Cah. Biol. Mar. (2007) 48 : 1-7

The use of trophic resources by a generalist eolid nudibranch: *Hermissenda crassicornis* (Mollusca: Gastropoda)

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Abstract: We are presenting the first of a series of studies describing the different trophic strategies of hydroids-eating eolid nudibranchs. *Hermissenda crassicornis* represents the most euriphagous strategy within this trophic guild. We studied the natural diet of this eolid based on the analysis of gut content of wild slugs from three different stations along the northern California coast, supplemented by laboratory observations. According to our results, *H. crassicornis* has a broad diet, which can vary widely among different environmental situations, but it still exhibits a certain degree of selectivity and some preferences. A general trend can be observed in the studied environments: despite its phenotypical specialization to exploit cnidarians, *H. crassicornis* preferred colonial tunicates (mainly *Aplidium solidum*). Anemones were not frequently consumed and probably only the smallest polyps are eaten in the studied environments. Although this species is evolutionarily associated with hydroid-eating eolids, hydroids were frequently eaten but always in limited quantity. This pattern of consumption led us to suggest two possible explanations that will need further experimentation: (1) hydroids could be consumed to obtain a complement of the diet, probably the defensive nematocysts or (2) there is a maximum consumable quantity of hydroids conditioned by their toxicity for the nudibranchs.

Résumé : *L'utilisation des ressources trophiques par le nudibranche éolidien généraliste* Hermissenda crassicornis *(Mollusca : Gastropoda).* La première étude d'une série portant sur les différentes stratégies trophiques chez les nudibranches éolidiens se nourrissant d'hydraires est présentée. *Hermissenda crassicornis* représente la stratégie la plus euryphage. Une étude du régime alimentaire naturel de cet éolidien a été réalisée, se basant sur l'analyse du contenu de tube digestif d'animaux sauvages provenant de trois stations différentes de la côte californienne, et complétée par les observations au laboratoire. Selon nos résultats, *H. crassicornis* dispose d'un régime alimentaire riche qui peut varier fortement en fonction de l'environnement. Toutefois, elle fait preuve d'un certain degré de sélectivité et de préférence. Une tendance générale est observée dans les environnements étudiés : en dépit de sa spécialisation phénotypique à tirer parti des cnidaires, *H. crassicornis* préfère les tuniciers coloniaux (principalement *Aplidium solidum*). Les anémones ont été rarement consommées et probablement seuls les polypes les plus petits ont été mangés dans les environnements étudiés. Bien que cette espèce soit associée du point de vue évolutif aux éolidiens se nourrissant d'hydraires, ceux-ci ont été fréquemment consommés mais en quantité réduite. Ce modèle de consommation suggère que les hydraires pourraient être consommés pour recueillir des compléments d'alimentation, les nématocystes défensifs, ou alternativement présenter une limite dans la quantité maximale d'hydraires consommés en raison de leur toxicité.

Keywords: Eolid • *Hermissanda crassicornis* • Trophic strategy • Euryphagous • Tunicates • Hydroids

Reçu le 15 février 2006 ; accepté après révision le 31 janvier 2007.
Received 15 February 2006; accepted in revised form 31 January 2007.

Introduction

Nudibranch molluscs are predominantly a group of specialized marine epibenthic carnivores generally associated with one or a few phylogenetically related prey species (monophagy or oligophagy) (Todd et al., 2001). Specifically, eolid nudibranchs are specialized predators of cnidarians (Todd, 1983) from which they obtain nematocysts, reusing them for their own defence (Greenwood & Mariscal, 1984). In temperate coastal ecosystem, hydroid-eating eolids are of particular interest because they are fairly common and may play a role in controlling hydroid populations (Miller, 1961; MacLeod & Valiela, 1975; Chester et al., 2000). Nevertheless, the available information regarding the association of hydroid-eating eolids with their prey usually comes from occasional observations or from studies not specifically dealing with this topic. Very little is known about how specific populations use the available trophic resources. A revision of this information (MacDonald & Nybakken, 1997) shows that some species have only been recorded in association with one prey species (apparently monophagous), whereas others have been recorded in association with a variety of hydroid species.

We present the first of a series of studies characterizing how hydroid-eating eolids use the available trophic resources within specific habitats. *Hermissenda crassicornis* (Eschscholtz, 1831) represents the most euriphagous extreme in the range of the different trophic strategies within this trophic guild. This eolid feeds on a variety of prey belonging to different phyla; cnidarians are the most frequently recorded prey in the literature, mostly hydroids, but also hexacoralian and octocoralian anthozoans, scyphozoans, tunicates, crustaceans, dead animals, nudibranchs (including cannibalism) (see McDonald & Nybakken, 1997, for a revision). Our study has an additional interest because this species is one of the few eolids that has expanded its trophic range beyond the cnidarians.

The information available provides a list of possible prey of *H. crassicornis*, but many essential aspects of its trophic strategy are still unknown. For instance, we do not know how many prey a specific population of *H. crassicornis* uses in particular habitats. Neither we know whether its diet is preferentially concentrated in a single or a few prey, or whether it prefers hydroids as main prey. The degree of dietary plasticity is also unknown: has the diet a more or less fixed structure and composition or may it vary among different habitats? Does the main prey change among habitats? The present study provides quantitative information on the diet and the use of trophic resources of three populations of *H. crassicornis* in its natural habitats. We compare various habitats to ascertain trends in natural behaviour. Lastly, we studied the foraging behaviour of *H. crassicornis* in aquaria to determine the actual degree of association with both cnidarian and non-cnidarian prey.

Methods

Field work

We randomly colleted twenty individuals of *Hermissenda crassicornis* in spring, at each of three stations along the California coast (Fig. 1). Monterey Marina (MM) and Pillar Point Marina (PPM) are harbour stations characterized by an artificial hard substrate with low species diversity but a high abundance of some fouling organisms (those living on hard artificial substrates). We sampled these subtidal stations by SCUBA. Pillar Point Beach (PPB) is an undisturbed natural rocky shore. At this station we collected *H. crassicornis* into large tide pools. To terminate the digestion in the field we fixed the individuals in 4% formaldehyde in sea water, immediately after collection.

Diet study

Individuals for gut content analysis were blotted on filter paper and weighed (body weight: BW; all weights in grams). They were dissected and the complete gut from buccal mass to anus was removed. The gut was blotted dry and weighed full of feeding material (full gut weight: FGW). Subsequently, the contents were extracted and the empty gut was dried and weighed (empty gut weight: EGW). Gut content weight (GCW) was calculated by subtracting EGW from FGW. A Repletion Index (RI) was then calculated dividing GCW by net weight of individuals:

$$RI = \frac{GCW}{BW - GCW} \qquad (1)$$

In order to detect differences in the intensity of feeding activity, we compared the log (*GCW*) of nudibranchs from the three populations by ANCOVA, with net weight as the covariate. To identify differences in the populations body condition (or nutritional state) we compared the log transformed body weights of individuals by ANOVA. A pos-hoc Tukey test was used for multiple comparisons.

The gut of *Hermissenda crassicornis* is divided in three different chambers: stomach, anterior intestinal chamber and posterior intestinal chamber (Fig. 2). Food remains from the stomach and anterior intestinal chamber were poorly digested and they were more easily identifiable than food remains from the posterior intestinal chamber. To avoid mistakes we calculated the percent occurrence of the different prey at each station (number of individuals having fed the prey i/total number of individuals examined) considering exclusively the material from the stomach and first intestinal chamber. We also calculated the diversity

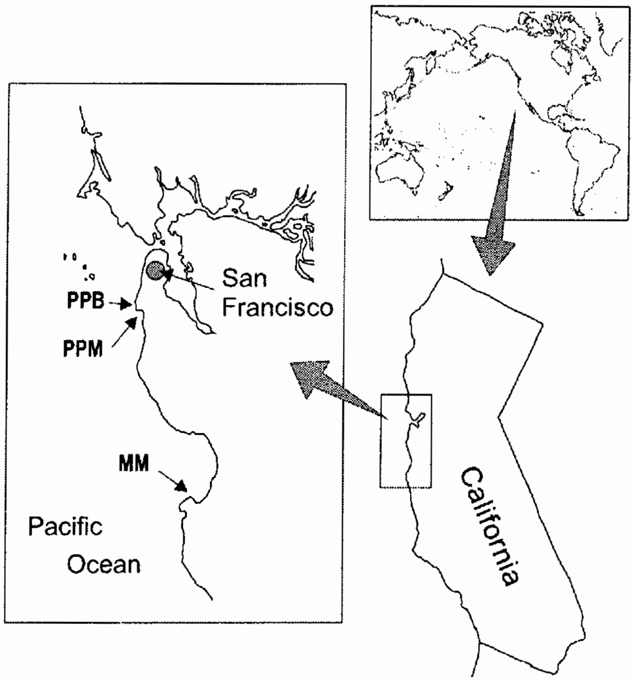

Figure 1. Location of the study area showing sampling stations. MM: Monterey Marina; PPB: Pillar Point Beach; PPM: Pillar Point Marina.

Figure 1. Zone géographique étudiée et localisation des stations d'échantillonnage. MM : Monterey Marina; PPB : Pillar Point Beach; PPM : Pillar Point Marina.

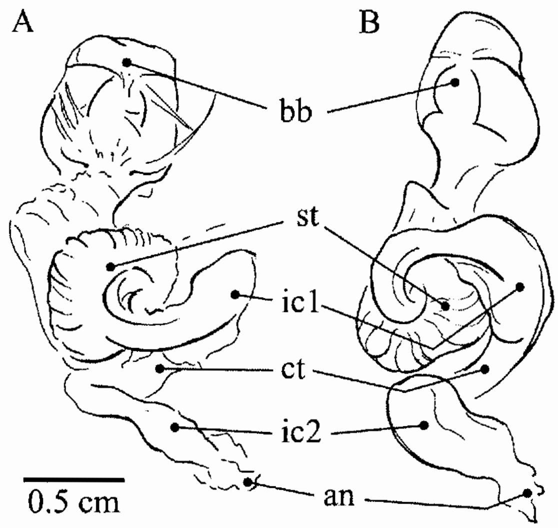

Figure 2. Scheme of *Hermissenda crassicornis* digestive system. **A.** Dorsal view. **B.** Dorso-lateral view (right side); (an) anus, (bb) buccal bulb, (ct) constriction that separates first and second intestinal chambers (ic 1 and ic 2), (st) stomach.

Figure 2. Schéma du système digestif de *Hermissenda crassicornis*. **A.** Vue dorsale. **B.** Vue dorso-latérale (côté droit) ; (an) anus, (bb) bulbe buccal, (ct) étranglement qui sépare la première et la deuxième cavités intestinales (ic 1 et ic 2), (st) estomac.

(H') and evenness (J) of the diet using the Shannon-Wiener index:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i \qquad (2)$$

$$J = \frac{H'}{H'\max} = \frac{H'}{\ln s} \qquad (3)$$

where p_i = number of individuals having fed prey i/ total number of occurrences of all prey categories; s = total number of prey categories

Laboratory observations and experiments

The observed diet of a predator depends both on its feeding preferences and on the availability of the different prey. To separate these two components we carried out laboratory observations in aquaria manipulating the availability of the principal prey categories. Given the small number of main prey identified (tunicates, hydroids and anemones), this method is simpler and more accurate than a quantitative comparison with the benthic assemblage.

We first observed the feeding behaviour of *Hermissenda crassicornis* in presence of the three main prey types: hydroids (*Obelia longissima* and *Plumularia* sp.), anemones (polyps of *Metridium senile* and *Corynactis californica* with pedal disc diameter of 1-2 cm) or tunicates (colonies of *Aplidium solidum* of 2-6 cm in diameter). We maintained 10 nudibranchs for 24 h., each one in a small tank (0.84 l) with flowing water pumped directly from the ocean, and containing one of the three prey types. This scheme was repeated three times till every experimental animal was maintained 24 h with every prey type; we varied the order in which the different prey were offered to distinguish possible effects due to this order (Table 1). We also offered a combination of the three prey types in similar detectable proportions (occupying similar volumes). The experimental tank was small enough to ensure the detection of all prey present. We checked periodically if consumption occurred.

After the results of previous trials, we wanted to compare quantitatively the consumption by *H. crassicornis* of hydroids or tunicates when they are the unique prey and their availability is not limited. Two groups of four individuals from PPM, with similar weights (average weight ± SD = 1.07 ± 0.43 g and 0.90 ± 0.35 g respectively; Man-Whitney U test p = 0.89), were starved for 24 h. Subsequently, they were individually held in the small tanks, containing a) tunicates (*Aplidium solidum*) or b) a

Table 1. *Hermissenda crassicornis.* Initial observation of feeding with different prey categories in the laboratory. The table shows the order in which the different prey were provided. An = anemones (*Metridium senile* and *Corinactis californica*); Hy = hydroids (*Obelia longissima* and *Plumularia* sp.); Tu = tunicates (*Aplidium solidum*); All: a combination of the three prey categories; in this last case the table shows which prey were consumed. +: consumed during observation period (24h for each treatment); -: not consumed.

Tableau 1. *Hermissenda crassicornis.* Observation de l'alimentation en function des différents types de proies au laboratoire. Le tableau indique dans quel ordre ont été présentées les proies. An = anémones (*Metridium senile* et *Corinactis californica*) ; Hy = hydraires (*Obelia longissima* et *Plumularia* sp.) ; Tu = tuniciers (*Aplidium solidum*) ; All: une combinaison des trois proies ; dans ce cas, le tableau indique quelles proies ont été consommées. + : consommées pendant la période d'observation (24 h pour chaque traitement); - : non consommées.

Experimental individual								An	Tu	Hy
1	An	-	Hy	+	Tu	+	All	-	+	+
2	An	-	Tu	+	Hy	+	All	-	+	+
3	Hy	-	An	-	Tu	+	All	-	+	+
4	Hy	+	Tu	+	An	-	All	-	+	+
5	Tu	+	Hy	+	An	-	All	-	+	+
6	Tu	+	An	-	Hy	+	All	-	+	+
7	Hy	+	An	-	Tu	+	All	-	+	+
8	Tu	+	An	-	Hy	+	All	-	+	+
9	An	-	Hy	+	Tu	+	All	-	+	+
10	Tu	+	Hy	+	An	-	All	-	+	-

mixture of the two hydroids (*Obelia* and *Plumularia*) for some additional 24 h. Prey were provided in higher quantity than what nudibranchs could consume. Then, the nudibrachs and faecal pellets were fixed. The sum of gut content weight and faecal pellets gives an estimation of material consumed. We finally did not consider faecal pellets because they were difficult to handle and its inclusion did not change the results (see *Results* and *Discussion*). We compared the gut content weight divided by net weight of the animal (RI, see *Diet study*) of the two groups by Mann-Whitney U test.

We checked if the occurrence of a limited consumption of hydroids by *H. crassicornis* maintained in laboratory also occurred in natural habitats. For this we combined the data from the three sampled stations and compared the RIs of individuals with just hydroids in their guts (having feed only hydroids in their last meal) with those with just tunicates in their guts, by a Mann-Whitney U test.

Results

Description of the diet

The diet of *Hermissenda crassicornis* was very similar between the two harbour stations, being composed by some prey categories that were abundant in the fouling assemblage, mainly massive colonial tunicates and hydroids (Table 2). Tunicates were largely represented by *Aplidium solidum*. At PPM, hydroids were represented by *Obelia longissima* (PPM 91%) and *Plumularia* sp. (PPM 9%). At MM, most hydroid remains could not be identified to the specific level because perisarc parts found lacked the characteristic sculptures or thecae.

Hydroids were frequently consumed (Table 2) but, within a given gut, they were usually found in small quantities, never filling the entire gut even when they were the only prey present in this gut. On the contrary, when tunicates had been consumed, they were usually the most abundant prey in the gut, frequently filling the digestive tract, regardless of the presence of secondary prey.

Remains of hexacoral anthozoans (distinguished by the occurrence of spirocysts) were less frequent (Table 2). Nematocyst and spirocyst composition of anthozoan remains from most individuals coincided with *Metridium senile* cnidome. We also found within the guts small crustaceans, mainly copepods as well as sedentary polychaetes, Foraminifera (*Eponides* sp.), and eolid remains (Table 2).

At PPB, 30 % of individuals had an empty gut. Foraminifera and hexacoral anthozoans were the most abundant components, but there was not any clearly dominant prey (Table 2). Consequently, both diversity and evenness of the diet are larger in PPB.

Repletion Index and body weight

Body weights of individuals collected at the two harbour stations were similar; individuals collected at the intertidal station were significantly smaller (Fig. 3). The repletion index of the individuals at the two harbour stations were also similar whereas individuals collected at the intertidal site had a significantly lower repletion index (Fig. 3).

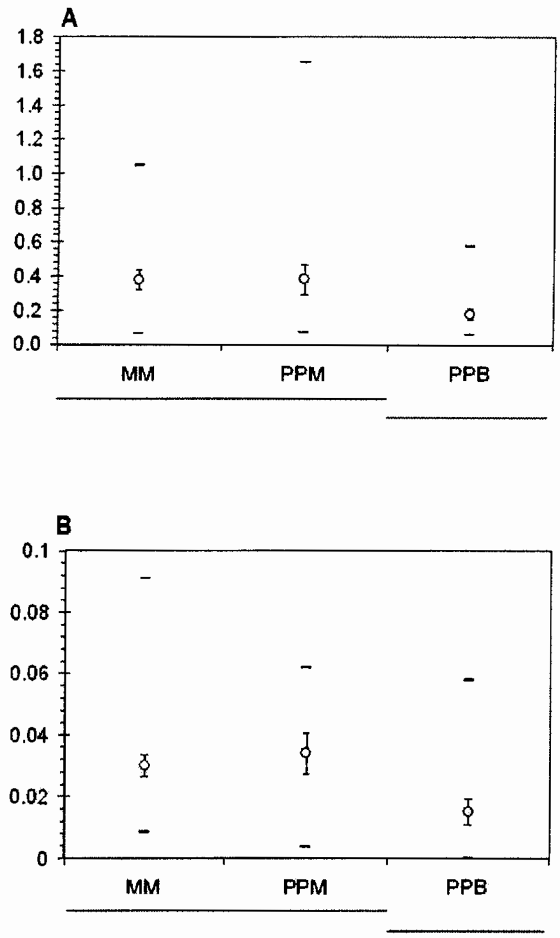

Figure 3. Body weight (A) and repletion index (B) of wild individuals from the three sampling stations: Monterey Marina (MM), Pillar Point Marina (PPM) and Pillar Point Beach (PPB). Averages (circles) ± standard error, and range (min-max, black dashes). Body weights were compared by ANOVA ($F = 5.63$; $p = 0.0059$). To compare the repletion of the guts we analyzed the weight of gut content by ANCOVA, with net weight of individuals as covariate ($F = 6.92$; $p = 0.0024$). Tukey test represented as lines (Body weight: PPB *vs* PPM, $p = 0.0441$; PPB *vs* MM, $p = 0.0077$; PPM *vs* MM, $p = 0.7796$; Repletion index: PPB *vs* PPM, $p = 0.0002$; PPB *vs* MM, $p = 0.0002$; PPM *vs* MM, $p = 0.9368$).

Figure 3. Le poids (A) et l'indice de remplissage (B) des individus sauvages provenant de trois stations d'échantillonnage : Monterey Marina (MM), Pillar Point Marina (PPM) et Pillar Point Beach (PPB). Les valeurs moyennes (cercles) ± erreur standard, et les variations (min-max, tirets noirs). Le poids des individus a été comparé par ANOVA ($F = 5{,}63$; $p = 0{,}0059$). Pour comparer le remplissage, le poids du contenu de l'intestin a été testé par ANCOVA, avec le poids net des individus comme covariant ($F = 6{,}92$; $p = 0{,}0024$). Test de Tukey représenté par des lignes (Poids du corps : PPB/PPM, $p = 0{,}0441$; PPB/MM, $p = 0{,}0077$; PPM/MM, $p = 0{,}7796$; indice de remplissage : PPB/PPM, $p = 0{,}0002$; PPB/MM, $p = 0{,}0002$; PPM/MM, $p = 0{,}9368$).

Table 2. *Hermissenda crassicornis*. Frequency of occurrence (%) of the different preys in the diet of the three populations studied: Pillar Point Marina (PPM), Monterey Marina (MM) and Pillar Point Beach (PPB).

Tableau 2. *Hermissenda crassicornis*. Prévalence (%) des différentes proies dans l'alimentation des trios populations étudiées : Pillar Point Marina (PPM), Monterey Marina (MM) and Pillar Point Beach (PPB).

Prey category	PPM	MM	Harbour Stations	PPB	Total
Tunicates	60.0	65.0	60.0	15.0	44.3
Hydroids	55.0	45.0	50.0	5.0	34.4
Hexacoral anthozoans	15.0	10.0	12.5	30.0	18.0
Aeolid remains	—	10.0	5.0	15.0	8.2
Foraminifers	—	5.0	2.5	30.0	11.5
Crustaceans	10.0	25.0	17.5	15.0	16.4
Others	15.0	5.0	10.0	5.0	8.2
Empty gut	—	—	—	30.0	11.5
n	20	20	40	20	60
Diversity (H'-ln)	1.36	1.56	1.53	1.77	1.76
Evenes (J)	0.85	0.80	0.78	0.91	0.90

RI of field individuals whose guts contained exclusively tunicates were significantly higher than those whose guts contained exclusively hydroids (Tunicates: 0.032 ± 0.0065, $N = 12$; Hydroids: 0.013 ± 0.0053, $N = 6$; Mann-Whitney U Test, $p = 0.025$).

Observations of feeding with different prey categories in laboratory

Neither ingestion nor attack by nudibranchs was observed when the two species of anemones were offered. *Hermissenda crassicornis* appeared to be stung by the anemones, withdrew and departed without concluding any attack.

The two species of hydroids as well as *Aplidium* were consumed (Table 1). Nevertheless, tunicates were regularly consumed throughout the experiment, while, hydroid were consumed with a low frequency.

In fact, during the experiments of hydroids-tunicates consumption, none of the individuals maintained with hydroids produced any faecal pellets, whereas those maintained with tunicates produced some. Additionally RIs of individuals maintained with hydroids were significantly smaller (Tunicates: 0.042 ± 0.0084, $N = 3$; Hydroids: 0.0086 ± 0.0021, $N = 4$; Mann-Whitney U Test, $p = 0.034$).

Discussion

Hermissenda crassicornis is an euriphagous predator (McDonald & Nybakken, 1997; this study), even considering that the consumption of some prey, for instance the small crustaceans like copepods, most probably occurred inadvertently while feeding other prey. An europhagous trophic strategy is common in many epibenthic grazers and predators (e.g. Birkeland, 1974; Giangrande et al., 2000; Boudouresque & Verlaque, 2001; Zupo, 2001; Kitsos et al., 2005;), but very unusual among nudibranchs, which usually feed on a homogeneous prey group (see McDonald & Nybakken, 1997, for a revision of previous data; Megina et al., 2002; Megina & Cervera, 2003). Nevertheless, *H. crassicornis* did not show unselective foraging strategy. In fact, the most surprising result was that, despite its morphological and anatomical specializations to exploit cnidarians, some of the studied populations of *H. crassicornis* principally consumed a non-cnidarian prey, the tunicate *Aplidium solidum*. The laboratory trials showed that this is not exclusively due to a higher abundance of this prey in the habitat: when hydroids were provided *ad livitum* as unique prey, they still were consumed in limited quantities, in contrast to the unrestricted consumption of tunicates (without considering the weight of faecal pellets we underestimated the consumption of tunicates; but the differences were still significant and the interpretation of the experiment is the same). But *Hermissenda* can not be considered a specialist predator of tunicates; the population in the intertidal habitat is not preferentially associated to tunicates as well as some others populations reported in the literature (Birkeland, 1974).

The diet of *Hermissenda crassicornis* can vary largely among different environments. None of the individuals collected in the two harbour sites had an empty gut and they presented higher RI's than nudibranchs on the rocky shore. This suggests a higher rate of encounter with prey and a more intense feeding activity. Accordingly, we found larger individuals in harbour habitats. With a higher food availability, predators are expected to be more selective, and consequently feeding activity more concentrated on preferred prey (Stephens & Krebs, 1986, among others); in this case mainly tunicates followed by hydroids. In contrast, in the intertidal environment (PPB) we found smaller individuals, a high percent of empty guts and significantly smaller repletion indexes. Additionally, the diet in PPB did not concentrate in any preferred prey. Other prey categories present in harbour habitats, but not preferentially consumed there (i.e. foraminifers and hexacoral anthozoans), were more frequently consumed in the intertidal, suggesting lower food availability in this habitat.

This eolid is not a specialist on anemones, but the consumption of anemones by *Hermissenda crassicornis* has been reported (Francis, 1973), and anemones have been used as food for *H. crassicornis* in aquaria (Avila & Kuzirian, 1995). In the studied habitats, however, anemones were not among the most exploited trophic resources, despite the fact that some species were common. Taking into account that the size of the polyps is a very important factor for their consumption by eolids, and that *H. crassicornis* and some other eolids prefer small anthozoans (Waters, 1973; Birkeland, 1974; Avila et al., 1998), it is plausible that only the very smallest anemones are preyed upon in these habitats.

The pattern of consumption of hydroids was also surprising. This frequent but quantitatively limited consumption can suggest a search for a complement to the diet. A plausible possibility is a dependence on hydroids' nematocysts for its defence. *Hermissenda crassicornis* is an aggressive nudibranch that uses the kleptocnides in its agonistic behaviour (Zack, 1975). But the maximum consumable quantity of hydroids may be conditioned by their toxicity (hydroids' nematocysts can cause injuries even to their specialist predators, Martin & Walter, 2003). Or more simply, hydroids may be less nutritionally profitable than tunicates. Hence, small quantities of hydroids would be frequently consumed to maintain the cnidosacs charged, while *Aplidium solidum* is consumed *ad libitum*. Nevertheless, specific experimentation would be required to test such suggestions.

Acknowledgements

We thank C. Avila, M.D. Subida, T. Ransome and M. Poddubetskaia for their help with the manuscript. This paper has been benefited partially by the project REN2001-1956-C17-02/GLO (Spanish Ministry of Education and Science).

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