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Insight into biting diversity to capture benthic prey in damselfishes (Pomacentridae)



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ABSTRACT

The cerato-mandibular (c-md) ligament, joining the hyoid bar to the coronoid process of the angular, allows Pomacentridae to slam their mouth shut in a few milliseconds. Previous works have revealed that such a mechanism is used to feed, but some variability in biting patterns has been observed between two damselfish species. The pelagic feeder Amphiprion clarkii performs two different kinematic patterns to bite fixed prey, one that does not depend on the c-md ligament (biting-1) and one that does (biting-2). The benthic feeder Stegastes rectifraenum only performs biting-2. The present study aims to shed light on the occurrence of biting-2 in the feeding behaviour of Pomacentridae. To test our hypothesis that biting-2 would be the only biting pattern for benthic feeders, we compared biting behaviours among four species: one pelagic feeder, A. clarkii, and three benthic feeders, Neoglyphidodon nigroris, Stegastes leucostictus and S. rectifraenum. Our results showed that the four species were able to perform biting-2, but they do not support that the use of this pattern is related to trophic habits. Contrary to S. rectifraenum, the two other benthic feeders randomly used biting-1 and biting-2 patterns, similar to A. clarkii. Two hypotheses are discussed for explaining this variability within Pomacentridae. Finally, it has been recently shown that some damselfishes do not possess the c-md ligament. We therefore included two species lacking the cmd ligament (Chromis chromis and Abudefduf troschelii) in our study and we demonstrate our expectation that they are unable to perform biting-2.

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1. Introduction

A vast majority of ray-finned fishes use suction to capture elusive or loosely attached prey (Case et al., 2008; Ferry-Graham et al., 2001; Norton and Brainerd, 1993; Oufiero et al., 2012; Van Wassenbergh and De Rechter, 2011; Wainwright et al., 2007, 2001; Waltzek and Wainwright, 2003). Despite the diversity of fishes using this feeding mode, the movements leading to suction are highly conserved in teleosts (Lauder, 1985, 1982; Sanford and Wainwright, 2002; Westneat and Wainwright, 1989). Conversely, the less common biting mode used to dislodge firmly attached prey seems highly diversified. Some taxa, such as Labridae, rely on a strong suction force used in combination with biting (Ferry-Graham et al., 2002). Other taxa rely more on their biting performance and often have a morphological novelty facilitating such a biting mode. The Scarinae are characterised by their fused beak-like jaws used to scrape or excavate algae and/or live coral from substrata (Bellwood and Choat, 1990). The Pomacanthidae are

able to occlude their oral jaws while they are still protruded thanks to an intramandibular joint between the angular and the dentary of the lower jaw. This functional novelty allows angelfish to adopt their particular "grab-and-tear" feeding behaviour to feed on cryptobenthic resources (Konow and Bellwood, 2005). In Acanthuridae, Girellidae, Poeciliidae and some Scarinae, an intramandibular joint has the opposite function since it allows a gape expansion to scrape a larger surface of the substratum (Ferry et al., 2012; Konow et al., 2008; Purcell and Bellwood, 1993; Streelman et al., 2002; Vial and Ojeda, 1990).

Recently, a new biting mechanism has been highlighted in Pomacentridae (damselfishes) (Olivier et al., 2015, 2014; Parmentier et al., 2007). This mechanism relies on the ceratomandibular (c-md) ligament, joining the ceratohyal of the hyoid bar to the coronoid process of the angular of the lower jaw (Fig. 1). Manipulations of freshly euthanised fish and the use of high-speed video recording of live fish feeding with X-ray and visible light sources allowed us to determine how this mechanism works (Olivier et al., 2015, 2014; Parmentier et al., 2007). When the neurocranium and the hyoid apparatus are held at rest, the c-md ligament is loose and cannot transmit movement to the lower jaw (Fig. 2a). Pulling along the line of action of the epaxial muscles rotates the

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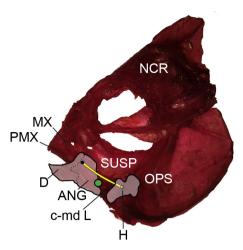
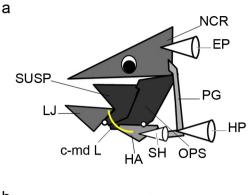
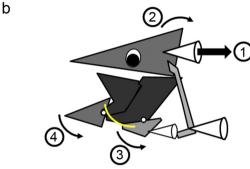


Fig. 1. Left lateral view of a *Neoglyphidodon nigroris* skull on a cleared and stained specimen. The left oral jaws, suspensorium, opercles, and hyoid bar have been removed allowing a view of the right part of the hyoid apparatus in the buccal cavity. The lower jaw and hyoid bar are highlighted. The green dot represents the quadrate articulation. The cerato-mandibular (c-md) ligament, highlighted in yellow, inserts on the inner (medial) part of the coronoid process of the angular and on the external (lateral) face of the ceratohyal of the hyoid bar. ANG: angular, c-md L: cerato-mandibular ligament, D: dentary, H: hyoid bar, MX: maxillary, NCR: neurocranium, PMX: premaxillary, OPS: opercular series, SUSP: suspensorium. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

neurocranium clockwise (left-facing lateral view). This rotation, via a four-bar linkage (see Muller et al., 1982 for details), causes the hyoid bar to rotate counterclockwise which induces mouth opening and gradually moves the insertion points of the c-md ligament away, until it is fully tightened (Fig. 2b). At this stage, additional elevation of the neurocranium and/or depression of the hyoid bar make(s) the taut ligament close the mouth by inducing rotation of the lower jaw around its quadrate articulation (Fig. 2c). High-speed video analyses revealed that the movements of the neurocranium and the hyoid apparatus are fast, which quickly tightens the ligament, ultimately allowing the fish to slam their mouth shut within 2–4 ms (Olivier et al., 2015, 2014; Parmentier et al., 2007).

It was first highlighted that the "mechanism involving the cerato-mandibular ligament" (hereafter, c-md mechanism) is used during acoustic communication in damselfishes, the sound being produced by an oral-teeth collision (College and Parmentier, 2012; Parmentier et al., 2007). It was later illustrated that the same mechanism is also used during feeding (Olivier et al., 2015, 2014). There are three main trophic guilds in damselfishes: (1) the pelagic feeders that feed mainly on planktonic copepods, (2) the benthic feeders that mainly graze filamentous algae and (3) an intermediate group including species that forage for their prey in the pelagic and the benthic environments in variable proportions (e.g. planktonic and benthic copepods, small vagile invertebrates and filamentous algae) (Frédérich et al., 2016, 2009). A study on a zooplanktivorous species, Amphiprion clarkii (Bennett, 1830), showed that the c-md mechanism is never used to capture elusive prey (Olivier et al., 2015). However, A. clarkii performs two different kinematic patterns to seize fixed prey items, which are called biting-1 (B1) and biting-2 (B2). Biting-1 does not look like the kinematic pattern for sound production and B1 is not dependent on the c-md ligament because the same kinematic pattern can be performed after its surgical transection; the fish uses the adductor mandibulae (AM) to close its mouth (Olivier et al., 2015). Conversely, B2 shows the same kinematic pattern as sound production and cannot be performed after the c-md ligament transection (Olivier et al., 2015). This study highlighted that the c-md mechanism is used in two different behaviours, i.e. to feed and to communicate. However, the





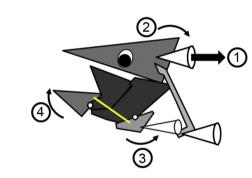


Fig. 2. Illustration of the cerato-mandibular ligament mechanism. As in Fig. 1, the left oral jaws, suspensorium, opercles, and hyoid bar have been removed to allow a view of right part of the hyoid apparatus in the buccal cavity. White cones indicate three muscles: the epaxial muscles (EP), hypaxial muscles (HP) and sternohyoideus muscle (SH). White circles indicate two articulations, one between the lower jaw and the suspensorium and another between the hyoid apparatus and the opercular series. c-md L: cerato-mandibular ligament, HA: hyoid apparatus, LJ: lower jaw, NCR: neurocranium, PG: pectoral girdle, OPS: opercular series, SUSP: suspensorium, In (a) no movement occurs and the c-md ligament is loose. In (b) a contraction on the epaxial muscle (1) induces a rotation of the neurocranium (2) provoking a rotation of the hyoid apparatus (3) which results in mouth opening (4) and in the tightening of the c- md ligament. In (c) additional contraction of the epaxial muscles (1) induces greater rotations of the neurocranium and hyoid apparatus (2 and 3) which results, as the c-md ligament is now fully tightened, in mouth closing (4). The same phenomenon of both mouth opening and closing can be obtained by pulling along the line of action of the sternohyoideus/hypaxial muscles but there is no neurocranium elevation in this case.

reasons for using two different biting patterns (*B1* and *B2*) to seize fixed prey remained unanswered. A different outcome has been observed in another damselfish, the grazer *Stegastes rectifraenum* (Gill, 1862) (Olivier et al., 2014). Instead of using two different patterns to seize fixed food items, this species only performs a *B2*-like kinematic pattern; a *B1*-like pattern being only performed after transection of the c-md ligament (Olivier et al., 2014). Such variability in the use of biting patterns between damselfish species is still unexplained. To better understand the diversity of biting in the feeding behaviours of Pomacentridae, we aim to test whether the use of one or two biting patterns could be related to trophic

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