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Cover image: *Macrophthalmus depressus* at Saco da Inhaca, Mozambique (© Jose Paula, 2014)

Sometimes hard to swallow: Attempted feeding on a porcupinefish results in death of both predator and prey

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Abstract

Predator-prey relationships are critical components of population dynamics across all ecosystems. Interactions between predators and dangerous prey are especially likely to result in a co-evolutionary arms race. To avoid predation, porcupinefishes (Diodontidae) present a suite of physical and chemical defences, including spines, inflation, and the potent neurotoxin, tetrodotoxin, which is concentrated in the internal organs. A failed predation attempt is described here on a longspined porcupinefish, *Diodon holocanthus*, by a benthopelagic predator, *Carangoides fulvoguttatus*, resulting in the death of both the predator and the prey.

Keywords: asymmetrical selection; co-evolution; coral reef; ecology; fishes; Indian Ocean; predation; Zanzibar

Predator-prey relationships are critical components of population dynamics and ubiquitous across all ecosystems (Gokhale and Wignall, 2019). They are often presented as an evolutionary arms race; selection pressures within these relationships are bi-directional and can be asymmetrical (Brodie and Brodie, 1999). For example, the *life-dinner principle* characterizes a race between predators and prey: if predators lose, they may be able to hunt again, but if the prey is caught and eaten, this removes it from the system and eliminates future reproductive potential. Therefore, the consequences are much more severe for the prey than for the predator (Dawkins and Krebs, 1979). Predator-prey relationships are also shaped by interactions between intra and inter-specific behavioural types (e.g. aggressive vs. docile; Chang *et al*., 2017). The type of predator-prey interaction that is most likely to result in a co-evolutionary arms race is in systems involving dangerous prey (Brodie and Brodie, 1999).

Porcupinefishes (Diodontidae) are circumtropical and inhabit a large variety of shallow water ecosystems (Nelson *et al*., 2016). They are slow swimmers that rely upon a suite of anti-predator adaptations: spines, pronounced inflation, and the potent neurotoxin tetrodotoxin, which is concentrated in the internal organs (Brainerd, 1994; Wainwright *et al*., 1995; Bane *et al*., 2014). This assemblage of defense mechanisms should effectively limit predation, however, a case is reported here where a benthopelagic fish attempted to prey upon an adult longspined porcupinefish (*Diodon holocanthus*), and died in the process. A yellow-spotted trevally, *Carangoides fulvoguttatus* (Carangidae, approximately 1 m TL) was retrieved, dead and floating at the surface off the east coast of Zanzibar, on 11 December 2018 (Fig. 1a). Upon close examination, a large longspined porcupinefish (approximately 30 cm TL) was found in the buccal cavity (Fig. 1b). The porcupinefish was barely alive, semi-inflated, with its spines lodged between the trevally's gill arches, and was thus unable to extricate itself from the mouth of its predator (Fig. 1c).

Considering the effectiveness of the suite of defensive strategies employed by porcupinefish, was this a naive predation attempt or a failed case of intentional consumption by an overly aggressive trevally? The literature reports a relatively high diversity of predators

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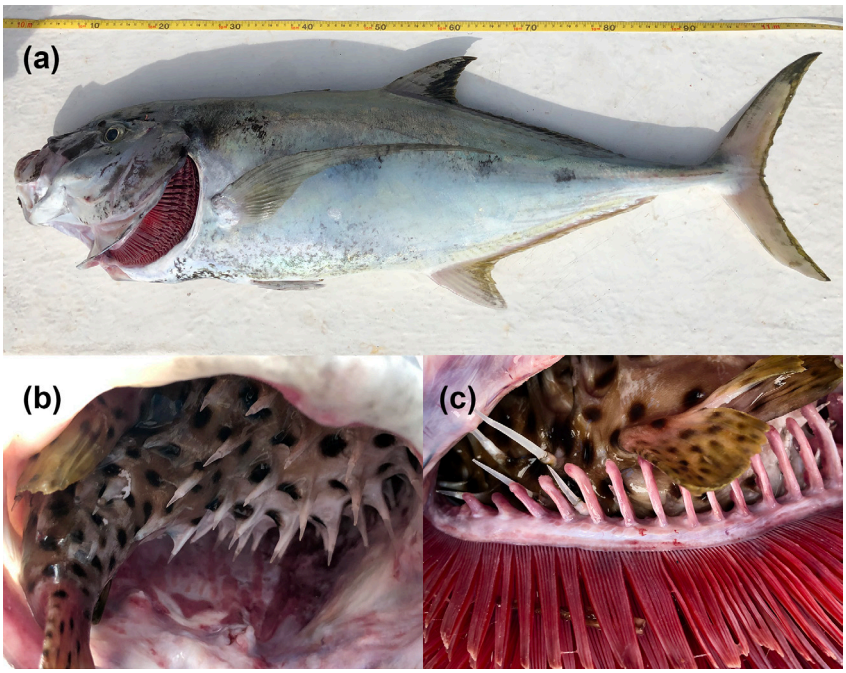

Figure 1. (a) Adult yellowspotted trevally, *Carangoides fulvoguttatus* (approx. 1 m TL), found dead, floating at the ocean surface off the east coast of Zanzibar. (b) *Diodon holocanthus* (approx. 30 cm TL) trapped in the buccal cavity, as viewed through the mouth of the trevally. (c) Detail of *Diodon holocanthus*, as viewed from beneath the operculum.

that feed upon juvenile porcupinefishes, including the pelagic and reef fishes *Coryphaena hippurus*, *Epinephelus itajara, Galeocerdo cuvier, Haemulon plumieri, Lutjanus analis, L. cyanopterus, L. griseus, L. synagris, Peprilus paru, Sphyraena barracuda* and *Tylosurus crocodilus* (Randall, 1967; Oxenford and Hunte, 1999). In May 2017, photographs circulated on the internet of a lemon shark, *Negaprion brevirostris*, dead on a beach in the Maldives, with a porcupinefish stuck in its mouth (Weisberger, 2017). Other marine animals also interact with porcupinefishes; there is a documented case of a bottlenose dolphin found dead with a slender-spined porcupinefish (*Diodon nichthemerus*) lodged in the posterior pharynx and upper esophagus (Byard *et al*., 2010), as well as reports of them being preyed upon by killer whales, *Orcinus orca*.

Porcupinefishes are slow swimmers that are regularly observed out in the open, including up in the water column, and are thus easy for predators to target. They depend upon physical (spines, inflation) and chemical (tetrodotoxin poison) defences to avoid this predation. Although selection pressure is usually stronger on the prey, predators that capture dangerous prey will experience a severe consequence with a high predictability, and therefore also face strong selection pressure (Brodie and Brodie, 1999). Predators will respond evolutionarily, and in the arms race model, can, in time, evolve mechanisms to overcome the physical defences of porcupinefishes and variable resistance to their internal toxins, as in other taxa (Geffeney *et al*., 2002). Therefore, this predation attempt could have been intentional, reinforced by the trevally's (hypothetical) prior experiences of successfully feeding on smaller porcupinefishes. The documentation of mortalities in individuals from other species that have attempted to prey upon porcupinefishes supports the assertion that this is not an uncommon event.

The longspined porcupinefish's spines, one of its primary defense mechanisms, locked the fish inside the predator and prevented it from escaping. Is this a case where an anti-predator adaptation has gone too far? Spines evolved as a defence mechanism (Shono *et al*., 2018), ostensibly to prevent the fish from being taken into the mouth of a predator. However, spines are not necessarily a guarantee of protection (Willman, 2007). In the case of the porcupinefishes, if the fish is swallowed head first, it will easily slide into the predator's mouth, due to the orientation of the spines and their biomechanical erection mechanism (Brainerd, 1994). Nevertheless, selection pressure might be stronger for the prey here as well. Following Brodie and Brodie (1999), the two main factors that shape the asymmetrical selection between prey and predators are the consequence of individual interactions and predictability of the consequence. Porcupinefishes are very

characteristic in their shape and behavior, so the predictability of the consequence to the predator is therefore high. Differences at the individual level, including predator aggressiveness, and individual variability in prey behaviour, interact to impact predator foraging performance (Chang *et al*., 2017). More aggressive predators perform better when facing unpredictable prey behaviours, while more docile predators perform better with more predictable prey (Chang *et al*., 2017). Previous successful consumption, or an overly aggressive behaviour might have encouraged the trevally's attempt, resulting in a serious and unpredicted consequence. In this case, despite an asymmetrical selection pressure, the result was the same for both predator and prey - neither survived the interaction.

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