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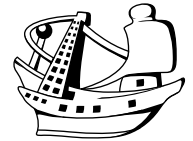
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SHORT NOTE

The absence of gas bladder in the Atlantic mackerel *Scomber scombrus* Linnaeus, 1758 (Actinopterygii: Teleostei: Scombridae). A review

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Abstract: The present article reviews the absence of gas bladder in the Atlantic mackerel *Scomber scombrus* (Actinopterygii: Teleostei: Scombridae). Four to five extant species are recognized to belong to the genus *Scomber*. Among them, only the Atlantic mackerel does not possess a gas bladder. The comparison of the swimming performances of the different species of the genus *Scomber* shows that the fastest one is the Atlantic mackerel. We may then hypothesize that the absence of this organ in this species is an adaptation to fast swimming, where the presence of a gas bladder would hamper fast accelerations.

Résumé : *L'absence de vessie gazeuse chez le maquereau atlantique Scomber scombrus Linnaeus, 1758 (Actinopterygii : Teleostei : Scombridés).* Une revue. Le présent article est une revue sur l'absence de vessie gazeuse chez le maquereau atlantique *Scomber scombrus* (Actinopterygii : Teleostei : Scombridés). Quatre à cinq espèces sont reconnues au sein du genre *Scomber* L., 1758). Parmi elles, seul le maquereau atlantique ne possède pas une vessie gazeuse. La comparaison des performances de nage des différentes espèces du genre *Scomber* montre que le maquereau atlantique est le plus rapide. Il est donc possible de considérer que cette absence est une adaptation à la nage rapide, au cours de laquelle la présence d'une vessie gazeuse empêcherait les accélérations rapides.

Keywords: *Scomber scombrus* • Gas bladder • Anatomy • Swimming performances • Adaptation

Introduction

The gas-bladder is a gas-filled sac present in the foregut region of most in actinopterygian species and mainly used for buoyancy (McCune & Carlson, 2004). Some species

can use it as well for breathing and sounds production and reception (McCune & Carlson, 2004) and its absence is a recurrent phenomenon among these animals (McCune & Carlson, 2004). The reasons of the regression of this organ can be multiple, from the adaptation to benthic habitats, like anglers (order Lophiiformes) or flatfishes (order Pleuronectiformes), or to deep sea environments, like Aulopiformes, to inheritance from an ancestral loss (like

notothenioids), to frequent diving (like Oceanic sunfish (Molidae, order Tetraodontiformes) and fast swimming, like some tunas (order Scombriformes, family Scombridae) (McCune & Carlson, 2004).

The species of this family are known to be “astounding bundles of adaptations for efficient and rapid swimming” (Magnuson, 1978). This ability is linked to their high-performance aquatic locomotion via, at least, oscillation of a homocercal forked caudal fin (Nauen & Lauder, 2002). In scombrids, this absence of gas bladder has been documented many times (Carpenter et al., 1995; McCune & Carlson, 2004), and seems to have occurred independently in several lineages within this group. But, even if quoted, it has been never linked to swimming performances for the genus *Scomber* to support this absence.

The genus *Scomber*, Scombridae, is composed of four to five extant species: the Atlantic mackerel, *Scomber scombrus* Linnaeus, 1758, present in North Atlantic ocean (Collette et al., 2001), the chub mackerel *Scomber japonicus* Houttuyn, 1782, inhabiting Pacific Ocean (Collette et al., 2001), the Atlantic chub mackerel *Scomber colias* Gmelin, 1789, present in warm waters of Atlantic Ocean (Collette et al., 2001), the blue mackerel *Scomber australasicus* Cuvier, 1832, present in indo-West Pacific (Collette et al., 2001) and the recently described Indian chub mackerel, *Scomber indicus* Abdussamad, Sukumaran & Ratheesh, 2016, collected from the eastern Arabian Sea (Abdussamad et al., 2016). The latter is considered as a probable synonym of *Scomber australasicus* by B. Collette (pers. comm. to W. Eschmeyer in Eschmeyer & Fricke, 2010). Among all these species, a gas bladder has been described in adult stages, except for the Atlantic mackerel, *Scomber scombrus*. This absence has been viewed as an adaptation to fast swimming (Collette et al., 2001; McCune & Carlson, 2004) linked to food collecting and escape from predators (marine mammals) (Zardoya et al., 2004). But, this ability has never been put in relation with the swimming performances of this species. Our purpose here is to compare, when possible, the anatomical data for the gas bladder of the different species of the genus *Scomber* with their swimming performances, when available in the literature, in order to explain a case of absence of this organ in *Scomber scombrus*.

Material and Methods

The present study is a review gathering already published observations and data obtained by different authors on the anatomy and biology of mackerels, genus *Scomber*.

Following McCune & Carlson (2004), we use the term “gas bladder” rather than “swim bladder” as this organ is a gas-filled sac not only used for swimming and control of buoyancy but also, at least in some groups of fishes, in

breathing, auditory reception, and sound production (McCune & Carlson, 2004).

Results

The observations from Chanet et al. (2009) on dissected specimens (Fig. 1) and from Chanet et al. (2011) on RMI (Magnetic Resonance Imaging) examined specimens (Fig. 2) of Atlantic Mackerel assess the absence of gas bladder in this species.

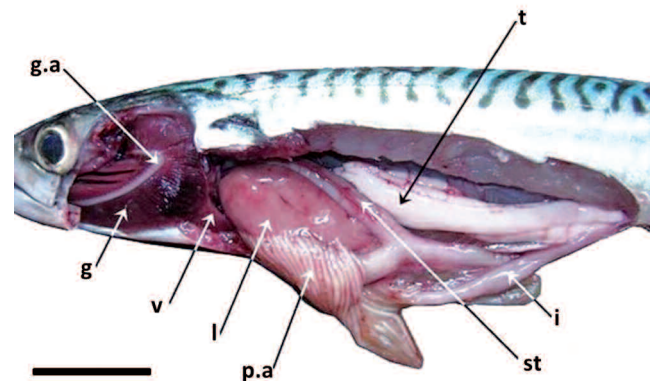


Figure 1. Visceral gross anatomy of an Atlantic mackerel (modified from Chanet et al., 2009), left lateral view. (Scale bar = 50 mm). (g = gills ; g.a = gill arch ; i = intestine ; l = liver ; p.a = pyloric appendages ; st = stomach ; t = testes ; v = ventricle).

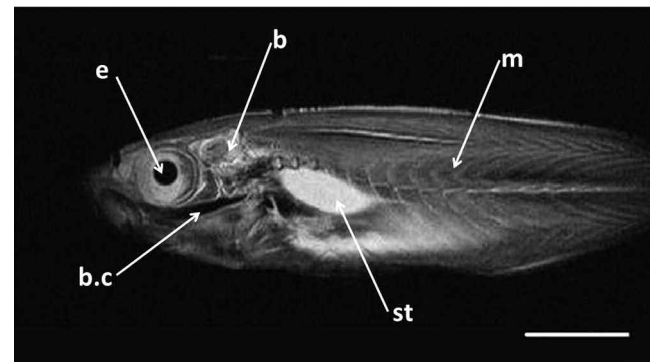


Figure 2. Virtual parasagittal section obtained by MRI on an Atlantic mackerel, modified from Chanet et al., 2011. (Scale bar = 50 mm). (b = brain ; b.c = buccal cavity ; e = eye ; m = muscles ; st = stomach).

The gas bladder is absent in Atlantic mackerel at any stage. It is a well-known phenomenon (Mendiola et al., 2007), while the presence of such a bladder has been reported in chub mackerel (Nauen & Lauder, 2002), *Scomber indicus* (Abdussamad et al., 2016) and all the

Table 1. *Scomber*: Swimming performances and presence of gas bladder in the different species of the genus. b.l.s⁻¹: body length per second; fl.s⁻¹: fork length per second.

^a The swimming performances of *Scomber colias* are here considered be similar to *Scomber japonicus* as the first one has often been confused with *S. japonicus* (Eschmeyer & Fricke, 2010).

^b The swimming performances of *Scomber indicus* might be similar to *Scomber australasicus*, Eschmeyer & Fricke (2010) doubting about the validity of Indian chub mackerel.

Species	Gas bladder	Swimming performances
<i>Scomber scombrus</i>	absent	3.5 b.l. s ⁻¹ (for a 33 cm specimen, at 11.7°C) (Wardle & He, 1988) accelerations to 18 b.l. s ⁻¹ (Wardle & He, 1988)
<i>Scomber japonicus</i>	present	1.16 b.l. s ⁻¹ (Castro Hernández & Santana Ortega, 2000) 1.2 to 2.2 fl.s ⁻¹ (Nauen & Lauder, 2002) accelerations to 8.35 b.l. s ⁻¹ (Sambalay, 1990)
<i>Scomber colias</i>	present	swimming performances unknown ^a
<i>Scomber australasicus</i>	present	0.3 b.l.s ⁻¹ with accelerations to 4.5 b.l.s ⁻¹ (1.4 m.s ⁻¹) Nauen & Lauder (2000), Heagney et al. (2007)
<i>Scomber indicus</i>	present	swimming performances unknown ^b

other species of the genus *Scomber* (McCune & Carlson, 2004; Trucco & Buratti, 2017).

The presence or absence of gas bladder in species of the genus *Scomber* has been here put in relation with swimming performances (Table 1). Then, even if methodologies can be different among these works, it is possible to observe that the Atlantic mackerel is able of the highest swimming abilities compared to all the other species of the genus *Scomber*, both in cruise swimming and accelerations. Unfortunately, no statistical analysis can be performed here at least with the low number of studied species and the different measuring methods used by previous authors.

Discussion

The different species reported in the genus *Scomber* form a clade (Collette et al., 2001; Miya et al., 2013). The Atlantic mackerel, *S. scombrus*, appears to be the fastest species of the *Scomber* clade (Table 1) and the only one to not possess a gas bladder. The absence of this organ can be then viewed as a loss linked to fast swimming, where such an organ would act as a buoy which would hamper the velocity of the animal. Several authors linked this high swimming speeds developed by the Atlantic mackerel to a way to avoid predation by marine mammals (Zardoya et al., 2004) or a way to collect fast swimming preys (B. Collette pers. com.). Karachle (2017) showed that Atlantic mackerel feed largely on fishes - particularly anchovies and sardines, which swim actively - while the co-occurring Atlantic Chub Mackerel feed largely on planktonic preys like fish larvae and crustaceans.

In terms of patterns, as this loss of the gas bladder is

unique to the Atlantic mackerel compared to its closest relatives (Collette et al., 2001), this can be viewed as an adaptation of this species to fast swimming. But, in terms of processes, it is impossible to determine whether this trait has been acquired or not by natural selection.

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