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Reef fishes stalking box crabs in the southern Caribbean

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Feeding interactions between fish species and crustaceans are not rare, such as the relations between cleaner shrimps and reef fishes (Horká et al. 2018) and between parasitic isopods and their fish hosts (Baeza 2015). In most of these cases, the fish plays the main role as host and the crustacean a secondary role as associated species (Karplus 2014). This report presents an example of the opposite.

Members of the Calappidae, also known as "shamefaced crabs" or "box crabs", mainly prey on marine mollusks, which they crack open by use of their specialized right claw (Ng and Tan 1984, Ng and Tan 1985, Hughes and Elner 1989). This family is represented by nine genera and approximately 80 species (Ng et al. 2008). These species can be found in tropical and temperate waters, where they inhabit coral rubble, sea-grass beds and various kinds of sandy substrates in shallow and deep water (Bellwood 1998). Calappids have the ability to hide from predators by digging themselves in the sand. When the threat is diminished, they exhume themselves and walk away. This process results in the displacement of sand and therefore calappid crabs are believed to play an important role in the bioturbation of sandy substrates in coral reef areas (Thomassin 1974).

While snorkeling at the Canary Islands (eastern Atlantic), Den Hartog (1987) noticed a facultative association between the calappid Cryptosoma cristatum Brullé, 1937 and three fish species: the flounder Bothus podas (Delaroche, 1809), and the weevers Trachinus draco L., 1758 and T. cf. araneus Cuvier, 1829. The fish followed the crabs at close distance and made "snapping movements", presumably feeding on small prey that became dislodged by the walking crab. The trailing flounders and weevers dug themselves in whenever the crab ceased to move. If the crab remained stationary, the weevers left the crab. When a new crab showed up, some fish changed partners. Den Hartog (1987) illustrated the crab and the fish species as separate collected specimens but did not illustrate their feeding interactions in situ. The only published illustration of fish stalking concerns a blenny, Labrisomus nuchipinnis (Quoy & Gaimard, 1824), following a hermit crab, Paguristes sp., at Brazil (Sampaio et al. 2008).

During field studies on the dietary habits of three calappid species on shallow reef flats (<5 m deep) at the leeward sides of Curaçao and Bonaire (southern Caribbean) we photographed and filmed fish-crab interactions that appeared to be similar to those reported from the other side of the Atlantic by Den Hartog (1987). However, the crab and fish species were different. As identification references we used the works by Holthuis (1958) and Humann et al. (2013) for the box crabs and a field guide by Robertson and Van Tassell (2019) for the fishes.

Box crabs of the species Calappa ocellata Holthuis, 1958 and Cryptosoma balguerii (Desbonne, 1867) were followed by fish belonging to four common species: the channel flounder (Syacium micrurum Ranzani, 1842), the maculated flounder (Bothus maculiferus (Poey, 1860) (Fig. 1), the pearly razorfish Xyrichtys novacula (Linneaus, 1758), the slippery dick wrasse Halichoeres bivitattus (Bloch, 1791). This behavior was observed in Caracas Bay (12°04'33.2" N 68°51'47.3" W) and Piscadera Bay (12°07'20.3" N 68°58'09.0" W) in Curaçao, and at two dive sites near Playa (12°09'02.5 "N 68°16'39.6" W) and Sorobon (12°05'43.2" N 68°14'14.9" W) in Bonaire. In total, more than 50% of all observed crabs (about 20 individuals) were followed by fish. Video footage of two species of fish (maculated flounder and slippery dick wrasse), both chasing a different Calappa ocellata at Bonaire, is available as Video S1 and Video S2.

There are no indications of fish trying to steal food away from the crabs (Video S1 and Video S2). By plowing through the sandy substrate, the calappids appeared to dislodge and expose small prey, which were eaten by



FIG. 1. A Calappa ocellata with a maculated flounder in the background at Bonaire (photographer credit: A. Ozten Low).

the trailing fish. The flounders used a passive approach of stalking by digging themselves in when the crab was dug in as well, until the crab moved again (Fig. 1, Video S1). The flounders followed the crabs at an approximate distance of 20 to 30 cm, but dug themselves in as close as 1 cm away from the crab. The razorfishes used a more active stalking approach by swimming around the crab, following at distances of 5 to 15 cm, but coming as close as touching the crab as they circled around (Video S2). In addition, when the calappids stopped walking, the razorfishes made snapping movements at the crabs until the crabs started walking again. This disturbance might be disadvantageous for the crabs, leaving them vulnerable to attacks by predators. The Caribbean flounders and razorfish operated alone or in groups of up to three individuals. They did not chase away conspecific individuals unlike the weevers in the East Atlantic, which only tolerated the presence of flounders but not of other weevers (Den Hartog 1987).

It is remarkable that crab-stalking fish are only known from shallow coastal waters in the West and East Atlantic. Since Indo-Pacific relatives of the calappids (Bellwood 1998) and their fish partners (e.g. Allen et al. 2015) occur in similar habitats, this kind of relation is expected to be geographically more widespread than presently known. The fossil record suggests that the Calappidae originated in the deep-sea of the Oligocene, while a reconstruction of the family's phylogeny indicates that only three out of eight evolutionary lineages contain extant shallow-water species (Bellwood 1998). Observations on more box crab species, in particular from the Indo-Pacific, but also from deeper-water ecosystems are needed to find out if stalking in fish-crab associations is taxonomically more widespread (involving other crabs and fishes) and not limited to shallow waters of the Atlantic. It would be interesting to examine the implications of this behavior for soft-bottom environments and their communities in shallow and deep waters around the world. Follow-up questions could relate to the dependency of the fish species on the crab's behaviour for food intake, and to the disadvantage these interactions for the crabs. In order to observe and quantify the behavior of the fish and the crab, we suggest future experimental research in which one crab and one or more fishes are confined to fenced areas (e.g. of 2×2 m²) that allow the animals to move freely in sight of observers. Such enclosures should ideally be placed in shallow water (ca. 2 m deep) near a research station.

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