

# Activity budgets for the sedentary Argentine sea bass *Acanthistius patachonicus* inferred from accelerometer data loggers

LUCAS E. BELTRAMINO,<sup>1\*</sup>  LEONARDO A. VENERUS,<sup>1</sup> GASTÓN A. TROBBIANI,<sup>1</sup> RORY P. WILSON<sup>2</sup> AND JAVIER E. CIANCIO<sup>1</sup>

<sup>1</sup>Centro para el Estudio de Sistemas Marinos (CONICET), Edificio CCT CONICET – CENPAT, Blvd. Brown 2915, U9120ACD Puerto Madryn, Chubut, Argentina (Emails: beltramino@cenpat-conicet.gob.ar; lucasbem@hotmail.com); and <sup>2</sup>Swansea Lab for Animal Movement, Biosciences, College of Science, Swansea University, Swansea, Wales, UK

**Abstract** The amount of energy an animal uses to move may constitute a significant fraction of its energy budget, so detailed descriptions of wild animal activity budgets can help to understand the ecology of a species, both at the individual and at the population levels. The rocky-reef fishes inhabiting the northern Patagonian gulfs of Argentina are important economic and recreational resources for which no activity or energy budgets are available. This fish assemblage may reach high aggregated biomasses (exceeding several hundreds of kilogrammes of fish distributed along a few hundred metres of linear reef ledges) and is not clear how such biomasses can be supported by the low productivity of the Patagonian coastal waters. We used animal-attached accelerometers to characterise the behaviours and activity budgets for the most abundant and ubiquitous species of this assemblage, the Argentine sea bass or ‘Mero’ *Acanthistius patachonicus* (Jenyns, 1840; Osteichthyes: Serranidae). Sixteen individuals were tagged (two in captivity and 14 free-living) and an ethogram was generated from acceleration recordings in varying environmental conditions. Two algorithms were used to classify the behaviours of wild fish. Both showed generally similar results during the cold-water season (8–10°C), but differed slightly in the warm-water season (16–18°C). Overall, sea bass were more active during warm season (mean time spent engaged in active behaviours; 46%, range; 24–60%). In contrast, during cold season fish only spent a mean of 29% of their time in active behaviours (range; 15–49%). No clear response to tidal state or ambient light was found, but some fish were more active during the night in the cold water season. Here, we provide the first activity budgets for the conspicuous Argentine sea bass, which contribute to our understanding of rocky-reef fish behaviour in Patagonia.

Abstract in French is available with online material.

**Key words:** accelerometer, behaviour, ethogram, rocky-reef fish, Serranidae.

## INTRODUCTION

The way in which animals allocate energy to different processes is considered to be strongly shaped by natural selection. Energy expenditure can be divided into four basic demands; activity (i.e. movement), growth, energy for basal metabolic rate and reproduction, all of which are described within overall energy budgets (Nisbet *et al.* 2000). Depending on the life-cycle stage, the energy used by an animal to move can represent a significant fraction of this budget (Mcnab 2002), so the estimation of accurate activity budgets and the associated energy expenditure of free-living organisms are pivotal in understanding species ecology, both at the individual and at the population levels (Masman *et al.* 1988).

There are two prime methodological approaches to study the behaviour and activity of wild animals; direct observation (Mueller *et al.* 2006) and using animal-attached tags (Ropert-Coudert & Wilson 2005; Hooker *et al.* 2007; Broell *et al.* 2013; Metcalfe *et al.* 2016). Direct observation is powerful, but animal behaviour may be affected by the presence of observers (Schneirla 1950) and, in general, animals can only be observed when they are in direct line of sight (Jolivet *et al.* 2015). This makes the study of aquatic organisms particularly challenging, although many studies have successfully used video cameras (e.g. Santos & Barreiros 1993; Pagel *et al.* 2016). Animal-attached tags, however, allow behavioural states to be inferred (Shepard *et al.* 2008) as well as to provide proxies for metabolic rate (e.g. Halsey *et al.* 2011) and environmental variables (Ropert-Coudert & Wilson 2005), even when animals cannot be seen. This approach is particularly useful for fish

\*Corresponding author.

Accepted for publication November 2018.

studies, as is manifest by the substantial increase in the numbers and types of tag deployments in recent years. The two major tag types used are; (i) transmitting devices (Hines *et al.* 1995; Jonsen *et al.* 2007), which do not require the recapture of the animals but have restricted transmission ranges and are additionally limited in the rate at which data can be transmitted (Woakes *et al.* 1995); and (ii) data loggers (most notably those containing accelerometers, hereafter ‘accelerometers’; Yoda *et al.* 1999; Moreau *et al.* 2009; Gleiss *et al.* 2011a), which store data and require the recovery of the tags in order to access the information (Woakes *et al.* 1995). This important restriction is, however, partially compensated by the large amounts of data that can be recorded. In particular, high-frequency tri-axial accelerometers show a great promise for monitoring animal activity (Robert *et al.* 2009; Diosdado *et al.* 2015; Soltis *et al.* 2016), behaviour (Shepard *et al.* 2008), ‘state’ (Wilson *et al.* 2014) and even provide proxies for energy expenditure (Wilson *et al.* 2006).

Fishes are particularly apt for behavioural studies using animal-attached accelerometers, but such studies come with challenges like the need to ensure the recovery of the tags. This has led to many behavioural studies of fish being undertaken in mesocosms (Brownscombe *et al.* 2014), confined spaces (Kawabe *et al.* 2003) or aquaria (Wright *et al.* 2014), whereas free-living fish studies generally encompass just a few hours in order to maximise the chances of tag recovery (e.g. Gleiss *et al.* 2011b), but nowadays more studies are successfully tagging free-living fish (mostly sharks) in the wild for longer periods of time (Tsuda *et al.* 2006; Gleiss *et al.* 2017; Bouyoucos *et al.* 2018).

The Argentine sea bass *Acanthistius patachonicus* (Jenyns, 1840; Osteichthyes: Serranidae) is a sedentary, long-lived, slow-growing and site-attached species (Irigoyen 2010). It is mostly found within 3–5 m of the Patagonian reef ledges and hardly ever observed, or fished, away from the reef areas (Irigoyen *et al.* 2013). The fish are mostly observed either just outside reef crevices, up to a few metres above the seabed at near neutral buoyancy, or resting inside crevices at different roll angles. Patagonian reefs can harbour large biomasses of Argentine sea bass (Di Bussolo & Minotti 1980) although it is not clear how these large biomasses can be supported by the low productivity that typifies these areas (Galván *et al.* 2009). Preliminary results using accelerometers indicate that fish spend large periods inactive, at least during the cold water seasons (Ciancio *et al.* 2016) so this may help reduce energy costs.

The high fidelity to specific crevices and/or reefs (Irigoyen 2010) and the large body size of the sea bass make them particularly good study animals for tagging with accelerometers. Indeed, *A. patachonicus*

represents an excellent opportunity to study how animals modulate movement in general, in response to environmental forcing variables. To evaluate potential differences in the activity patterns between seasons, tide and ambient light levels, we first created an ethogram for the species; that is a catalogue of descriptions of the discrete species typical behaviour patterns that forms the basic behavioural repertoire (Martin *et al.* 1993). Then, by quantifying the amount of time engaged in each of those behaviours we constructed an activity budget for each individual based on tri-axial accelerometer records. In this work, we study the behaviour and activity patterns of free-living Argentine sea bass with the aim of assessing the extent to which different environmental variables (water temperature-season-, tide and ambient light levels) affect their activity. In addition, we aimed to create activity budgets to inform bioenergetic models of the species.

## METHODS

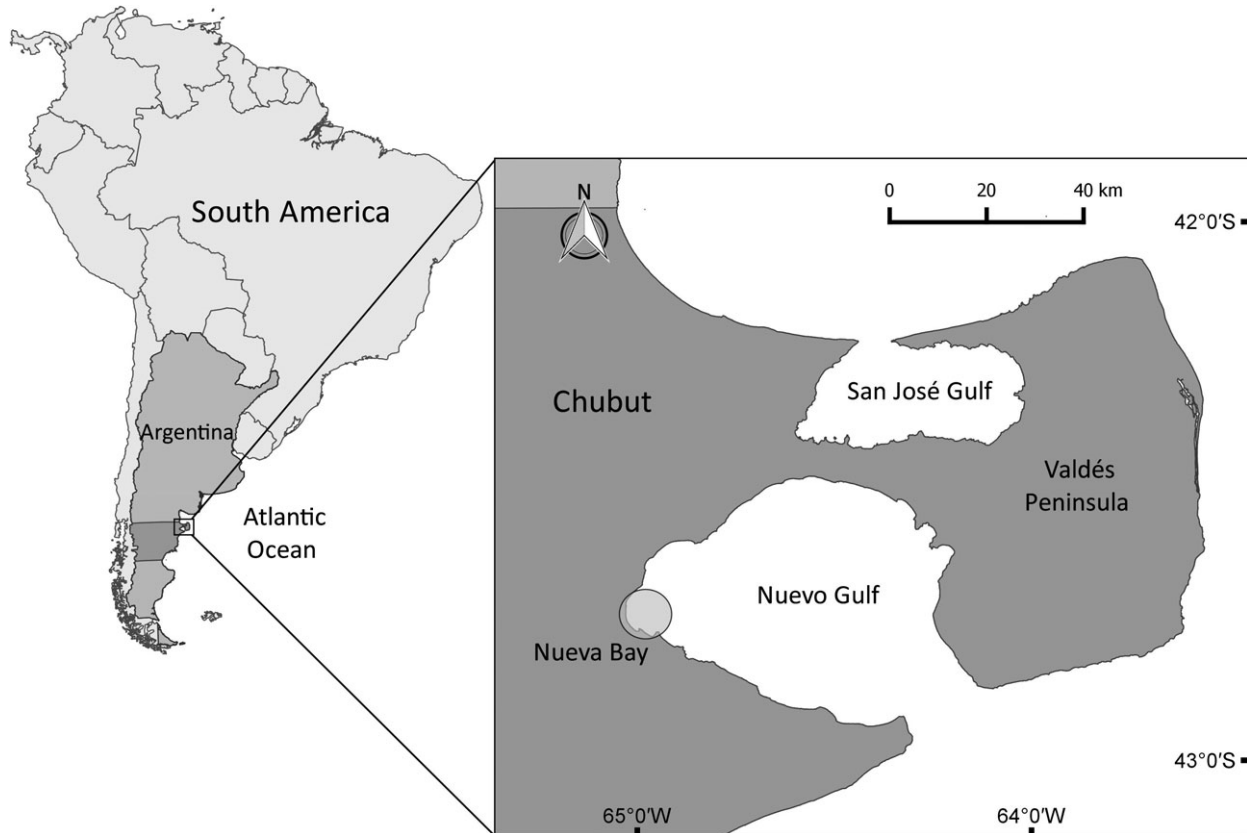
### Model species

The Argentine sea bass reaches 65 cm total length (TL) and about 4 kg weight. It inhabits rocky reefs and is distributed in the southwest Atlantic from Brazil (23°S) to Argentina (48°S; Irigoyen *et al.* 2008). Maximum age recorded for a 53-cm-TL fish was 41 years (Rubinich 2001). Due to its great abundance in terms of biomass and number of individuals, it is considered a key component of the temperate northern Patagonia reef fish assemblage (Irigoyen 2006). Males are morphologically indistinguishable from females (Getino 2012) and the length at 50% maturity for females is estimated to be 29 cm total length (Dell’Arciprete *et al.* 1987).

### Experimental design, method of capture and accelerometer attachment method

Mean water temperature in the Golfo Nuevo (42°47’S 65°00’W, Fig. 1) ranges between 8 and 18°C, with a maximum in March and a minimum in September (Rivas & Beier 1990; Dellatorre *et al.* 2012). We defined two sampling seasons based on water temperature, warm (16–18°C) and cold (8–10°C). Tagging, undertaken in February, March and April, was considered representative of the warm season, whereas fish tagged in July, September and November, were considered representative of the cold season. During the tagging experiments, fish experienced many tidal cycles and different ambient light levels (‘Day’, ‘Night’ and ‘Twilight’). The absence of sexual dimorphism precluded us from studying sexual differences in the activity patterns during the experiment.

Between 2013 and 2017, 17 fish ranging in TL between 26 and 35 cm were captured in natural and artificial reefs located in the Golfo Nuevo, at depths between 5 and 10 m (Table 1). Fish were pole-hooked (Irigoyen & Venerus



**Fig. 1.** Map of the study area showing the locations of the Golfo Nuevo where the Argentine sea bass were tagged with tri-axial accelerometer loggers.

2008) or captured inside crevices with a fishing landing net by scuba divers. Three of them were slowly brought to the surface in a dip net to avoid sudden changes in pressure and were then relocated to the CENPAT (Centro Nacional Patagónico) experimental aquarium; one of these fish was not equipped because it showed abnormal swimming behaviour. The remaining fish were tagged underwater to prevent barotrauma, and were used to provide data on the activity of free-living fish. Fish were equipped with an accelerometer fixed to the right side of the body using plastic straps following the procedure described in Ciancio *et al.* (2016). The length of each fish was recorded and spaghetti tags (Floy FD-68B) of different colours were attached at different positions below the dorsal fin for individual fish identification (see Venerus *et al.* 2013). Some fish were video-recorded at the moment of their release at the reef, which provided a few verified seconds of 'swimming' behaviour in the wild. After the tag batteries were exhausted (3–9 days), fish were recaptured inside crevices with a fishing landing net by scuba divers. Due to their high fidelity to crevices, all devices were recovered, although two had water ingress so recorded data were not further considered (Table 1).

Three different tri-axial accelerometer models were used for the experiments with captive and free-living fish: the X8M-3 ( $n = 2$ ) and the X16-mini ( $n = 13$ ; both from *Gulf Coast Data Concepts* Company, 611 Nicholson Avenue, Waveland, MS 39576, United States), and the AXY-Depth

( $n = 2$ ; *Techno SmArt* Company, Rome, Italy). All devices recorded acceleration data at a frequency of 25 Hz.

### Aquarium experiments

Fish were kept together in a 400 L circular tank. Salinity and water temperature were 35‰ and 12°C, respectively. The photoperiod was set at 12 h light (8.00–20.00 hours) and 12 h dark. The captivity acclimatisation and adaptation period lasted 1 week. During that period, fish were fed with squid.

Two of the fish kept in the aquarium were fitted with plastic rectangular plates (3 × 7 cm) bearing a piece of Velcro using plastic straps attached to the body in the same place as the free-living fish. The accelerometers had also a piece of Velcro glued to their waterproof exterior (the accelerometers were encapsulated with heat-shrink tubing before being deployed) so that they could be attached to the fish. This procedure allowed the attachment and removal of the accelerometer easily, multiple times, with minimal effects on the fish. Individuals were video-recorded as they undertook different behaviours during designated periods in the aquarium. After three recordings periods in one fish and four in the other (Table 1), the plates were removed. The individuals were maintained in the aquarium to monitor their recovery. After 4 months, no marks from the tag fitting procedure remained.

**Table 1.** Details of the tagged individuals, type of experiment (aquarium or reef) and starting date and number of hours recorded

Individual	TL (m)	Estimated weight (kg)	Experiment	Water temperature (season)	Date	Acceleration data registered (in hours)
1Le	0.29	0.42	Reef	Cold	11/13/2013	69.5
2Ga	0.31	0.5	Reef	Cold	11/13/2013	69
3Le	0.31	0.6	Aquarium	Cold	09/04/2014	46.3
				Cold	09/09/2014	45.9
				Cold	09/17/2014	56.4
4Ga	0.33	0.7	Aquarium	Cold	09/04/2014	36.1
				Cold	09/09/2014	40.8
				Cold	09/17/2014	49.9
				Cold	09/24/2014	20.0
5Lu†	0.30	0.46	Reef	Warm	04/27/2016	7.16
6Sa	0.28	0.38	Reef	Warm	04/27/2016	105
7Pd3	0.31	0.7	Reef	Warm	02/22/2017	193.8
8Tn	0.26	0.33	Reef	Warm	02/22/2017	116.3
9Tn†	Unsize	–	Reef	Warm	03/10/2017	108.6
10Pd1	0.28	0.38	Reef	Warm	04/20/2017	172.4
11Pd4	0.28	0.38	Reef	Warm	04/20/2017	171.9
12An	0.35	0.7	Reef	Warm	04/20/2017	141.4
13Sr	0.30	0.46	Reef	Warm	04/20/2017	140.1
14Pd2	0.28	0.38	Reef	Cold	09/13/2017	215.1
15Pd4	0.30	0.46	Reef	Cold	09/13/2017	196.2
16Pd10	0.29	0.42	Reef	Cold	09/13/2017	199.3

Each individual was given a specimen number (1–16), and a code of two letters identifying the accelerometer used. Free-living fish weight was estimated based on the length–weight relationships by Rubinich (2001). TL refers to total length. In the cases identified with a † (5Lu and 9Tn), the accelerometer got wet and the device stopped logging.

### Video analysis and ethogram definition

After synchronising the video timeline with that of the acceleration data, the video footages obtained were scrutinised to list the main behaviours observed (both in the aquarium and in the wild). Initially, six behavioural categories were chosen; three of which had already been defined by Brownscombe *et al.* (2014) *viz.*: ‘Swimming’, ‘Resting’ (‘Static on the bottom’ in Table 2) and ‘Feeding’. In addition, three other behaviour categories observed in the video footages were recognised; an extreme roll body angle behaviour described by Ciancio *et al.* (2016; ‘Lying on its side’), ‘Hovering’ and ‘Gliding’ (Table 2). A total of 3.26 h of acceleration data, extracted from the two specimens maintained in the aquarium, was synchronised with the video footages. After analysing the accelerometer signal for each particular behaviour, we discarded two of the originally selected behaviours (‘Gliding’ and ‘Feeding’; see Table 2).

### Data analysis and activity budget estimation

In addition to the raw accelerometer data (‘Surge’, ‘Heave’ and ‘Sway’), we derived other variables that included the vectorial dynamic body acceleration (VeDBA), a proxy for activity (Qasem *et al.* 2012; see Ciancio *et al.* 2016 for details on its estimation), and the variances of the raw sway (‘VariSway’) and roll (‘VariRoll’; Fig. 2). The variances of different signals had been successfully used for discriminating between distinct behavioural phases in other systems

(e.g. Chimienti *et al.* 2016). A three-second running mean was used for estimating each of these variables. A training data set was compiled by putting together the corresponding accelerometer raw values and the derived variables, along with the categorisation of particular behaviours observed in the video footages obtained both in the aquarium and in the wild. Overall, video footage from a total of seven fish was used (wild and captive), and using this entire training data set, we classified the acceleration signals of the free-living fish into the four behaviour categories previously selected.

Additionally, urchin graphs (Wilson *et al.* 2016) were plotted to visually compare the four different behaviours between warm and cold seasons. The process for creating this visualisation is as follows: first, the smoothed acceleration values are plotted in a tri-axial graph, which results in each point falling on the surface of a sphere. This sphere surface is then divided into equal facets and all data points that fall within each facet are summed and then divided into frequency bins of VeDBA. This is then presented in the form of discs on a central spine radiating from the facet. Greater radial distances from the sphere surface indicates greater VeDBA values, whereas greater disc diameter indicates larger numbers of data points with that particular value.

With the aim of choosing the best classification approach for estimating the activity budgets (time allocated to defined behaviours) for the sea bass, we compared the performance of two machine learning algorithms: K nearest neighbour (KNN, Bidder *et al.* 2014) and decision trees (TREE, De’ath & Fabricius 2000; see methodological details and results in Appendix S1). As both methods

**Table 2.** Description of the behaviours identified from the videos, and descriptions of the selection criteria according to the data recorded by the accelerometers

Behaviour	Description	Reasons to accept or reject the behaviour
<b>Static on bottom</b>	<b>The fish rests at the bottom with limited movement</b>	<b>This behaviour was selected because it has distinctive accelerometer signal features</b>
<b>Lying on its side</b>	<b>The fish rests at extreme roll angles (see Ciancio <i>et al.</i> 2016)</b>	<b>This behaviour produces a distinctive signal, especially through the heave, sway and roll variables. This has been hypothesised as an energy saving mechanism (Ciancio <i>et al.</i> 2016)</b>
<b>Hovering</b>	<b>The fish holds its position in the water column using only its pectoral fins</b>	<b>This behaviour was selected because it is frequently observed by divers when the fish is not in a cave. The accelerometer signal of this behaviour can be differentiated from other behaviour signals</b>
Gliding	Body translocation	Sea bass usually glides for a few seconds after moving their propulsive fins slowly. Gliding does not generate a characteristic signal that allows differentiation from static behaviours. For this reason, the tail movement intervals were classified as 'Swimming', and hence 'Gliding' was not used as a valid behaviour category for the classification process
<b>Swimming</b>	<b>The fish is propelled by tail movements. This behaviour is functionally different from 'Gliding'</b>	<b>The signal produced for swimming is characterised by extreme sway and high VeDBA values</b>
Feeding	The fish attacks food, swallowing it rapidly	Sea bass in captivity did not really attack food as they do in the wild, so the behaviour was discarded

The behaviours selected for the activity budget estimation are shown in bold letters.

tested had similar performance, the accelerometer recordings of the free-living sea bass were assigned to different behaviours using both the KNN and TREE algorithms. Before the classification process, the free-living fish data set was down-sampled from 25 to 1 Hz, in order to reduce the temporal correlation between successive recordings and to diminish computational time. To avoid potential bias caused by the use of unbalanced training data sets (i.e. training data sets composed by a different number of observations in each behavioural category), we constructed one hundred training data sets by randomly sampling 2983 observations from each behavioural category (that being the number of instances of 'Hovering', the least exhibited behavioural category). The two algorithms were then run with the same training data sets using a combination of the six classification variables described above, and the mode of the classifications obtained for each observation used as the classified behaviour for each algorithm. First, we created activity budgets for each fish, and then we averaged the proportions for all fish to obtain an overall activity budget. Finally, as the results obtained with KNN and TREE showed some differences, we averaged the proportion of each behaviour obtained with these two methods (see Results). *Ad hoc* R codes (R Core Team 2016) were programmed to randomise the training data sets and to run the KNN and TREE algorithms. KNN requires the 'class' package (Venables & Ripley 2002), whereas TREE requires 'MASS' (Venables & Ripley 2002) and 'party' (Hothorn *et al.* 2006) libraries.

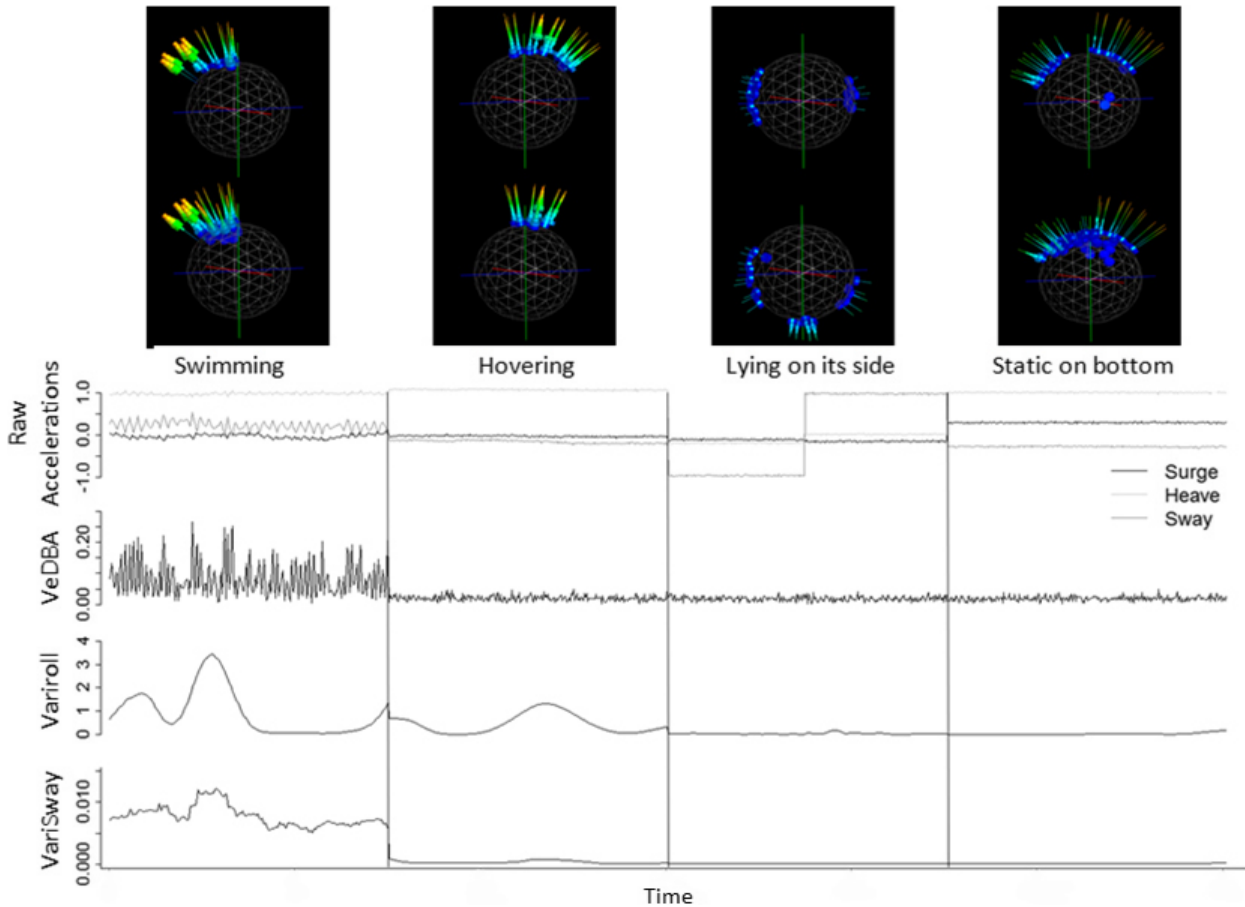
Non-metric multidimensional scaling analyses (NMDS, Clarke & Warwick 2001) were performed prior to testing for potential differences in the proportion of time that fish spent engaged in each of the four behaviours. We considered that

Kruskal stress values <0.2 are indicative of the usefulness of the 2D plots to make some conclusions (Clarke 1993). The effects of the ambient light (with three levels: 'Day', 'Night' and 'Twilight'), tide (with four levels: 'Low', 'Flow tide', 'High' and 'Ebb tide') and season ('Warm' and 'Cold') were evaluated. Due to the time of the year in which the fish were tagged during the cold and the warm seasons, the length in hours for the ambient light levels was similar between seasons. Due to the absence of strong patterns in the proportion of time engaged into the four different behaviours caused by the ambient light and tide (see Results), the potential effects of these variables were not further investigated. In order to test for the effect of the water temperature (season) on the activity patterns, we performed an analysis of similarity (ANOSIM) and a similarity percentage analysis (SIMPER) for the proportions of time spent in each behaviour, using the software PRIMER 6 (Clarke & Warwick 2005).

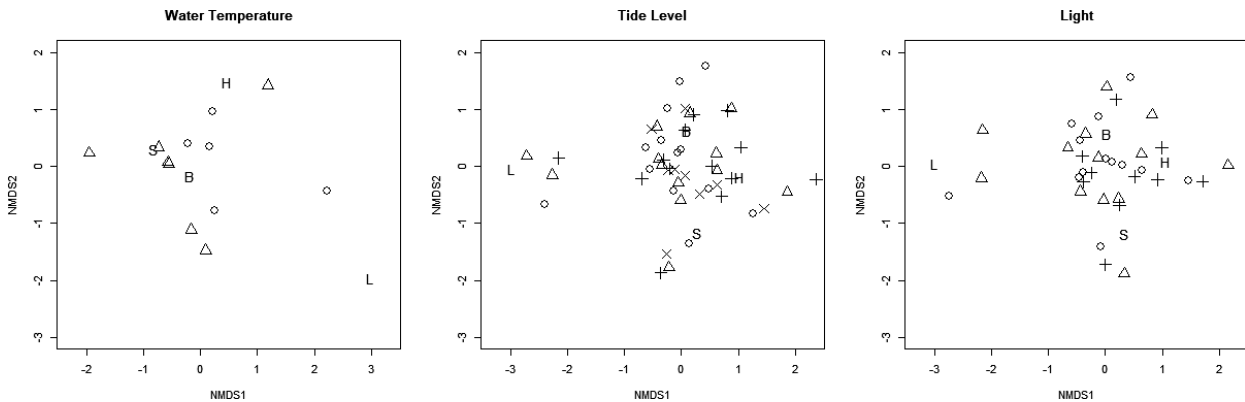
## RESULTS

We accumulated a total of 295.4 h of acceleration data from two fish in captivity and 1905.2 h from the fourteen free-living sea bass (each fish was recorded between 3 and 9 days, Table 1). All free-living tagged sea bass were recaptured and released with no observable indication of abnormal behaviour.

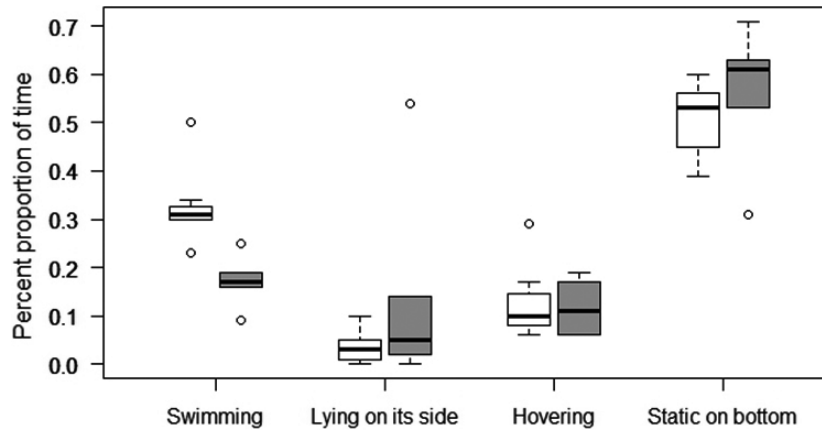
The NMDS analysis only suggested a seasonal effect on the proportion of the different behaviours displayed (Fig. 3), so we focused our analyses on this variable. In line with this, the activity budgets showed water temperature (season) to be an important driver of sea bass



**Fig. 2.** Examples of the raw accelerations signals (i.e. ‘Surge’, ‘Heave’ and ‘Sway’), ‘VeDBA’, ‘VariRoll’ and ‘VariSway’ for the four different behaviours selected in the Argentine sea bass. Each period represents 10 s of each behaviour taken from different individuals. The sampling frequency was set at 25 Hz. Urchin plots on top represent the different behaviours for cold (upper panel) and warm (lower panels) seasons. ‘Lying on its side’ behaviour was recorded in the aquarium, whereas all other behaviours occurred in wild fish.



**Fig. 3.** Non-metric multidimensional scaling ordination of the Argentine sea bass behaviour, using a Bray–Curtis dissimilarity matrix of the proportion of time engaged in different behaviours (%), grouped by water temperature (left plot; Stress = 0.15), tide (middle plot, Stress = 0.13) and light level (right plot, Stress = 0.13). B: ‘Static on bottom’, H: ‘Hovering’, L: ‘Lying on its side’ and S: ‘Swimming’. Left plot: cold season (circles), warm season (triangles). Middle plot: high tide (circle), ebb tide (triangles), low tide (plus sign), flow tide (cross). Right plot: day (circle), twilight (triangles), night (plus sign).



**Fig. 4.** Boxplots showing the activity budgets estimated for free-living Argentine sea bass in two water temperature ranges: warm (white boxes) and cold (grey boxes). The per cent proportions of time engaged in each behaviour resulted from combining the classifications obtained with the KNN and the TREE algorithms (see details in the text). The line within the boxes indicates the median proportion, and the box edges, the 1st and 3rd quartiles.

behaviour. The proportion of the time invested in active behaviours ('Swimming' and 'Hovering') was higher, on average, during the warm-water season (46% of the time) than in the cold one (29% of the time; Fig. 4). Conversely, overall results showed that in cold water, fish spent approximately 70% of their time engaged in inactive behaviours ('Static on bottom' and 'Lying on its side'). When both algorithms were used to classify the same data set for the free-living fish, some differences were evident in the classifications obtained (Appendix S2), particularly for the warm season. The TREE method assigned a higher proportion of fish to 'Static on bottom' and lower proportions of fish to 'Swimming' and 'Hovering' than the KNN algorithm. When the proportion of time engaged in the four behaviours by KNN and TREE were averaged, a greater proportion of fish 'Swimming' and a lower proportion of fish 'Lying on its side' became apparent for the warm season (Fig. 4). The ANOSIM showed a significant effect of the water temperature (season) on the proportion of different behaviours (Global  $R = 0.234$ ,  $P = 0.04$ ). SIMPER analysis showed an average similarity between individuals of 84.4% for the 'Warm' group and 71.8% for the 'Cold' one. In the warm-water season 'Static on bottom' was the behaviour that contributed most to the dissimilarity (54.3%), followed by 'Swimming' (33.8%), whereas for the cold water season 'Static on bottom' (65.4%) followed by 'Swimming' (19.1%) were the main causes of dissimilarity between the two groups.

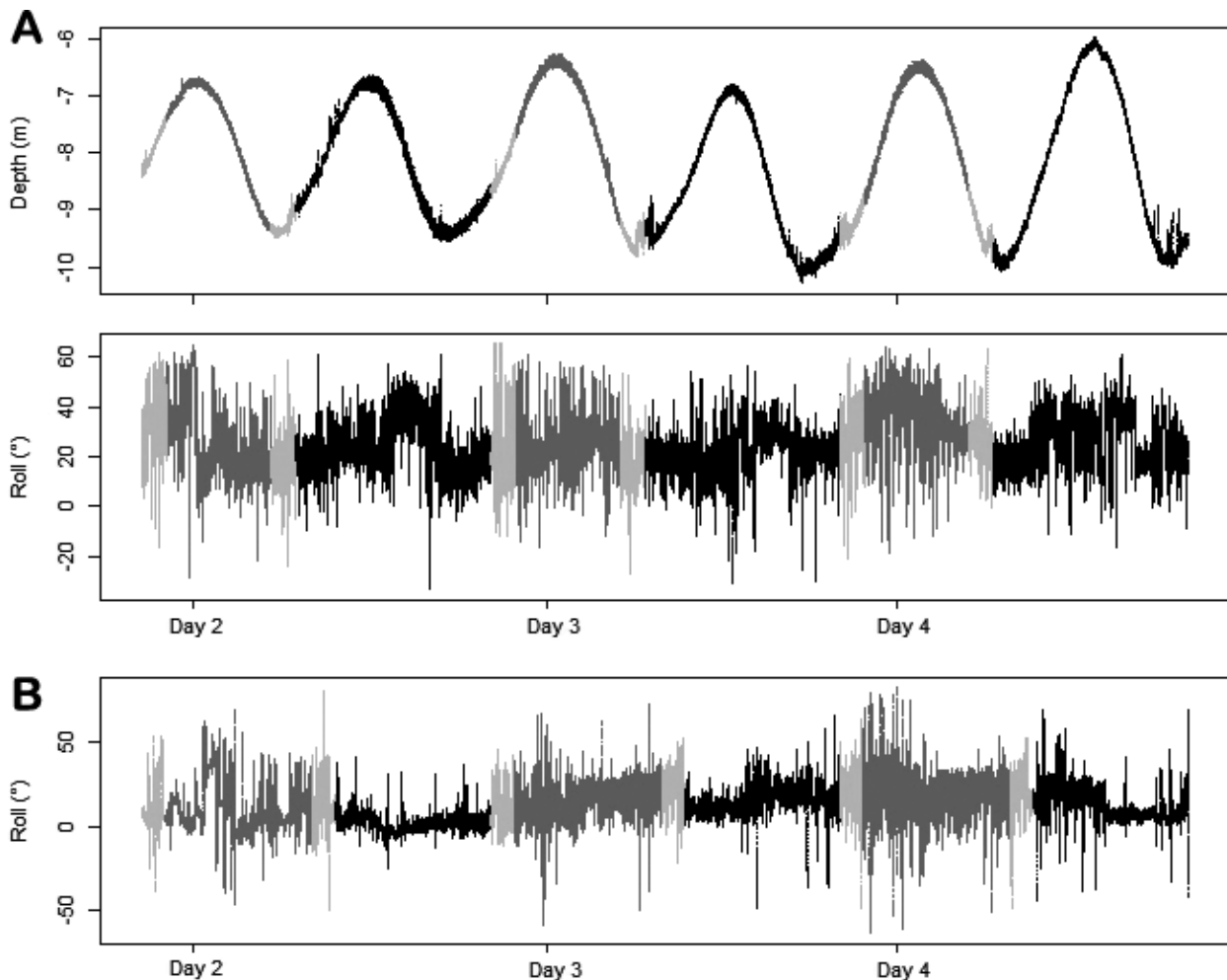
## DISCUSSION

Here, we have provided the first definition of an ethogram and the corresponding estimation of the activity budget for free-living Argentine sea bass in

contrasting conditions of water temperature. Most notable was that this species spent most of its time inactive, engaged in energetically low cost behaviours (between 54% and 71% of the time, Fig. 4). At the same time, a significant seasonal effect was apparent in sea bass activity, with fish being less active during the cold-water season than in the warm one.

Comparable studies have been undertaken most in tropical or subtropical environments (Brownscombe *et al.* 2014, 2017; Broell *et al.* 2016; Payne *et al.* 2016; but see Gannon *et al.* (2014), and Gleiss *et al.* (2017) for a few examples in temperate waters), where fish do not experience large temperature fluctuations between seasons. The metabolic rate and other physiological processes in non-aestivating ectotherms are a function of body temperature (Angilletta *et al.* 2004). Thus, when temperate or warm-temperate species, such as the Argentine sea bass, are exposed to large seasonal fluctuation in temperature, it is expected to affect their metabolism and hence their behaviour and activity budgets (Schurmann & Steffensen 1997; Guderley 2004). This accords with our observation of more active behaviours during the warmer period but also occurs during the periods of increased food availability (Rivas *et al.* 2006) which presumably helps balance the increased energy expenditure. Similarly, other studies supported the energetic benefit of being inactive during resource -or performance capacity- limited environments such as winter (Speers-Roesch *et al.* 2018).

To date, it has not been possible to identify a common behavioural or activity response of fishes under different forcing variables. Indeed, a diverse array of fish studies suggest that even the same species may behave differently according to the reproductive season (Zabala *et al.* 1997), daylight (Fraser *et al.* 1993),



**Fig. 5.** Roll angles for two Argentine sea bass tagged in February (a, lower panel, fish 8Tn in Table 1) and in April (b, fish 6Sa in Table 1). The upper plot in a) show the depth of the tagged fish, which is mainly affected by the tidal level. Line colours indicate the ambient light levels: black = ‘Day’, medium grey = ‘Twilight’ and grey = ‘Night’. Note that the activity patterns differ between individuals. The fish in panel b) did not used different roll angles during the day. In contrast, the fish in panel (a) fluctuated around a mean roll angle of approximately  $20^\circ$  (this angle may be due to the position of the accelerometer logger on the fish body rather due to the fish attitude), but there is little difference between ‘Day’ and ‘Night’. Furthermore, tidal height did not have an obvious effect on fish attitude.

or location (Gibran 2007; Hackradt 2012; Koeck *et al.* 2014). Nevertheless, some responses to environmental light have been described for the different trophic guilds in temperate kelp-forest fish in the California Current (Helfman 1986). In this habitat, piscivorous species are primarily nocturnal or crepuscular, whereas shoaling zooplanktivores, foragers on small invertebrates and cleaner fishers are diurnal (Helfman 1986). Irigoyen *et al.* (2013) studied the instantaneous variation in fish counts of the carnivorous Argentine sea bass (Galván *et al.* 2009) using underwater visual censuses to examine count variability with time-of-day, tidal state and time elapsed between censuses (minutes, days, weeks and months), finding no effect of those variables (although censuses were made only during daylight). Indeed, the

instantaneous variation in counts for the Argentine sea bass was the smallest among all the species studied, emphasising its sedentary habits. These results are in line with the findings of our study because, when all fish were pooled together, we found no general response to environmental light or tide. We note, however, that the behaviour of individuals might accord with one or the other of these environmental variables, with inter-individual variability tending to blur patterns (Magurran 1986). Certainly, some marine fish species display ‘personalities’ and particular individuals may indeed show different responses in behaviour to circadian patterns (e.g. Alós *et al.* 2017). This was suggested by the behaviour of certain individuals during this study (Fig. 5), and for fish sampled during the cold water season by Ciancio *et al.*



(2016). Further analyses of different fish personalities should help to clarify this.

The use of accelerometers to describe animal behaviour obviates the need for direct observation and increases the period over which animals can be monitored (Moreau *et al.* 2009). However, while this approach is useful for studying organisms that are difficult to observe (e.g. cryptic or aquatic organisms, see Gleiss *et al.* 2010), some limitations were apparent for our study of the Argentine sea bass. This species spends most of the time resting (Fig. 4) or inside caves, so it was difficult to video-record tagged free-living fish engaged in active behaviours to create representative training set for the classification algorithms (Brewster *et al.* 2018). Nonetheless, the analysis allowed us to classify four of the most common behaviours of these fish with reasonably accuracy. Despite the fact that we paid particular attention to the precise mounting position of the tags, some variation during this procedure was apparent in our data. The two metrics 'VariRoll' and 'VariSway', both less affected by animal body attitude in comparison with Ay and Az raw acceleration, were crucial in providing most accurate classification of behaviours. We were also able to test the tagging and monitoring protocol for captive and free-living sea bass, which included tagging fish underwater. Of special note is that our underwater tagging procedure avoided potential barotrauma or stress due to exposure to air, increased temperatures or pressure changes. This meant that our model species adapted well to the manipulation conditions, setting up a framework for future studies.

As in previous comparisons (e.g. Dutta *et al.* 2015; Sur *et al.* 2017), this work did not find one classification method (KNN versus TREE) consistently better than the other, and some mismatch were observed, in particular for the 'Hovering' and 'Static on bottom' behaviours (Appendix S1). Both behaviours produce a low amplitude signal for all the variables, which may explain why the classification methods confused them. Both classification methods proved easy to implement and do not require software licenses. Even with the limitations reported here (i.e. some differences were evident among the classifications obtained with the two methods, Appendix S2), the methods provided the first estimations of an activity budget for the Argentine sea bass under different environmental conditions (water temperature). For many years, fish bioenergetics modelling studies have not incorporated potential changes in activity, essentially assuming all behaviours occur with constant frequency and intensity through time (e.g. Ciancio *et al.* 2010). The combination of the activity budgets, such as the one provided here, with knowledge on the energy consumption associated with different behaviours, should provide more accurate energy estimates of individuals as well as that

of community needs. These are key parameters necessary to understand the energy flux in ecosystems (Brodie *et al.* 2016), which could be greatly influenced by temperature in temperate oceans.

## SPECIES NOMENCLATURE

*Acanthistius patachonicus* (Jenyns, 1840; Osteichthyes: Serranidae).

## ACKNOWLEDGEMENTS

We thank A. Biasotti, S. Fernández, A. Lhose, M. Matos, N. Ortíz, M. Piuñca, D. and M. Pollicelli, and F. Quiroga for their help during fieldwork. M. Moris helped us with the aquarium work, the Área Náutica de la Universidad de la Patagonia San Juan Bosco provided logistic support and *Techno SmArt* Company donated one of the accelerometers used. Financial support was provided by the Youth Activity Fund (The Explorers Club, granted to LEB), PADI Foundation (granted to JEC), the Agencia Nacional de Promoción Científica y Tecnológica (PICT 2015-3340, granted to JEC) and the Secretaría de Ciencia, Tecnología e Innovación Productiva del Chubut, Argentina (granted to LEB).

## REFERENCES

- Alós J., Martorell-Barceló M. & Campos-Candela A. (2017) Repeatability of circadian behavioural variation revealed in free-ranging marine fish. *R. Soc. Open Sci.* **4**, 160791.
- Angilletta M. J. Jr, Steury T. D. & Sears M. W. (2004) Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integr. Comp. Biol.* **44**, 498–509.
- Bidder O. R., Campbell H. A., Gómez-Laich A. *et al.* (2014) Love thy neighbour: automatic animal behavioural classification of acceleration data using the k-nearest neighbour algorithm. *PLoS One* **9**, e88609.
- Bouyoucos I. A., Suski C. D., Mandelman J. W. & Brooks E. J. (2018) In situ swimming behaviors and oxygen consumption rates of juvenile lemon sharks (*Negaprion brevirostris*). *Environ. Biol. Fish.* **101**, 761–73.
- Brewster L. R., Dale J. J., Guttridge T. L. *et al.* (2018) Development and application of a machine learning algorithm for classification of elasmobranch behaviour from accelerometry data. *Mar. Biol.* **165**, 62.
- Brodie S., Taylor M. D., Smith J. A., Suthers I. M., Gray C. A. & Payne N. L. (2016) Improving consumption rate estimates by incorporating wild activity into a bioenergetics model. *Ecol. Evol.* **6**, 2262–74.
- Broell F., Noda T., Wright S. *et al.* (2013) Accelerometer tags: detecting and identifying activities in fish and the effect of sampling frequency. *J. Exp. Biol.* **216**, 1255–64.
- Broell F., Taylor A. D., Litvak M. K., Bezanson A. & Taggart C. T. (2016) Post-tagging behaviour and habitat use in

- shortnose sturgeon measured with high-frequency accelerometer and PSATs. *Anim. Biotelem.* **4**, 11.
- Brownscombe J. W., Gutowsky L. F., Danylchuk A. J. & Cooke S. J. (2014) Foraging behavior and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers. *Mar. Ecol. Prog. Ser.* **505**, 241–51.
- Brownscombe J. W., Cooke S. J. & Danylchuk A. J. (2017) Spatiotemporal drivers of energy expenditure in a coastal marine fish. *Oecologia* **183**, 689–99.
- Chimienti M., Cornulier T., Owen E. *et al.* (2016) The use of an unsupervised learning approach for characterizing latent behaviors in accelerometer data. *Ecol. Evol.* **6**, 727–41.
- Ciancio J. E., Beauchamp D. A. & Pascual M. A. (2010) Marine effect of introduced salmonids: prey consumption by exotic steelhead and anadromous brown trout in the Patagonian Continental Shelf. *Limnol. Oceanogr.* **55**, 2181–92.
- Ciancio J. E., Venerus L. A., Trobbiani G. A. *et al.* (2016) Extreme roll angles in Argentine sea bass: could refuge ease posture and buoyancy control of marine coastal fishes? *Mar. Biol.* **163**, 90.
- Clarke K. R. (1993) Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* **18**, 117–43.
- Clarke K. R. & Warwick R. M. (2001). *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd edn. Natural Environment Research Council, Plymouth Marine Laboratory, Plymouth.
- Clarke K. R. & Warwick R. M. (2005) *Primer-6 Computer Program*. Natural Environment Research Council, Plymouth Marine Laboratory, Plymouth.
- De'ath G. & Fabricius K. E. (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* **81**, 3178–92.
- Dell'Arciprete O. P., Christiansen H. E. & Diaz de Astarloa J. M. (1987) Observaciones sobre el ciclo reproductivo del mero, *Acanthistius brasilianus* (Serranidae, Pisces). *Rev. Invest. Desarr. Pesq.* **7**, 67–84.
- Dellatorre F. G., Pisoni J. P., Barón P. J. & Rivas A. L. (2012) Tide and wind forced nearshore dynamics in Nuevo Gulf (Northern Patagonia, Argentina): potential implications for cross-shore transport. *J. Mar. Syst.* **96**, 82–9.
- Di Bussolo R. A. & Minotti P. G. (1980) Estudio de la estructura de población del mero (*Acanthistius brasilianus*, Cuvier & Valenciennes); patrones de distribución, biomasa y rendimiento potencial. *Bachelor Thesis, Instituto Nacional de Investigación y Desarrollo Pesquero, Buenos Aires, Argentina*.
- Diosdado J. A. V., Barker Z. E., Hodges H. R. *et al.* (2015) Classification of behaviour in housed dairy cows using an accelerometer-based activity monitoring system. *Anim. Biotelem.* **3**, 15.
- Dutta R., Smith D., Rawnsley R. *et al.* (2015) Dynamic cattle behavioural classification using supervised ensemble classifiers. *Comput. Electron. Agr.* **111**, 18–28.
- Fraser N. H., Metcalfe N. B. & Thorpe J. E. (1993) Temperature-dependent switch between diurnal and nocturnal foraging in salmon. *Proc. R. Soc. Lond. B Biol. Sci.* **252**, 135–9.
- Galván D. E., Botto F., Parma A. M., Bandieri L., Mohamed N. & Iribarne O. O. (2009) Food partitioning and spatial subsidy in shelter-limited fishes inhabiting patchy reefs of Patagonia. *J. Fish Biol.* **75**, 2585–605.
- Gannon, R., Taylor, M. D., Suthers, I. M., *et al.* (2014). Thermal limitation of performance and biogeography in a free-ranging ectotherm: Insights from accelerometry. *J. Exp. Biol.* **217**, 3033–7.
- Getino L. (2012) Evaluación de la distorsión óptica y del efecto de arqueo en la captura de datos morfogeométricos. El mero *Acanthistius patachonicus* (Jenyns 1840) como caso de estudio. *Bachelor Thesis, Universidad Nacional de la Patagonia San Juan Bosco, Chubut, Argentina*.
- Gibrán F. Z. (2007) Activity, habitat use, feeding behavior, and diet of four sympatric species of Serranidae (Actinopterygii: Perciformes) in southeastern Brazil. *Neotrop. Ichthyol.* **5**, 387–98.
- Gleiss A. C., Dale J. J., Holland K. N. & Wilson R. P. (2010) Accelerating estimates of activity-specific metabolic rate in fishes: testing the applicability of acceleration data-loggers. *J. Exp. Mar. Biol. Ecol.* **385**, 85–91.
- Gleiss A. C., Wilson R. P. & Shepard E. L. C. (2011a) Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods Ecol. Evol.* **2**, 23–33.
- Gleiss A. C., Norman B. & Wilson R. P. (2011b) Moved by that sinking feeling: variable diving geometry underlies movement strategies in whale sharks. *Funct. Ecol.* **25**, 595–607.
- Gleiss A. C., Morgan D. L., Whitty J. M., Keleher J. J., Fossette S. & Hays G. C. (2017) Are vertical migrations driven by circadian behaviour? Decoupling of activity and depth use in a large riverine elasmobranch, the freshwater sawfish (*Pristis pristis*). *Hydrobiologia* **787**, 181–91.
- Guderley H. (2004) Metabolic responses to low temperature in fish muscle. *Biol. Rev.* **79**, 409–27.
- Hackradt C. W. (2012) Population ecology and mobility patterns of groupers (Serranidae: Epinephelinae) on temperate rocky reefs on south-western Mediterranean Sea: Implications for their conservation. *Doctoral Thesis, Universidad de Murcia, Murcia, España*.
- Halsey L. G., Shepard E. L. & Wilson R. P. (2011) Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **158**, 305–14.
- Helfman G. S. (1986) Fish behaviour by day, night and twilight. In: *The Behaviour of Teleost Fishes* (ed. T. J. Pitcher) pp. 366–87. Springer, Boston.
- Hines A. H., Wolcott T. G., González-Gurriarán E., González-Escalante J. L. & Freire J. (1995) Movement patterns and migrations in crabs: telemetry of juvenile and adult behavior in *Callinectes sapidus* and *Maja squinado*. *J. Mar. Biol. Assoc. U.K.* **75**, 27–42.
- Hooker S. K., Biuw M., McConnell B. J., Miller P. J. & Sparling C. E. (2007) Bio-logging science: logging and relaying physical and biological data using animal-attached tags. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **3**, 177–82.
- Hothorn T., Hornik K. & Zeileis A. (2006) Unbiased recursive partitioning: a conditional inference framework. *J. Comput. Graph. Stat.* **15**, 651–74.
- Irigoyen A. J. (2006) Distribución espacial y temporal del mero (*Acanthistius brasilianus*) en la plataforma argentina. *Bachelor Thesis, Universidad Nacional de la Patagonia San Juan Bosco, Chubut, Argentina*.
- Irigoyen A. J. (2010) Efecto del alga invasora *Undaria pinnatifida* sobre la comunidad de peces de arrecife en los golfos Norpatagónicos. *Doctoral Thesis, Universidad Nacional del Comahue, Río Negro, Argentina*.
- Irigoyen A. J. & Venerus L. A. (2008) The pole-hooking method: a novel and economical technique for *in situ* tagging small to medium-sized fishes. *Fish. Res.* **91**, 349–53.

- Irigoyen A. J., Gerhardinger L. C. & Carvalho-Filho A. (2008) On the status of the species of *Acanthistius* (Gill, 1862) (Percoidae) in the South-West Atlantic Ocean. *Zootaxa* **59**, 51–9.
- Irigoyen A. J., Galván D. E., Venerus L. A. & Parma A. M. (2013) Variability in abundance of temperate reef fishes estimated by visual census. *PLoS One* **8**, e61072.
- Jolivet A., Chauvaud L., Thébault J. *et al.* (2015) Circadian behavior of *Tectus (Trochus) niloticus* in the southwest Pacific inferred from accelerometry. *Mov. Ecol.* **3**, 1–12.
- Jonsen I. D., Myers R. A. & James M. C. (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Mar. Ecol. Prog. Ser.* **337**, 255–64.
- Kawabe R., Kawano T., Nakano N., Yamashita N., Hiraishi T. & Naito Y. (2003) Simultaneous measurement of swimming speed and tail beat activity of free-swimming rainbow trout *Oncorhynchus mykiss* using an acceleration data-logger. *Fish. Sci.* **69**, 959–65.
- Koeck B., Pastor J., Saragoni G., Dalías N., Payrot J. & Lenfant P. (2014) Diel and seasonal movement pattern of the dusky grouper *Epinephelus marginatus* inside a marine reserve. *Mar. Environ. Res.* **94**, 38–47.
- Magurran A. E. (1986) Individual differences in fish behaviour. In: *The Behaviour of Teleost Fishes* (ed. T. J. Pitcher) pp. 338–65. Springer, Boston.
- Martin P., Bateson P. P. G. & Bateson P. (1993) *Measuring Behaviour*, 2nd edn p. 222. Cambridge University Press, New York.
- Masman D., Daan S. & Beldhuis H. J. A. (1988) Ecological energetics of the kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labeled water methods. *Ardea* **76**, 64–81.
- Mcnab B. K. (2002) *The Physiological Ecology of Vertebrates: A View from Energetics* p. 576. Cornell University Press, Ithaca.
- Metcalfe J. D., Wright S., Tudorache C. & Wilson R. P. (2016) Recent advances in telemetry for estimating the energy metabolism of wild fishes. *J. Fish Biol.* **88**, 284–97.
- Moreau M., Siebert S., Buerkert A. & Schlecht E. (2009) Use of a tri-axial accelerometer for automated recording and classification of goats' grazing behavior. *Appl. Anim. Behav. Sci.* **119**, 158–70.
- Mueller R. P., Brown R. S., Hop H. & Moulton L. (2006) Video and acoustic camera techniques for studying fish under ice: a review and comparison. *Rev. Fish Biol. Fisher.* **16**, 213–26.
- Nisbet R. M., Muller E. B., Lika K. & Kooijman S. A. L. M. (2000) From molecules to ecosystems through dynamic energy budget models. *J. Anim. Ecol.* **69**, 913–26.
- Pagel C. D., Scheer M. & Lück M. (2016) Swim encounters with killer whales (*Orcinus orca*) off Northern Norway: interactive behaviours directed towards human divers and snorkellers obtained from opportunistic underwater video recordings. *J. Ecotourism* **16**, 1–11.
- Payne N. L., Smith J. A., Meulen D. E. *et al.* (2016) Temperature dependence of fish performance in the wild: links with species biogeography and physiological thermal tolerance. *Funct. Ecol.* **30**, 903–12.
- Qasem L., Cardew A., Wilson A. *et al.* (2012) Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS One* **7**, e31187.
- R Core Team (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Rivas A. L. & Beier E. J. (1990) Temperature and salinity fields in the north Patagonian gulfs. *Oceanol. Acta* **13**, 15–20.
- Rivas A. L., Dogliotti A. I. & Gagliardini D. A. (2006) Seasonal variability in satellite-measured surface chlorophyll in the Patagonian Shelf. *Cont. Shelf Res.* **26**, 703–20.
- Robert B., White B. J., Renter D. G. & Larson R. L. (2009) Evaluation of three-dimensional accelerometers to monitor and classify behavior patterns in cattle. *Comput. Electron. Agr.* **67**, 80–4.
- Ropert-Coudert Y. & Wilson R. P. (2005) Trends and perspectives in animal-attached remote sensing. *Front. Ecol. Environ.* **3**, 437–44.
- Rubinich J. P. (2001) Edad y crecimiento del mero *Acanthistius brasiliensis* (Pisces, Serranidae) en el Golfo San Matías, Argentina. *Bachelor Thesis, Universidad Nacional de la Patagonia San Juan Bosco, Chubut, Argentina*.
- Santos R. S. & Barreiros J. P. (1993) The ethogram of *Parablennius sanguinolentus parvicornis* (Valenciennes in Cuvier & Valenciennes, 1836) (Pisces: Blenniidae) from the Azores. *Arquipel. Life Mar. Sci. Suppl.* **11**, 73–90.
- Schneirla T. C. (1950) The relationship between observation and experimentation in the field study of behavior. *Ann. N.Y. Acad. Sci.* **51**, 1022–44.
- Schurmann H. & Steffensen J. F. (1997) Effects of temperature, hypoxia and activity on the metabolism of juvenile Atlantic cod. *J. Fish Biol.* **50**, 1166–80.
- Shepard E. L., Wilson R. P., Quintana F. *et al.* (2008) Identification of animal movement patterns using tri-axial accelerometry. *Endanger. Species Res.* **10**, 47–60.
- Soltis J., King L., Vollrath F. & Douglas-Hamilton I. (2016) Accelerometers and simple algorithms identify activity budgets and body orientation in African elephants *Loxodonta africana*. *Endanger. Species Res.* **31**, 1–12.
- Speers-Roesch B., Norin T. & Driedzic W. R. (2018) The benefit of being still: energy savings during winter dormancy in fish come from inactivity and the cold, not from metabolic rate depression. *Proc. Biol. Sci.* **285**, 20181593.
- Sur M., Suffredini T., Wessells S. M. *et al.* (2017) Improved supervised classification of accelerometry data to distinguish behaviors of soaring birds. *PLoS One* **12**, e0174785.
- Tsuda Y., Kawabe R., Tanaka H. *et al.* (2006) Monitoring the spawning behaviour of chum salmon with an acceleration data logger. *Ecol. Freshw. Fish* **15**, 264–74.
- Venables W. N. & Ripley B. D. (2002) *Modern Applied Statistics with S*, 4th edn p. 495. Springer, New York.
- Venerus L. A., Irigoyen A. J., Galván D. E. & Parma A. M. (2013) Spatial dynamics of the Argentine sandperch, *Pseudoperca semifasciata* (Pinguipedidae), in temperate rocky reefs from northern Patagonia, Argentina. *Mar. Freshw. Res.* **65**, 39–49.
- Wilson R. P., White C. R., Quintana F. *et al.* (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J. Anim. Ecol.* **75**, 1081–90.
- Wilson R. P., Grundy E., Massy R. *et al.* (2014) Wild state secrets: ultra-sensitive measurement of micro-movement can reveal internal processes in animals. *Front. Ecol. Environ.* **12**, 582–7.
- Wilson R. P., Holton M. D., Walker J. S. *et al.* (2016) A spherical-plot solution to linking acceleration metrics with

- animal performance, state, behaviour and lifestyle. *Mov. Ecol.* **4**, 22.
- Woakes A. J., Butler P. J. & Bevan R. M. (1995) Implantable data logging system for heart rate and body temperature: its application to the estimation of field metabolic rates in Antarctic predators. *Med. Biol. Eng. Comput.* **33**, 145–51.
- Wright S., Metcalfe J. D., Hetherington S. & Wilson R. (2014) Estimating activity-specific energy expenditure in a teleost fish, using accelerometer loggers. *Mar. Ecol. Prog. Ser.* **496**, 19–32.
- Yoda K., Sato K., Niizuma Y. *et al.* (1999) Precise monitoring of porpoising behaviour of Adélie penguins determined using acceleration data loggers. *J. Exp. Biol.* **202**, 3121–6.
- Zabala M., Louisy P., Garcia-Rubies A. & Gracia V. (1997) Socio-behavioural context of reproduction in the Mediterranean dusky grouper *Epinephelus marginatus* (Lowe, 1834) (Pisces, Serranidae) in the Medes Islands Marine Reserve (NW Mediterranean, Spain). *Sci. Mar.* **61**, 79–89.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Performance comparison between the KNN and TREE methods for classifying tipified behaviours in the Argentine sea bass *Acanthistius patachonicus*.

**Appendix S2.** Median and quantile values of the classifying variables for each tipified behaviour, and results obtained with the two classification methods (KNN and TREE) applied on data from free-living Argentine sea bass *Acanthistius patachonicus*.