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Deep-sea in situ observations of gonatid squid and their prey reveal high occurrence of cannibalism

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ABSTRACT

In situ observations are rarely applied in food web studies of deep-sea organisms. Using deep-sea observations obtained by remotely operated vehicles in the Monterey Submarine Canyon, we examined the prey choices of more than 100 individual squids of the genus *Gonatus*. Off the California coast, these squids are abundant, semelparous (one reproductive cycle) oceanic predators but their diet has remained virtually unknown. *Gonatus onyx* and *Gonatus berryi* were observed to feed on mesopelagic fishes (in particular the myctophid *Stenobrachius leucopsarus*) as often as on squids but inter-specific differences in feeding were apparent. Gonatids were the most common squid prey and while cannibalism occurred in both species it was particularly high in *Gonatus onyx* (42% of all prey items). Typically, the size of prey was similar to the size of the predator but the squids were also seen to take much larger prey. Post-juvenile gonatids are opportunistic predators that consume nektonic members of the meso-and bathypelagic communities, including their own species. Such voracious feeding is likely necessary to support the high energetic demands associated with the single reproductive event; and for females the long brooding period during which they must depend on stored resources.

1. Introduction

Squids are pelagic cephalopod molluscs that are particularly abundant and diverse in the open ocean and deep sea (Hoving et al., 2014). In the North Pacific the Gonatidae dominate, and their biomass may regionally exceed that of commercially exploited fish (Radchenko, 1992). The most abundant gonatids in the California Current region are members of the genus *Gonatus*, in particular *G. onyx* (Young, 1972). Vertical distribution profiles for *G. onyx* show a bimodal pattern (Roper and Young, 1975; Hunt, 1996; Hunt and Seibel, 2000), with younger individuals (ML $<$30–35 mm) closer to the surface and sexually mature adults occurring deeper. This species has one of the highest metabolic rates among cephalopods (Seibel et al., 1997). Female gonatids invest a great portion of their energy into their single reproductive event, and after spawning all their eggs at once, the eggs are brooded in the middle of the water column, at bathypelagic depths, for approximately 9 months (Seibel et al., 2000; Seibel et al., 2005; Laptikhovsky et al., 2007). During brooding, feeding is arrested and energy is mobilized from lipids stored in the digestive gland (Arkhipkin and Bjørke, 1999). Spent females attain a mantle length of 132–145 mm (Seibel et al., 2000). Very little has been reported about the diets of *G. onyx* and its sympatric congener *G. berryi*.

Gonatid squids comprise an essential trophic link between top predators in the California Current's pelagic ecosystem, and consumers at the primary and secondary levels (Brodeur et al., 1999). Knowledge of gonatid diets and feeding behavior is thus important for understanding food web structure and nutrient energy flow within this highly productive offshore system. The last two decades have seen significant changes within the system, with the appearance of invasive predators (Zeidberg and Robison, 2007; Stewart et al., 2014) and a decline in populations of secondary consumers (Koslow et al., 2011).

Most diet studies of squid rely on specimens obtained via nets and jigging. While these methods certainly have advantages, such as the collection of a large sample size, they may induce unnatural feeding behaviors. Net feeding has been experimentally proven for mesopelagic fishes (Lancraft and Robison, 1980) and since many squids are voracious feeders, it is likely that squid, too, feed unnaturally once they are captured in a net (Markaida and Sosa-Nishizaki, 2003; Ibañez et al., 2008). Jigging for squid may result in excitement and stress in the fished population, which may also induce unnatural feeding, including cannibalism. Underwater observations show that in jigged populations, cannibalism occurs regularly, both on free-swimming individuals as well as on jig-caught squid (Markaida and Sosa-Nishizaki, 2003). Finally, certain behaviors of squid, such as the discard of fish heads after feeding

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(and with that the otoliths, which are typically used for prey identification), may influence the results obtained from visual examination of stomach contents (Markaida et al., 2008).

In situ observations using SCUBA have been used to study natural feeding in coastal octopod species (Mather, 1991; Hanlon and Messenger, 1996) but this method is not feasible for most animals that live in the open ocean, in particular not in the deep pelagic zone. The application of remotely operated vehicles in ocean science has made the pelagic zone more accessible to research, opening new areas of investigation (Robison, 2000), and resulting in novel insights into the behavior of pelagic animals, including the feeding behavior of gelatinous organisms (Robison et al., 1998) and cephalopods (Hoving and Robison, 2012; Hoving et al., 2013). Using real-time and recorded ROV observations of the midwater communities in the Monterey Submarine Canyon, we studied the prey choice and feeding behavior of gonatid squids.

2. Material and methods

For this study we used data from annotated video observations obtained between 1995 and 2015 by the MBARI ROV program in the Monterey Canyon. Observations were collected by ROVs *Tiburon*, *Ventana* and *Doc Ricketts*, principally at the time series station, Midwater 1 (waypoint 36.7°N–122°E) at depths from 160 to 2056 m (average 741 ± 293 m) using standard ROV observational techniques (Bush et al., 2009; Burford et al., 2015). We performed queries in MBARI's Video Annotation and Reference System database (Schlining and Jacobsen Stout, 2006; Bush et al., 2009; Burford et al., 2015). The video tapes from which predator/prey pairing had been annotated, were viewed again and re-analyzed. While some data were collected when the vehicles were transiting with relatively high forward or vertical speed and thus no detailed footage was obtained, in most cases the ROV hovered a few meters away from the feeding squid and close-up video was recorded with a telephoto lens. The recorded specimens were categorized as either predator or prey, depending on who was ingesting whom, and both were identified to the lowest possible taxonomic level. The squids were distinguished using characteristics described on the Tree of Life webpage (www.tol.org), in particular the presence of large tentacular hooks in *Gonatus berryi*. When possible, we oriented the ROV to provide an orthogonal perspective, and we measured the mantle length of the predator as well as the mantle length or total fish length of the prey. Since there was no reference scale in the video image, the relative sizes of the predator and prey were measured in pixels using an image analysis tool (GIMP 2). We collected 6 squid pairs with the ROV, which allowed measurement of the absolute mantle length as well as confirmation of the identification of the observed specimens (Table 1). In November 2014 we collected 17 gonatid squids to determine the relative abundance of each species of *Gonatus* encountered by ROV, and for validation of ROV video identifications. All of these specimens were *Gonatus onyx*.

Table 1
Direct measurements of the size of ROV-collected pairs of *Gonatus* species.

ROV sample	Predator species	Predator size (mm)	Prey species	Prey size (mm)
D695-SS8	*Gonatus berryi*	96	*Gonatus onyx*	70
D695-SS3	*Gonatus onyx*	81	*Gonatus onyx*	69
D214-D6	*Gonatus onyx*	80	*Gonatus onyx*	75
D218-	*Gonatus berryi*	201	*Gonatus berryi*	210
V3611-SS2	*Gonatus berryi*	150	*Gonatus onyx*	100
V3699	*Gonatus onyx*	58	*Gonatus onyx*	58

3. Results

Of the 109 predator/prey pairs that we encountered: in 36 cases *G. onyx* was the predator, in 17 cases the predator was *G. berryi*, and on 56 occasions the species of the gonatid predator could not be determined from the video footage. *Gonatus onyx* and *G. berryi* both consumed fish and squid in roughly equal proportions (Fig. 1). All prey were held head-first in the arm crown of the squid predator (Fig. 2).

Fifteen of 36 *G. onyx* had captured other *G. onyx* as prey and 9 had seized the common myctophid fish *Stenobrachius leucopsarus* (Figs. 1 and 2; Table 2). Ten of 17 *G. berryi* had captured fish, including 5 *S. leucopsarus*, while 2 were holding other *G. berryi* and 3 had caught *G. onyx* (Figs. 1 and 2; Table 2). Gonatids that could not be identified to species were seen to be feeding chiefly on fish and squid, and on a few occasions crustaceans had been taken by small individuals. In about one quarter of the

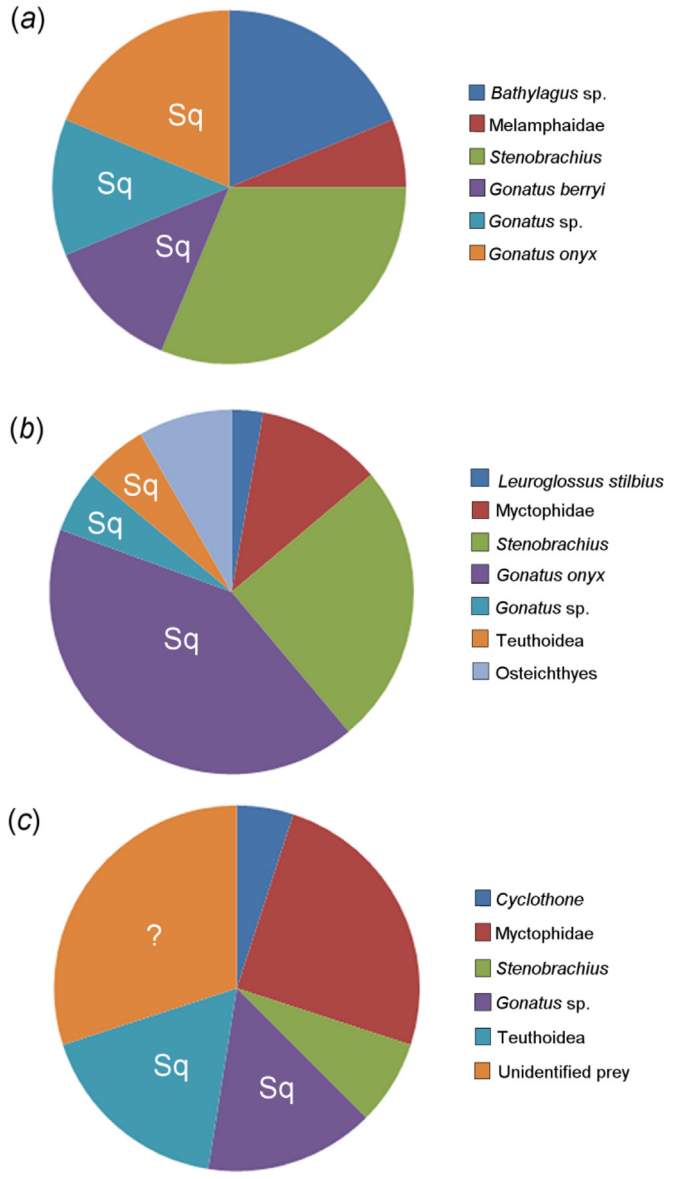

Fig. 1. The relative contribution of prey types to the predator-prey associations of *Gonatus* spp. observed by ROV in the Monterey Submarine Canyon (*a*) *Gonatus berryi* ($n=17$), (*b*) *Gonatus onyx* ($n=36$) and (*c*) *Gonatus* sp. ($n=56$). The squid diet components are indicated by (Sq) and unknown prey by (?). All other unlabeled diet components are fish prey.