

Specialization and Noncompetitive Resource Partitioning Among Sponge-Eating Dorid Nudibranchs

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Summary. Habitat and food resource partitioning ecologically isolate six species of Pacific Northwest dorid nudibranchs. Food resources along a gradient of sponge skeletal structure are partitioned between two exploitive guilds. The guilds are characterized by mutually exclusive predatory and digestive adaptations which allow efficient processing of sponges with poorly- or well-organized skeletons. Habitats along a depth gradient are partitioned within guilds. For a dorid species, feeding rates, extraction efficiencies and food quality are virtually identical for sponges with the appropriate extreme (either poorly- or well-organized) and intermediate skeletal organizations, but growth and reproductive rates supported by the former prey type are twice those supported by the latter prey type. Prey types with the appropriate extreme skeletal organization are thus optimal food and specialization to that food is expected. When two divergent specialist species co-occur, food resource partitioning is demonstrable but arises from self-stabilizing specializations to maximize net energy accumulation and not from competitive interactions. Habitat partitioning is viewed as arising from prey distributions and dorid physiological tolerances. This system represents an example of morphological and behavioral specializations giving rise to resource partitioning as opposed to competition giving rise to resource partitioning and subsequent morphological and behavioral specializations.

Introduction

Resource partitioning can be operationally defined as the subdivision of some resource(s) (food, habitat, time, etc.) by a group of utilizers. Typically, the utilizers are viewed as sympatric and ecologically similar species possessing resource-utilization patterns that peak over different resources with overlap occurring primarily in the tails of the utilization functions (MacArthur and Levins 1967; Colwell and Futuyma 1971; Roughgarden 1972, 1974; May 1974; Sale 1974). Given a partitioning pattern, the next step is to ascertain the causal mechanism behind the partitioning. Competition is by far the dominant hypothesis accounting for partitioning (Cody 1968; DaCunha et al. 1951; Edington and Edington 1972; Emery 1973; Fraser 1976; Gatz 1979; Hartley 1948; Heinrich 1976; Huey and Pianka 1977; Jones 1968; Leviten 1979; MacArthur 1958; MacArthur and Levins 1964; Nybakken and Eastman 1977; Pianka 1969; Rose 1976; Schoener 1968; Shonman and Nybakken 1978; Werner 1977, etc.). The view that competition and resource partitioning are interlinked is strongly supported by manipulative studies showing competitive release, i.e. expansion of resource utilization

by one consumer in the absence of the potential competitor (Connell 1961; Jaeger 1971; Menge 1972; Reynoldson and Davies 1970; Werner and Hall 1977, 1979) and an extensive body of theoretical models (see Whittaker et al. 1973; May 1974; MacArthur 1972). The suggestion has been made that if the prey is capable of evolving, i.e. is biotic rather than abiotic, partitioning patterns of consumers may become progressively more distinct as prey evolve away from zones of overlap that are presumably subjected to greater predatory stress (Caswell 1978). Coevolution of predator and prey can also sharpen partitioning patterns (Culver 1976). Such evolution would result in morphological or behavioral specializations which would preclude the demonstration of competitive release. Even in cases where there is no direct evidence of competition in the form of competitive release or competitive interactions, competition may still be viewed as the causal force behind the partitioning (Schoener 1974). Logically, the competitive hypothesis would then be non-falsifiable, i.e. the reason that there is no evidence of competition is due to non-observable competition in the past.

Such an assertion can be challenged not only on logical grounds but on practical ones as well. Competitive interactions are not necessarily implied by overlapping resource utilization (Vandermeer 1972; Dayton 1973; Pianka 1974; Rathcke 1976; Sale 1977; Schoener 1974; and see Abrams 1980 for a relevant discussion of overlap measures), and clear partitioning patterns have been linked to noncompetitive mechanisms such as response to environmental gradients (Whittaker 1967; Harris 1972 among others), predation (Connell 1970a, b) and mixtures of mechanisms such as food distributions and predation (Dunham et al. 1978).

While competition may often be responsible for partitioning and subsequent specialization, it is also possible to examine partitioning in some systems from an energetic rather than a competitive orientation (Miller 1967). A potential cause of resource partitioning without competitive interactions is specialization of a consumer to maximize net energy accumulation (also see Mitchell 1969). The theoretical basis for such specialization, a feedback loop between a food's use and its value leading to increased specialization on somatic and genetic levels, has been clearly delineated by Emlen (1968). If specialization occurred in different places along a prey resource gradient, clear partitioning among species or among guilds (if multiple species happen to specialize on the same resource) might result.

Central to the energetic argument is the appropriate prey resource gradient. If the extremes of the prey resource gradient require divergent specializations for efficient utilization, then intermediate prey types would be poorly utilized by the specialists

on either end of the gradient and no consumer would specialize on intermediate prey types. This *watershed effect* can best be appreciated by picturing the system as an adaptive response surface. The extremes of the gradient would be represented as depressions with the intermediate expression of the gradient being represented by a ridge between the troughs. The ridge represents a successful anti-predator adaptation by the prey, i.e. to efficiently utilize such prey, mutually exclusive adaptations would be required. Consumers would tend to accumulate evolutionarily in the depressions, i.e. they would evolve into one or the other adaptive mode to utilize prey resources most efficiently. If the prey distributions are patchy and any prey patch is too small to support a predator for any significant length of time, sufficient plasticity should be maintained to allow consumption of intermediate prey types for short periods so the search for optimal patches can continue. If the habitat happens to support species that are adapted to exploit different ends of the gradient, partitioning of the prey resource would be demonstrable but would have nothing to do with competition. Given the coexistence of divergent specialists, partitioning patterns may give the illusion of competition rather than being evidence of ecological interactions between consumers.

To demonstrate the *watershed effect*, a resource gradient requiring predator specializations must exist, the predators must be demonstrably adapted to the extremes of the gradient, and consumption of intermediate prey types must result in lower evolutionary fitness relative to consumption of prey from the appropriate gradient extreme. Such a system does exist among the sponge-eating dorid nudibranchs of Pacific Northwest in-shore marine environments and their sponge prey.

Sponges can be ranked according to the degree of organization of their skeletons (Bloom 1976). At one extreme are sponges in which the spongin fibers and spicules are independent of one another. Upon digestion, great quantities of loose, sharply pointed spicules are liberated. Any predator must pass these spicules without perforating its own digestive tract. At the other end of the gradient are sponges in which the spicules are firmly bound into interconnected spongin ropes. A predator faces the problem of fragmenting the sponge to ingest it and the problem of transporting and processing a bulky bolus of food with a complex, nondigestible matrix (Bloom 1976).

Dorid nudibranchs have countered either one or the other of these extremes of sponge skeletal organization by adopting distinct and mutually exclusive suites of adaptive predatory characteristics. Dorids that consume sponges with poorly organized skeletons tend to have a radula with many fine teeth (a 'leaf rake' radula), a caecum in the floor of the stomach which packages loose spicules into spicule-mucus ropes, and a narrow-bore intestine moving fecal material primarily by ciliary means. All of these characters enable the animal to deal efficiently with loose spicules and easily fragmented sponges. On the other hand, dorids that consume sponges with well-organized skeletons tend to have radulas with fewer but larger teeth (a 'garden rake' radula), a stomach without a caecum, and a muscular intestine which moves material peristaltically. These characters aid the animal in fragmenting tougher sponges and in processing bulky fragments. These two adaptive modes can be viewed as forming the basis for dividing sponge-eating dorids into two guilds (*sensu* Root 1967), the caecate dorid guild and the caecate dorid guild (Bloom 1976).

The general conclusion that caecate dorids prey on sponges with poorly-organized skeletons and acaecate dorids prey on sponges with well-organized skeletons has been shown to hold for virtually all sponge-eating dorids whose diets have been deter-

mined (Bloom 1976). This demonstration, however, is based on observations of field diets and is therefore highly influenced by prey availability.

To further test the hypothesis that there are two guilds among dorid nudibranchs and that the observable resource partitioning patterns are likely to have arisen through the *watershed effect*, this paper examines six Pacific Northwest nudibranchs, *Archidoris montereyensis* (Cooper), *Archidoris odhneri* (MacFarland), *Cadlina luteomarginata* MacFarland, *Diaulula sandiegensis* (Cooper), *Anisodoris nobilis* (MacFarland) and *Discodoris heathii* MacFarland. Partitioning is demonstrated for both habitat and food resources. Energy input for a dorid species (as influenced by feeding rates, processing efficiencies and quality of food) is virtually identical regardless of prey type consumed while significantly greater growth and reproductive output is supported by prey from the appropriate extreme of the gradient as opposed to intermediate prey types. These data are shown to support specialization and to be consistent with the *watershed effect*, and thus constitute an alternative to competitive interactions as an explanation for resource partitioning among sponge-eating dorid nudibranchs.

Methods and Materials

Resource Utilization Patterns

Specimens of the six dorid species were collected from several intertidal and many subtidal stations in the San Juan Archipelago, Washington (by SCUBA diving) between March 1970 and December 1973. Species of nudibranch and the location and depth of the station were recorded for all specimens. Six hundred and sixty-four individuals were taken overall. The dorids were returned to the laboratory and placed in holding chambers (one-liter plastic containers with screened sides to allow water circulation) in clean shallow aquaria with flowing, filtered seawater.

In order to identify prey species, feces were collected and the spicules were extracted and mounted on permanent microscope slides (Light et al. 1954). The slides were examined to determine the spicule types and thus the species of sponge that had been eaten by the dorid. Identifications were made according to Bakus (1966) and de Laubenfels (1932, 1961). All identifications of species were verified by Dr. Bakus. The taxonomic ordering of the genera is primarily based on that given by Bergquist et al. (1971), Bergquist and Hartman (1969) and Bakus (1966, pers. comm.).

Paralleling the data-summation technique used by DaCunha et al. (1957) for yeast in *Drosophila* diets, the data for a particular dorid-sponge combination were compiled by summing the number of times a given species of sponge was observed in the feces of a given species of dorid, regardless of whether other sponge species were also present in the feces. The resulting dietary profiles for the six dorids listed above feeding on twelve sponges (representing 99% of all sponge observations in dorid feces) were analyzed by a FORTRAN IV program, TRELIS (described in Bloom et al. 1972).

Feeding Rates

Due to the nature of sponge prey, no feasible method exists for measuring the amount of sponge ingested during a feeding bout. However, an accurate and efficient indirect method does exist. The first element in the method is the fractionation of whole sponge into digestible organic, spongin and spicule fractions. This is accomplished by sequential digestion in KOH and NaOCl.

The four most common sponges occurring in dorids' diets (*Haliclondria panicea* (Pallas), *Haliclona permollis* (Bowerbank), *Myxilla incrustans* (Esper) and *Mycale adhaerans* (Lambe)) were fractionated by digesting 2,000 mg of powdered sponge dried at 80° C in 20 ml of 1 molar KOH for 4 h. This treatment dissolves up to 98% of the digestible organic material while having a negligible effect (less than 5% loss) on spongin (Bloom 1974). Residues were washed with distilled

Table 1. Percentages of major components of the four most common sponges in dorid diets (see text for fractionation procedure)

Sponge component	Sponge species							
	<i>Halichondria panicea</i>		<i>Haliclona permollis</i>		<i>Myxilla incrustans</i>		<i>Mycale adhaerans</i>	
	mean	stn. dev.	mean	stn. dev.	mean	stn. dev.	mean	stn. dev.
Digestible organic fraction	48.67	3.43	56.82	5.38	50.97	6.90	46.60	1.73
Spongin (KOH-resistant) fraction	8.77	2.81	5.74	1.81	6.45	4.01	4.62	1.91
Spicule (inorganic) fraction	42.55	3.03	37.40	4.48	42.94	5.85	48.80	1.72
Sample size	14		15		18		15	

water and sedimented three times. The residues were dried at 80° C and reweighed. They were then digested with 5.25% sodium hypochlorite, washed twice in distilled water, washed twice in 95% ethanol and dried by combustion of the alcohol. The residues, now consisting only of inorganic materials, e.g. spicules, were reweighed. The resulting data (total dry weight, weight of the KOH-resistant fraction and the weight of the sodium hypochlorite-resistant fraction) were used to determine estimates of digestible organic, spongin and spicule fractions of the four sponges. These data will be used in estimation of digestive efficiencies as well as feeding rates (Table 1).

Measurements of total processing time (grams digestible organic material consumed per unit time per gram consumer) were attempted for the six species of dorids consuming the four sponge species listed above. An accurate feeding rate can be determined for any given feeding bout if the time spent feeding and the amount of inorganic material in the feces are known. Each feeding bout consisted of first starving the individual for 3 to 5 days, a period of time sufficient to allow the dorid to clear its digestive tract of inorganic materials from previous feedings. The dorid was then weighed (Carefoot 1967) and placed in a clean holding chamber in a shallow aquarium with filtered flowing seawater, several hours before food was made available. Either newly collected clumps of *H. panicea* or *H. permollis* or fresh *M. incrustans* or *M. adhaerans* encrusting one valve of the scallop *Chlamys hastata herica* or *C. rubida* were added to the chamber. The dorid was placed on the sponge and whether the dorid was feeding or not was monitored and scored at 30 minute intervals. Temperature was monitored and approximated 10° C for all experiments.

Due to the morphology of these dorids, actual observations of the feeding apparatus in use were impossible without physically removing the animal from the food and thus ending the feeding bout. For a dorid to be scored as feeding, the dorid must have been on or adjacent to the food and the food must have been in contact with the head and mouth region of the dorid.

Total time spent feeding was the sum of the intervals during which feeding (as defined above) was observed. Experiments were terminated for various runs at 10, 15, 24, 72, and 168 h. Some intervals between monitoring for long experiments were greater than 5 h. Data were excluded from consideration if the sponge was unharmed at the end of a run, if the dorid died within five days of the termination of a bout, or if the monitoring period was greater than three hours and the animal changed feeding states.

All feces from each container were collected for five days after the termination of an experiment. The feces were digested with NaOCl as described above, dehydrated in 95% ethanol, dried by combustion, and weighed.

The data derived from these experiments included dorid wet weight, dry weight of spicules in the total fecal content and the time spent feeding for various combinations of dorids and sponges. Spicule weight was converted into estimated digestible organic input by the formula:

$$D_{ijk} = \frac{S_{jk}}{P_i} O_i$$

where D_{ijk} is the digestible organic material in milligrams, S_{jk} is the spicule weight (mgm) of the feces, P_i and O_i are the spicule fraction and the digestible organic fraction respectively of the i th sponge,

the j th feeding bout and the k th dorid species. Carefoot (1967) has used a similar procedure for determining the dietary input in another sponge-rasping dorid nudibranch.

Not all dorids ate all sponges under laboratory conditions. After twenty unsuccessful attempts to feed a particular sponge species to a particular dorid species, that particular dorid-sponge combination was excluded from further testing. Due to extremely specific diets of very rare sponges and few dorid specimens, measurements were not possible for *C. luteomarginata* and *D. heathii*.

For each successful dorid-sponge combination, the feeding rates were divided into two groups, short-term (≤ 15 h) and long-term (> 15 h). The division at 15 h corresponds to the appearance of digestive gland wastes (degraded sponge pigments) in the feces of caecate dorids and was chosen to separate the effects of intermittent feeding from continuous feeding. Caecate dorids consuming easily fragmented prey stop ingesting food periodically so as to allow the digestive wastes to pass from the digestive gland through the temporarily quiescent stomach and into the intestine for elimination (Millott 1937; Forrest 1953) as opposed to continuous feeding by acaecate dorids (Fournier 1969). As a result, long-term feeding rates for caecate dorids eating easily fragmented prey should be slower than short-term rates and estimates made of energy input based on short-term rates will overestimate energy input.

Linear regression analyses for short- and long-term feeding rates for all dorid-sponge combinations (time spent feeding versus amount consumed per gram wet weight consumer) were performed. If the null hypothesis of a zero slope ($\alpha=0.05$) was accepted for short or long-term feeding rates of any dorid-sponge combination, those data were excluded from further analysis.

Covariance analyses (Sokal and Rohlf 1969) were performed between short- and long-term feeding rates for each dorid-sponge combination. If the covariance analysis indicated that the division was unwarranted, the data were pooled for that dorid-sponge combination. A covariance analysis was then run between all dorid-sponge combinations of independent standing.

Utilization Efficiencies

Feces resulting from the consumption of a variety of sponges were collected from specimens of the four dorid species and processed as described above for the fractionation of sponges. Care was taken to collect only fresh feces uncontaminated by extraneous particulate debris. Because fecal quantities per animal were too small for accurate analysis, total fecal material resulting from a feeding bout on a given sponge by several specimens of a given dorid species were pooled and analyzed. The feces from several feeding bouts were used to generate replicate measurements.

The efficiency of digestion, e.g. extraction of digestible organic material, was estimated for any dorid-sponge combination by the equation:

$$E = 100.0 \times \left(\frac{O \times S}{P} - R \right) / \left(\frac{O \times S}{P} \right)$$

where E is the efficiency of digestion, O and P are the digestible organic and spicule fractions respectively of the sponge, and R and S are the fecal digestible organic and spicule fractions respectively of the dorid species.

Growth Rates

A series of experiments was initiated to test the effects of food types on growth and reproduction of dorids. Due to collection difficulties, *A. montereyensis* consuming *H. panicea* and *M. incrustans*, and *A. nobilis* consuming *M. incrustans* and *M. adhaerens* were used. All dorids were collected and isolated for one week without food in holding chambers in shallow aquaria with flowing seawater. Ten specimens of *A. nobilis* fed on *M. incrustans* for 73 days and 11 animals fed on *M. adhaerens* for 84 to 159 days. Four individuals of *A. montereyensis* fed on *H. panicea* for 101 days but the bulk of information for this dorid species was gathered under an experimental procedure designed to eliminate individual and environmental effects on the differential results of food types on growth and reproduction. One group of 7 specimens was fed *M. incrustans* for 37 days while an equal-sized group was fed *H. panicea* for the same period. Food was withheld for 7 days and feeding recommenced with the first group now receiving *H. panicea* and the second group receiving *M. incrustans*. The result of these manipulations was that growth and reproduction for an individual dorid was measured on both food sources and that over all the data, the effects of the order of the food consumed or environmental effects (temperature, salinity, etc.) should have been equalized over the entire period. All experiments were run in the period between June 6 and November 12, 1973 with all experiments terminating on the latter date.

For all growth experiments, food was always present (with the exception noted above) and was replaced by fresh food every other day. At approximately weekly intervals, the dorids were gently damp-dried and weighed on a platform balance to a tolerance of 0.1 g (Carefoot 1967).

All egg masses were collected. Length and width of the ribbon, number of egg layers in the ribbon, number of eggs per capsule and five measurements of the number of capsules in a 0.967 mm² subsection of a microscope field were noted. The egg masses were dried at 80° C and weighed. Between 10% and 50% of the egg masses of each dorid-sponge combination were also weighed before drying so as to generate conversion factors for dry to wet weights. For each sampling date, the dry weights of the egg masses (if any) were converted to wet weights and added to the wet weights of the producers (Carefoot 1967).

The specimens for which growth and reproduction had been quantified had been selected to fall along a size gradient from very small to large so that the regression lines for those specimens consuming a given sponge would tend to overlap to some extent. The regression

statistics of smaller organisms of the same dorid species consuming the same sponge were used to predict the starting point of the regression for the next larger organism (Paul et al. 1977). In this way the various regression lines can be melded together. This procedure allows the fusion of growth rates for a variety of individuals of differing sizes into a 'species summation curve'. Growth data (*Archidoris pseudoargus* feeding on *H. panicea*) were extracted from the literature (Carefoot 1967) and compared to the growth results compiled by the 'species summation curve' method.

There was sufficient egg production by *A. montereyensis* to allow statistical testing (one-way analysis of variance) of the effects of different food species on egg production. Egg production (measured in grams dry weight of eggs per gram wet weight producer per day and also in units of numbers of eggs per gram wet weight producer per day) by this dorid species feeding on *H. panicea* was compared to egg production by the same specimens feeding on *M. incrustans*. The dry weights (and numbers of eggs) produced by an individual over the period of time it consumed a specific sponge were summed and divided by the product of the mean wet weight of the animal over that period and the number of days in the period. These data were then pooled according to the sponge consumed and tested to determine if a significant difference in egg production was associated with the food resource utilized.

Results

Resource Utilization Patterns

Intertidally, *A. montereyensis* and *D. sandiegensis* coexisted while subtidally *A. odhneri*, *C. luteomarginata*, *A. nobilis* and *D. heathii* occurred together (Fig. 1). Exact site locations can be found in Bloom (1974). The major habitats according to depth appeared to be partitioned along guild lines. Intertidally, the two common dorids belong to different guilds. Subtidally, the two dorids found at deeper depths (*A. nobilis* and *C. luteomarginata*) are also members of different guilds. Overall, each dorid species appears to have a restricted distribution with regard to depth and a partitioning pattern can be seen within each guild.

The diets of the dorids are presented in Table 2 along with diversity values (Shannon-Weaver H' calculated in decits). *A. montereyensis* was the most specialized of the dorids and it pri-

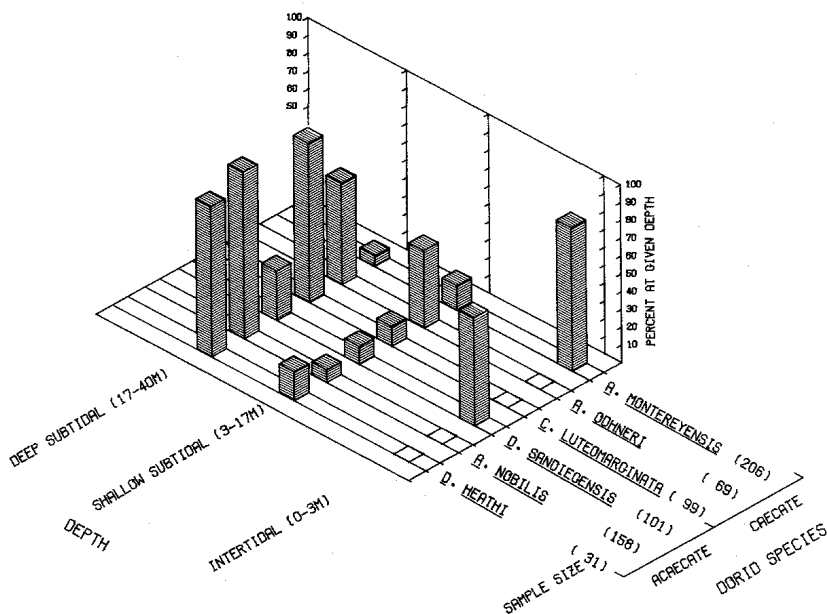


Fig. 1. Distributions of six dorid nudibranchs according to depth (see text for generic names of species)

Table 2. Percent occurrence of sponges in dorid diets. Values in table represent percent of individuals of dorid species above that had eaten sponge species at left. Sponge species which occurred at frequencies of less than 1% for all dorid species were excluded. See text for generic names of dorids

Order	Family	Genus and species	Caecate dorids			Acaecate dorids		
			<i>A. monte- reyensis</i>	<i>A. odhneri</i>	<i>C. luteo- marginata</i>	<i>D. sandie- gensis</i>	<i>A. nobilis</i>	<i>D. heathii</i>
Halichondria	Halichondriidae	<i>Halichondria panicea</i> (Pallas)	76.2	37.3	15.3	34.9	5.0	14.3
		<i>Higginsia</i> sp.			35.1			
Hadromerida	Suberitidae	<i>Terpios</i> sp.	4.3	26.5	2.7	1.7	1.3	4.8
Haplosclerida	Halicionidae	<i>Haliclona permollis</i> (Bowerbank)	2.3	2.4		32.6	0.6	4.7
Poecilosclerida	Amphilectidae	<i>Biemma rhadia</i> (de Laubenfels)				0.6	25.6	
	Myxillidae	<i>Myxilla incrustans</i> (Esper)	9.4	16.9	18.0	16.3	25.0	19.0
	Mycalidae	<i>Lissodendoryx firma</i> (Lambe)		3.6	5.4	1.2	3.1	4.8
		<i>Mycale adhaerens</i> (Lambe)	4.3	4.8	5.4	8.1	13.8	19.0
		<i>Mycale lingua</i> (Bowerbank)	0.4	2.4	5.4	4.7		23.8
		<i>Mycale psila</i> (de Laubenfels)	2.7	1.2	3.6		8.8	9.5
		<i>Mycale richardsoni</i> Bakus					1.3	
		<i>Zygerherpe hyaloderma</i> (de Laubenfels)	0.4	4.8	8.1		15.6	
		food species diversity ($H' - \log_{10}$)	0.40	0.72	0.82	0.66	0.81	0.83
		sample size	256	172	83	160	111	21

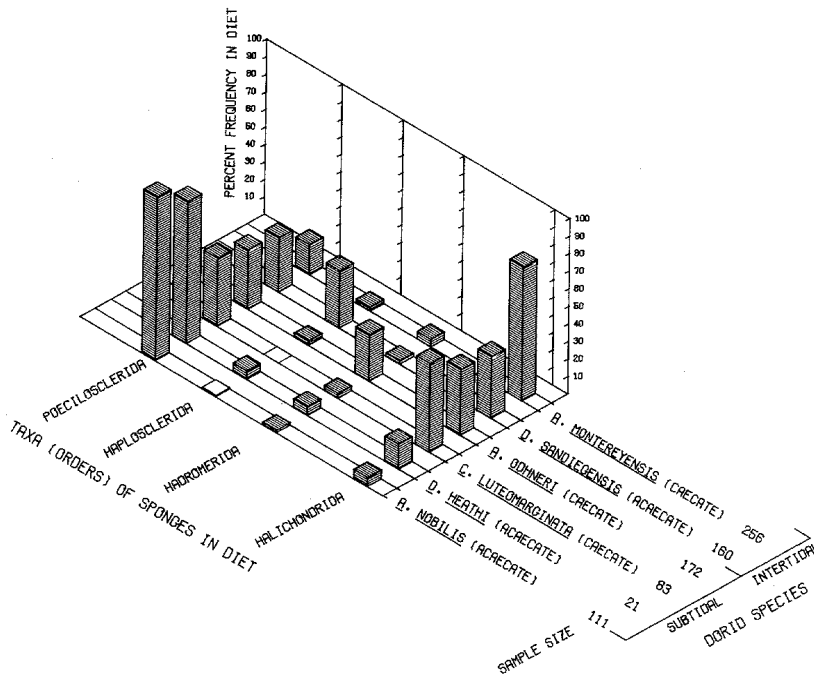


Fig. 2. Dietary patterns of six dorid nudibranchs (see Table 2 for Complete diets by sponge species)

marily consumed *H. panicea*. The other intertidal dorid, *D. sandiegensis*, had a broader diet consisting of the commonly occurring *H. panicea* and the less common *H. permollis*. The subtidal dorids had fairly consistent diversity values. In deeper subtidal areas, the two co-occurring dorids had widely different diets; *A. nobilis* consumed poeciloscleridan sponges while *C. luteomarginata* consumed halichondrid sponges.

The effect of sponge skeletal organization on the dietary patterns can best be appreciated by pooling the dietary data by sponge orders (Fig. 2). The orders Halichondrida and Hadromerida are characterized by poorly-organized skeletons (de Laubenfels 1932, 1961; Hyman 1940). Isodictyal skeletons (spicules

connected by small amounts of spongin into a 3-dimensional network) are characteristic of the Haplosclerida (de Laubenfels 1961) and reticulated meshes or well-organized skeletons characterize the Poecilosclerida (Hyman 1940). The diets of the caecate dorids are clearly dominated by the first two orders while the last two sponge orders constitute the bulk of food items of acaecate dorids. These data support quantitatively the hypothesis of two guilds of dorids advanced primarily on qualitative evidence (Bloom 1976).

Of the four major sponges that appear in these dorid diets, *H. panicea* represents the easily fragmented, poorly-organized skeletal extreme of the sponge gradient. *M. adhaerens* represents

Table 3. Statistical analysis of feeding rates ($Y = B_0 + B_1X$ where Y = milligrams digestible organic content per gram wet weight dorid; X = hours spent feeding). All regressions significant at $\alpha = 0.05$. Covariance coding: '.' = coincident; 'p' = parallel not noncoincident; 'n' = noncoincident and nonparallel regression lines at $\alpha = 0.05$

Dorid-sponge combination		Length of feeding bout	Sample size	Regression statistics		Correlation coefficient r	Covariance analyses dorid-sponge combination number														
Dorid	Sponge			B_0	B_1		1	2	3	4	5	6	7	8	9						
<i>A. montereyensis</i>	<i>H. panicea</i>	0-15 h	170	3.695	0.844	0.44	1														
	<i>H. permollis</i>	0-15 h	24	0.476	1.094	0.69	2	.													
	<i>M. incrustans</i>	>0 h	74	7.206	1.094	0.66	3	.	.												
<i>A. odhneri</i>	<i>M. adhaerens</i>	0-15 h	4	-2.712	1.555	0.99	4	.	.	.											
	<i>H. panicea</i>	0-15 h	11	-0.017	0.800	0.81	5	.	.	.	n										
<i>D. sandiegensis</i>	<i>M. incrustans</i>	>0 h	10	6.202	0.260	0.53	6										
	<i>H. panicea</i>	0-15 h	5	0.099	0.567	0.97	7	.	.	.	n	.									
<i>A. nobilis</i>	<i>H. permollis</i>	>0 h	12	2.987	0.702	0.76	8	.	.	.	n	.	.								
	<i>M. incrustans</i>	>0 h	57	3.722	0.305	0.76	9	.	n	p	n	p	
	<i>M. adhaerens</i>	>0 h	16	2.263	0.229	0.90	10	.	n	p	n	n	p

Table 4. Fractionation of dorid feces. Statistical coding: '.' = nonsignificant; '*' = significant difference at $\alpha = 0.05$. See text for procedure of estimating extraction efficiencies

Dorid-sponge combination		Fecal component percentages						Extraction efficiency		Mann-Whitney U-test dorid-sponge combination number							
Dorid	Sponge	Sample size	Spicule		Spongin		Digestible organic		Mean	S.D.	1	2	3	4	5	6	
			Mean	S.D.	Mean	S.D.	Mean	S.D.									
<i>A. montereyensis</i>	<i>H. panicea</i>	8	82.1	1.99	11.8	2.39	6.2	2.80	93.5	3.06	1						
	<i>M. incrustans</i>	5	80.1	4.21	13.9	4.76	6.0	1.29	93.7	1.27	2	.					
<i>A. odhneri</i>	<i>H. panicea</i>	6	70.8	1.70	23.8	1.16	5.5	0.72	93.2	1.03	3	.	.				
<i>D. sandiegensis</i>	<i>H. permollis</i>	3	85.3	0.65	7.3	0.31	7.4	0.95	94.3	0.78	4	.	.	.			
	<i>M. incrustans</i>	2	68.3	2.19	14.6	2.47	17.3	0.35	78.7	0.25	5	*	*	*	.		
<i>A. nobilis</i>	<i>M. incrustans</i>	4	82.4	1.65	2.2	1.76	15.5	0.31	84.1	0.56	6	*	*	*	*	.	
	<i>M. adhaerens</i>	5	79.0	3.24	8.9	1.68	12.1	1.78	83.8	2.91	7	*	*	*	*	*	.

the other extreme, sponges with well-organized skeletons. *H. permollis* and *M. incrustans* fall into the intermediate category of sponge skeletal structure. Two common caecate dorids, *A. montereyensis* and *A. odhneri* consume *H. panicea* more often than other sponges but do take the intermediate sponge *M. incrustans*. The two common acaecate dorids, *A. nobilis* and *D. sandiegensis*, consume more well-organized sponges (Families Mycalidae and Haliclionidae respectively) than other skeletal types but also take sponges with intermediate skeletal organization.

The dietary overlap between dorids consuming sponge species was calculated using the Bray-Curtis Index (also known as the Index of Affinity, the Least Common-Percentage Index or Czekanowski's Quantitative Index) (see Boesch 1977 for a general discussion) after a percent transformation had been performed. Overlaps ranged from 23% to 64% with an overall mean of 46.2% (S.D. 10.8%). There were no clear patterns of overlap between or within guilds or habitats probably due to the limited number of cells in the matrix and species-specific distributional patterns of the sponges.

Feeding Rates

Feeding rates were successfully measured for 11 of the 16 combinations of the four common dorids with the four most common sponges in dorid diets (all taxa listed immediately above). The

combinations involving *A. odhneri* and *D. sandiegensis* with *M. incrustans* were excluded from consideration due to small sample sizes and statistically insignificant regressions. These species were either not common or not hardy under laboratory conditions. Long-term feeding rates for *A. montereyensis* on *H. panicea* were also excluded for similar reasons.

In general, a dorid species ingested the same amount of sponge tissue per gram consumer regardless of the sponge being consumed, i.e. the null hypothesis of coincident regression lines could not be rejected ($\alpha = 0.05$) (Table 3). The one exception to this rule was that *A. nobilis* had parallel rather than coincident feeding rates with the intermediate sponge, *M. incrustans*, being consumed in greater quantity than *M. adhaerens*.

Utilization Efficiencies

Fecal component percentages and estimated digestive extraction efficiencies are presented in Table 4 along with a pairwise comparison of the extraction efficiencies using a Mann-Whitney U-test (Siegel 1956). The digestible organic content of the feces consists of unused sponge, digestible organic material and mucus from the dorid. Overall efficiency should reflect nonutilized resources plus expended organic material due to processing the food, and this is accomplished with the method used here (Eadie 1969).

Extraction efficiencies within a dorid species were statistically

Table 5. Statistical analyses of dorid nudibranch growth ($Y=B_0+B_1X$ where Y =grams wet weight; X =days). All regressions significant at $\alpha=0.05$. Data for *A. pseudoargus* from Carefoot 1967. Only covariance analyses sharing a dorid or sponge species are displayed (see Table 3 for symbol code; numerical values are growth rate of category to the left divided by category above for noncoincident and nonparallel lines at $\alpha=0.05$)

Dorid-sponge-weight class combination			Sample size	Regression statistics		Correlation coefficient r	Covariance analyses dorid-sponge-weight combination number							
Dorid	Sponge	Weight class		B_0	B_1		1	2	3	4	5	6	7	
<i>A. pseudoargus</i>	<i>H. panicea</i>	0-20 g	16	-1.66	0.261	0.98	1							
<i>A. montereyensis</i>	<i>H. panicea</i>	0-20 g	125	-4.51	0.330	0.90	2							
		>20 g	43	-35.30	0.656	0.92	3	2.51	1.99					
<i>A. nobilis</i>	<i>M. incrustans</i>	>0 g	92	3.64	0.338	0.98	4		p	0.52				
		0-20 g	71	2.65	0.269	0.84	5				0.80			
	>20 g	43	-11.60	0.451	0.92	6				1.33	1.68			
	<i>M. adhaerens</i>	0-20 g	80	-1.65	0.072	0.91	7				0.27	0.16		
>20 g		52	-180.0	0.737	0.96	8				2.74	1.63	10.2		

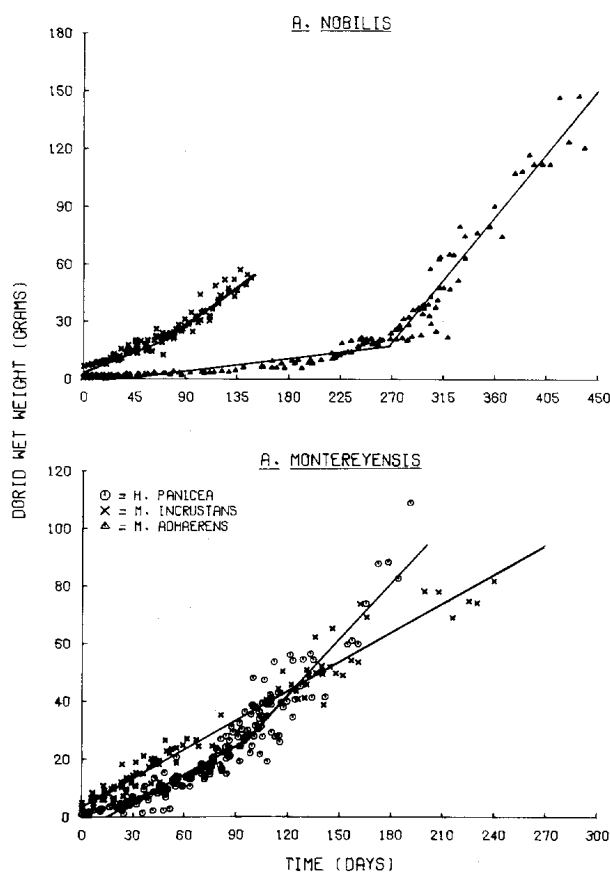


Fig. 3. Species summation curves of dorid nudibranch growth consuming the sponges indicated. Lines are least square estimates for animals 0 to 20 g and greater than 20 g wet weight. See text for the procedure by which these data were generated

indistinguishable ($\alpha=0.05$) regardless of the sponge consumed while the same sponge was processed at different levels of efficiency by different dorid species. *A. montereyensis* extracted approximately 93% of the available organic material regardless of sponge types while *A. nobilis* consistently extracted 84%. It would thus appear that extraction efficiencies are controlled pri-

marily by dorid digestive processes and are not greatly influenced by the sponge structure even when it ranges from the appropriate extreme of the sponge skeletal gradient to intermediate prey types.

Growth Rates

Growth rates (corrected for egg output) for the dorids *A. montereyensis* and *A. nobilis* were controlled by the size of the animal and the food resource. Visual examination of the plotted growth data indicated a change in rate at approximately 20 g wet weight for most dorid-sponge combinations (Fig. 3). Growth data for each combination were arbitrarily divided into small (0 to 20 g) and large (over 20 g) segments. A linear regression analysis for each segment and a covariance analysis between segments for each combination were performed (Table 5). Only for *A. montereyensis* feeding on *M. incrustans* was the null hypothesis of coincident growth rates of small and large dorids accepted ($\alpha=0.05$). The data for this combination were pooled for further analysis. For all other combinations, the larger weight class exhibited faster growth (Table 5).

For comparative purposes, growth data of *Archidoris pseudoargus* feeding on *H. panicea* were analyzed. There was no statistical difference between growth of small specimens of *A. montereyensis* and comparatively-sized specimens of *A. pseudoargus* when both were feeding on *H. panicea* ($\alpha=0.05$). This result justifies the data summation procedure outlined above.

Within a dorid species, large specimens grew faster on prey with the appropriate extreme of the sponge skeletal gradient than they did on intermediate prey types. *A. montereyensis* had comparable growth curves for small individuals feeding on *H. panicea* and *M. incrustans* but large specimens grew nearly twice as fast on the former (Fig. 3, Table 5). Large specimens of *A. nobilis* consuming *M. adhaerens* grew at 1.63 times the rate their counterparts did consuming *M. incrustans* (Fig. 3, Table 5).

If food were available for one year, *A. montereyensis* could attain a wet weight of 130 g feeding on *M. incrustans* and 210 g if the food were *H. panicea*. If a specimen of *A. nobilis* grew for that period, it would attain a weight of 90 g eating *M. adhaerens* or 150 g eating *M. incrustans*. However, if it ate *M. incrustans* until it reached 20 g and then switched to *M. adhaerens*, it would attain a mass of 250 g. This switch of food types from intermediate to extreme skeletal types by acaccate dorids is supported by field distributions and diets of *D. sandiegensis* (Bloom in prep.).

For both dorid species, maximal growth is supported by

Table 6. The influence of food types consumed on egg production by *Archidoris montereyensis*. Units are number of eggs or grams dry weight of eggs per gram wet weight producer per day

Sponge	Measure	Sample size	Mean	Standard deviation	One-way ANOVA ($\alpha=0.05$)
<i>H. panicea</i>	numbers	25	653.86	425.50	nonsignificant
<i>M. incrustans</i>		15	772.49	718.00	
<i>H. panicea</i>	weight	25	0.9032	0.5257	nonsignificant
<i>M. incrustans</i>		15	1.0710	0.6622	

a sponge possessing the appropriate extreme of the sponge skeletal gradient. In terms of growth, the optimal food for *A. montereyensis* is the easily fragmented *H. panicea* and the optimal food for *A. nobilis* is the well-organized sponge *M. adhaerens*.

Growth rates, while not necessarily directly related to reproductive effort or evolutionary fitness in all organisms, appear to be a direct measure of egg production (and presumably fitness) in these dorid nudibranchs, as well as other opisthobranchs (Kandel and Capo 1979; Chia and Skeel 1973). There was no statistical difference ($\alpha=0.05$) in egg production by *A. montereyensis* when feeding on *H. panicea* or *M. incrustans* regardless of whether production was measured as the number of eggs or the grams dry weight of eggs per gram wet weight producer per day (Table 6). A similar comparison cannot be made for *A. nobilis* due to poor spawning during the growth experiments. Since egg production was measured for the same individuals feeding on different foods, the prime factor controlling egg production was the size of the producer and not the food utilized. Growth appears to have precedence over reproduction in the allocation of energy resources in these animals in that growth rates double on the optimal food while reproductive rates remain constant. Since the optimal food, i.e. a sponge characterized by an extreme position on the sponge skeletal gradient, supports greatly increased growth, overall egg production would be significantly higher for a dorid consuming this food relative to a more intermediate food type.

Discussion

The concept of resource partitioning has been so closely interwoven with that of competition that the existence of resource partitioning has often been taken as proof of competitive interactions, even if there is little or no descriptive or experimental evidence to support that contention. Taken to extremes, competition as the ultimate cause of resource partitioning can become a non-falsifiable hypothesis. Even if a partitioning is due to specializations in diet or habitat that are self-stabilizing, the assertion can always be made that the original impetus was competition and that the specializations were subsequent adaptations. The essential question is whether resource partitioning leads to specialization or whether specialization can lead to resource partitioning. While there is no logical way to refute the competitive assertion, it is possible to advance a hypothesis that is falsifiable at the proximal level and thus has equal standing with competition as an ultimate cause.

An extensive examination of resource-utilization patterns revealed distinct patterns of habitat and dietary resource partitioning among six species of dorid nudibranchs (Figs. 1 and 2, Ta-

ble 2). All species are ecologically isolated from one another by habitat and/or diet.

The argument for competitive interactions would follow the line that since there are no observable behavioral interactions (individuals of the four most common species will simultaneously crop sponge from a single scallop shell in the laboratory), scramble rather than contest competition (*sensu* Nicholson 1955) would be expected. Since the distributions of sponges and dorids are extremely patchy (predictably these dorids are cross-fertilizing hermaphrodites with the ability to store sperm for extended periods of time), generalist foraging strategies are predicted (MacArthur and Pianka 1966). These generalist strategies however do not preclude the possibility of distinct food preferences. Since utilizing a patch does not preclude the use of the same patch by other individuals of the same or different species if any sponge remains, competition would be via exploitation rather than interference (Birch 1957 and also see de Jong 1976) and would be mediated by resource availability. Specialization in both food and habitat might be expected to occur and this would prevent the observation of competitive release on the time scale of a human observer. Since exploitation/scramble competition is notoriously difficult to document (Reynoldson and Davies 1970), the observed resource partitioning patterns could have arisen competitively without any evidence remaining of the causal mechanism.

There are several features of this evolutionary scenario that should be noted. Logically, there is no way to refute the scenario. Lack of direct evidence supporting the role of competition can be dismissed by the assertion that competition occurred in the past and subsequent evolution has erased any traces except the partitioning patterns. Secondly, the scenario hinges on the question of resource availability. Direct measurements of resource availability were hindered by observational difficulties involving estimation of sponge patch volume, extremely patchy sponge distributions subtidally and limited investigator search time due to diving limitations. Qualitatively, intertidal sponge resources appear to be superabundant (Bakus 1966, personal observations) and in all habitats almost all dorids tested (92%) were found to have recently eaten. Food is not likely to be a limiting or limited (Darlington 1972) resource. A second scenario can be erected that incorporates the evidence cited above, is evolutionarily reasonable, and can be falsified. Specializations may have arisen out of energetic considerations without reference to other dorid species. These specializations would be self-stabilizing and resource partitioning would occur when two divergent specialists happen to coexist.

This scenario requires that (1) there be a resource gradient such that mutually exclusive adaptive suites of characters are needed to exploit the ends of the gradient; (2) consumers do exist with those suites of characters; and (3) consumers of both ends of the gradient happen to coexist. Given these conditions, a resource partitioning pattern can be observed that has little or nothing to do with competition. If multiple specialists on the same extreme happened to coexist, the resource partitioning would be between guilds rather than between species. If guild members happened to coexist in the same habitat, competition might be expected to occur within the guild.

Sponge-eating dorid nudibranchs appear to be an example of such a system. Sponges are orderable according to the degree of skeletal complexity. Dorid nudibranchs can be divided into two guilds featuring appropriate specializations for the exploitation of the extremes of the sponge gradient (Bloom 1976). Furthermore, examination of their utilization abilities reveals that the food resource partitioning is self-stabilizing. *A. montereyensis*

serves as the best example. It consumes optimal (here defined as the unorganized extreme of the sponge gradient) prey at the same rate as intermediate prey (Table 3). Short and long-term feeding rates for this dorid eating intermediate prey (*M. incrustans*) are statistically indistinguishable from each other and from short-term feeding rates on the optimal sponge (*H. panicea*). Since feeding rates on the optimal sponge are likely to be overestimated due to intermittent feeding (Millott 1937; Forrest 1953), the amount of these foods consumed over a long period would either be the same or the intermediate food would be consumed in greater quantity.

Utilization efficiencies by *A. montereyensis* on the two sponges are virtually identical (Table 4) and the intermediate prey type has a slightly greater quantity of digestible organic material than does the optimal prey (Table 1). Combining ingestion rates, digestible organic contents and utilization efficiencies, the intermediate prey would seem to be as good if not a better source of energy that the optimal prey.

Examination of the growth rates shows this not to be the case. The optimal prey supports approximately twice the growth that the intermediate prey does once the dorid reaches a size at which its digestive adaptations come into full play. Thus the difference in net food worth is almost certainly due to increased internal utilization costs. The same or greater amount of food is processed per unit time with the same degree of energy extraction, yet the overall effect is less growth when the intermediate food is consumed. Since egg production and presumably fitness (see Menge 1972 or Vance 1973 for arguments linking fitness and egg production in planktotrophic organisms) is a direct function of size (Table 6), consumption of *H. panicea* by *A. montereyensis* should result in significantly higher fitness, i.e. the dorid would transmit more copies of its genome into the next generation, and specialization on the optimal prey would be expected. Morphologies and quantitative measurements of feeding, utilization and growth of other dorids supports this general conclusion.

The argument that energy input (as measured by feeding rates, extraction efficiencies and prey quality) is virtually identical for the optimal and suboptimal prey categories rests on potentially challengeable statistical grounds. Acceptance of the null hypothesis of no difference can be due to two reasons, the null hypothesis is true or insufficient data (too few observations and/or data with high variance) were collected. In that the internal patterns within the data sets are reasonable [intermittent versus continuous feeding for appropriate dorid-sponge combinations (Table 3), consistent extraction efficiencies for a dorid species but different efficiencies for the same sponge when consumed by different dorid species (Table 4)], the latter reason does not seem likely. Moreover, if the highly distinct growth rates (Table 5) were due to differences in feeding rates or extraction efficiencies, it would seem unlikely that differences of those magnitudes could have escaped detection during the direct measurements of those parameters.

It is thus reasonable to predict that if a dorid species were introduced into a habitat containing no other sponge consumers but a variety of sponges falling along the sponge-skeletal gradient, eventually the dorid species would have specialized on one extreme of the gradient. If in such a system, species specializing on different ends of the gradient happened to coexist, the food resource gradient would be partitioned even if there never were competitive interactions. I thus conclude that in the dorid system, the guilds partition the sponge resource due to self-stabilizing energetic considerations rather than due to competitive interactions.

If competition is not occurring between guilds, is it occurring within guilds and could this lead to habitat partitioning? Not only are there theoretical models to support such a suggestion (MacArthur and Pianka 1966 and see Schoener 1974), but the most likely place to find underutilized sponge resources would be in a habitat occupied by members of the other guild. A tidy way to explain the observable food and habitat partitioning patterns among these dorid species would be to postulate self-stabilizing specializations to maximize energy acquisition combined with competitive interactions within the guilds. However, there is little or no evidence to support the role of competition in the observed habitat partitioning. The intertidal dorids are more resistant to desiccation and exposure than are subtidal dorids (based qualitatively on laboratory hardiness and the results of occasional aquarium failures). Physiological tolerances plus homing in on specific sponge resources may account for the partitioning. Since sponges are known to have distinct spatial distributions proximately caused by larval substrate selection (Bergquist et al. 1968, 1970), and opisthobranchs are well known to have the ability to delay metamorphosis and preferentially settle out on adult food sources (Thompson 1958; Hadfield 1963, 1977; Franz 1975; Paige 1979), dorids may be found in certain habitats due solely to the fact that their optimal prey are found in the same habitats. The ability to delay metamorphosis until the adult food is encountered can be viewed as simply another character in the suite of adaptive characteristics for the exploitation of one or the other extreme of the sponge gradient. While admittedly this hypothesis pushes the question back to the sponge level, it suggests that competition need not be evoked to explain dorid habitat partitioning.

In summary, food resource and habitat partitioning are demonstrable among Pacific Northwest sponge-eating dorid nudibranchs. While competition can be evoked to 'explain' the partitionings as a non-falsifiable hypothesis, there is no evidence of competition. Rather, the food resource partitioning can be seen as arising from two co-occurring guilds, each specializing on different ends of a food gradient due to self-stabilizing energetic considerations, and habitat partitioning may be due to prey distributions and dorid physiological tolerances. Competition need not be evoked to explain partitioning among these nudibranchs and it is conceivable that in other systems of resource partitioning characterized by morphological and behavioral specializations, the driving selective force was not competition but self-stabilizing adaptations to maximize net energy acquisition.

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