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Diet, prey selection and cannibalism in the hunter opisthobranch *Roboastra europaea*

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The diet and predatory behaviour of the nudibranch *Roboastra europaea* (Mollusca) is described and compared with other nudibranch-hunting opisthobranchs. The natural diet in the Strait of Gibraltar was studied by the analysis of gut contents. *Roboastra europaea* is a specialist predator of nudibranchs, and the diet is comprised essentially of the polycerids *Polycera* sp., *Polycerella emertoni*, *Limacia clavigera* and conspecific *R. europaea*. One or several *Polycera* species appeared as the most dominant prey.

The complete assemblage of potential prey of this predator—the fundamental diet—was assessed in laboratory trials that included all likely prey groups. This predator consistently rejected both non-nudibranch species and non-polycerid nudibranchs. *Roboastra europaea* is exclusively a predator of polycerids and previously unencountered polycerids are also potential prey items.

As most of the hunter opisthobranchs, *R. europaea* exhibited cannibalistic behaviour, to the extent that aggressiveness prevailed over mating in intraspecific encounters. *Roboastra europaea* as prey showed a complex result in laboratory trials: (a) if one individual was small enough complete ingestion proceeded; (b) if there was not enough difference in size, a cannibal attack proceeded, but if ingestion was not possible, it could result in mating behaviour.

INTRODUCTION

Nudibranch molluscs are considered among the most specialized elements of benthic marine trophic systems, both as predators and as prey. As predators, nudibranchs are a group of highly specialized carnivores (Clark, 1975; Todd, 1981, 1983; Rudman & Willan, 1998). However, although good qualitative knowledge of their predator–prey relationships exists, quantitative data are very scarce. As prey, nudibranchs generally have such effective defence mechanisms that specific predators are not known for most species (Todd, 1981; Harris, 1987; Rudman & Willan, 1998).

Among the few predators of nudibranchs known are other opisthobranchs, such as cephalaspideans of the genus *Navanax* Pilsbry, 1895 (Paine, 1965), notaspideans of the genus *Pleurobranchaea* Meckel in Leue, 1813 (Cattaneo-Vietti et al., 1993; Battle & Nybakken, 1998), some eolid nudibranchs (Cooper, 1978; Harris, 1987, among others) and phanerobranch nudibranchs of the genus *Gymnodoris* Stimpson, 1855 (Jonhson & Boucher, 1983; Rudman & Darvell, 1990; Rudman, 1998) and *Roboastra* Bergh, 1877 (Farmer, 1978; Carté & Faulkner, 1986). Furthermore, most of these hunters of nudibranchs are also cannibalistic (Paine, 1965; Rutowski, 1983; Rudman & Darvell, 1990; Tsubokawa & Okutani, 1991; Cattaneo-Vietti et al., 1993; Debelius, 1997; Battle & Nybakken, 1998) so there is a conflict between predatory opportunities and mating opportunities which require cross-fertilization.

This study deals with the single representative of genus *Roboastra* in Europe, *R. europaea* García-Gómez, 1985. This is the biggest European polycerid and, until now, the only biological information published is the description of the animal itself and the egg mass (García-Gómez, 1985). Data on the feeding of *Roboastra* spp. are mainly confined to the Pacific species *R. tigris* Farmer, 1978 (Farmer, 1978; Carté & Faulkner, 1983, 1986; Kerstitch, 1989; Debelius, 1997). The present study reports on the feeding of *R. europaea* and comparisons are drawn with other species of *Roboastra*, and other hunting opisthobranchs.

First, from gut content analysis, the realized diet of *Roboastra europaea* along the Strait of Gibraltar was quantified. Second, by means of laboratory trials, we qualitatively determined the complete assemblage of potential prey—the fundamental diet—that might be exploited by this species. In laboratory trials we also allowed intraspecific encounters to investigate the possibility of cannibalistic behaviour in *R. europaea*.

MATERIALS AND METHODS

Field study of the diet

Forty-nine specimens of *Roboastra europaea* were collected at 5–30 m depth by SCUBA from southern Spain (Figure 1). Ten specimens from Tarifa (Figure 1, E3) and two from Trafalgar (Figure 1, E4) were maintained alive and used for the experimental laboratory study (see below). Thirty-seven specimens, 35 to 50 mm in length (0.60–3.98 g), were anaesthetized and fixed immediately after collection in order to stop digestion. Nudibranch remains were identified to species whenever possible, and quantitative estimates were made from radulae and jaws. From nudibranch prey with jaws (i.e. *Polycera* spp.) each radula was matched with one pair of jaws, and recorded as one individual. Remaining unmatched radulae or pairs of jaws were counted as additional individuals.

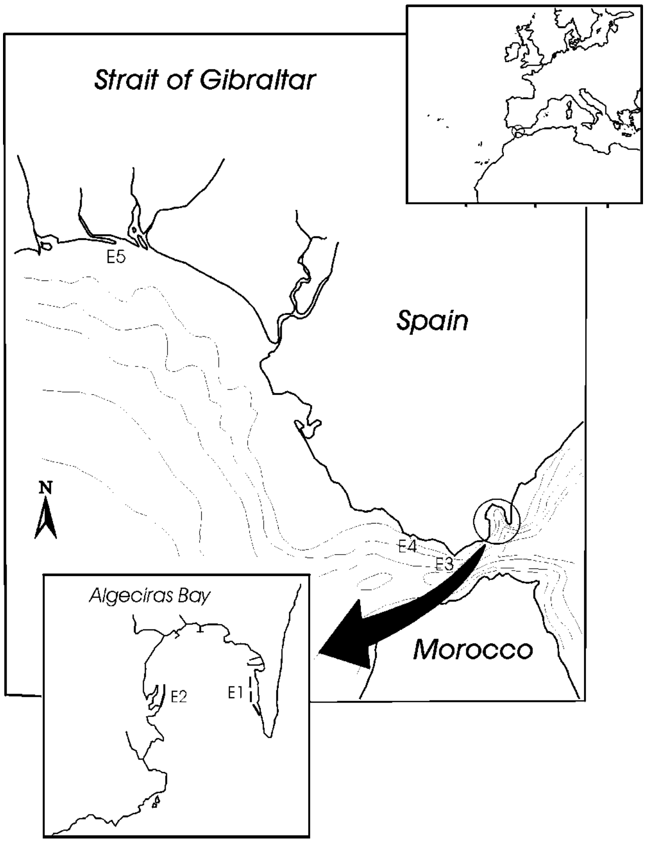

Figure 1. Location of the study area showing sampling stations. E1, Gibraltar Harbour; E2, Algeciras Harbour; E3, Tarifa; E4, Trafalgar; E5, El Portil.

Table 1. *Gut contents of* Roboastra europaea *in the Strait of Gibraltar.*

Prey category	F.O. (%)	N.I. (%)*
Polycerella emertoni	45.95	7.49
Polycera spp.	89.19	91.62
Limacia clavigera	5.41	0.60
Roboastra europaea	2.70	0.30
TOTAL Polycerid nudibranchs	94.59	
BRYOZOAN	35.14	
OTHER	18.92	
Empty stomachs	5.41	

F.O., frequency of occurrence; N.I., numerical importance; *, numeric importance was only calculated for prey that could be enumerated as individuals (i.e. nudibranch).

The frequency of occurrence of different prey was calculated (FO_i = proportion of *Roboastra europaea* for which prey i was recorded). The numerical importance of each prey species (NI_i = proportion of the total prey item attributable to prey species i) was calculated from remains of prey that could be enumerated as individuals.

Although feeding diversity is a fundamental parameter to evaluate and classify the trophic strategy and the dietary specialization of any predator, however, no agreement exists to express the feeding diversity in the literature about the diet of opisthobranchs, what precluded the comparison of different strategies. As an attempt to standardize this measure we propose the calculation of the mean individual feeding diversity (H_i) and the overall population feeding diversity (H_p), using diversity measures calculated for prey taken (gut contents) (Tokeshi, 1991). Although Shannon index has been previously used as a summary statistic for inclusion in this methodology (Tokeshi, op. cit.; Marshall & Elliot, 1997), we propose the use of the Brillouin diversity index (H), as a standard method for the evaluation of feeding diversity in predator opisthobranchs, on the grounds that it is mathematically more appropriate in the study of gut content analysis (Hurtubia, 1973). The most valuable use of this methodology is the graphical comparison among multiple predator species, each one represented by a simple point in a plot of H_i against H_P. Although presently, data are available only for *Roboastra europaea*, we consider fundamental the calculation of these indices that will permit informative comparisons with other hunter opisthobranchs if similar data can be obtained in the future.

$$H_i = \frac{\sum_{j=1}^{N} \frac{1}{n_j} \times \left(\log_2 n_j! - \sum \log_2 n_{ij}! \right)}{N}$$

$$H_P = \frac{1}{n} \times \left(\log_2 n! - \sum \log_2 n_i! \right)$$

where N = total number of *R. europaea* studied, n = total number of individuals of all prey observed for all *R. europaea* studied, n_i = total number of individuals of prey i observed for all *R. europaea* studied, n_j = number of individuals of all prey observed for the individual j of *R. europaea*, n_{ij} = number number of individuals of prey i observed for the individual j of *R. europaea*. The curve stabilization method proposed by Hurtubia (op. cit.) was applied.

Experimental study of the diet

Some potential prey may not actually be observed in the gut contents of field-collected individual predators due to its absence or low availability in the study area. Furthermore, certain undesired prey items can occasionally be ingested inadvertently.

With this in mind, we offered specimens of different taxa as putative prey in order to permit a qualitative assessment of the full potential extent of the diet of *Roboastra europaea* (the fundamental diet). The inclusion of a test organism was based upon observations of the locally available fauna and the results of the field study of the diet, and included bryozoans, small crustaceans, polycerid and non-polycerid nudibranchs and opisthobranchs from other suborders (Table 2).

We tested almost all the species of polycerid reported in the Strait of Gibraltar as potential prey (Table 2). Three specimens of *Polycera aurantiomarginata* collected in El Portil (Huelva) (Figure 1, E5), a very uncommon species in the Strait of Gibraltar, were utilized in the experiments.

Ten specimens of *Roboastra europaea*, ranging from 40 to 48 mm in length, were maintained in an aquarium for at least two days to clean the gut and ensure hunger. Contacts between *R. europaea* and a specimen of putative prey

Table 2. *Prey species test material.*

Tested prey-species	No. trials (no. individuals)	Attacks	Ingestion
Bryozoans			
Bugula neritina	5(5)	0	0
Zoobotryum verticillatum	5(5)	0	0
Crustaceans*			
Amphipoda sp.	5(5)	0	0
Copepoda sp.	5(5)	0	0
Nudibranchs			
Polycerids***			
Limacia clavigera	5(5)	5	5
Polycera quadrilineata	12(12)	12	12
P. aurantiomarginata	3(3)	3	3
P. faeroensis	2(2)	2	2
Polycerella emertoni	9(9)	9	9
Thecacera pennigera	1(1)	1	1
*Tambja ceutae***	3(1)	3	1
Non polycerids			
Dorids			
Crimora papillata	5(2)	0	0
Doriopsilla areolata	5(3)	0	0
Hypselodoris bilineata	5(5)	0	0
H. orsini	5(5)	0	0
H. midatlantica	5(5)	0	0
Chromodoris purpurea	5(2)	0	0
C. luteopunctata	5(3)	0	0
Eolids			
Flabellina affinis	5(5)	0	0
F. ischitana	5(5)	0	0
F. babai	5(3)	0	0
Dondice banyulensis	5(5)	0	0
Dendronotids			
Marionia blainvillie	5(2)	0	0

*, Crustaceans were anaesthetized by cooling, in order to avoid mobility; **, two individual *Tambja ceutae* successfully escape after being attacked; ***, the definition of the family Polyceridae provided by Thompson & Brown (1984) was used, and we included the genus *Tambja*.

Table 3. *Results of intraspecific encounter trials.*

Individuals confronted	Behaviour sequence			
1	NR			
2	NR			
1	NR			
3	NR			
1	E	A2	F	M
4	A1	H	F	M
1	A2	F		
5	A1	F		
2	NR			
3	NR			
2	A2	F	E	M
4	A1	F	H	M
2	A2	F	M	
5	A1	F	M	
3	A2	F	M	
4	A1	F	M	
3	A1	F	M	
5	A2	F	M	
4	A1	F	M	
5	A2	F	M	

NR, no reaction; A1, attack; A2, response attack; F, fighting; E, escape; H, hunting; M, mating. See text for the explanations of typified behaviours. Sizes of individuals (1, 3.22 g, 60 mm length; 2, 3.85 g, 68 mm length; 3, 4.69 g, 70 mm length; 4, 5.07 g, 71 mm length; 5, 6.68 g, 77 mm length).

species were permitted in an experimental tank (1000 cc, water temperature 15–16°C), and the behaviour, attack and ingestion were recorded. If neither ingestion nor attack occurred, the two animals were kept together in small floating tanks (1200 cc) with flowing seawater. The tanks were small enough to ensure exposure to any waterborne chemical cue, direct contact between animals and the detection of mucus trails. If neither attack nor ingestion were noted after 24 h the test species was not considered a possible prey. Each experimental *R. europaea* specimen was used in several prey encounters. To ensure the positive and negative choices being made every specimen of *R. europaea* used in the experiment was periodically offered a known prey species [i.e. *Polycera quadrilineata* (O.F. Müller, 1776) or *Polycerella emertoni* (Verrill, 1880)] and confirming attack and ingestion to ensure that they were trophically active. Whenever possible five trials with different individuals of *Roboastra europaea* were undertaken for each prey species. For especially scarce prey species some specimens had to be reused in several trials. If ingestion occurred, the number of trials was limited to the number of individuals available.

Cannibalism

Five experimental specimens of *Roboastra europaea* were measured and weighed (Table 3), and individually identified to allow the assessment of individual behaviour. Each animal was used in several trials for the recording of conspecific responses and all ten possible individual combinations were assessed.

The association between body size and aggressiveness (aggressive/non-aggressive behaviour) was analysed by means of Spearman's rank correlation.

Finally, it was possible to confront two specimens of *Roboastra europaea* of markedly different size (2.55 g, 58 mm; 0.19 g, 25 mm) from Trafalgar (Figure 1, E4), that permitted assessment of the possibility of cannibalism (i.e. complete ingestion) in this species.

RESULTS

Field study of diet

The most frequent gut remains throughout all the specimens of *Roboastra europaea* examined were of polycerid

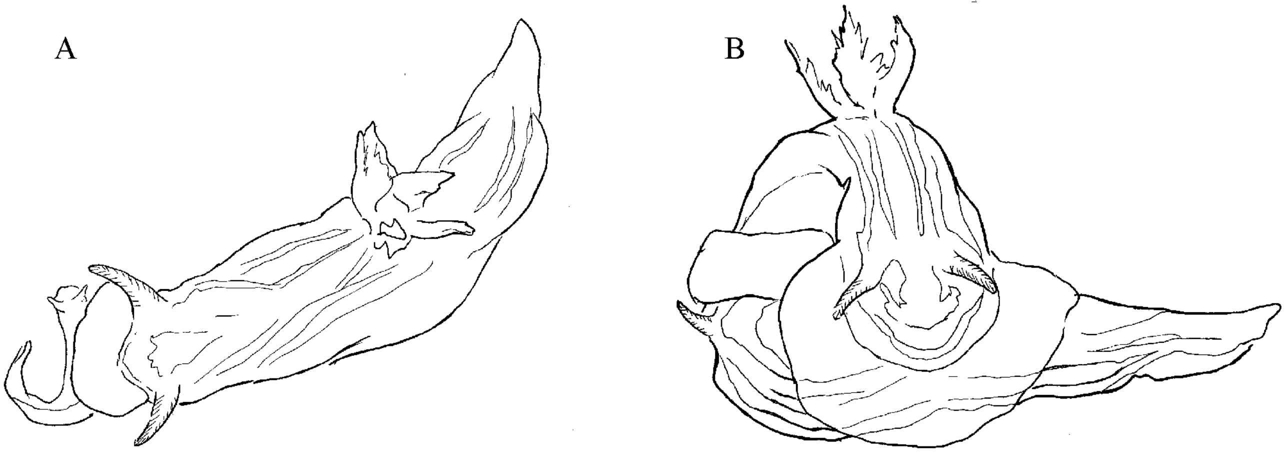

Figure 2. (A) *Roboastra europaea* attacking a small prey individual. (B) Two similar sized *Roboastra europaea* fighting.

Figure 3. An individual of *Roboastra europaea* showing damage and marks around the tail posterior to the gills (arrows). This damage was produced during the fight, after one attacker engulfed the tail of this individual apparently attempting to excise it.

nudibranchs (Table 1). Most other gut remains were uncommon (Table 1) and, when present, comprised a very small proportion of the gut contents. Bryozoans were the most frequent among the non-nudibranch remains.

Amongst the polycerid nudibranchs, the genus *Polycera* appeared to be the principal prey. It was not possible to further specify *Polycera* spp. from the jaws and radulae but two undamaged specimens of *P. quadrilineata* were found within the buccal cavity of one specimen of *R. europaea*.

The remains of a *R. europaea* prey item were found in the biggest specimen studied. It was of a poorly digested mass of blue and grey striped epidermal tissue, and hence positively identifiable, but neither the radula of *R. europaea* nor other identifiable remains of other species were found in its gut.

Most individuals examined contained several prey specimens in the gut, with numbers ranging up to 29 specimens and an average of 9.0 ($SD = 8.2$; $N = 37$). A low diversity of the diet at both the populational and mean individual level was found ($H_p = 0.44$; $H_i = 0.24$), which indicates a specialized diet with few between-individual differences for *R. europaea*.

Experimental study of the diet

None of the non-nudibranch species, and none of the non-polycerid nudibranchs were attacked even when the specimens of *R. europaea* had been starved for more than a week. Conversely, all the polycerid species were attacked and consumed immediately following first contact. Any contact of the oral tentacles of *R. europaea* with the body of a polycerid elicited an instantaneous reaction of the predator, which abruptly extruded the buccal mass towards the prey and expanded the velum to cover it (Figure 2A). *Roboastra europaea* was shown to be able to detect the slime trail of any polycerid and became excited, everting the buccal mass and following the mucus trail.

Tambja ceutae García-Gómez & Ortea, 1988 exhibited effective defensive behaviour to *R. europaea* attack by undulating the body in convulsions and thereby effecting an escape swimming response. This response was immediate when it touched or was touched by *R. europaea*, and this species evaded capture by the predator in two trials. In the third trial it was captured, and the prey item produced a whitish secretion, which possibly was defensive, although no reaction was exhibited by *R. europaea*. No other tested polycerid species displayed any response which could be interpreted as a defensive behaviour.

Cannibalism

When two specimens of *R. europaea* meet, they touch and examine each other with their oral tentacles. The observed behaviours were classified into the following categories:

(a) **No reaction (NR):** animals touch each other with the oral tentacles without apparent reaction. Finally both move apart.
(b) **Attack (A1):** one individual abruptly begins the attack by extruding the buccal mass towards the opponent, expanding widely the velum over the body of the opponent in an attempt to swallow it (Figure 2B).
(c) **Response attack (A2):** an animal receiving an attack answers in the same way. This normally results in a fight with the two animals trying to engulf the other (Figure 2B).
(d) **Fighting (F):** the animals can continuously fight for a long time as they attempt to engulf one another (up to 30 min was recorded). Due to the large and similar size of all the experimental animals none of individuals could actually swallow another, and these attacks never resulted in consumption. It was frequently observed that during the fight one attacker could engulf the tail of the opponent (Figure 2B), apparently attempting to excise it. No excision was actually observed during the trials, but damage and marks around the tail were inflicted upon two animals during encounters (Figure 3). Similar marks have been observed in field-collected individuals.
(e) **Escape (E):** after initial contact some animals withdraw and crawl apart rapidly.
(f) **Hunting (H):** the animal pursues an escaping opponent.
(g) **Mating (M):** the fighting behaviour can develop into mating behaviour, with one or both animals protruding the penis while fighting, apparently soliciting copulation, or a more complex behaviour that includes a kind of courtship. This behaviour can be very easily interrupted by normal fighting and alternations between both behaviours occur repeatedly.

The results of the cannibalism behaviour trials are shown in Table 3. The initial aggressive response (A1 or A2) was positively correlated with body weight and the non-aggressive responses (NR or E) were negatively correlated with body weight (Spearman $R=0.94$, $P=0.014$). Most observed attacks (except two) were initiated by the bigger individual. Smaller individuals tend to be less aggressive, and NR and E behaviours were observed for specimens 1, 2, and 3.

The encounter between the two individuals of very different size from Trafalgar resulted in the immediate and complete ingestion of the smaller individual.

DISCUSSION

Fundamental and realized diet of Roboastra europaea

The realized diet of *Roboastra europaea* in the Strait of Gibraltar is specialized, comprised of a few species of polycerid nudibranchs, and primarily dominated by individuals of the genus *Polycera*. This dominance does not necessarily imply preference, but perhaps a greater availability of this kind of prey. Since *Polycera quadrilineata* is the most abundant polycerid species in the Strait of Gibraltar and, although not identifiable to species from the radula and jaws, the majority of the gut contents of most *R. europaea* individuals studied probably belong to this species.

The incidental occurrence of bryozoans and other taxa may be the result of inadvertent ingestion during a prey attack, or they may derive from the stomach contents of bryozoan eating prey (i.e. polycerids). Laboratory experiments show that trophically active and hungry *R. europaea* will not feed on bryozoans, or any other non-nudibranch prey offered, whilst they avidly attack polycerid nudibranchs.

The laboratory studies confirmed the field results and show that the fundamental diet of *R. europaea* is restricted to nudibranchs of its own family, Polyceridae, and the diet probably extends to the whole family (*sensu* Thompson & Brown, 1984, including *Tambja* and *Roboastra* itself). The abrupt attack of *R. europaea* is probably nonselective, and prey species which are very uncommon in the sampling area (specially *Polycera aurantiomarginata*) were immediately ingested. This suggests evolutionarily derived trophic association between predator and prey which is not based on previous dietary experience (Hall et al., 1984).

Comparison of predatory strategy of hunter opisthobranchs

Most cannibalistic predators have very generalized feeding habits and may also take a large number of alternative food items (Fox, 1975). The few existing quantitative data on hunting opisthobranchs are in accordance with this. *Pleurobranchaea meckelii* (Blainville, 1825) and *P. californica* MacFarland, 1966 have wide diet ranges, comprising prey belonging to nine and six phyla respectively (Cattaneo-Vietti et al., 1993; Battle & Nybakken, 1998). These species hunt mobile individual prey but also graze on sessile and modular taxa. *Navanax inermis* (Cooper, 1863) takes a variety of prey belonging to different phyla, but it appears to be primarily a specialist on opisthobranchs, including cephalaspideans, dorid nudibranchs and eolid nudibranchs (Paine, 1963, 1965). *Dirona albolineata* Cockerell & Eliot, 1905 is a non-selective predator, taking practically every benthic prey type available (bryozoans, hydroids, ascidians, sponges, prosobranchs, crustaceans, etc.) (Robilliard, 1971).

Among nudibranchs, a directed hunting strategy seems to be developed mainly within phanerobranch dorids, because the few eolids that prey upon other nudibranchs seem actually to be primarily grazers of sessile epifauna (principally cnidarians) that occasionally hunt other eolids (McDonald & Nybbaken, 1997). Species of the dorid genus *Gymnodoris*, however, have been reported as more specific predators, hunting only upon opisthobranchs (different species of *Gymnodoris* prey upon species belonging to different suborders) or preying upon the eggs (Kay & Young, 1969; Johnson & Boucher, 1983; Rudman & Darvell, 1990; Rudman, 1998; Marshall & Willan, 1999; Johnson, 2000). Rudman (op. cit.) suggested that each species of *Gymnodoris* apparently feeds specifically on one prey species, although there are no published reports of specific studies on the diet of any *Gymnodoris* species.

The few published data on the feeding of other species of *Roboastra* are confined to *R. tigris*, and these show that it also preys upon opisthobranchs, and preferentially upon the polycerids *Tambja abdere* Farmer, 1978 (Farmer, 1978; Carté & Faulkner, 1983, 1986; Kerstich, 1989) and *T. eliora* (Marcus & Marcus, 1967) (Farmer, 1978; Carté & Faulkner, 1983, 1986). But a variety of other opisthobranchs have been reported as potential prey of this species, including anaspideans, arminids, dendronotids, eolids, other polycerids and non-polycerid dorids (Debelius, 1997; Lance, 1997). Despite its wider fundamental diet, *R. tigris* does not show generalist behaviour, because some other species have been shown to be rejected by this predator (Lance, op. cit.).

Paine (1965) considered it unlikely the evolution of a predator such as *Navanax inermis* exclusively specialized on nudibranchs, because the latter generally are of sporadic and unpredictable occurrence and are comparatively small. However, *R. europaea* is not only a specialist predator of nudibranchs, but it exclusively feeds on species of the one family, the Polyceridae.

Cannibalism

Sexual cannibalism in gonochoric species normally takes place after mating (Elgar, 1992). This often is explained as a paternal investment in future offspring, or the contribution of the male to increase female fecundity and hence augment its own offspring fitness. Such does not appear to extend to hunter opisthobranchs, such as *Roboastra europaea*, in which aggressiveness seems to prevail over mating behaviour on initial contact. *Hermissenda crassicornis* (Eschscholtz, 1831), *Pleurobranchaea* spp., *Navanax inermis* and *Gymnodoris citrina* (Bergh, 1875), *Roboastra tigris* and *R. europaea* will often cannibalize a partner prior to mating (Paine, 1965; Zack, 1975; Rutowski, 1983; Debelius, 1997; Willan, 1998; Johnson, 2000; this study).

Elgar & Nash (1988) concluded pre-mating sexual cannibalism to be a form of female sexual selection, because smaller males were more likely to be cannibalized than larger ones. Although *R. europaea* is a simultaneous hermaphrodite, pre-mating cannibalism may be acting as a kind of sexual selection that facilitates size assortative mating. This optimizes the mating effort investment, in particular for larger individuals (Todd et al., 2001). Female fecundity of nudibranchs is directly correlated to body size (Thompson, 1967; Todd, 1981) and therefore, smaller individuals are less profitable females. The cannibal attack is most often initiated by the larger individual in all reported hunter opisthobranchs (Paine, 1965; Cattaneo et al., 1993; Battle & Nybakken, 1998; Johnson, 2000; this study). If insufficient size differences occur between partners it seems to be impossible for the one to swallow its opponent (Paine, 1965; this study; although see Leonard & Lukowiak, 1984), thereby preventing the elimination of a suitable mating partner. If one of the partners is sufficiently small, complete ingestion occurs before mating can be effected, and an inappropriate mating partner becomes a profitable prey item.

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