also potential energy gain. It is, however, important to

note that it is foraging behaviour, not necessarily successful feeding, that is being measured. Future research could identify foraging success rates in laboratory-based observational studies or even behavioural signatures of successful foraging events using accelerometry.

ODBA is a well-established metric for predicting locomotory speeds and energy expenditure across a wide range of taxa (Gleiss et al. 2011). Indeed, there was a strong positive correlation between bonefish swimming speed and ODBA from the swim tunnel, while recent research has shown that acceleration and swimming speeds are both strong predictors of metabolism in teleost fishes (Wilson et al. 2013, Wright et al. 2014). Active metabolism can represent a major component of an animal's energy budget (Boisclair & Leggett 1989, Giacomini et al. 2013), and quantification of activity has applications for developing bioenergetics models and understanding habitat requirements. For example, further work may determine the relationship between bonefish swimming speed and metabolic rate, enabling field estimates of daily and seasonal energetic requirements using accelerometry. Indeed, tri-axial accelerometer biologgers show promise for quantifying fine-scale energy dynamics (both energy expenditure and gain) of fishes in the wild. However, it is important to recognize that estimating the active metabolism of fishes based on steady state movement is a simplified representation of their energetics, which vary with complex manoeuvres (Boisclair & Tang 1993).

While in the wetland, bonefish exhibited predominantly slow swimming behaviour (mean 0.18 m s⁻¹). However, bonefish commonly exhibited burst and coast swimming behaviour (mean of 17% of time spent coasting), with burst speeds estimated up to 4.2 to 6.4 m s⁻¹ across individuals, which are similar to maximum swimming speeds estimated for sockeye salmon *Oncorhynchus nerka* using EMG radiotelemetry (Hinch & Rand 1998). In bonefish, these speeds were never observed in the confines of the swim tunnel, and these estimates are based on extrapolations from the predictive model. Nevertheless, the majority of ODBA values recorded in the wetland were within the range measured in the swim tunnel and therefore provide reliable estimates of swimming speeds, which future research could use to predict metabolism. There was also significant inter-individual variability in bonefish swimming behaviour, swimming speeds, and foraging behaviour in the wetland. Animal behaviour in general is often highly variable within species due to genetic, ontogenetic, physiological, or experiential factors,
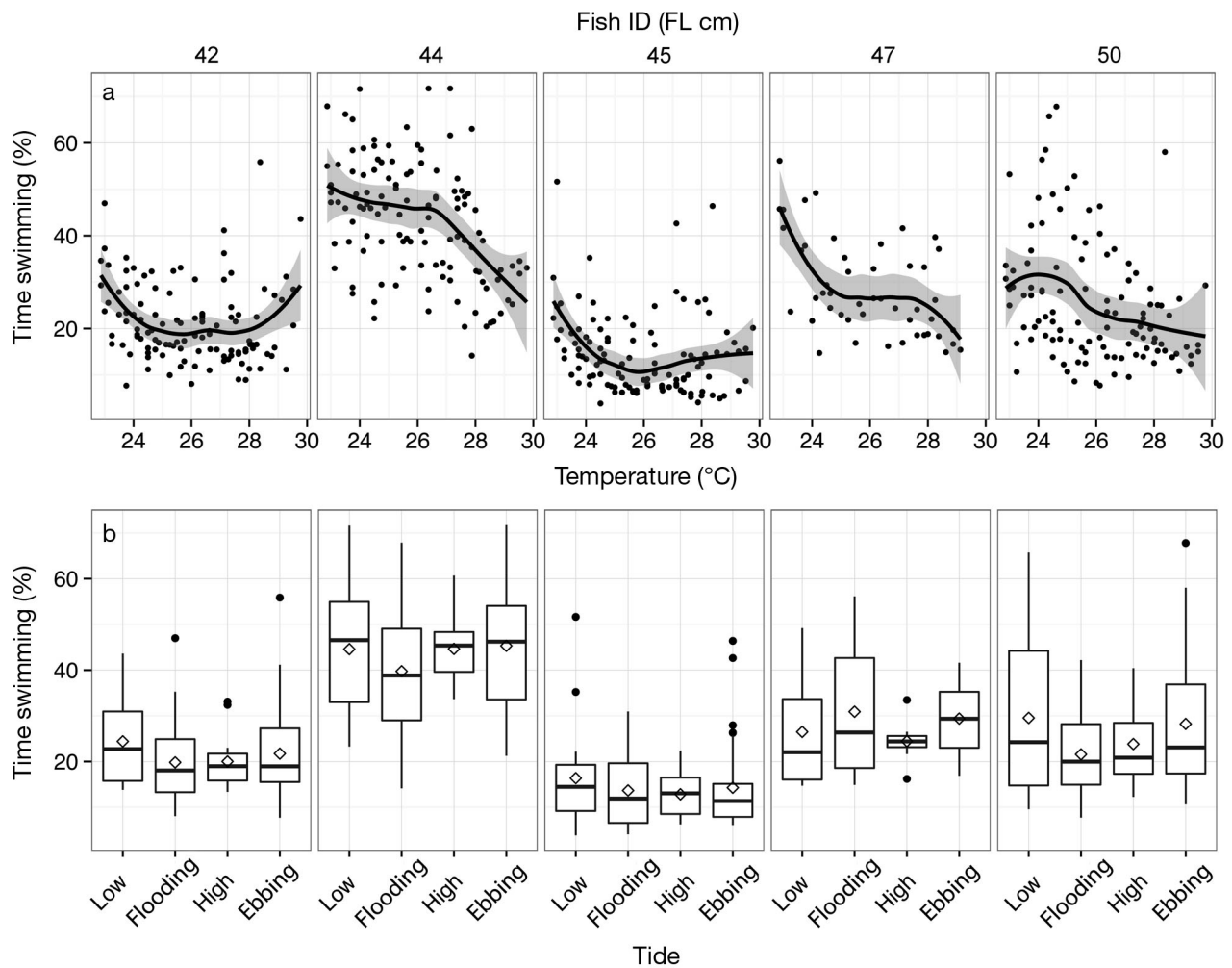
Fig. 5. Individual bonefish swimming behaviour (% time) across (a) temperature and (b) tidal periods while in the wetland mesocosm. In (a), dots are individual measurements, lines indicate means, and shading indicates 95% confidence intervals. In (b) boxes: 1st and 3rd quartiles; horizontal lines: medians; whiskers: 1.5 × inner quartile range; diamonds: means; dots: outliers; FL: fork length

but individuals commonly exhibit consistent behavioural types (personalities; Magurran 1993, Dall et al. 2004, Sih et al. 2004). Such individual variability may have important ecological (e.g. population dynamics or environmental interactions) and evolutionary (e.g. evolvability and speciation) implications and, on a population level, may be important for survival in changing environments (Wolf & Weissing 2013). The sample size of this study (n = 5) has revealed how variable bonefish behaviour can be between individuals, and larger sample sizes may indicate the relative prevalence of these behavioural types in the population.

Despite the high inter-individual variability, bonefish behaviours showed some consistent patterns across environmental factors. Diel period was a strong predictor of all the aforementioned bonefish behaviours, while temperature and tidal period also explained swimming behaviour. Both light and temperature often have strong influence on biological rhythms in fish (Zhdanova & Reebs 2006), while tides are important drivers of behaviour in species that live in nearshore marine ecosystems (Gibson 1986). While all of these factors may influence bonefish behavior, it is impossible to untangle the effects of light, temperature, and tide on bonefish behaviour in the wetland mesocosm over a 5 d period. As the technology of accelerometer loggers advances, longer-term studies in the wild should enable observations across a greater range of environmental parameters (e.g. across entire tidal periods) and increase the ability to identify cues for certain behaviors in bonefish.

Across the diel cycle, the majority of bonefish were most active (swimming) at dawn and during daylight hours; however, some fish were also highly active at night. Light intensity often affects fish behaviour because it influences their ability to forage, rest, avoid predators, aggregate, or reproduce (Helfman 1986, Zhdanova & Reebs 2006). It is interesting that although bonefish exhibited foraging behaviour throughout the diel cycle, most of the foraging behaviour was detected at night (Fig. 4). Given that bonefish were not directly observed during the night period, it is possible that bonefish exhibit behaviours unobserved during the day that have a similar accelerometric signal (e.g. a sleep-like state). However, it is certainly plausible that bonefish foraged most often night. In the wetland, bonefish were actively swimming during the night periods, and fish that were highly active swimming at night also exhibited high frequencies of foraging behaviour (e.g. Fish 44). Further, in the wild, bonefish often migrate into near-shore tidal areas during nighttime hours, a migration that is associated with foraging (Colton & Alevizon 1983b, Murchie et al. 2013).

Bonefish spent the most time swimming while temperatures were lowest (~22 to 25°C; coinciding with early morning to early day) and became less active as temperatures increased during the day and into the evening hours. They also exhibited the highest mean swimming speeds during daytime and evening hours when temperatures were highest (26 to 30°C; Fig. 5). Preliminary data on bonefish thermal biology suggests that maximum aerobic scope occurs at approximately 26 to 28°C, while in winter months (i.e. during this study), preferred temperatures are ~24°C (L. Nowell unpubl. data). It is not surprising that bonefish were most active at their preferred temperatures, which they were likely acclimatized to in the wild. Higher swimming speeds at higher temperatures may reflect higher aerobic scope or that bonefish are seeking more optimal temperatures. Indeed, bonefish live in environments with high thermal variability and strong thermal gradients where behavioral thermoregulation can occur on small spatial scales (Murchie et al. 2011).

Over the tidal cycle, bonefish were generally most active during ebbing and low tides and least active at flooding, although the differences in activity were relatively small. Interestingly, water levels in the wetland mesocosm were not directly influenced by tides because although the wetland is adjacent to the ocean, it is on a higher elevation and typically disconnected. Bonefish typically reside in shallow, near-shore seas that are tidally influenced, and make feeding migrations with flooding tides (Colton & Alevizon 1983b, Murchie et al. 2013). Many species that live in these areas have sensory systems that detect changes in pressure associated with changing tides (Gibson 1986). Bonefish may have sensed declines in pressure associated with ebbing tides that triggered activity that would normally be required to leave near-shore feeding areas with ebbing tides. Indeed, responses to tides may be an entrained biological rhythm despite the fact that water levels are static. Future studies of bonefish in areas under direct tidal influence are needed to better understand the influence of tides on their behaviour.

In summary, tri-axial accelerometers provided a reliable means for measuring a range of bonefish behaviours and swimming speeds and, when applied to bonefish in a wetland mesocosm, revealed high inter-individual variability and potential influences of environmental factors including diel period, temperature, and tide on bonefish behaviour. The ability to measure fine-scale behaviour such as foraging may identify habitat requirements and inform bioenergetics models, providing insight into population dynamics, mechanisms of animal behaviour, and energy landscapes. To this end, further work should estimate the relationship between bonefish swimming speeds and energy expenditure, the relative energetic costs of active metabolism and digestion, and foraging efficiency. Given the relationship between energy acquisition, growth, and reproductive investment, the ability to study feeding ecology in free-ranging fish provides scientists with new opportunities for tracking fitness.

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