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# Extreme roll angles in Argentine sea bass: Could refuge ease posture and buoyancy control of marine coastal fishes?

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**Abstract** The swim bladder provides a mechanism for buoyancy regulation in teleosts. However, in certain species, its location can result in an unstable body position, with associated energetic costs assumed for maintaining posture in addition to the energetic demands from swim bladder volume regulation. Direct observations show that some body-compressed, cave-refuging teleosts that nominally operate near neutral buoyancy may adopt unusual body attitudes within crevices. We hypothesize that these fishes may relax their buoyancy and posture control mechanisms during periods of rest. A prediction derived from this is that resting fish may adopt a wide range of roll angles (i.e., rotation about their longitudinal axis) inside caves. To quantify this behavior and for testing this hypothesis, tri-axial accelerometers were deployed on free-living, cave-refuging Argentine sea bass *Acanthistius patachonicus*, and

the relationship between roll angle and a proxy for activity (defined as the vectorial dynamic body acceleration, VeDBA) was analyzed. The results were compared with data available for three other species of fishes with disparate body forms and lifestyles: the pelagic whale shark *Rhincodon typus*, the dorsoventrally compressed benthic great sculpin *Myoxocephalus polyacanthocephalus*, and the fusiform and demersal Atlantic cod *Gadus morhua*. Inactive Argentine sea bass adopted a wide variety of roll angles, including extreme ones exceeding 80°, but had lower roll angles closer to an upright posture primarily associated with higher activity levels. In contrast, the great sculpin and Atlantic cod both rested at a close to upright roll angle but had higher activity levels associated with larger roll angles. Whale shark did not rest for the duration of the recorded period and also showed higher activity levels associated with larger roll angles. We propose that relaxation of buoyancy and posture control may help to reduce the metabolic rate in laterally compressed, cave-refuging fishes during periods of rest within crevices.

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## Introduction

Traits that minimize energy expenditure are strongly shaped by natural selection (Brown et al. 2004), particularly those related to locomotion (Priede 1977), where metabolic costs are among the highest of any activity (McNab 2002). Less obvious are the costs of maintaining posture when animals are stationary or moving at low speeds, although the extended periods that animals spend in these behaviors (e.g., see Gruber et al. 1988; Brownscombe et al. 2014; Gannon et al. 2014, for fish examples) imply that such costs may represent a significant proportion of the overall energy budget. It is well acknowledged that the costs of maintaining posture in terrestrial animals counteracting gravity may be appreciable (Alexander 2002), but the problem is not absent in aquatic animals (Blake 1979; Eidietis et al. 2002). Stabilizing forces in the water can be created in two ways: by flow over a control surface (e.g., fins) during swimming (trimming), or from the active motion of a control surface (powered control, e.g., using fins Webb 2002). Powered control can occur at all speeds, but it is the only option at zero or low speeds (Webb 2002, e.g., hovering).

In addition to the need for posture control, most aquatic animals without buoyancy-generating mechanisms are expected to sink because their tissues have a greater density than water (Alexander 1990 and references therein). Thus, primitive elasmobranchs exploiting nonbenthic habitats swim to generate lift by using their fins or by angling their body. Indeed, this obliges those fishes to swim to maintain constant depths, with the energetic consequences that this engenders (Alexander 1990; Gleiss et al. 2015). Many teleosts, however, exploit the low density of gases compared to water to control their buoyancy by regulating the volume of gas in their swim bladder (McCutcheon 1966). This obviates the need to swim to maintain depth and posture (e.g., while hovering), which is theorized to reduce attendant metabolic power required for trimming (Alexander 1990). Despite the energy savings related to swimming and trimming, secreting gas into the swim bladder of physoclistous fishes (based on their anatomy, teleosts can be divided into physostomous fishes, in which the swim bladder is connected to the esophagus by the pneumatic duct, and physoclistous fishes, which regulate gases with a gas gland) demands energy, especially since bladders are leaky and changes in ambient pressure (given by swimming depth, tide height) can result in changing bladder volume, which needs to be compensated (e.g., Strand et al. 2005). Additionally, the swim bladder location in many fishes results in an unstable body position. This forces tending to roll or pitch (roll angle represents the rotation around the longitudinal axis of the fish and pitch, the nose-up or nose-down rotation) the fish body (Webb and Weihs 1994). As

a consequence, stability in nonswimming teleosts having a swim bladder is achieved by powered control, which entails an energetic cost (Webb 2002). In essence, even though teleosts bearing a swim bladder can be close to neutrally buoyant without the need to swim to generate lift, there still appears to be a metabolic cost to their buoyancy strategy.

In contrast, benthic fishes, which typically are either dorsoventrally compressed (described also as depressed-body fishes) or fusiform, may lie on the seabed and rest, avoiding any postural costs (example being cottids and pinguipedids). For nonbenthic, laterally compressed teleost fishes, this strategy is problematic because, even if they adjusted their buoyancy to be denser than water to allow them to rest on the seabed, they would have an inappropriate body form to lie in an upright body position, which may also reduce the effectiveness of any countershading coloration. Hundreds of hours of underwater observations of northern Patagonia rocky reef fishes in the wild (JEC, LAV and GAT, see also Irigoyen et al. 2013; Venerus et al. 2014) demonstrate that several species commonly lie on their sides in crevices or caves, either being negatively buoyant on the bottom or positively buoyant and pressed against the cave roof (e.g., Patagonian rockfish *Sebastes oculatus*, or Argentine sea bass *Acanthistius patachonicus*, see Online Resource 1). The same species, however, have never been reported adopting anything other than an upright posture when outside their refuges.

We hypothesized that some physoclistous cave-refuging species may relax their buoyancy and posture controls during periods of rest within their refuge to help minimize energy expenditure, a benefit from refuging not previously considered. To test this, we equipped the cave-refuging Argentine sea bass with high-frequency triaxial accelerometers, which give information on both posture and activity (Shepard et al. 2008b), to compare with other contrasting body form and lifestyle fishes. Postural attitudes were derived directly from the raw acceleration. The value of acceleration-derived metrics for quantifying activity was enhanced by deriving the vectorial dynamic body acceleration (VeDBA a derived metric from dynamic component of acceleration) a proxy for activity and activity-derived power use (cf. Qasem et al. 2012; Williams et al. 2014).

A prediction derived from our hypothesis is that body-compressed, cave-refuging fishes may adopt a larger range of roll angles during resting periods within the caves, accompanied by low VeDBA values, while they should have highly constrained roll angles with higher VeDBA values during foraging or other activities that imply movement of the animal. In order to put our results into broader perspective, we explored the relationship between VeDBA and roll angles in fishes with contrasting lifestyles, body form, and mechanisms for buoyancy regulation. Specifically, we compared Argentine sea bass data with available

data from other noncave-refuging fishes that exemplified three major lifestyles and feeding habits of marine fish: the whale shark *Rhincodon typus*, a cosmopolitan large pelagic elasmobranch (with no swim bladder, and pelagic feeding lifestyle); the great sculpin *Myoxocephalus polyacanthocephalus*, a fusiform or body-depressed benthic-feeding teleost lacking a swim bladder distributed in the North Pacific Ocean; and the Atlantic cod *Gadus morhua*, a fusiform body benthopelagic species bearing a swim bladder distributed in the North Atlantic Ocean.

## Materials and methods

### Species studied

The Argentine sea bass is a long-lived, slow-growing species that reaches 65 cm total length (TL) and 4 kg weight. Until recently, this species had been misclassified as *A. brasiliensis*, giving rise to a nomenclatural confusion, which was clarified by Irigoyen et al. (2008). Maximum age recorded for a 53-cm-TL fish was 41 years (Rubinich 2001). The Argentine sea bass is a sedentary, site-attached species (Irigoyen 2010), mostly found within 3–5 m of the reefs ledges (Irigoyen et al. 2013). Dietary analysis shows that their main prey is reef- and soft-bottom species that live close to, and around, reefs, in agreement with the local distribution of fish (Galván et al. 2008, 2009b). These fish are mostly recorded in an upright body position outside the caves, up to a few meters above the seabed at near neutral buoyancy, or negatively buoyant resting on the seabed at the caves' entrances. Extreme roll body angles are only observed when fish are inside the caves, a behavior frequently reported by spear fishers using flashlights to locate inactive fish hidden in deep cave nooks during daytime.

### Northern Patagonia temperate reefs

The coastal seafloor in the Northern Patagonian gulfs of Argentina is characterized by a preponderance of soft muddy and sandy bottoms, from which isolated, small patches of rocky outcrops emerge. Most commonly, the reefs are linear ledges of up to a few 100 m long and less than 30–50 cm height. These temperate rocky reefs, as well as other artificial structures generated by the intentional deployment of scrap metal pieces and shipwrecks, offer habitat complexity in an otherwise flat bottom and attract a particular fish assemblage composed by about 29 species (Galván et al. 2009a). Only a few of these fishes are common, and the Argentine sea bass is one of the most abundant species that may reach very high densities of more than 300 individuals along a 50 m × ~4 m transect laid onto the reef ledge. Previous studies have shown that

some soft-bottom prey is depleted by fishes around these reefs (Galván et al. 2008) and suggested that food may be a limiting factor of fish inhabiting this type of reef (Galván et al. 2009b).

This study was conducted in 'Parque Nuevo,' a shallow artificial reef at 10 m depth (ebb tide) located within Bahía Nueva, Golfo Nuevo, Argentina. Field data were recorded in July and November of 2013. The daily mean semidiurnal tidal amplitude for 2013 was 4.1 m (during the experiments tidal amplitude ranged between 1.26 and 4.84 m in July, and between 1.18 and 5.07 m in November). Weak tidal currents of less than 5 cm/s have been recorded for the area (Dellatorre et al. 2012).

### Field and aquaria work

We chose the Argentine sea bass as a model species because it is one of the species often seen adopting a nonupright position inside crevices in Northern Patagonian reefs; is large enough to carry accelerometer tags able to record several days of activity and posture; and has a strong site fidelity to crevices. We decided to tag both free-living and captive fish with accelerometers to allow us to compare and validate the data from wild fish with those in captivity of certain behaviors such as acceleration records during resting. For this, we deployed X8m-3m Gulf Coast Data Concepts triaxial accelerometers (weight in air 11 g), encapsulated in heat-shrink tubes with air enough to achieve slight negative buoyancy of the whole package (cross-sectional profile of the tag is approximately an ellipse with radii of 25 and 4 mm axes), on four free-living Argentine sea bass (size range = 29–33 cm total length, weight range 500–750 g) and four fish held in aquaria (31–33.2 cm, 500–610 g). For the free-living fish experiment, we checked the weather forecast to avoid occurrence of waves within Bahía Nueva for a time window of at least 3 days. Because of the depth (5–10 m) and location of the reef, northerly and easterly winds create waves that could produce noise in the accelerometer signal due to water movement rather than fish activity. The largest fish observed in the reef were captured in situ at low tide (5 m depth) by pole-hooking (Irigoyen and Venerus 2008) before they were placed in a net cage underwater. Subsequently, the cage was slowly taken to the surface where the accelerometers were fitted to the fish trunk by plastic straps threaded laterally, close to the fish center of mass (Online Resource 2). Standard spaghetti tags (Floy™ FD-68B) were also attached below the dorsal fin for identification. A diver gently released the fish close to a reef cave after tagging, and remained in place for a few minutes to check that their swimming behavior was normal. Fish were recaptured by pole-hooking 4 days after deployment. After capture, the device-retaining straps were released underwater before the fish were placed again

**Table 1** Summary of fish tagged

Species	<i>N</i>	Size range (cm)	Habit	Swim bladder	Body form	Experiment	Time recorded (hours)	Tag attachment procedure
Whale shark	5	350–800	Pelagic	No	Depressed	Free-living	110	Gleiss et al. (2013)
Atlantic cod	4	56–70	Benthopelagic	Yes	Fusiform	Captivity	96	Wright et al. (2014)
Great sculpin	2	29–35	Benthic	No	Depressed	Captivity	20	Broell et al. (2013)
Argentine sea bass	8	33–41	Cave-refuging	Yes	Compressed	Free-living ( <i>n</i> = 4) and captivity ( <i>n</i> = 4)	316	This study

in their caves. Potential effects of tagging on fish behavior are discussed in Online Resource 3. We recovered all the deployed tags due to the strong fidelity of Argentine sea bass to crevices. Triaxial acceleration was recorded at a frequency of 25 Hz until the batteries died (between 48 and 72 h after tagging). In total, we obtained nine recorded days of data, which we assume covers the complete set of posture and swimming patterns displayed for this species. Field work for tagging whale sharks was carried at Ningaloo Reef, Western Australia. Atlantic cod and great sculpin were tagged in aquaria in the Centre for Environment, Fisheries and Aquaculture Science (CEFAS), UK, and in Friday Harbor Laboratories, San Juan Island, Washington, USA, respectively. Tags were attached by surgical implantation into the peritoneum of Atlantic cod, below the dorsal fin and close to the center of mass of the great sculpin, and to the second dorsal fin in whale sharks. Details on device deployment for these species are given by Wright et al. (2014) for Atlantic cod, Gleiss et al. (2013) for whale shark, and Broell et al. (2013) for great sculpin. The numbers of fish, attachment methods, types of experiment (free-living and captivity), and recording times for those species are detailed in Table 1.

### Data analysis

Acceleration data were measured in three orthogonal axes and were subsampled (by removing two lines of every three of the 25-Hz data to produce an effective recording frequency of 8.33 Hz) to approximate the lowest value used in any of our fish studied (~8 Hz for whale shark). The acceleration data from each axis were then separated into their static and dynamic components following Shepard et al. (2008a). Roll angles for each fish were calculated by using the derived estimate of the gravity-based acceleration (i.e., static, Shepard et al. 2008a), following Wilson et al. (2008). Animal-based dynamic body acceleration (DBA) has been shown to be a powerful proxy for activity and energy expenditure in a suite of vertebrate taxa (Halsey et al. 2009) including fish (Gleiss et al. 2010; Wright et al. 2014). Here,

we estimated the vectorial dynamic body acceleration (VeDBA, Gleiss et al. 2011; Qasem et al. 2012), a standardized quantity of DBA, a better proxy for activity when the orientation of the device is not aligned precisely with respect to the vertical. VeDBA was given by:

$$\text{VeDBA} = \sqrt{D_x^2 + D_y^2 + D_z^2}$$

where *D* is the dynamic acceleration for the respective axes (*x*, *y*, *z*), itself calculated by subtracting a smoothed running mean from the raw acceleration from each channel (Shepard et al. 2008a). The time window for calculating the running mean to estimate the dynamic acceleration was 2 s (Shepard et al. 2008a). Raw data for the whale shark, great sculpin and Atlantic cod were treated in the same manner as for the Argentine sea bass. Finally, the resulting data were subsampled with frequency of one record every 2 s, which reduced the temporal autocorrelation in the data. Hereafter, in the text, ‘accelerometer record’ will refer to data processed as follows.

We defined acceleration data as either those manifesting ‘stationary’ or ‘moving’ behaviors. This was necessary for us to test the prediction derived from our hypothesis. To categorize data accordingly, we performed two experiments. First, we recorded the VeDBA of all the devices motionless while placed on a table. This allowed us to define a critical value,  $\text{VeDBA}_{\text{crit}}$ , above which the fish were considered to be ‘moving,’ and below (or equal to) which, they were considered to be ‘stationary.’ We verified that these criteria held by comparing those VeDBA values with activity in captive fish. For this, we attached accelerometers to 4 fish held in aquaria and simultaneously filmed them for ~1 h to identify the time periods during which they were visually assessed as being ‘resting.’

Accelerometer data were used to test the prediction derived from our hypothesis about relaxation of buoyancy and posture control in Argentine sea bass, using a randomization test (Manly 1991). The same analysis, adapted from the ideas by Perry and Smith (1994), was repeated for the other three species. As we observed only slight differences



between the distributions of VeDBA obtained for the stationary captive fish and those from the loggers stable on a table, we used the latter to estimate  $\text{VeDBA}_{\text{Crit}}$ . To account for device noise (Evans et al. 2014), we used the median of maximum VeDBA values as the  $\text{VeDBA}_{\text{Crit}}$ . Based on this procedure,  $\text{VeDBA}_{\text{Crit}}$  was fixed at 0.035 g. Given computer processing constraints, a subset of VeDBA and roll angle data were used for hypothesis testing: 1000 records were randomly taken for each combination of individual fish and movement category ('stationary' and 'moving') in Argentine sea bass and Atlantic cod. However, as the number of records above and below  $\text{VeDBA}_{\text{Crit}}$  for great sculpin and whale shark, respectively, was limited, only 150 (great sculpin) and 131 (whale shark, only 3 of 5 fish could be used for this analysis) records for each combination of individual fish and movement category were used. For each subset, the absolute values of the roll angles were randomly permuted with respect to VeDBA under the null hypothesis that those variables were uncorrelated. Monte Carlo permutations ( $n = 1000$  for Argentine sea bass and Atlantic cod, and  $n = 10,000$  for great sculpin and whale shark) were stratified by individual fish since differences in activity patterns and roll angles were evident among individuals (see 'Results' section). To test our prediction (see above), the cumulative distribution function of absolute roll angles for moving fish was compared with the 95 % confidence bounds of the corresponding distribution estimated by stratified Monte Carlo permutations under the null hypothesis. Calculations were performed using an ad hoc code programmed in R language (R Development Core Team 2011).

## Results

Beyond intraspecific differences, each species showed a distinctive signature composed of a characteristic relationship between roll and VeDBA values, which suggested different posture and activity patterns in the four fishes studied (Fig. 1). Figure 1 shows the general pattern of VeDBA (activity) and its association with roll (body posture) for the four species studied (Fig. 1b, right panel). In addition, a spherical plot (Fig. 1a, left panel), using 'Crystal Ball' visualization software (Grundy et al. 2009), shows the relationship between duration and body posture. In this, the position of the bars projecting from the sphere corresponds to fish orientation, while the height of the bars denotes the total time spent at the corresponding orientation. A fish in the normal vertical position will have a single bar at the north pole of the sphere, and an inverted fish would have a bar at the south pole. Increasing roll places bars between the north pole and the equator in the direction of the red arrow while increasing pitch places bars between the north pole and the equator in the direction of the black arrow.

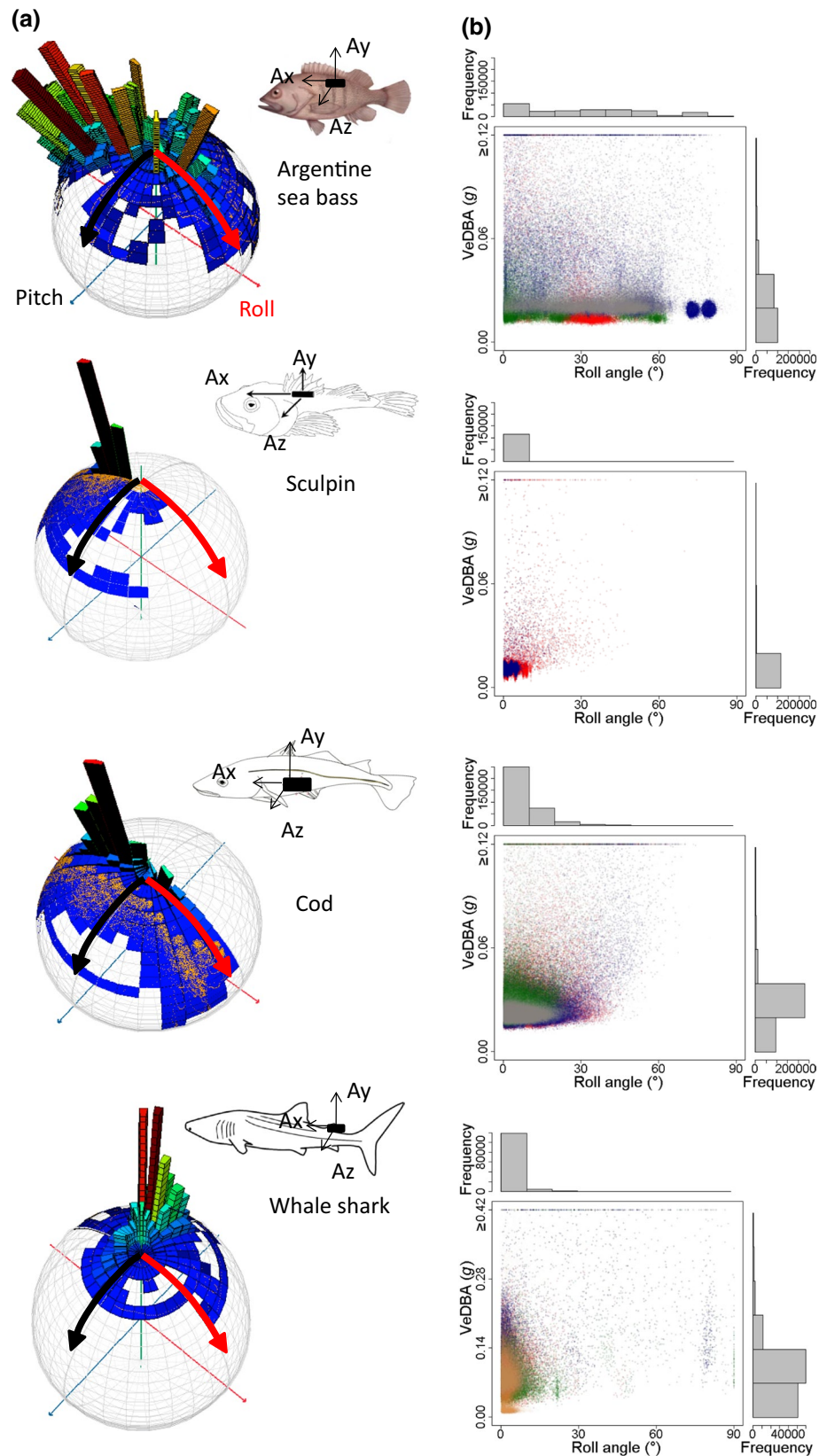
The most relevant result of this study is that the four free-living Argentine sea bass showed extreme roll values (between  $60^\circ$  and  $90^\circ$ ), infrequently recorded for the other three studied species (Fig. 1b, Online Resource 4). Indeed, Argentine sea bass showed the most variable pattern in the frequency distribution of absolute roll angles, with larger roll values at low VeDBA values (Fig. 1b), suggesting a relaxation of body posture in support of our hypothesis.

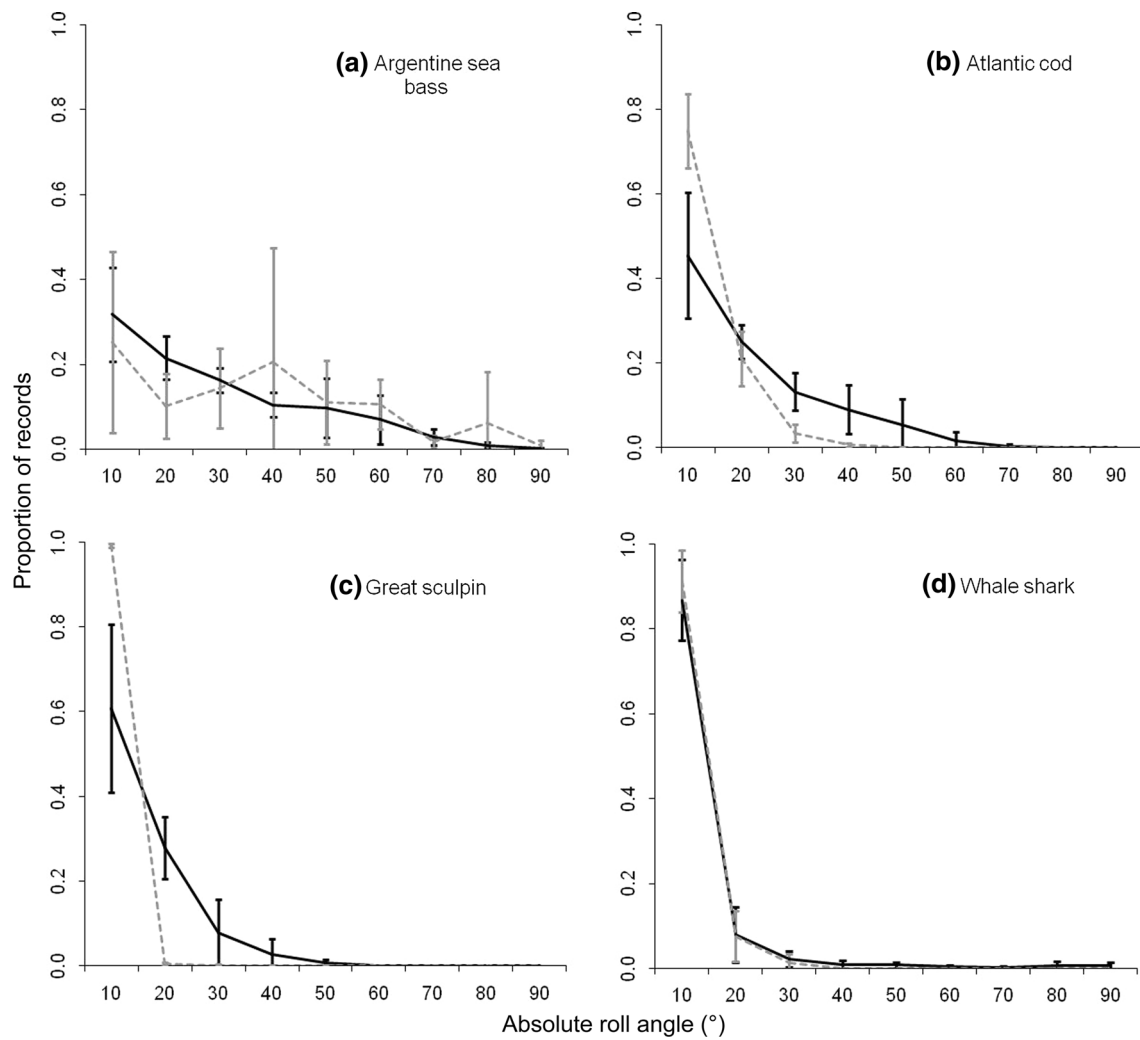
When data for all free-living Argentine sea bass were pooled and grouped into  $10^\circ$  roll angle classes, the average proportions of records for the four individuals were similar for 'stationary' and 'moving' fish (Fig. 2a). However, below an absolute roll angle of  $30^\circ$ , the average proportions for stationary fish tended to be below of those for moving fish. This trend was reversed over  $30^\circ$  roll angles (Fig. 2a). Indeed, the cumulative proportion of records with absolute roll angles  $\leq 30^\circ$  was higher for moving than stationary fish (0.69 vs. 0.49, Fig. 2a). This same trend was observed when a subset of the data was used ( $n = 8000$ ): The cumulative frequency distribution of records belonging to moving fish was larger than the 95 % upper confidence limit under the null hypothesis of no association between VeDBA and roll angle (Fig. 3a). Furthermore, the incidence of the absolute roll angle in Argentine sea bass was linked with time of day, with most extreme angles being recorded during daylight, when fish were less active and most probably refuging in their caves (Fig. 4).

Overall, between 81 and 91 % of the accelerometer records for each free-living Argentine sea bass had VeDBA values  $\leq \text{VeDBA}_{\text{Crit}}$ , which indicated very low activity levels for all the individuals tagged. In contrast, only 0–12 % of the records from whale sharks, the other free-living species tagged in this study, were below  $\text{VeDBA}_{\text{Crit}}$ , which suggests whale sharks did not rest during the recording period, likely performing burst-and-coast swimming (intermittent swimming) (Gleiss et al. 2013).

Although the proportion of time engaged in different activities or postures is not directly comparable between the species studied, none of the other species showed such extreme roll angles (Fig. 1b), and the proportion of records with large roll angles was significantly lower in all other species than those recorded in Argentine sea bass (Online Resource 4). Furthermore, the overall trends in the relationship between VeDBA and roll angle for the other species revealed an opposite pattern to that shown in Argentine sea bass (Fig. 1b). In Atlantic cod, great sculpin, and whale shark, the cumulative frequency distribution of records belonging to fish moving was lower than the 95 % lower confidence limit under the null hypothesis of no association between VeDBA and roll angle (Fig. 3b, c). In a manner different to that observed in Argentine sea bass, the average proportions of stationary Atlantic cod and great sculpin records with roll angles  $\leq 10^\circ$  were greater than those

**Fig. 1** **a** Visualization of relative frequencies in fish body posture (*left-hand side*) using a spherical plot, whereby the precise position of each *bar* on the *sphere* denotes the pitch and roll values of the fish and the percentage of time spent in each body angle class is depicted by the height of each bar (Grundy et al. 2009). The *color scale* corresponds to the percentage of time spent with certain body angles. *Black* and *red* arrows indicate, respectively, the directions in which pitch and roll increase with respect to the upright position. Data for a single fish are shown as representative of each species. The *right-hand side b* shows the relationship between dynamic body acceleration (VeDBA) and absolute (the nonnegative value without regard to its sign) roll angle value for all individuals tagged (shown with *different colors*). Data were then subsampled up to a frequency of one record every 2 s to highlight major trends (see details in the text). The y-axis was truncated for clarity at 0.12 g for teleosts and at 0.42 g for the whale shark. Larger values were condensed in the upper section of each plot. *Ax*, *Ay*, and *Az* arrows on fishes indicate the axes where acceleration was measured





**Fig. 2** Average proportion of records and standard deviations with absolute roll angles in 10° classes, among all fish tagged. Stationary fish: gray line; moving fish: black line. **a** *Acanthistius patachonicus* (Argentine sea bass): 205,203 records corresponding to 4 fish;

**b** *Gadus morhua* (Atlantic cod): 345,598 records corresponding to 4 fish; **c** *Myoxocephalus polyacanthocephalus* (great sculpin): 117,066 records corresponding to 2 fish; **d** *Rhincodon typus* (whale shark): 125,718 records corresponding to 5 fish

observed for moving fish, and decreased more abruptly (Fig. 2b, c). This pattern is coincident with the expected for fusiform or body-depressed fishes, which may maintain an upright position when resting on the bottom. Differently in the whale shark, the average proportions of stationary and moving fish were similar for all the absolute roll angle range (Fig. 3d).

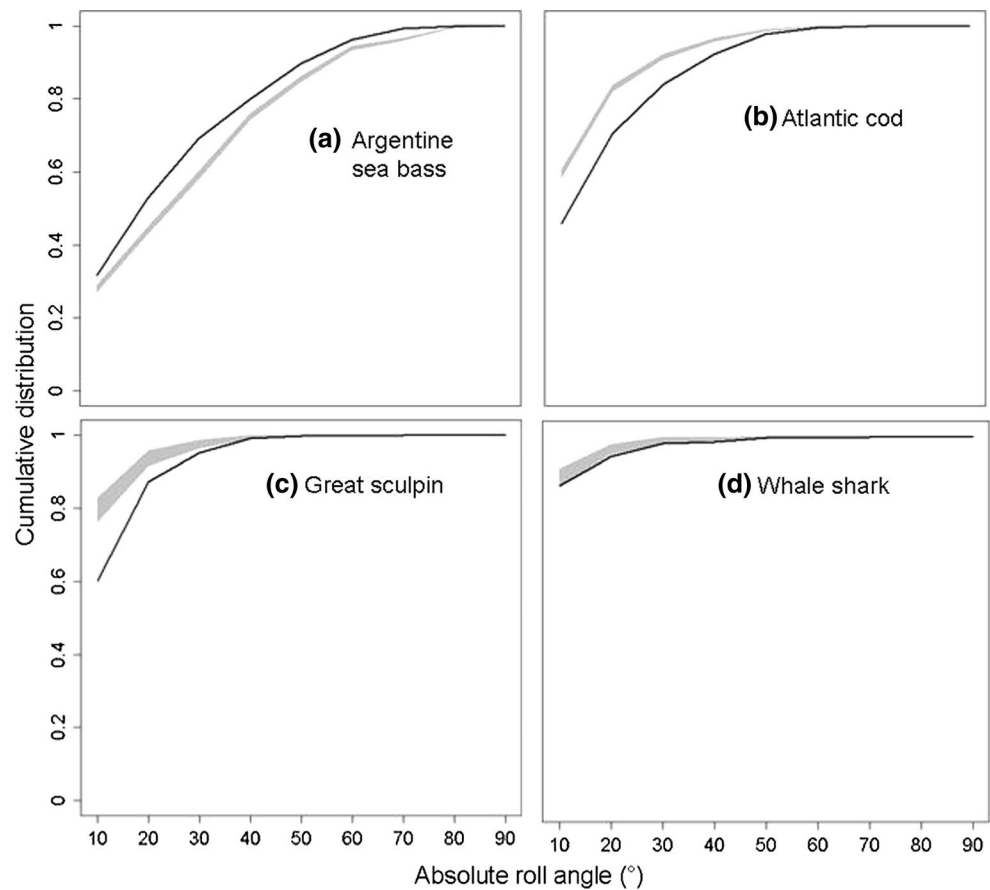
## Discussion

In this study, we showed that the laterally body-compressed Argentine sea bass, a cave-refuging species, rests at a wide range of roll angles including almost lying at their sides. This suggests that this species may relax posture and buoyancy controls during resting periods. Both the

higher proportion of records with absolute roll angles  $\leq 30^\circ$  adopted by moving fish, and the wide range of roll angles observed in stationary Argentine sea bass, which could exceed  $80^\circ$ , agreed with this notion. Such extreme roll angles were not recorded in such proportions for the other three species during monitoring of different activities including resting. Furthermore, the remaining three species: Atlantic cod, great sculpin, and whale shark showed an inverse relationship between VeDBA and roll angle, suggesting that these fishes had lower VeDBA values when close to the upright position. Our results point to a novel function of refuging in marine reef fishes (e.g., Hixon and Beets 1993; Anderson 2001), not previously considered in the literature. Refuge is mostly regarded as protection from predation (Steele 1999; Anderson 2001) or from hydrodynamic forces from currents (Gerstner 1998). We postulate



**Fig. 3** Evaluation of the prediction about an association between absolute roll angle and VeDBA. Shaded gray area represents 95 % confidence regions for cumulative distributions under the null hypothesis, approximated by Monte Carlo permutations (1000 replicates for Argentine sea bass and Atlantic cod, and 10,000 replicates for great sculpin and whale shark). The solid lines represent the empirical cumulative distribution. **a** Argentine sea bass: 8000 records corresponding to 4 fish; **b** *Gadus morhua* (Atlantic cod): 8000 records corresponding to 4 fish; **c** *Myoxocephalus polyacanthocephalus* (great sculpin): 600 records corresponding to 2 fish; **d** *Rhincodon typus* (whale shark): 786 records corresponding to 3 fish

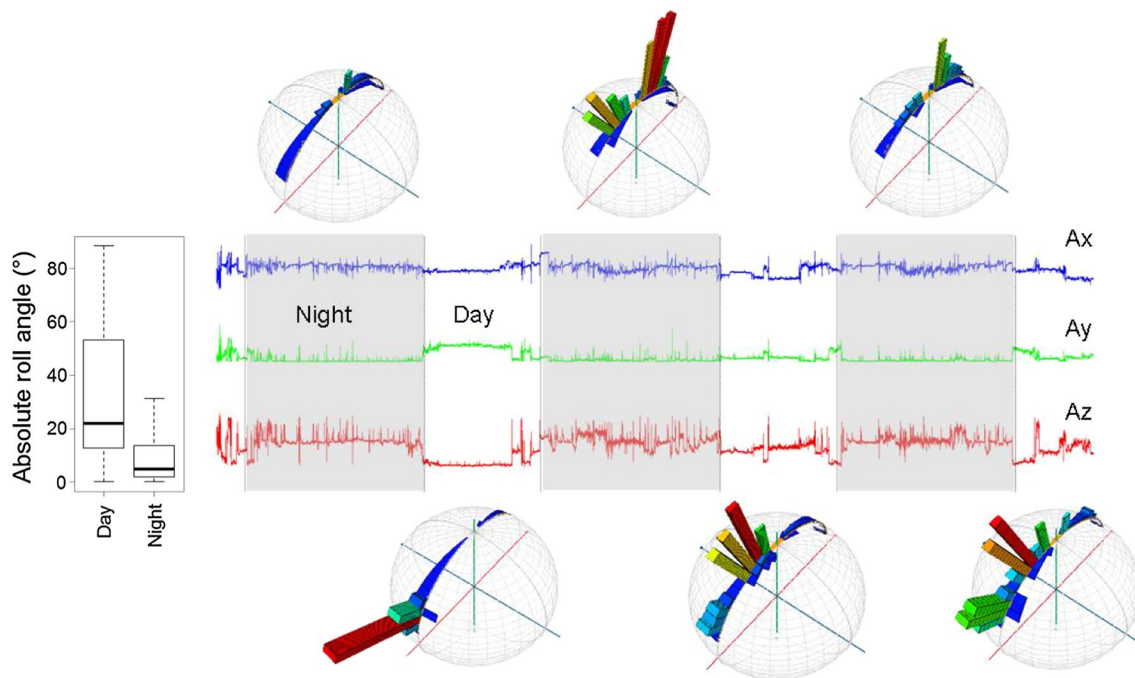


that in laterally body-compressed fishes, the use of refuges may provide an additional opportunity for relaxation of posture and buoyancy control mechanisms in periods of low activity, which may save part of the energy demands of maintaining posture and depth in an environment with daily pressure changes (see Strand et al. 2005 for an example of modeled energy demands of hovering or hydrodynamic lift by swimming, which could be as high as  $1.5 \text{ J s}^{-1} \text{ kg}^{-1}$  for the Atlantic cod performing nocturnal migrations).

Lateral body compression in fishes is believed to have evolved for better maneuverability (Helfman et al. 2009) at the expense of increasing the metacentric height and hence their instability (Webb 2002). This could entail an increased energetic cost for maintaining posture (but see also Webb and Weihs 1994). In essence, as long as such a fish remains perfectly upright, there is no moment arm tending to cause the fish to roll upside down. However, the slightest roll will tend to exert a torque to roll the fish, with greater rolls exerting proportionately greater torque (Eiditis et al. 2002) requiring correspondingly greater energy expenditure required to correct it. For teleosts that normally operate near neutral buoyancy to forage, the relaxation of its buoyancy control to rest on the bottom is commonly observed in dorsoventrally compressed (i.e., depressed body) or fusiform fishes. However, laterally compressed

body fishes still will have to maintain their posture control when resting on the bottom. Our results showed that the cave-refuging Argentine sea bass, which has a laterally compressed body (see Online Resource 5 for a detail of body shape and swim bladder location in the Argentine sea bass), appears able to rid itself of the problems of posture and buoyancy control during periods of inactivity and rest at positive or negative buoyancy within the refuge, at virtually any roll angle. Given the energetic costs of powered control and maintaining swim bladder volume (Speers-Roesch et al. 2004; Strand et al. 2005), such a strategy would be expected to reduce daily energy expenditure.

As tidal amplitude in the study area ranges between 3 and 5 m, fish buoyancy would be expected to change during periods of sheltering, which spanned a significant part of a single tidal cycle (semidiurnal). Tidal changes in the shallow reefs where fish were tagged effectively resulted in ambient pressure changes of about 25 % four times a day, which would require adjustments of the volume of gas into the swim bladder to maintain constant buoyancy. Beyond being energetically demanding, it may not be even possible, due to the time required to add or to remove gases from the swim bladder of a physoclistous fish (Strand et al. 2005, Mehner 2012). Moreover, positive buoyancy is often considered a particular danger to physoclistous fish as



**Fig. 4** Activity patterns denoted by the raw  $x$ ,  $y$ , and  $z$  (orthogonal) acceleration values over time of a free-living Argentine sea bass in Patagonia with the corresponding body posture values summarized in a spherical plot (*upper spheres* show nighttime and *lower ones* daytime hours, respectively, see Grundy et al. 2009) (cf. Fig. 1). The fish shown was tagged on July 2013 (austral winter) during a new moon

period (sunrise 8:50 a.m., sunset 6:00 p.m.). Note that during the night, when the fish was more active (*gray areas*), acceleration levels were higher and the body roll was close to the upright position (*Box-plot* in the left of figure). During the day, when the fish most probably rested in caves, activity levels dropped and body roll values were more extreme

it may result in barotrauma if a fish is unable to overcome these hydrostatic forces (e.g., Shasteen and Sheehan 1997). This represents particular challenges for fish resting on the seabed in areas that are shallow and have large tidal amplitudes (as is the case in Patagonia). Resting in caves may therefore be a necessity for Argentine sea bass, our physoclistous model species, to prevent acquiring positive buoyancy and being transported to the surface during low tides, when buoyancy is expected to increase.

As a byproduct, accelerometer data obtained from free-living fish allowed us to estimate a gross (i.e., ‘moving’ vs. ‘stationary’), infra-second activity budget for this species in the wild, which pointed to a sedentary lifestyle. Despite activity being one of the main energy sinks for any aquatic predator, this quantity has been most commonly underestimated (Halsey et al. 2015) or considered constant in bioenergetics modeling (see, e.g., the commonly used ‘Wisconsin model of fish bioenergetics’ in Hanson et al. 1997). Due to the obvious logistic difficulties in quantifying it, only a few works have provided estimates of activity budgets for free-living fish (e.g., Gruber et al. 1988; Brownscombe et al. 2014; Gannon et al. 2014). Brownscombe et al. (2014), for example, reported that ‘resting’ made up a significant proportion of time (57 %) for bonefish *Albula*

*vulpes* (Linnaeus 1758) in a mesocosm experiment, which is well below our estimates of stationary *Argentine sea bass* (81–91 %). Our work also suggested that the scatter plots of VeDBA versus roll angle (Fig. 1b) could provide a characteristic signature for each species, which could be used to represent an average posture and activity pattern and to show the degree of intraspecific variability in behavior.

Finally, although our conclusions are not based on direct estimates of energy use, VeDBA has been shown to correlate linearly with power use in teleost fish (Wright et al. 2014, but see Webb and Weihs 2015) and in a large array of vertebrates (Williams et al. 2014). Hence, the strategy described in this study (i.e., relaxing posture and/or buoyancy controls while inactive), only possible within caves or in crevice habitats, could provide a potential energy-saving mechanism. This strategy might help fishes to exploit ecosystems where food is limited and the ambient pressure very variable, such as the small rocky outcrops that typify the home of the reef-dwelling Argentine sea bass. This being the case, the use of crevices by cave-refuging species may provide an additional advantage by allowing animals to save posture and/or buoyancy costs, beyond the benefits of offering refuge from predation or currents.

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