THE DIET OF *PLATYDORIS ARGO* (GASTROPODA: NUDIBRANCHIA) AND THE DIETARY SPECIALIZATION OF SPONGE EATING DORIDS

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ABSTRACT

The diet of the dorid nudibranch *Platydoris argo* was studied in relation to prey availability, and under different environmental conditions to evaluate richness, evenness, and plasticity of its diet. In order to assess the availability of possible prey, the sponge assemblage at two different habitats was characterized. The results showed that *P. argo* is a relatively specialized benthic carnivore, feeding exclusively on spiculated demosponges. However, it has a relatively polyphagous diet (16 prey-species) and adapts well to contrasting patterns of prey availability at different sites. At the location with lower sponge diversity, the diet of *P. argo* included more prey categories, was more diverse, and less selective (lower dietary evenness), foraging preferentially on the most frequent resource, *Stylopus dujardini*. In contrast, at a station with a clearly more diverse and abundant sponge assemblage, the diet was more selective, and *Phorbas tenacior* was its principal component. Despite its trophic plasticity, *P. argo* displayed a specialized pattern of resource exploitation in terms of niche breadth within a given habitat. Foraging was focussed on one preferred prey (which changed from one habitat to another) as indicated by the significant positive selection indexes (*S. dujardini* $= +0.29$, *P. tenacior* $= +0.74$). The revision of quantitative data on the diet of so-called 'sponge eating dorids' indicates the existence of a more specialized guild of 'spiculated demosponge eating dorids'. Most species revised are 'non-stereotyped specialist', which indicates that they have a polyphagous and plastic diet but only exploit one or few main prey species in each habitat. However, *obligate specialists*, with a monophagous (or rather oligophagous) diet also seem to be present.

INTRODUCTION

Nudibranch molluscs are common elements of trophic networks in benthic marine ecosystems present in almost all seas, at all latitudes and depths, from the inter-tidal zone to the deep ocean, and have undergone a great evolutionary radiation, clearly influenced by dietary adaptations (Todd, 1981, 1983; Rudman & Willan, 1998). Despite their considerable morphological and ecological diversity, they have often been considered a group of highly specialized predators, habitually reported as extremely stenophagous, associated with one or few related prey species (monophagy or oligophagy). Besides, it is often accepted that these trophic mono-or oligospecific relationships are obligated and rigidly fixed (stereotyped) (Swennen, 1961; Miller, 1961; Clark, 1975; Cattaneo-Vietti, Chemello & Gianuzzi-Savelli, 1990; Rudman & Willan, 1998). However, as various authors have pointed out (e.g. Todd, 1981; Cattaneo-Vietti & Balduzzi, 1991; Todd, Lambert & Davies, 2000), this generalization perhaps requires a re-appraisal due to the scarcity of quantitative systematic studies.

To evaluate trophic specialization it is necessary to consider two different concepts: *dietary niche breadth* and *dietary plasticity* (Morse, 1971; Sherry, 1990). The latter is defined as the capacity to adapt the diet to different short-term ecological situations (Morse, 1971). The former is defined as the extent of the hyper-volume representing the realized niche (Hutchinson, 1957; Pianka, 1994). When we evaluate the dietary niche breadth, we must consider both the number of prey categories included in the diet (we will call this *dietary richness*) and how close the frequency of use of different preys matches their availability (we will call this *dietary evenness*). The more similar the both frequencies, the broader the species' dietary niche (Glasser, 1982).

It is particularly important to distinguish between an *obligate specialist* with very few prey categories included in its potential diet and a *facultative specialist* with a richer potential diet, but concentrated in few preferred categories (low dietary evenness). Obligate specialists have both restricted niche breadth and low dietary plasticity (stereotypy), while facultative strategists have more plastic diets, and can behave as specialist or generalist feeders depending on ecological circumstances.

The main objective of this research was to study the diet of the dorid *Platydoris argo* (Linneaus, 1767) as it relates to the availability of prey, by studying the diet and the prey assemblage together. *P. argo* is one of the largest nudibranchs from the Atlantic–Mediterranean coasts, and references to its diet are imprecise and based on indirect data. There are some discrepancies concerning the nature of its main trophic resource, which has been reported to be bryozoans (Ros, 1973; Ros & Gili, 1985) and sponges (García, García-Gómez & Medel-Soteras, 1988; Cattaneo-Vietti & Balduzzi, 1991). In order to understand the trophic plasticity, and the degree of opportunism or stereotypy, the diet of *P. argo* was studied under two different environmental conditions. Our working hypothesis was that if the diet of *P. argo* is rigidly fixed, it should not vary significantly between different environments. On the other hand, if this species is able to change its diet according to the habitat, these changes should be clearly reflected in different situations.

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MATERIAL AND METHODS

Composition of the diet

The composition of the diet of *Platydoris argo* was studied by examining the gut contents of 63 specimens from seven locations throughout the Strait of Gibraltar (Figure 1). Sponge remains were identified following the technique traditionally employed in the study of this phylum (Carballo Cenizo, 1994).

The percentage of occurrence, calculated by the data summation technique (Da'Cunha, Shehata & De Oliveira, 1957), applied for the study of the sponge eating dorids (SED) diet by Bloom (1981), was used to quantitatively characterize the diet. The number of slugs in which each prey species occurs was counted and referred to the total individuals examined.

Dietary plasticity

Like many nudibranchs, *Platydoris argo* appears irregularly and in low frequency (Todd, 1983; Rudman & Willan, 1998) and most explored locations did not contain a population large enough to allow an accurate quantification of the diet. To establish the degree of plasticity in the trophic resource exploitation of *Platydoris argo,* we selected the locations with both different prey assemblages and populations large enough to allow the comparison of the diets (E1 and E2). Station E1 is an oil refinery port zone, characterized by an artificial hard substrate, spatially homogeneous, and colonized by a simple benthic community. Station E2 is a natural rocky area, with a spatially heterogeneous substrata, inhabited by a highly diverse benthic community. Both stations were sampled by SCUBA diving. All the specimens of sponges visualized along determined underwater runs (from depth of 0–30 m) were collected to establish the proportion of each species in its environment (42 sponge specimens at E1 and 139 at E2; Alcolado 1985). The sponge assemblage at each station was subsequently characterized using the Shannon diversity index (H'; Shannon & Weaver, 1963). The K-dominant curves were used to compare the sponge communities (Platt, Shaw & Lambshead, 1984): the cumulative abundance expressed in percentages is represented against the logarithm of species range, arranged from the most abundant to least abundant species.

Trophic niche breadth

Two indices of trophic niche breadth were calculated. The Smith index (FT; Smith, 1982) is less sensitive to scarce species and varies between 0 and 1. The Hurlbert index (Hurlbert, 1978), which is more sensitive to scarce species, was standardized (B'_A) to also vary between 0 and 1, and be comparable to FT (Krebs, 1989). These indexes are very useful to measure

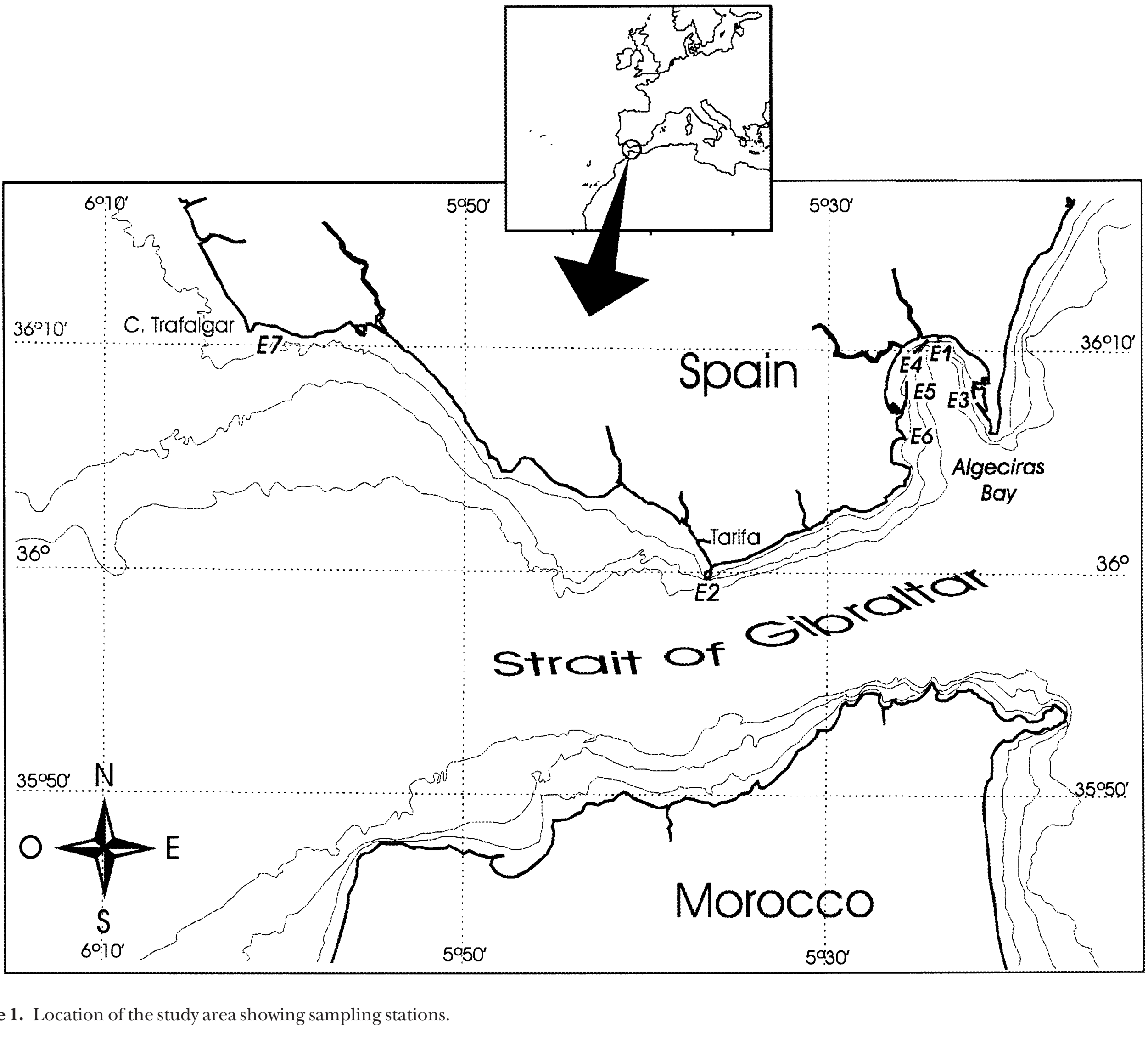

Figure 1. Location of the study area showing sampling stations.

dietary evenness, as they consider the availability of prey and the composition of the diet. The maximum evenness is reached when the frequencies of use of different prey match those of the prey available. However, these indexes do not consider the dietary richness. The Shannon diversity index (H') has been proposed as a good indicator of diet complexity (Colwell & Futuyma 1971; Marshall & Elliott 1997). Although there are some reasons not to use indices that do not consider prey availability (e.g. Hurlbert, 1978), we conceive H' useful to estimate the trophic niche breadth when it is associated with the number of used resources, and FT and B'_A. We calculated H' of the diet of *Platydoris argo* and other SED on which quantitative information is available (Bloom, 1981; Hellou, Andersen & Thompson, 1982; Thompson, Walker, Wratten & Faulkner, 1982; Cattaneo-Vietti, Angelini & Bavestrello, 1993) for comparative purposes. The data from Bloom (1981) was recalculated from H' based on *log10* to H' based on *ln* in order to standardize all the measurements. Hellou *et al.* (1982) and Thompson *et al.* (1982) provided absolute frequencies of the different prey species. Cattaneo-Vietti *et al.* (1993) provided approximated data. Except for our investigations there are no data available on prey communities, which makes it impossible to calculate indexes such as B'_A or FT to be compared.

Prey selection

In order to detect any association of *Platydoris argo* with spiculated (siliceous) and keratose demosponges, and calcareous sponges, their frequencies in the diet were compared with those in the environment (only at E1 and E2) on 2-way contingency Tables.

All calculations were subsequently repeated using spiculated demosponges as 100% of the diet.

In order to express *Platydoris argo* preference for each prey species (only at E1 and E2), we calculated the C index (selection of prey index; Pearre, 1982), which varies between –1 and +1, where 0 is no selection. This index was also calculated by placing the absolute frequency of the tested prey species *versus* the rest of the preys grouped according to diet and habitat on two-way contingency Tables. It derives from the formulation of chi-squared and its significance is statistically testable (Fisher exact test). The value of the index is affected by its statistical probability and it behaved the best in cases of complete association (prey species found in the diet and not in field census, Pearre, 1982). Only statistically significant results ($P < 0.05$) were considered here.

RESULTS

Composition, complexity, and extent of the diet

The main component of the mollusc diet is represented by sponges, with only a few individuals containing remains of other organisms such as bryozoans, crustaceans, or even algae or detritus (2.74, 2.74, 1.37 and 4.11% of the total, respectively). Moreover, when these remains appeared, they occupied a minor percentage of the stomach volume and sponges were almost always the main component.

A total of 16 species of demosponges were found (Table 1): *Mycale microacanthoxea* Buizer & Soest, 1977, *Esperiopsis fucorum* (Esper, 1794), *Hymedesmia peachi* Bowerbank 1882, *Stylopus dujardini* (Bowerbank, 1866), *Leptolabis cf. brunnea* (Topsent, 1904), *Phorbas tenacior* (Topsent, 1925), *Pronax lieberkuhni* (Burton, 1939), *Myxilla iotrochotina* (Topsent, 1892), *Cliona vastifica* Hancock, 1894, *Batzella inops* (Topsent, 1891), *Ulosa stuposa* (Esper, 1794), *Geodia* sp., besides four other unidentified species. No keratose or calcareous sponges appeared in the diet.

The identified prey belonged to eight different families from four orders (Table 1) and were therefore qualitatively heterogeneous. Frequently up to three species were found in a single stomach (average: 1.33 spp./individual). There were 49 stomachs that contained food remains (77.78%) and 14 were empty (22.22%; Table 1).

Characterization of the sponge assemblage at E1 and E2

We found a total of 16 sponge species at station E1, with *Stylopus dujardini* (19.05 %), *Pleraplysilla spinifera* (14.29 %), and *Cliona viridis* (11.90 %) as the most frequent. 72 species were found at station E2: *Axinella damicornis* (6.94 %), *Ircinia variabilis* (4.17 %), and *Sarcotragus spinosula* (3.47 %) were the most frequent. At both stations, the spiculated demosponges were the most abundant (Table 2). Keratose demosponges were also well represented at both stations, with similar percentages of abundance (28.57% at E1 and 29.17% at E2). There were no calcareous sponges at E1, while they made up 4.17% of the assemblage at E2 (Table 2). Data show that E2 has a more diverse and better structured sponge assemblage than E1, as can be inferred from the higher diversity found for the former station (Table 2, Figure 2).

Predator–prey relationships and selection of prey

A significantly positive association exists between the nudibranch and the spiculated demosponges, which made up 100% of the sponge remains found (Fisher exact test, E1: $P = 0.0026$; E2: $P = 0.0069$). None of the specimens we studied contained remains of horny demosponges (spongin fibres), although these sponges were frequent at both stations, and represented among the dominant species at E1 and E2 (as in E2 *S. spinosula*, 3.47%, or *I. variabilis*, 4.17%; or *P. spinifera*, 14.29%, in E1). This negative association is significantly different from randomness at the two stations (Fisher exact test, E1: $P = 0.0026$; E2: $P = 0.015$).

No calcareous sponges were found among the diets either but, given their scarce representation in the environments we studied, this negative association was not statistically different from randomness.

On the other hand, there was a primary prey species at both stations, to which *Platydoris argo* was associated and C was significantly positive (Table 1). In both cases, it was a Poecilosclerid species of the same family, *S. dujardini* (59.26% of the diet) at E1, and *P. tenacior* (76.92% of the diet) at E2.

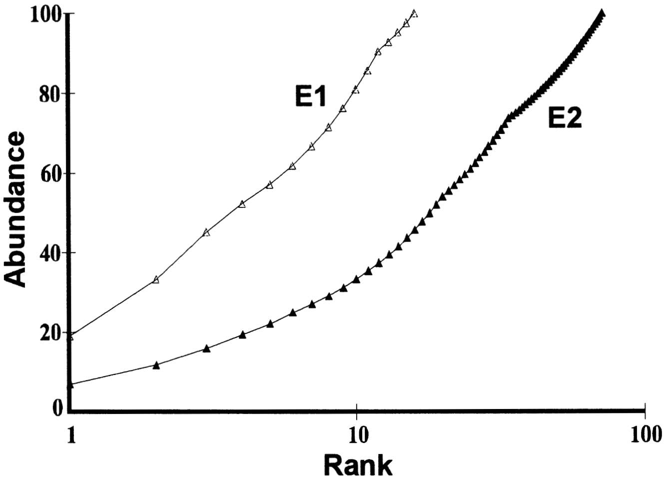

Figure 2. K-dominance curves for sponge community at E1 and E2. The lower curve represents the community with greater diversity and more evenly distributed species, and the upper curve corresponds to communities dominated by few, but very abundant species.

Table 1. Diet characteristics of *Platydoris argo* at each station: occurrence percentage of sponges in the diet (see text for generic names of sponges). At E1 and E2 occurrence percentage of sponges in the environment is also provided, as well as trophic niche breadth indexes (Smith –FT-, Hulbert standardize -B'_{A}-), Shannon diversity index (H'), and prey selection index (C).

	E1			E2								
	Diet	Environment	*C*	Diet	Environment	*C*	E3	E4	E5	E6	E7	Total
O. Poecilosclerida												
F. Micalidae												
M. microacanthoxea							20.0	11.1				3.1
E. fucorum										33.3		3.1
F. Hymedesmiidae												
H. peachi	14.8	0.0*	+0.22					11.1				7.7
S. dujardini	59.3	26.7	+0.29	7.7	1.0	NS	40.0	33.3	66.7	50.0		41.5
L. cf. brunea	3.7	0.0	NS									1.5
F. Anchinoidae												
P. tenacior				76.9	3.1	+0.69						15.4
P. lieberkuhni	3.7	0.0*	NS									1.5
F. Myxiliidae												
M. iotrochotina								22.2				3.1
O. Hadromerida												
F. Clionidae												
C. vastifica									33.3			1.5
O. Halichondriida												
F. Halichondriidae												
B. inops	7.4	0.0*	NS					11.1			100	7.7
F. Dictyonellidae												
U. stuposa				7.7	0.0*	NS		11.1		16.7		4.6
O. Astrophorida												
F. Geodiidae												
Geodia sp.				7.7	0.0*	NS						1.5
Not identified												
sp. 1	7.4		—			—						3.1
sp. 2	3.7		—			—						1.5
sp. 3			—			—	20.0					1.5
sp. 4			—			—	20.0					1.5
n	29	30		16	96		2	7	2	5	2	63
Empty stomach (%)	27.6			25.0			0	0	0	0	0	22.2
Prey number	7			4			4	6	2	3	1	16
Diversity (H' – ln)	1.34			0.79								2.07
B′A	0.75			0.04								
FT	0.4			0.18								

*Species not detected in field census due to its low frequency. This cases can occur in field data (Pearre, 1982). C index behaves as if field frequency is lower than 1, this is, the value is just slightly higher (Pearre, 1982) and its statistical probability is testable.

Table 2. Characterization of the sponge assemblages.

		Sponges total	Demosponges total	Spiculated demosponges	Horny demosponges	Calcareous
E1	Abundance (%)*	–	100	71.43	28.57	0
	Sp. of max. Abund. (%)†	19.05	19.05	19.05	14.29	0
	Sp. of min. Abund. (%)†	2.38	2.38	2.38	2.38	0
	Num. Sp.	16	16	11	5	0
	Diversity (H' – ln)	2.55	2.55	2.19	1.36	–
E2	Abundance (%)*	–	95.83	66.67	29.17	4.17
	Sp. of max. Abund. (%)†	6.94	6.94	6.94	4.17	1.39
	Sp. of min. Abund. (%)†	0.69	0.69	0.69	0.69	0.69
	Num. Sp.	72	67	50	17	5
	Diversity (H' – ln)	4.05	3.98	3.67	2.66	1.56

*Relative abundance of each group within the whole sample.

†Maximum and minimum relative abundance found within each group, considering the whole sample as 100%.

Some secondary sponges found in the diet were not found in the field censuses. This can occasionally occur in field data (Pearre, 1982). In these cases, the value of the index is slightly higher than with field frequency of prey equal to 1, this is, it behaves as if the field frequency is just lower than 1. However, most of these complete associations can be dismissed, as they are not statistically significant (Table 1).

Dietary plasticity

The characteristics of the diet varied substantially between animals inhabiting the two types of stations, both in qualitative composition as well as in number of prey species and diversity (Table 1). At station E1, where some sponges were dominant and diversity and species richness were low, the diet of *Platydoris argo* was richer and more diverse (seven prey species and *H*′ = 2.07). In contrast, at E2 the diet was more restricted (four prey species and *H*′ = 1.34) despite the sponge assemblage was clearly more diverse. This is made evident by trophic niche breadth indexes, noticeably greater at E1 than at E2 (Table 1). *P. argo* exploits the most frequent resource at E1, which is *S. dujardini* (26.67% of the spiculated sponge assemblage), while at E2, the preferred prey was not among the most abundant sponge species.

DISCUSSION

The diet of Platydoris argo

Ros (1973, 1975) and Ros & Gili (1985) indicated the bryozoan '*Sertella cellulosa*' as *Platydoris argo* prey, while García *et al.* (1988) suggested a diet composed mainly of sponges, on the basis of the functional anatomy of the digestive system. Cattaneo-Vietti & Balduzzi (1991) pointed out as surprising that the diet of *P. argo* is based on '*S. cellulosa*', since its radula is typical of sponge eating dorids (SED). Our results confirm the hypothesis of García *et al.* (1988) with quantitative data. Consequently, *P. argo* should be placed within the SED group, like the rest of the species from the genus *Platydoris* (Young, 1969; Mulliner & Sphon, 1974) and the majority of the species in the family (Mulliner & Sphon, 1974). We consider the remains of diverse origin found (hydrozoans, bryozoans, algae, and detritus) as the result of an accidental ingestion. The diet of this species seems to be exclusively made up of spiculated demosponges.

Spiculated Demosponge-Eating Dorids (SDED)

The most significant studies on the diets of the SED support the existence of a trophic guild exclusively specialized in spiculated demosponges. Cattaneo-Vietti & Balduzzi (1991), on the basis of the relationships between the morphology of the radula and the type of prey sponge to which the dorid is associated, recognized two trophic guilds within the SED: a group of calcareous sponge-eating dorids and a group of demosponge-eating dorids. The latter group would further be divided into a group of keratose demosponge-eating dorids (mainly chromodorids) and a group associated with spiculated demosponges, specifically the order Poecilosclerida.

The latter group appear to be exclusively associated with spiculated demosponges (no keratose or calcareous sponges were ever found in their guts). This behaviour was found in all the species studied (*Anisodoris nobilis*, *Archidoris montereyensis*, *A. odhneri*, *Diaulula sandiegensis*, *Discodoris heathii*, *Cadlina luteomarginata*, *Discodoris atromaculata*, and *Platydoris argo*), in different geographical areas and different zones within the same geographical area (Bloom, 1981; Hellou *et al.*, 1982; Thompson *et al.*, 1982; Cattaneo-Vietti *et al.*, 1993; this study). Doubt still remains on whether *C. luteomarginata* can be included in this guild or if it has a wider trophic niche, as its radular morphology seems to fit better a keratose sponges eater (Cattaneo-Vietti & Balduzzi, 1991). Thompson *et al.* (1982), based on several indirect evidence, proposed keratose demosponges as a part of the diet of this species. However, their speculations are not supported by data despite this being an SED species for which quantitative data are available, given that Bloom (1981), Hellou *et al.* (1982), and Thompson *et al.* (1982) examined 83, 84, and 99 specimens, respectively, and no keratose sponges remains were ever found.

Polyphagy

With respect to the idea of extreme stenophagy that dominates the literature on SED, the diet of *Platydoris argo* is relatively polyphagous because it includes at least 16 species (*H*′ = 2.07; Tables 1 and 3). Most SDED displayed a similar pattern of resource exploitation (Table 3), with more or less polyphagous diets (from eight to 13 prey species), although we found populations with less polyphagous diets, for example, *P. argo* at E2 or *Cadlina luteomarginata* at Barkley Sound. Diets were also qualitatively heterogeneous, since they included prey species with very different structural characteristics (belonging to different orders and families; Bloom, 1981; Hellou *et al.*, 1982; Thompson *et al.*, 1982; present study), which affect handling and digestive processes (see Bloom, 1981, for a discussion on this topic). In general, diets of SDED may include every spiculated demosponge (at least, no more restrictive limit has been found up to now).

Trophic plasticity and non-stereotyped specialization

One principal prey usually dominated the diet of *Platydoris argo*, and its consumption occurred with a significantly higher frequency than its availability in the environment would predict for a non-selective forager (C was significantly positive). That is, foraging is actively concentrated on the preferred prey. Available quantitative data on SDED support this idea, since only one or a few preferred prey (1–3 species) occur within each

Table 3. Summary of quantitative data regarding feeding characteristics of SED. Shannon Index (*H*′) was calculated with data published by other authors, except those of *P. argo*. In *C. luteomarginata*: I: San Juan Archipelago* (Washington, Eastern Pacific); II: Barkley Sound (British Columbia, Eastern Pacific); III: Howe Sound (British Columbia, Eastern Pacific); IV: Pt. Lomas (California, Eastern Pacific). References: (I) Bloom, 1981; (II) Hellou *et al.*, 1982; (III) Thompson *et al.*, 1982; (IV) Cattaneo-Vietti *et al.*, 1993; (V) present study.

Species	Total number of prey	% Empty stomachs	Diversity (H' – ln)	References
Anisodoris nobilis	10	–	1.87	(I)
Archidoris montereyensis	8	–	0.93	(I)
Archidoris odhneri	9	–	1.66	(I)
Cadlina luteomarginata I	10	–	1.90	(I)
Cadlina luteomarginata II	4	20.6	1.12	(II)
Cadlina luteomarginata III	6	40.0	1.20	(II)
Cadlina luteomarginata IV	10	52.7	1.51	(III)
Cadlina luteomarginata Total	13	–	2.33	(I) + (II) + (III)
Diaulula sandiegensis	8	–	1.53	(I)
Discodoris heathi	8	–	1.91	(I)
Discodoris atromaculata	2	60*	0.10*	(IV)
Platydoris argo E1	7	25.0	1.34	(V)
Platydoris argo E2	4	27.5	0.79	(V)
Platydoris argo Total	16	22.2	2.07	(V)

*Approximate data: calculated from approximate data provided by Cattaneo-Vietti *et al.* (1993).
–, Data not available in referred studies.

habitat, and a group of quantitatively secondary prey complete the diet (Bloom, 1981; Hellou *et al.*, 1982; Thompson *et al.*, 1982).

Although specialized within a given habitat, the diet of *Platydoris argo* widely varies in qualitative composition (including the principal prey species), diversity, number of prey (dietary richness), and selectivity (dietary evenness, measured as the *trophic niche breadth indexes*) between E1 and E2 (Tables 1 and 3). Therefore, the resource exploitation pattern of SDED is also plastic, and a process of adaptation in their feeding strategy exists in order to obtain an optimal ecological fitness under different circumstances. The assessment of the precise causes explaining the differences found is out of the scope of the present study. However, although no quantitative measurements were done, a lower abundance of sponges at E1 (the oil refinery port) was evident. A higher abundance of a certain prey generally produce a stronger feeding selectivity and, consequently, a more restricted diet ('Optimal Foraging Theory'; Emlen, 1966, 1968; MacArthur & Pianka, 1966; see Stephens & Krebs, 1986, for a review).

The comparison of quantitative studies on the diet of the same species under different circumstances support the existence of plasticity in the use of trophic resources by SDED. *Cadlina luteomarginata* feeds on a different number and diversity of prey in different geographical localities (Table 3; although data on the sponge assemblages are not supplied, sponge abundance presumably varies among localities). The qualitative diet composition also varies conclusively among localities, with the diet dominated by diverse spiculated demosponges: the halichondrids *Halichondria* sp. and *Higginsia* sp., the poecilosclerids *Hymedesmia* sp. or *Myxilla incrustans*, or the Axinellid *Axinella* sp. (Bloom, 1981; Hellou *et al.*, 1982; Thompson *et al.*, 1982).

The observed pattern of resource exploitation by SDED does not exactly fit the concept of facultative strategists, or obligate specialist. Most species reviewed are 'non-stereotyped specialist', which indicates that they have a polyphagous and plastic diet, but only exploit one or few main prey species in each habitat.

Obligate specialists

There is also an extensive study on the diet of *Discodoris atromaculata*, where the elevated trophic specificity of this species is evident (two prey species and $H' = 0.10$), strongly associated with the sponge *Petrosia ficiformis* (Poiret, 1789) (98% of the diet, Table 4) (Cattaneo-Vietti *et al.*, 1993). The almost monophagous (or rather oligophagous) diet of *D. atromaculata* suggests the existence of a second type of strategy with much more restricted limits (*obligate specialist*). More quantitative data are necessary to correctly interpret this point.

These two types of dietary specialization have different functional implications: obviously, obligate specialists present a marked dependence on their prey species, their biology matches with that of the prey populations, and they show a similar distributional range. Non-stereotyped specialists, in contrast, may have a less concurring biology and their distribution may be wider than that of prey.

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