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RESEARCH ARTICLE

Oil gland and oil pores in billfishes: in search of a function

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ABSTRACT

Billfishes are well known for their distinctive elongated rostra, i.e. bills. The functional significance of billfish rostra has been frequently discussed and the recent discovery of an oil gland (glandula oleofera) at the base of the rostrum in swordfish, *Xiphias gladius*, has added an interesting facet to this discussion regarding the potential co-evolution of gland and rostra. Here, we investigated the oil gland and oil pores (through which the oil is brought to the skin surface) of four billfish species – swordfish, Atlantic blue marlin (*Makaira nigricans*), Indo-Pacific sailfish (*Istiophorus platypterus*) and striped marlin (*Kajikia audax*) – and provide detailed evidence for the presence of an oil gland in the last three. All four species had a high density of oil pores on the forehead which is consistent with the hypothesis of hydrodynamic benefits of the oil. The extension of the pores onto the front half of the rostrum in sailfish and striped marlin, but not in swordfish or blue marlin, suggests that the oil may have additional functions. One such function could be linked to the antibacterial and anti-inflammatory properties of the oil. However, the available evidence on predatory rostrum use (and hence the likelihood of tissue damage) is only partly consistent with the extension of pores on rostra across species. We conclude that the oil gland probably serves multiple, non-mutually exclusive functions. More detailed information on rostrum use in blue marlin and swordfish is needed to better link behavioural and morphological data with the aim of accomplishing a full comparative analysis.

KEY WORDS: Comparative method, Functional morphology, Rostrum, Glandula oleofera, Rete lubricans, Fatty acids, Co-evolution

INTRODUCTION

Pelagic predators possess an array of morphological adaptations thought to facilitate prey detection and/or capture. Examples of these adaptations include the hammerhead shark's (Sphyrnidae) dorsoventrally flattened cephalofoil (McComb et al., 2009) and the billfishes' (Istiophoridae and Xiphiidae) elongated rostra (Habegger et al., 2015). Speculations on the role of these morphological structures are numerous, but detailed investigations are scarce because of the logistical complexity of open-ocean research.

In the case of billfishes, the rostrum has been shown to serve as a weapon to stab or strike prey (Domenici et al., 2014; Shimose et al., 2007). Additionally, it was hypothesized to create turbulence in the boundary layer, reducing pressure drag because of a delay in flow separation (Aleyev, 1977; Kozlov, 1973; Videler, 1995). Drawing on the functional morphology approach, researchers have analysed the morphology of the bill to gauge its function. Recently, Habegger et al. (2015) reported the presence of a poorly calcified structure in front of the eyes at the base of the rostrum on billfish specimens. This structure, first mentioned by Gudger (1940), was recently analysed in detail by Videler et al. (2016) in swordfish, *Xiphias gladius*. They described it as an oil-producing gland (glandula oleofera) connected via a capillary network (rete lubricans) to micro-pores on the forehead and the base of the rostrum. The presence of this gland, especially in connection with the capillary network running into the rostrum, adds an interesting angle to the debate on bill functionality, particularly regarding the potential co-evolution of gland and rostra.

The prime function of the oil gland put forward by Videler et al. (2016) is that it lubricates the fish's forehead, creating a hydrophobic layer on the skin. The authors analysed the oil's chemical composition and properties and studied the distribution and size of the pores on the swordfish forehead. The oil was found to consist of fatty acids and to congeal at 8°C. The authors suggested that the oil stays fluid at the swordfish's typical foraging depths thanks to a heat-producing muscle located behind the eyes (Videler et al., 2016). Low dynamic pressure over the concave front part of the head has been proposed as the oil's passive excretion mechanism. The hydrophobic layer resulting from the oil lubrication, associated with micro-protrusions on the skin, is thought to decrease frictional drag (Luo et al., 2015; Videler et al., 2016). Therefore, these findings placed functional explanations of the oil gland and capillary system in the context of a hydrodynamic benefit that reduces the metabolic costs of swimming (Videler et al., 2016).

In this study, we investigated and compared the presence and characteristics of the oil gland of four billfish species: the Atlantic blue marlin (*Makaira nigricans* Lacepède 1802), striped marlin [*Kajikia audax* (Philippi 1887)], Indo-Pacific sailfish [*Istiophorus platypterus* (Shaw 1792)] and swordfish (*Xiphias gladius* Linnaeus 1758). First, we used computed tomography (CT) scans to image the region in which the oil gland was found in swordfish to identify similar structures in the other billfish species. Second, we took oil samples from all species and determined the fatty acid composition of the oil. Third, we measured the pore distribution along the bill to quantify potential species differences in pore extension along the rostrum, and quantified pore density and size. We discuss our results, considering what is known about behavioural differences between the billfish species.

If hydrodynamic benefits are indeed the main function of the oil gland, then we would predict that, in all four species, oil pores

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would be primarily present on the forehead and base of the bill, as these regions face the greatest frictional drag in billfish (Aleyev, 1977). However, if the oil gland also relates to other functions such as predatory rostrum use, then we would expect to find among-species differences in the extension of the pores along the rostrum. Sailfish are known to use their rostrum frequently in prey capture (Domenici et al., 2014; Hansen et al., 2020). Striped marlin also use their rostrum for prey capture, although less frequently than sailfish (Hansen et al., 2020). Blue marlin (Shimose et al., 2007) and swordfish (Stillwell and Kohler, 1985) are thought to rely less on their bill for prey capture, though this evidence is circumstantial as it is inferred from stomach content analyses rather than direct observation. The rostra of billfish are subject to exceptionally high biomechanical stress and show signs of tissue damage (Atkins et al., 2014; Kurvers et al., 2017). Given the antibacterial properties of some of the fatty acids found in swordfish oil (i.e. oleic and palmitic acid; Yff et al., 2002; Le et al., 2010; Videler et al., 2016), one potential function in connection with the rostrum's use as a weapon could also be tissue repair. If the oil is linked to tissue repair, we hypothesize that the oil pores would be more abundant on the rostrum and would extend further towards the rostrum tip in sailfish and striped marlin as compared with blue marlin and swordfish.

MATERIALS AND METHODS

We obtained the heads of four individuals of each billfish species from Cancun, Mexico (sailfish), Reunion Island, France (striped marlin, blue marlin, sailfish) and Sardinia, Italy (swordfish). Rostra were collected by observers embarking on commercial longliners in Mexico and France, and provided directly by commercial fishermen in Italy.

Oil gland: CT-scans and oil composition

To document the presence of the oil gland across species, we carried out scans of the heads of every collected specimen at the Centre for Computed Tomography at the Leibniz Institute for Zoo and Wildlife Research using CT-Scanner Toshiba Aquilion CX operating at a 0.25 mm resolution.

Videler et al.'s (2016) analysis of the chemical composition of the oil focused on fatty acids and we did the same to facilitate comparisons with the original discovery. Three oil samples (~7 mg) were collected from one specimen of each of the four species for chemical analysis. The extraction was carried out with 4.5 ml chloroform–methanol (2:1 v/v). Samples were shaken for 3 h on ice in the dark and subsequently centrifuged. The upper layers containing the lipid extracts were removed and samples were washed twice with 5 ml of a 2:1 chloroform–methanol solution. The combined extracts were then dried, dissolved in methanol and stored at 5°C overnight. The fatty acids were methylated by heating for 4 h at 80°C in a solution of 5% sulphuric acid in methanol and subsequently extracted 3 times with hexan (4.5, 2 and 2 ml, respectively). The upper layers of the extracts were measured 3 times (directly and diluted or concentrated 10-fold, respectively). A gas chromatograph/mass spectrometer (GC/MS Agilent 6890/5973-N) equipped with a fused silica capillary column (CP Sil 88, 100 m×250 µm×39 µm) was used to detect fatty acid methyl esters (FAMEs). The fatty acids were identified based on their respective retention times and mass spectra in full scan mode calibrated with fatty acid standards (FAME Mix 47885-4, PUFA No1–47033 and PUFA No3–47085, Supelco). The most intensive ion of the molecular ion cluster was used to quantify FAMEs, and estimation of the concentration of additional fatty acids – not contained in the standard solutions – was done by comparison of the intensities of similar fatty acids in the standard solutions. The limit of detection was 0.1 µg mg^{-1} and the limit of quantification was 0.5 µg mg^{-1}.

Pore distribution, density and size

In all four species, oil pores as described by Videler et al. (2016) were found, but only on the dorsal surface. Therefore, we focused on the dorsal side for our study. We examined the pore distribution on the bill by measuring the dorsal extension of the pores. We used a microscope (Leica Wild MZ, lens: Planapo 1.0×) to measure how far towards the bill-tip the dorsal pores were present. To standardize the extent of the pores across individuals (and species), we measured, for each individual, the distance from the anterior eye edge to the maximum dorsal pore extension point and divided this by the total rostrum length (RL). The RL was measured as the distance from the anterior eye edge to the rostrum tip. This approach thus provides a measure that quantifies how far the pores extend relative to the total length of the rostrum.

Pore density (number of pores per cm^2) was sampled at six equidistant dorsal locations starting at the eye edge and ending at the bill tip (Fig. 1). At each sampling point, the size (mm) of the four pores closest to the centre of the area was measured. Assessments of pore density and size were conducted using a Mitutoyo microscope (Vision Measuring Machine, Quickscope) and its image processing software (QSPAK). Full raw data for pore extension, pore density and size are in Tables S1 and S2.

Data analysis

Data analysis was performed in R (v3.6.2; http://www.R-project.org/). We tested our hypothesis that pore extension would be different between species using a linear model with pore extension as a response variable and species as a fixed effect. We used Tukey's HSD to investigate *post hoc* pairwise comparisons. Statistical assumptions were checked by plotting residuals and *Q*–*Q* plots with the library *gvlma* (https://CRAN.R-project.org/package=gvlma).

To test whether pore density and pore size differed between species, we performed two mixed effect models with individual bill as a random effect. This was done to control for the repeated measurement within samples (i.e. individual bill). For pore density, we fitted a zero-inflated generalized linear mixed model (as these data contained many zeros) using maximum likelihood estimation (*glmmTMB*; Brooks et al., 2017). Species was included as a fixed effect in interaction with sampling location, and the probability distribution was set to Poisson. Pairwise comparisons were investigated using the library *emmeans* (https://CRAN.R-project.org/package=emmeans) with Tukey's adjustment method. Statistical assumptions were checked by plotting residuals, *Q*–*Q* plots and with the library *DHARMa* (https://CRAN.R-project.org/package=DHARMa). For pore size, we fitted a linear mixed model (*lme4*; Bates et al., 2015) by maximum likelihood *t*-tests with species included as a fixed factor in interaction with sampling point, and we used Satterthwaite approximations for degrees of freedom to

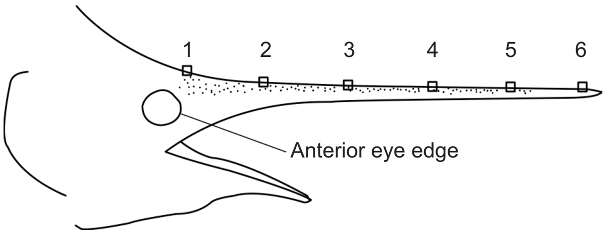

Fig. 1. Schematic representation of a billfish head. Pore density and pore size were measured at six equidistant sampling points along the rostrum length (1–6). The rostrum length was measured from the anterior eye edge to the tip of the rostrum.

approximate P-values. Pore size was log transformed to meet statistical assumptions.

RESULTS

Oil gland: CT-scans and oil composition

The CT scans showed evidence for the presence of oil-filled cavities at the base of the rostrum in all four billfish species (Fig. 2). Chemical analysis of the oil showed that docosahexaenoic (DHA), oleic and palmitic acids were the three most abundant fatty acids in all species (Fig. 3). In swordfish, the most abundant fatty acid was oleic acid whereas in the other three *Istiophoridae* species, DHA was the most abundant. Palmitic acid was the second most abundant fatty acid in all four species.

Pore distribution, density and size

Oil pores were found on the base of the bill of all four billfish species (Fig. 4). The extension of pores towards the tip of the rostrum relative to the total RL was significantly different between all species apart from sailfish and striped marlin (Table 1, Fig. 5A). In sailfish, the pores extended the furthest towards the tip proportionally to the length of the rostrum, closely followed by striped marlin. In blue marlin, the pores extended to less than half the rostrum, and in swordfish, the pores were only found at the base of the bill (see Table 1).

Pore density was significantly lower in swordfish than in the other three species (Tukey tests, log estimated mean±s.e. difference: blue marlin 4.62±0.67, $P<0.0001$; striped marlin 5.46±0.66, $P<0.0001$; and sailfish 4.76±0.66, $P<0.0001$; Fig. 5B). No other pairwise comparison reached significance (i.e. all $P>0.05$). Pore density decreased along the bill towards the tip in swordfish (estimate±s.e. −1.07±0.2, $P<0.0001$) and sailfish (−0.37±0.04, $P<0.0001$; Fig. 5B).

Striped marlin had a larger pore size than all the other species (mean±s.d. pore size 0.21±0.05 mm, $n=16$; Tukey tests, log estimated mean±s.e. difference: blue marlin 0.74±0.18, $P<0.005$; sailfish 0.5±0.15, $P<0.05$; swordfish 0.79±0.23, $P<0.05$; Fig. 5C). There was no significant difference in pore size between the three other species (mean±s.d. pore size: sailfish 0.13±0.03 mm, $n=20$; blue marlin 0.09±0.008 mm, $n=9$; swordfish 0.13±0.08 mm, $n=8$). There was no effect of sampling point on pore size.

DISCUSSION

Our results provide evidence for the presence of a morphological structure similar to that described as an oil gland in swordfish in each of the three species of *Istiophoridae* we investigated. Videler et al. (2016) hypothesized that the main function of the oil gland is to reduce frictional drag on the forehead by lubricating it. This hypothesis seems plausible in swordfish and blue marlin, where the pores do not extend very far onto the rostrum. However, in sailfish and striped marlin, the pores lubricate more than 70% of the rostrum. It seems likely that the oil gland has functions beyond hydrodynamic benefits.

Billfish rostra have often been conjectured to facilitate prey capture (Fierstine, 1997; Fierstine and Voigt, 1996; Frazier et al., 1994), and this was confirmed in the case of sailfish, striped marlin and blue marlin (Domenici et al., 2014; Hansen et al., 2020; Shimose et al., 2007). Sailfish use their rostrum to slash or tap at fish, typically injuring prey before capture and ingestion (Domenici et al., 2014; Herbert-Read et al., 2016; Krause et al., 2017). Hansen et al. (2020) compared the hunting behaviour of striped marlin and sailfish and concluded that striped marlins use their rostra less in prey capture and in particular slash less at fish schools. In a stomach content analysis of blue marlin, Shimose et al. (2007) found that 62% of undigested prey did not show signs of rostrum-attributed injury. Similar studies on

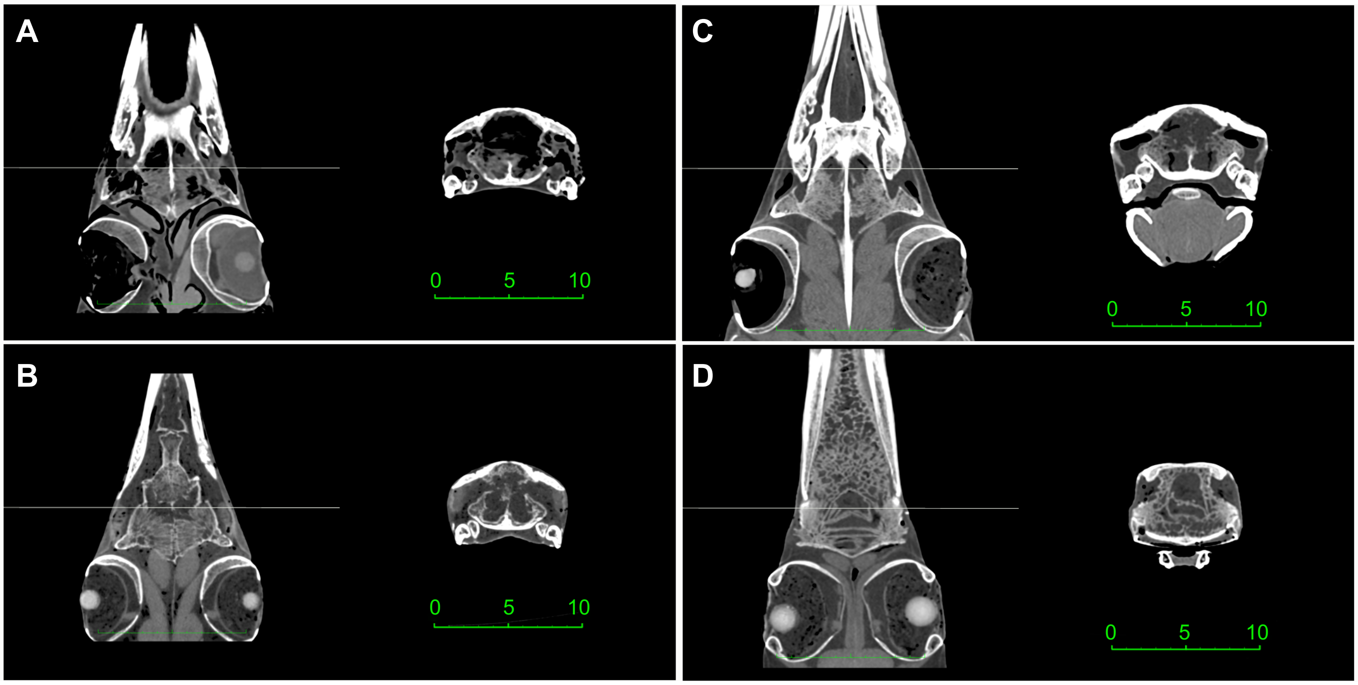

Fig. 2. Computed tomography (CT) scans of billfish heads. (A) Sailfish, (B) striped marlin, (C) blue marlin and (D) swordfish. The oil gland is visible right in front of the eyes in the dorsal views (left) and in the cross-section of the cranium (right). The spongy soft tissue of the oil gland shows up in grey and the oil-filled cavities are black, whereas bones are white. The dorsal views were taken at the point of maximum eye width and the cross-sections were taken half an eye width in front of the most anterior part of the eye, as indicated by the white line. The scale bar is in centimetres.

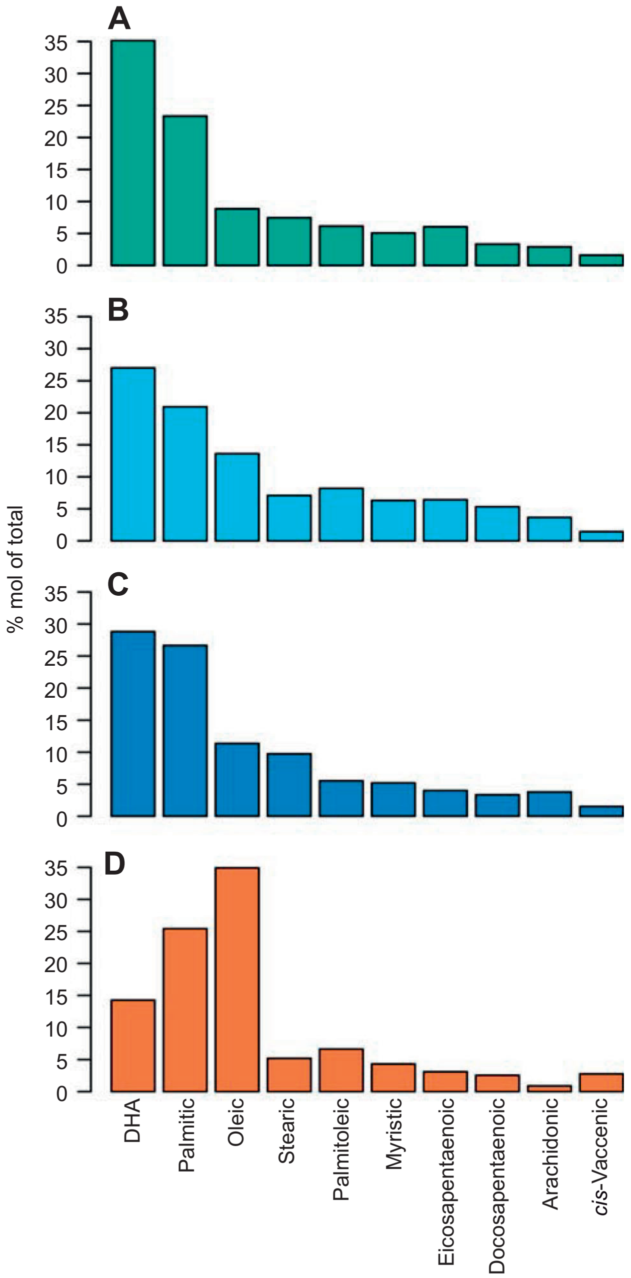

Fig. 3. Oil composition. The oil composition is shown for the 10 most abundant fatty acids for (A) sailfish, (B) striped marlin, (C) blue marlin and (D) swordfish. DHA, docosahexaenoic acid.

swordfish described that some of the larger undigested prey items (e.g. cephalopods 25–30%; Stillwell and Kohler, 1985) showed lacerations and were often cut into pieces (Markaida and Sosa-Nishizaki, 1998; Stillwell and Kohler, 1985). Although these observations are not directly comparable, it seems possible that sailfish and striped marlin make different and more extensive rostrum use in prey capture than blue marlin and swordfish, which coincides with predicted differences in pore extension, suggesting that oil may play a role in a hunting context. However, we did not find significant differences in pore extension or density between sailfish and striped marlin despite their behavioural differences.

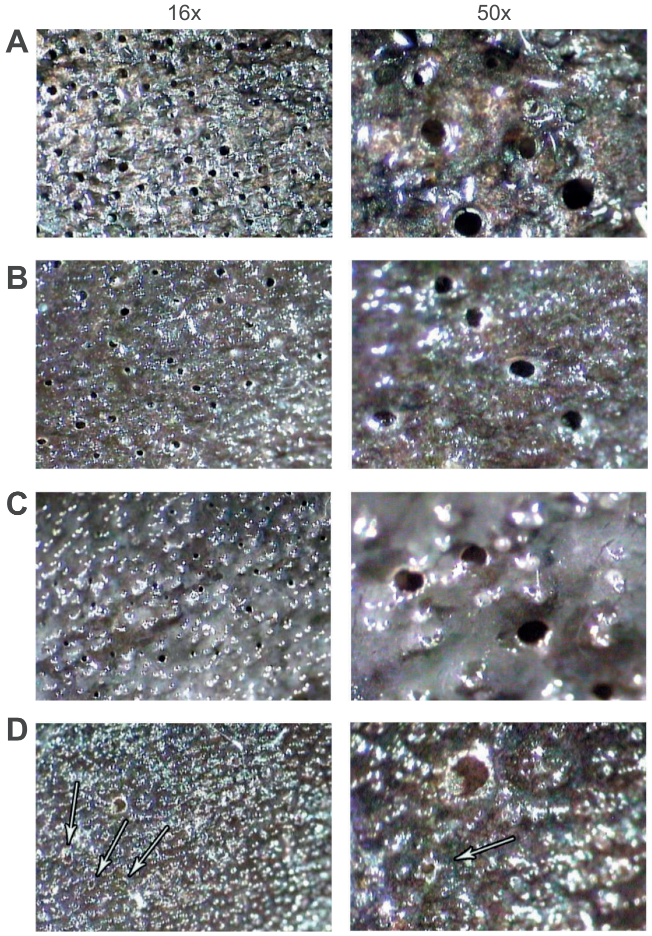

Fig. 4. Magnified images of the oil pores on the dorsal surface of the base of the rostra. (A) Sailfish, (B) striped marlin, (C) blue marlin and (D) swordfish. Images are provided at two different magnifications. In swordfish (D), small pores are indicated with arrows.

We propose three main possible functions for the presence of oil on the surface of the rostrum in the context of hunting. First, the oil could play a role in tissue repair. Three fatty acids were particularly common in all four species: DHA, oleic acid and palmitic acid. Oleic and palmitic acid are known to have antibacterial properties (Le et al., 2010; Yff et al., 2002), which supports the hypothesis that the oil is secreted for antibacterial reasons. The oil might serve a similar function to fish mucus, which is also known to have antibacterial properties (Shephard, 1994; Subramanian et al., 2008) and shares some of its fatty acid composition (Sar and Rosenberg, 1989). For instance, in striped snakehead, *Channa striata*, oleic acid constituted 21.25% of the total lipid content of mucus and palmitic acid constituted 16.65% (Jais et al., 1998). One difference between most fish mucus and the billfish oil is the higher presence of DHA in the latter (i.e. no DHA in *C. striata*; Jais et al., 1998). One function of DHA is to inhibit the production of inflammatory cytokines (Calder, 2009). Oleic acid is also known to modulate inflammation in wounds (Cardoso et al., 2011), which suggests that the oil could fulfil a role in wound healing by reducing inflammation and

Table 1. Individual data points and mean±s.d. of the dorsal pore extension relative to rostrum length (RL) for each species

	Individual data points (RL)				Mean±s.d. (RL)
Sailfish	0.8	0.8	0.79	0.84	0.81±0.02
Striped marlin	0.62	0.76	0.76	0.84	0.72±0.07
Blue marlin	0.33	0.37	0.3	0.36	0.36±0.06
Swordfish	0.19	0.23	0.2	0.2	0.21±0.01

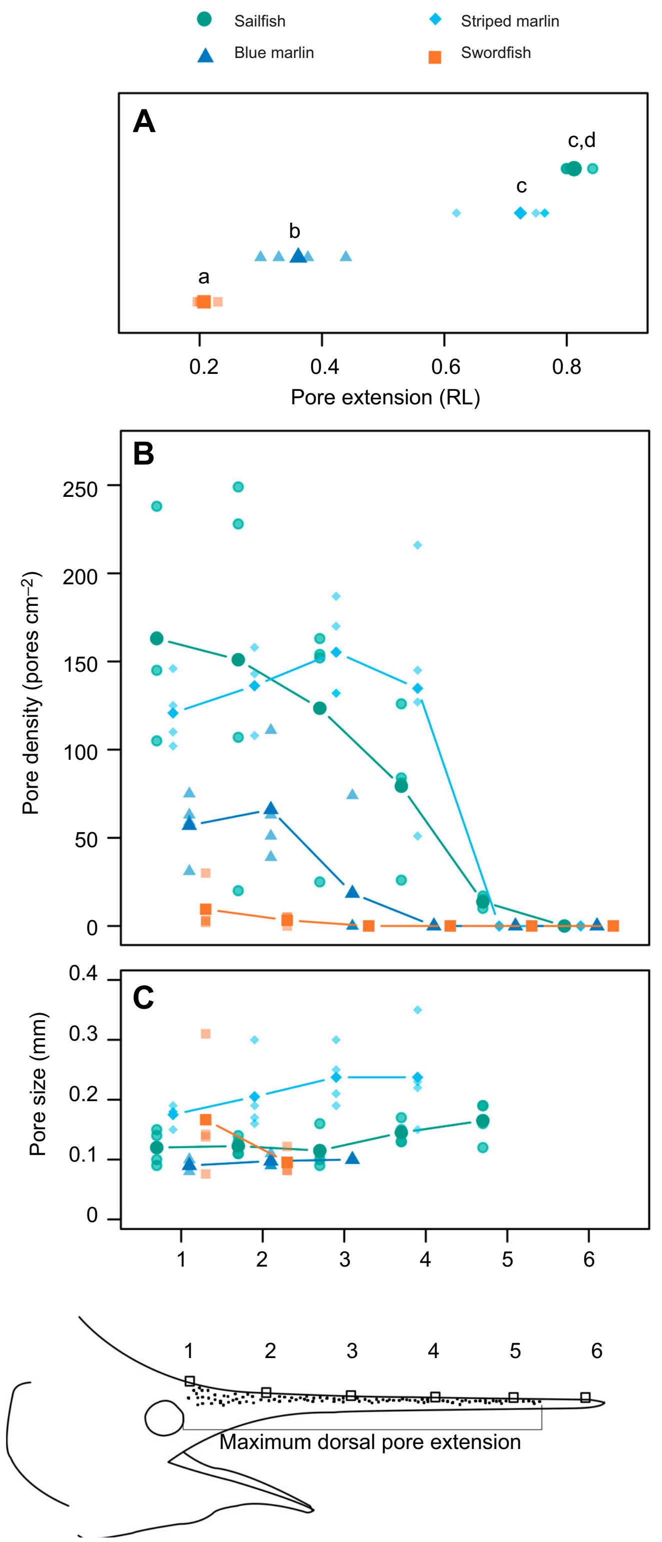

Fig. 5. Maximum pore extension, pore density and pore size in sailfish, striped marlin, blue marlin and swordfish. (A) Maximum pore extension was calculated as the distance of the pore furthest away from the eye edge, in rostrum lengths (RL). Different letters indicate statistically significant differences between species (all $P<0.005$). (B) Pore density for each billfish species at six equidistant sampling points (1–6, indicated in the diagram below) along the rostrum. (C) Pore size for each billfish species at six equidistant sampling points (1–6) along the rostrum. In all panels, light-coloured symbols represent individual measurements, and dark-coloured symbols are means at the species level. Note that data points are staggered on x-axis for clarity.

preventing bacterial infections on the skin. This potential function of the oil is supported by the fact that Atkins et al. (2014) used billfish rostra as a study model for remodelling in bone because of the high biomechanical stresses on them. They described intensive tissue repair in areas where high loads were expected. A repair function of the oil would therefore be consistent with the presence of the oil gland in all four species we investigated. Although we focused here on fatty acids, the oil gland might secrete other lipid classes. For instance, sphingosines, which are known to have strong antimicrobial properties, are commonly found in cell membranes and on the animal's skin, making them a potential candidate (Bibel et al., 1992). Future research would benefit from a broader chemical investigation of the oil.

A second possible hunting-related function of rostra oil relates to slashing behaviour. It has been shown that during sideways slashing, the tip of the rostrum in sailfish can attain much higher speeds than its potential prey (Domenici et al., 2014). The oil, associated with the micro-protrusion on the rostrum, could be a determining factor in the achievement of such speeds by decreasing drag on the rostrum as shown in other examples of drag-reducing surfaces (Luo et al., 2015). Because of their dorsoventrally flattened rostra, swordfish were hypothesized by Habegger et al. (2015) to have superior lateral slashing capability compared with other billfish species. The lubrication from the oil along the bill might in this case be more relevant for *Istiophoridae*, as they do not benefit from a dorsoventrally flattened bill for lateral striking.

Third, sailfish introduce up to a third of their bill into prey schools before slashing or tapping (Domenici et al., 2014; Herbert-Read et al., 2016; Krause et al., 2017). The prey species have been found to not react to this insertion of the bill, despite being extremely close to the dangerous weapon (Domenici et al., 2014). It is possible that the oil plays a role in such stealth attacks on fish schools, for example, by changing the viscous properties of the water near the bill, which might make the rostrum harder to detect for the prey's lateral line.

We further propose three potential non-exclusive functions of the oil gland. Structures composed of a solid outer layer and a hollow core are common in nature and are thought to prevent buckling while reducing weight (Meyers et al., 2013). A property of these honeycombed structures is that they can take different shapes according to the directional stress they are subjected to (e.g. in avian feathers: Sullivan et al., 2017). Given that swordfish probably slash mainly horizontally, whereas marlins and sailfish use multi-directional slashing (Habegger et al., 2015), it is relevant to consider the shock-absorption properties of the different species' rostra. Using finite element analysis, Habegger et al. (2020) suggested that the round rostrum of the blue marlin may be suited for a wide range of slashing motions, while the flat rostrum of the swordfish is more specialized for lateral swiping. In this case, the oil gland could be speculated to play a role in shock absorption (Gudger, 1940; Habegger, 2014).

Poorly calcified bones filled with lipids are known to increase buoyancy in the aquatic environment (Lee et al., 1975; Sullivan et al., 2017). Billfishes can control their buoyancy via a multi-chambered swim bladder which grants them neutral buoyancy at constant depths but cannot be filled/emptied as fast as necessary during descent/ascent, forcing them to use high swimming speed during depth changes (Block et al., 1992; Carey and Robison, 1981). Storage of lipids in the cranium has been shown in castor oil fish, *Ruvettus pretiosus*, to increase buoyancy at the surface, making the fish rest with its head pointing up at 45 deg, and is assumed to permit neutral buoyancy at depth (Bone, 1972). The oil gland can therefore be hypothesized to increase buoyancy at the front end of billfishes, which could be both an advantage and a drawback. Whilst it could scale down the increased energetic cost of negative buoyancy at depth (Strand et al., 2005), it could also make vertical manoeuvres near the water surface more costly. Buoyancy (just like hydrodynamic benefits and shock absorption) is a good candidate for the primary function of the oil gland in the evolution of the bill. As the rostra of billfishes grew longer, there might have been an increasing need to deal with buoyancy problems.

Finally, a further function that does not exclude other ones is related to the eye heater system in billfishes. The eyes and the brain of swordfish are known to be maintained at a temperature 10–15°C higher than ambient due to a highly specialized heating system (Block, 1986; Carey, 1982). This increases the temporal resolution of their visual system (in terms of the flicker fusion frequency), improving the detection of rapid motion relevant for predator–prey interaction (Fritsches et al., 2005). It is possible that the oil produced in the gland positioned right in front of the eyes protects and insulates the eyes further, allowing superior vision in swordfish and providing a crucial advantage over their prey.

To conclude, all four billfish species showed a high density of oil pores on the forehead, which is consistent with the hypothesis of hydrodynamic benefits of the oil. However, the extension of the oil pores onto the front half of the rostrum in some species suggests that the oil may have additional functions. One such function could be the antibacterial and anti-inflammatory qualities of some of the fatty acids found in the oil. We also argue that the oil might facilitate hunting behaviour such as slashing. However, the available evidence on rostrum use (and hence the likelihood of tissue damage) is insufficient to test either of these hypotheses. In conclusion, the oil gland is likely to serve multiple functions in billfishes that are not mutually exclusive. More detailed information is needed on rostrum use, in particular in blue marlin and swordfish, to link behavioural and morphological data to strengthen a comparative analysis.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: F.D., M.J.H., J.J.V., P.D., J.F.S., P.B., P.S.S., R.H.K., J.K.; Methodology: S.D.B., J.J.V., P.D., J.F.S., T.H., A.K., J.K.; Software: T.H., G.F.; Formal analysis: F.D., M.J.H.; Investigation: F.D., M.J.H., S.D.B., T.H., G.F., J.K.; Resources: J.J.V., P.D., J.F.S., P.B., P.S.S.; Data curation: A.K.; Writing - original draft: F.D., R.H.K., J.K.; Writing - review & editing: M.J.H., S.D.B., J.J.V., P.D., J.F.S., T.H., G.F., P.B., P.S.S., A.K., R.H.K., J.K.; Visualization: F.D.; Supervision: J.K.

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Supplementary information
Supplementary information available online at https://jeb.biologists.org/lookup/doi/10.1242/jeb.224956.supplemental

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