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The Diet of *Diodon hystrix* (Teleostei: Tetraodontiformes): Shell-crushing on Guam's Reefs

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Abstract. The spiny puffer *Diodon hystrix* is one of the most powerful shell-crushing predators on tropical coral reefs. We counted, measured, and identified molluscan and hermit crab prey remains in the digestive tracts of twelve spiny puffers collected on Guam between 1975 and 1981. Individual fish contained up to 142 prey belonging to a total of 27 gastropod and 8 hermit-crab species. Recovered shell fragments ranged up to 31.5 mm in length and up to 3.5 mm in wall thickness. *D. hystrix* is a voracious consumer of well-armored shell-bearing reef animals.

Introduction

The spiny puffer or porcupinefish *Diodon hystrix* (Linnaeus, 1758) (Diodontidae) stands out as one of the most powerful shell-crushing predators of molluscs on the world's tropical coasts (Vermeij 1978, Palmer 1979, Bertness *et al*. 1981). At a purported maximum length of 90 cm, *D. hystrix* is the largest member of the Diodontidae and, like its smaller congener *D. holocanthus* (Linnaeus, 1758), is found throughout the tropics except in West Africa (Leis 1974). In common with most other Diodontidae and Tetraodontidae, *D. hystrix* crushes its prey between upper and lower plates (each composed of fused teeth) in a vise-like jaw (Fig. 1) (Tyler 1980, Ralston & Wainwright 1997, Wainwright & Bellwood 2002, Korff & Wainwright 2004). Along with the digestible parts, skeletal fragments are ingested, whose diagnostic features make species-level identification possible.

Few of the hundreds of studies of diets of reef fishes report species identifications of prey consumed in the wild. Ingested molluscan prey have been documented at the species level for the bonefish *Albula vulpes* (Linnaeus, 1758) in Puerto Rico (Warmke & Erdman 1963), the labrid wrasses *Lachnolaimus maximus* (Walbaum, 1792) in the Caribbean (Randall & Warmke 1967, Wainwright 1987) and *Cheilinus undulatus* (Ruppel, 1835) in the Indo-West Pacific (Randall *et al*. 1978), tetraodontid puffers of the genus *Sphoeroides* in Florida and the Pacific coast of Costa Rica (Targett 1978, Duncan & Szelistowski 1998), and numerous species including *D. hystrix* in the West Indies (Randall 1964, 1964, 1967). The only records of prey molluscs identified to species in *D. hystrix* from the Indo-West Pacific are those of Rehder & Randall (1975) at Ducie Atoll in southeast Polynesia.

Here we report the diet composition of *Diodon hystrix* in Guam. We dedicate this paper to the memory of Lucius G. Eldredge, who first introduced one of us (GJV) to the importance of shell-breaking predation of molluscs in 1970. Lu was not only a most generous host, along with his wife Jo and four daughters, but also freely shared his laboratory and extraordinary library of reprints during seven productive stays at the University of Guam Marine Laboratory from 1968 to 1984. Further personal details of our friendship with Lu and his family, and the influence Lu had on GJV's scientific development, are given in Vermeij (1997, 2010).

Materials and Methods

During extensive research on shell-breaking predation on molluscs in the field and laboratory in Guam in 1974, 1975, 1979, and 1981, we obtained 12 specimens of *Diodon hystrix*. These were caught from early morning to early afternoon on both the windward and leeward sides of the island by students and staff at the University of Guam Marine Laboratory in Mangilao. One of the 12 specimens was caught by an unidentified fisherman who participated in a spearfishing contest held at

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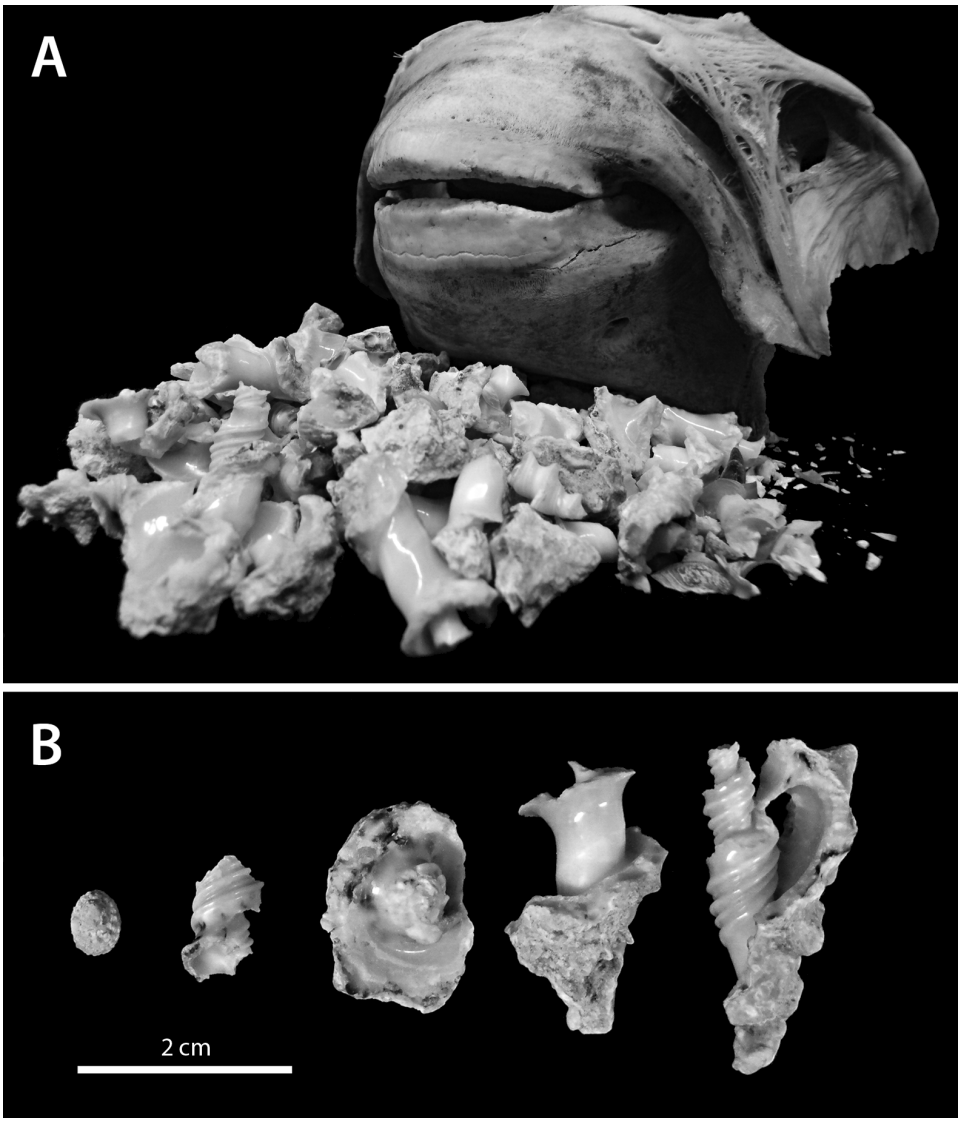

Fig. 1. A. Upper and lower jaw of a 47 cm long *Diodon hystrix*, together with the skeletal fragments in its digestive tract. **B**. Close-ups of five fragments, including a whole individual of the limpet-like *Sabia conica* (left) and a fragment of the columella of *Vasum turbinellus* (right); in between are fragments of *Drupa* spp.

Umatac on 5 and 6 August 1975. This specimen was examined with his permission and with prior agreement with the village commissioner of Umatac. Several other molluscivorous fish species were also examined for gut contents at Umatac.

We recorded the standard length (cm) and, where possible, the gape (mm) of the jaws for each specimen. All skeletal fragments in the digestive tract of each fish were recovered, counted, and identified when possible; and some of the larger fragments were measured. The number of prey per fish was estimated first by counting gastropod shell apices, opercula, and undamaged shells. The minimum number of hermit crab individuals was estimated by counting pairs of chelae. Apices with a glossy inner surface were considered to belong to prey gastropods that were alive when ingested.

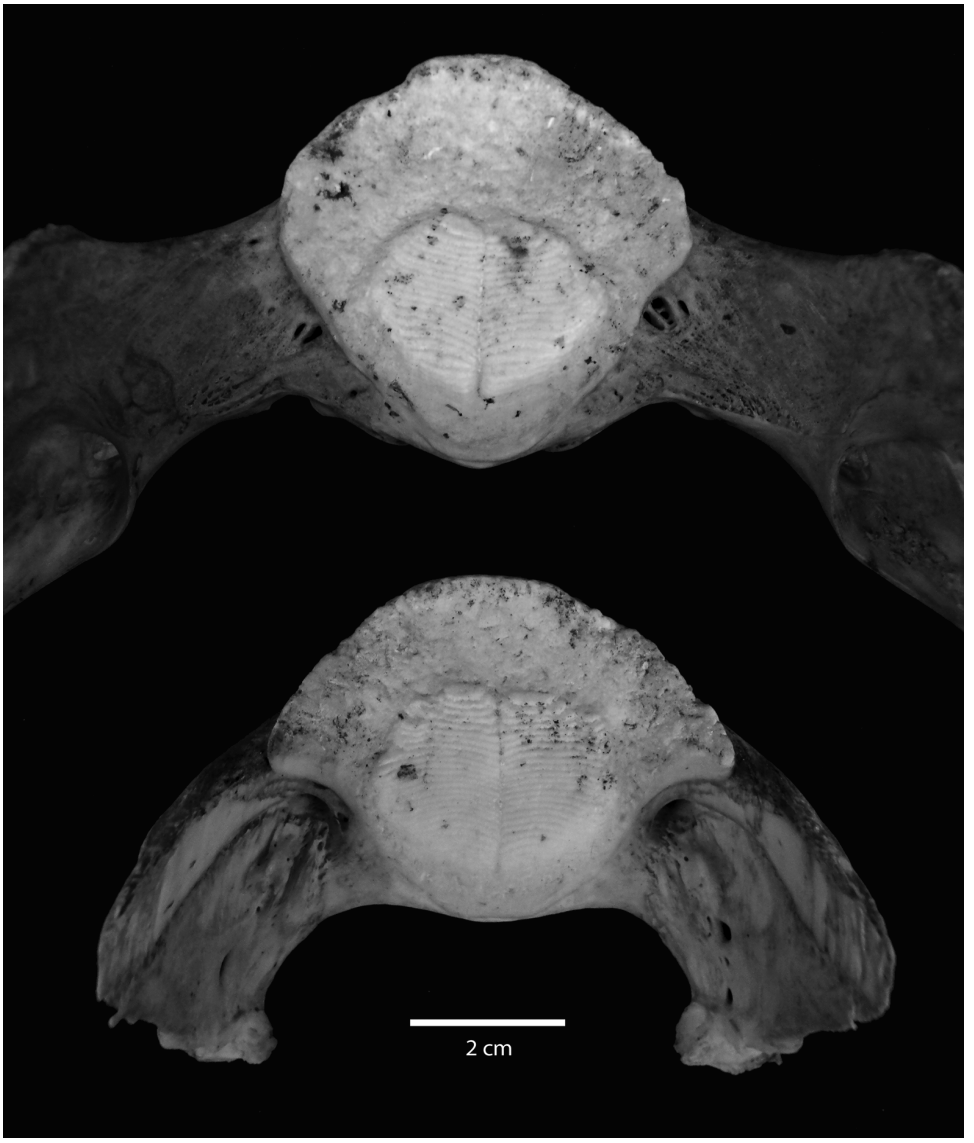

Fig. 2. Close-up of the crushing surfaces of the jaws of a 47 cm *Diodon hystrix*.

Where opercula were available, their number indicated the minimum number of living gastropod taken by the fish. The total number of ingested prey included items that could not be identified to species.

Results

The 12 puffer specimens we examined ranged in length from 23 cm (close to the lower limit of size at which individuals begin to feed in the benthos; see Leis 1974) to 56 cm (Table 1). The gape at the front of the mouth ranged from 15 mm in a 27 cm long specimen to 32 mm in a 47 cm puffer (Table 1).

Of the digestive tracts we examined, 11 (92%) contained skeletal remains of prey. All ingested fragments consisted of either gastropods or hermit crabs. Estimated numbers of prey per fish, includ-

Table 1. Length (cm), gape (mm), and number of prey ingested in individual *Diodon hystrix*.

Length	gape	prey
23	-	16
25.5	-	95
25.5	-	142
27	19	19
27	15	0
34	25	6
34.5	-	134
37	-	38
45	-	33
46	23	52
47	32	14
56	-	49

ing unidentified prey individuals, ranged from 0 to 142 (Table 1), with a mean and standard deviation of 50 +/- 48.5. All fish were caught during daylight hours, indicating that *Diodon hystrix* is a voracious shell-crushing predator, which likely feeds at night or near dawn (see also Hobson 1974).

We identified 27 species of living gastropod and 8 species of hermit crab in the digestive tracts of *D. hystrix* (Table 2). All prey species are common inhabitants of reef flats and the reef margin. No bivalves, barnacles, or sea urchins were found in any of the gut contents. Given that the remains of these other groups are common in the digestive tracts of other shell-crushing fishes, it is likely that *D. hystrix* in Guam is specialized to feed on shell-bearing gastropods and hermit crabs.

Nearly all skeletal material in the digestive tracts was highly fragmented, consisting of shell apices and columellas (Fig. 1). Among these fragments, outer lips of gastropod shells were never recovered and were likely spit out before ingestion. The only intact shells found were a few very small naticids, three individuals of the small cerithiid *Semivertagus nesioticus*, and the limpet-like hipponicid *Sabia conica* (Fig. 1). The last-named species excavates a pit on the exterior of host gastropods (Vermeij 1998) and was ingested together with host specimens of the genera *Drupa* and *Vasum*.

Two of the larger puffers ingested and crushed impressively large and thick-shelled prey. The 56 cm puffer contained 5 apices of *Virgiconus flavidus*, one of which was associated with a fragment 29.9 mm long and 1.8 mm thick at a broken edge. This same individual ingested 32 individuals of *Drupa* spp. (represented by opercula) including *D. morum*; one of the fragments was 25 mm in length and 2.1 mm thick. It also contained two individuals of *Menathais intermedia*, one of which had a diameter of 21.4 mm and a thickness of 2.6 mm at a broken edge. A 46 cm puffer ingested 27 *Drupa* individuals as represented by opercula, of which at least 15 belong to *D. rubusidaeus* (Fig. 2). Some fragments of *D. rubusidaeus* were 25.5 mm long and 3.5 mm thick. Of the 8 *Vasum turbinellus* individuals (as represented by opercula) ingested by this puffer, one fragment was a 31.4 mm long segment of the columella.

Discussion

Our data show that the puffer *Diodon hystrix* is a highly specialized shell-crushing predator on gastropods and hermit crabs. Within this category, however, the fish feeds on a wide variety of species, and shows little discrimination with respect to either shell architecture or occupancy by a living snail or a hermit crab. Other diodontid or tetraodontid puffers whose diets have been studied are smaller and have more generalized feeding habits. For example, we found molluscs, hermit crabs, and sea urchins (*Echinometra* sp.) spines in the digestive tracts of two specimens of *Diodon holocanthus*

Table 2. Prey species in the digestive tracts of *Diodon hystrix* in Guam.

Taxon	N_f	N_{pmax}
Hermit crabs		
Aniculus aniculus (Frabricius, 1787)	1	1
Aniculus sp.	1	1
Calcinus elegans H. Milne Edwards, 1836	1	1
C. laevimanus Randall, 1840	1	1
C. latens Randall, 1840	5	120
C. morgani Rahayu and Forest, 1999	5	8
Ciliopagurus strigatus (Herbst, 1804)	2	1
Clibanarius humilis (Dana, 1851)	1	18
Gastropods		
Turbinidae		
Astralium rhodostoma (Lamarck, 1822) s.l.	1	3
Neritidae		
"Puperita" bensoni (Récluz, 1850)	2	1
Theliostyla albicilla (Linnaeus, 1758)	2	1
Cerithiidae		
Cerithium columna Sowerby, 1855	3	16
"C." punctatum Bruguiére, 1792	1	30
Clypeomorus nympha Houbrick, 1985	1	17
Semivertagus nesioticus (Pilsbry and Vanatta, 1906)	1	3
Strombidae		
Canarium mutabile Swainson, 1821	2	16
Gibberulus gibbosus (Röding, 1798)	2	12
Hipponicidae		
Sabia conica (Schumacher, 1817)	2	6
Naticidae		
Notocochlis gualteriana (Récluz, 1844)	3	4
Tectonatica bougei (Sowerby, 1908)	1	1
Cypraeidae		
Mauritia maculifera (Schilder, 1832)	1	3
Ranellidae		
Monoplex nicobaricus (Gmelin, 1791)	1	1
Muricidae		
Drupa morum Röding, 1798	3	24
D. ricinus (Linnaeus, 1758)	2	1
D. rubusidaeus Röding, 1798	1	27
Drupina grossularia (Röding, 1798)	1	1
Ergalatax fiscella (Gmelin, 1791)	1	1
Menathais intermedia (Kiener, 1835)	1	2
Nassa serta (Bruguiére, 1789)	1	1
Tenguella granulata (Duclos, 1832)	1	1
Buccinidae		
Pollia fumosa (Dillwyn, 1817)	1	1
P. undosa (Linnaeus, 1758)	1	1
Vasidae		
Vasum turbinellus (Linnaeus, 1758)	5	8
Costellariidae		
Costellaria semifasciata (Lamarck, 1811)	1	1
Conidae		
Rhizoconus rattus (Hwass in Bruguiére, 1792)	2	2
Virgiconus flavidus (Lamarck, 1810)	2	5

N_f Number of fish containing the species

N_{pmax} Maximum number of prey in one fish

from New Guinea (pers. observ.); and studies of American *Sphoeroides* spp. show these puffers to consume a wide range of invertebrate prey (Targett 1978, Ralston & Wainwright 1997, Duncan & Szelistowski 1998, Korff & Wainwright 2004).

Many other species of reef fish consume gastropods, bivalves, and hermit crabs by crushing these prey either in the oral jaws or with the pharyngeal bones. In Guam, perhaps the most powerful of these is the wrasse *Coris aygula* Linnaeus, 1758 which, at a maximum length of 36 cm, consumes relatively small prey including young individuals of *Astralium rhodostoma*, *Trochus ochroleucus* Gmelin, 1791, small conids, and the hermit crabs *Calcinus guamensis* Wooster, 1984, *C. lineopropodus* Morgan & Forest, 1991, *C. minutus* Buitendijk, 1937, *C. morgani*, *C. pulcher* Forest, 1958, and *Ciliopagurus strigatus* (pers. observ. on 4 individuals from Guam ranging in length from 23.5 to 36 cm). Neither this wrasse nor any other mollusk-eating fish in Guam matches the size and power of *Diodon hystrix*.

Together with reef-dwelling carpiid and parthenopid crabs (see Zipser & Vermeij 1978), *Diodon hystrix* is able to crush exceptionally strong shells. Specimens of *Drupa morum* comparable in size to those crushed by *Diodon hystrix* were estimated to break under a load of up to 5000 N (Vermeij & Currey 1980). Experiments with relatively small (29 cm) individuals of *Diodon hystrix* in Panama indicated that the presence of large knobs on the shell surface increased the effective size of prey and prevented the puffers from successfully crushing gastropods near the upper limit of size that could fit in the puffer's jaws (Palmer 1979). We have seen specimens of *Drupa morum, D. ricinus*, and *Vasum turbinellus* in the field in Guam with broken knobs or spines, potentially indicating the role of these protrusions in defense against shell-crushers like *Diodon*. As a relatively common and voracious predator, *Diodon hystrix* is likely to be an important selective agent for reef-dwelling shell-bearing animals.

In the modern fauna, *Diodon hystrix* has a nearly circumtropical distribution, in part owing to an exceptionally long pelagic phase (Leis 1974). It would be interesting to know where this most powerful diodontid evolved. The genus *Diodon* is known from the Early Eocene onward in Europe and the Indo-West Pacific (Bellwood 1996, Tiwari & Ralte 2012) and from the Middle Eocene to the present in Florida in the western Atlantic (Hulbert 2001), but the sparse fossil record of this genus has not yet revealed where and when *D. hystrix* arose.

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