Morphological Correlations Between Dorid Nudibranch Predators and Sponge Prey

BY

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(1 Text figure)

INTRODUCTION

MORPHOLOGICAL AND BEHAVIORAL specializations of a predator to its prey have been noted for birds (EDINGTON & EDINGTON, 1972; LACK, 1947; PERKINS, 1903), reptiles (PIANKA, 1969), fish (EMERY, 1973; FRYER, 1959; JONES, 1968; KEAST & WEBB, 1966), grasshoppers (ISELY, 1944) and opisthobranchs (EVANS, 1953; GRAHAM, 1938; HURST, 1965; LALLI, 1970; YOUNG, 1969). These specializations have been inferred to have arisen due to competition (BROWN & WILSON, 1956; CODY, 1968; DARLINGTON, 1972; HUTCHINSON, 1966) or due to selection to minimize utilization costs on patchy, divergent prey (BLOOM, 1974).

While feeding and digestive morphologies of sponge-rasping dorid nudibranchs (*sensu* YOUNG, 1969) are well known (see Discussion below for references), and skeletal morphologies of the sponge prey are available in the taxonomic literature, little attention has been paid to correlations of predator-to-prey morphologies within the sponge-rasping dorid nudibranch category.

By critically examining dorid nudibranch and sponge morphologies with regard to predatory correlations, certain logical predictions of prey-preferences by the predators result. The prediction that dorids with certain character-sets should preferentially consume sponges with certain skeletal organizations can be tested with laboratory preference studies and observations of diets of dorids in nature. Partial literature reviews exist (FOURNIER, 1969; MILLER, 1961; THOMPSON, 1964), although many of the reported observations do not fulfill the criteria listed by SWENNEN (1961) that the animal be found on or near the food, that the animal be observed to ingest the food, and that the animal be known to subsist on the food. The combination of these 3 reviews, recent work by many authors and my own observations provides an adequate data-basis to test the hypothesis that a correlation between dorid and sponge morphologies exists.

METHODS AND MATERIALS

Specimens of *Archidoris montereyensis* (Cooper, 1862), *A. odhneri* (MacFarland, 1966), *Cadlina luteomarginata* MacFarland, 1905, *Diaulula sandiegensis* (Cooper, 1862), *Anisodoris nobilis* (MacFarland, 1905) and *Discodoris heathi* MacFarland, 1905 were collected from several intertidal and many subtidal stations (by SCUBA diving) near San Juan Island, Puget Sound, Washington between March 1970 and December 1973. The estimated wet weight of each nudibranch, its species and the location and depth of the station were recorded. Over 600 individual nudibranchs were collected for study. The dorids were placed in thoroughly cleaned one liter capacity plastic containers with screened sides in clean shallow aquaria with flowing, filtered seawater at the Friday Harbor Marine Laboratories, Friday Harbor, Washington.

In order to identify prey species, feces were collected and processed according to the procedure outlined in LIGHT *et al.* (1954) and were examined to determine the spicule types present and thus the species of sponge consumed. Identifications were made according to BAKUS (1966) and DE LAUBENFELS (1932, 1961). Dr. Bakus kindly verified the identifications of all species of sponge.

The shape of the radula teeth for those dorids known to eat sponge and for which radular teeth drawings or specimens were available was quantified. Radulae of the dorid species mentioned above were removed from the animals, cleaned in dilute NaOCl, dehydrated in 70 and 100% ethanol and mounted in Canada balsam. Before placement of the coverslip, teeth from the functional area of the radula (anterior one-third of the rows, middle one-third of a pair of rows) were pulled free. Teeth were then drawn, using a camera lucida, at 100×.

Tooth shape, or the degree of "hook" of the teeth was defined as the amount of concavity of the inner margin of the tooth. The method for measuring the concavity is shown in Figure 1. Curvature was averaged over 3 teeth

Table 1

Sponge species reported in dorid nudibranch diets.

	Skeletal description	Skeleton described by
HEXACTINELLIDA		
ROSSELLIDAE		
Rossella racovitzae Topsent	moderately hard; crumbly; long spicules	(Burton, 1929; Dayton, per. comm.)
Rossella nuda Topsent	harder than *R. racovitzae;* long spicules	(Burton, 1929; Dayton, per comm.)
Scolymastra joubini		[1]
CALCAREA		
Calcinea		
LEUCETTIDAE		
LEUCASIDAE		
Leucetta barbata (Duchassing & Michelotti)[2]	confused mass of triaxons; resembles Demospongiae	(de Laubenfels, 1950)
DEMOSPONGIAE		
Tetractinomorpha		
HOMOSCLEROPHORIDA		
PLAKINDAE		
Plakortis simplex Schulze	confused mass of spicules	(de Laubenfels, 1950; 1954)
CHORISTIDA		
STELLETTIDAE		
Stelletta estrella de Laubenfels	cartilaginous with radiate tracts	(de Laubenfels, 1932)
HADROMERIDA		
CLIONIDAE		
Cliona celata Grant	confused mass of spicules	(Bergquist, 1965a; de Laubenfels, 1961)
SUBERITIDAE		
Stylotella columella	confused mass of spicules	(de Laubenfels, 1954[1]
Suberites ficus (Johnston)	confused mass of spicules	(de Laubenfels, 1932; Wells, 1960)
Terpios aploos de Laubenfels	confused mass to vague reticulation	(de Laubenfels, 1954)
Terpios sp.		[1]
Terpios zeteki de Laubenfels	confused mass of spicules	(Hechtel, 1965; de Laubenfels, 1950)
EPIPOLASIDA		
TETHYIDAE		
Tethya aurantia (Pallas)	radiate tracts without reticulation	(Bergquist, 1965a; de Laubenfels, 1932)
Ceractinomorpha		
HALICHONDRIDA		
HALICHONDRIIDAE		
Halichondria dura Lingren	confused mass of spicules	(de Laubenfels, 1951)
Halichondria panicea (Pallas)	confused mass of spicules; crumb-of-bread	(de Laubenfels, 1932)
Halichondria sp.		[1]
HYMENIACIDONIDAE		
Hymeniacidon perleve (Montagu)[3]	confused mass of spicules	(Bergquist, 1970)
Hymeniacidon sp.		[1]
Prianos phlox de Laubenfels	confused mass of spicules	(de Laubenfels, 1954)
Prianos sp.		[1]
HIGGINSIDAE		
Higginsia sp.	confused mass to vague reticulation	(Higgins, 1877[1])
HAPLOSCLERIDA		
DESMACIDONIDAE		
Desmacidon sp.	assumed to resemble other in order	(Bergquist, 1965b[1])
HALICLONIDAE		
Gellius sp.	confused mass to isodictyal	(de Laubenfels, 1932[1])
Haliclona permollis (Bowerbank)	unispicular isodictyal reticulation	(Wells, 1960; de Laubenfels, 1961)
Haliclona sp.		[1]
Reniera japonica Kadota	unispicular isodictyal reticulation	(de Laubenfels, 1936[1])
Reniera okadai Kadota		[1]
CALLYSPONGIIDAE		
Callyspongia diffusa (Ridley)	heavy fibro-reticulation	(de Laubenfels, 1954)

Table 1 (continued)

	Skeletal description	Skeleton described by
POECILOSCLERIDA		
MYXILLIDAE		
Acarnus erithacus de Laubenfels	large tracts without reticulation	(Bakus, 1966)
Myxilla agennes de Laubenfels	vague isodictyal reticulation	(de Laubenfels, 1932)
Myxilla incrustans (Esper)	confused mass to isodictyal reticulation	(Bakus, 1966)
MICROCIONIDAE		
Isociona lithophoenix de Laubenfels	dense isodictyal reticulation	(de Laubenfels, 1932)
Microciona astrasanguines Bowerbank	irregular reticulation	(Simpson, 1968)
Microciona coccinea Bergquist	prominent tracts without reticulation	(Bergquist, 1961)
Microciona haematodes de Laubenfels	isodictyal reticulation	(de Laubenfels, 1957)
Microciona seriata (Grant)[4]	prominent reticulation	(Simpson, 1968)
PSAMMASCIDAE		
Kaneohea poni de Laubenfels	isodictyal reticulation	(de Laubenfels, 1950)
OPHLITASPONGIIDAE		
Ophlitaspongia pennata (Lambe)	ladder-like tracts without reticulation	(Bakus, 1966)
PLOCAMIIDAE		
Hoplocamia neozelanicum	thinly-incrusting; spiculose	(Morton and Miller, 1968)
Plocamia karykina de Laubenfels	ladder-like tracts without reticulation	(Bakus, 1966)
ADOCIIDAE		
Petrosia dura	densely-packed spicules with stout reticulation	(Dendy, 1924[1]; de Laubenfels, 1951[1])
Toxidocia violacea de Laubenfels	isodictyal reticulation	(Bergquist, 1965b; de Laubenfels, 1950)
AMPHILECTIDAE		
Biemma rhadia de Laubenfels	spicules bound into bundles without reticulation	(Bakus, 1966)
MYCALIDAE		
Esperiopsis originalis de Laubenfels	reticulated with bound spicules	(Bakus, 1966)
Mycale adhaerens (Lambe)	massive reticulation with bundled spicules	(Bakus, 1966)
Mycale lingua (Bowerbank)	highly reticulated with bundled spicules	(Bakus, 1966)
Mycale macginitiei de Laubenfels	confused mass of spicules	(de Laubenfels, 1932)
Mycale maunakea de Laubenfels	large tracts without reticulation	(de Laubenfels, 1951)
Mycale psila (de Laubenfels)	highly reticulated with bundled spicules	(Bakus, 1966)
Zygerherpe hyaloderma de Laubenfels	ladder-like reticulations	(Bakus, 1966)
DICTYOCERTIDA		
APLYSILLIDAE		
Aplysilla glacialis (Dybowski)	many fibers without reticulation	(de Laubenfels, 1932)
DYSIDEIDAE		
Dysidea fragilis (Montagu)	irregular reticulation	(Bergquist, 1961; de Laubenfels, 1936)
SPONGIIDAE		
Cacospongia scalaria	soft consistency; skeletal form unclear	(de Laubenfels, 1936[1])

[1]skeletal characteristics assumed to be similar to other species in same genus or family
[2]synonomous with *L. solida* (de Laubenfels, 1950) and *L. floridana*, changed to above by Burton (1963)
[3]synonomous with *H. caruncula* and *H. sanguinea* (Bergquist, 1970)
[4]synonomous to *Ophlitaspongia seriata* (Simpson, 1968)

Table 2

Radular characteristics and caecate nature of known sponge-consuming dorid nudibranchs. (Literature citations coded by number and listed at end of table; r=radula description; c=caecum description; nd=not described.) See figure 1 for explanation of curvature of teeth.

Dorid	Caecate (C) or Acaecate (A)	Radular characteristics			
		Radular Mean	Formula Range	Curvature of teeth	Reference
DORIDIDAE					
Kentodoridinae				0.21	
Jorunna tomentosa (Cuvier)	(C)	19(23.0.23)	14-24(20-25.0.20-25)	0.21	r-[1, 26] c-[17]
Archidoridinae				0.22	
Archidoris montereyensis (Cooper)	(C)	32(53.0.53)	27-36(42-70.0.42-70)	0.12	r-[2, 14, 16, 20] c-[4]
Archidoris pseudoargus[a] (Rapp)	(C)	43(72.0.72)	29-56(37-100.0.37-100)	0.19	r-[1, 5, 11, 23] c-[8]
Archidoris stellifera (Vayssière)	(C)	30(42.0.42)	30(39-45.0.39-45)	0.23	r-[22, 23] c-nd
Archidoris odhneri[b] (MacFarland)	(C)	34(55.0.55)		0.36	r-[15] c-[4]
Archidoris flammea (Alder & Hancock)	(C)	25(36.0.36)			r-[1] c-nd
Archidoris wellingtonensis (Abraham)	(C)	42(61.0.61)	33-48(50-75.0.50-75)		r-[6, 7] c-[7]
Ctenodoris flabellifera (Cheeseman)	(C)	40(50.0.50)			r-[6, 7] c-nd
Doridinae				0.23	
Doris verrucosa (Cuvier)	(C)	32(37.0.37)	24-42(25-39.0.25-39)	0.20	r-[10, 22, 23] c-nd
Doriopsis granulosa Pease	(C)	34(44.0.44)	30-38(40-48.0.40-48)	0.11	r-[29] c-[29]
Doriopsis pecten (Collingwood)	(C)	31(35.0.35)	30-32(28-42.0.28-42)	0.21	r-[29] c-[29]
Doriopsis viridis Pease	(C)	28(25.0.25)	26-30(24-26.0.24-26)	0.38	r-[29, 30] c-[29]
Chromodoridinae				0.23	
Hypselodoris n.s.#1	(C)	28(21.0.21)		0.00	r-[29] c-[29]
Hypselodoris peasei (Bergh)	(C)	27(19.0.19)	26-28(17-20.0.17-20)	0.00	r-[29] c-[29]
Hypselodoris kayae Young	(C)	28(21.0.21)		0.13	r-[30] c-nd
Hypselodoris vibrata Pease	(C)	47(33.0.33)	38-56(28-38.0.28-38)	0.25	r-[29] c-[29]
Glossodoris macfarlandi[c] (Cockerell)	(C)	62(49.0.49)	62(47-50.0.47-50)	0.18	r-[15, 21] c-nd
Glossodoris amoena Cheeseman	(C)	79(99.0.99)	69-88(77-120.0.77-120)	0.42	r-[7, 20] c-nd
Glossodoris tricolor (Cantraine)	(C)				r-nd c-nd
Cadlina luteomarginata MacFarland	(C)	96(51.0.51)	90-114(47-58.0.47-58)	0.21	r-[14, 15, 21] c-[4]
Chromodoris dalli Bergh	(C)	112(28.1.28)	112(27-29.1.27-29)	0.22	r-[2] c-nd
Chromodoris lilacina (Gould)	(C)	64(40.0.40)	61-66(41-48.0.41-48)	0.25	r-[29] c-[29]

Table 2 [continued]

Dorid	Caecate (C) or Acaecate (A)	Radular characteristics: Radular Mean	Formula Range	Curvature of teeth	Reference
Chromodoris californiensis[d] (Bergh)	(C)	88(119.0.119)	82-92(98-132.0.98-132)	0.68	r-[2, 21] c-nd
Halgerdinae				0.63	
Halgerda rubra Bergh	(C)	34(53.0.53)		0.63	r-[29] c-[29]
Trippinae				0.13	
Trippa scabriuscula (Pease)	(A)	17(18.0.18)		0.13	r-[29] c-nd
Discodoridinae				0.11	
Discodoris heathi MacFarland	(A)	21(40.0.40)	20-22(36-42.0.36-42)	0.00	r-[14, 15, 17, 21] c-[4]
Discodoris fragilis (Alder & Hancock)	(A)	20(29.0.29)	18-22(28-30.0.28-30)	0.22	r-[29] c-nd
Aldisinae				0.33	
Austrodoris macmurdensis Odhner	(A)	18(25.0.25)	13-22(19-240.019-24)	0.32	r-[20] c-nd
Rostanga pulchra MacFarland	(A)	76(76.0.76)	65-80(39-90.0.39-90)	0.33	r-[14, 15, 16, 17, 21] c-[19]
Rostanga arbutus (Angas)	(A)				
Rostanga rubicunda (Cheeseman)	(A)	69(82.0.82)			r-[7] c-nd
Rostanga rufescens[e] Iredale & O'Donoghue	(A)				
Aldisa sanguinea (Cooper)	(A)	67(86.0.86)	60-70(70-100.0.70-100)		r-[14, 15, 17, 21] c-nd
Diaululinae				0.60	
Diaulula sandiegensis (Cooper)	(A)	21(29.0.29)	19-23(25-34.0.25-34)	0.37	r-[15, 15, 17, 21] c-[4]
Peltodoris atromaculata Bergh	(A)	20(56.0.56)		0.50	r-[22, 23] c-[9]
Anisodoris nobilis (MacFarland)	(A)	26(58.0.58)	23-27(55-62.0.55-62)	0.94	r-[14, 15, 17, 21] c-[4]
HEXABRANCHIDAE				0.29	
Hexabranchus marginatus (Quoy & Gaimard)	(C)	45(78.0.78)		0.29	r-[29] c-[29]
DENDRODORIDIDAE					
Dendrodoris nigra (Stimpson)	(A)	no radula			c-[29]
Doriopsilla albopunctata[f] (Cooper)	(A)	no radula			c-nd

[1]-Alder & Hancock, 1845
[2]-Bergh, 1879
[3]-Bergh, 1880
[4]-Bloom, 1974
[5]-Burn, 1968
[6]-Eliot, 1877
[7]-Eliot, 1907
[8]-Forrest, 1953
[9]-Fournier, 1969
[10]-Franz, 1970
[11]-Hancock & Embleton, 1852
[12]-Hutton, 1881
[13]-Iredale & O'Donoghue, 1923
[14]-MacFarland, 1905
[15]-MacFarland, 1966
[16]-Marcus, 1959
[17]-Marcus, 1961
[18]-Millott, 1937
[19]-Moore, unpublished
[20]-Odhner, 1934
[21]-O'Donoghue, 1927
[22]-Provot-Fol, 1951
[23]-Provot-Fol, 1954
[24]-Roller, 1970
[25]-Rose, 1971
[26]-Steinberg, 1961
[27]-White, 1938
[28]-Winckworth, 1951
[29]-Young, 1966
[30]-Young, 1967
[31]-Young, 1969

[a] synonomous with *A. brittanica* and *A. tuberculata*, [27, 28]
[b] *(Austrodoris odhneri)*, ([24]), [5]
[c] *(Chromodoris macfarlandi)*, [23]
[d] *(Hypselodoris californiensis)*, [24]; *(Glossodoris californiensis)*, [21]
[e] *(Doris coccinea)*, *(Rostanga coccinea)*, [13]
[f] *(Dendronotus fulva)*, [26]

Table 3

A global survey of dorid-sponge interactions. Sponges are ranked in increasing order of skeletal complexity and thus increasing difficulty of fragmentation (see Table 1 for taxonomic placement and skeletal descriptions). Dorids are divided into caecate, unknown and acaecate classes and further ranked by taxa and mean tooth curvature (see text for details). The numbers in the table refer to literature citations included as footnotes.

	Leucetta solida	Plakortis simplex	Halichondria dura	Halichondria panicea	Halichondria sp.	Hymeniacidon perleve	Hymeniacidon sp.	Prianos phlox	Prianos sp.	Cliona celata	Suberites ficus	Stylotella columella	Mycale macginitiei	Terpios zeteki	Terpios sp.	Terpios aploos	Higginsia sp.	Rossella racovitzae	Rossella nuda	Scolymastra joubini	Cacospongia scalaris	Dysidea fragilis	Tethya aurantia	Acarnus erithacus	Biemma rhadia
Hexabranchus marginatus	22																								
Jorunna tomentosa				24																					
Archidoris montereyensis				25							05														
Archidoris pseudoargus				26		20																	17		
Archidoris flammea						11																			
Archidoris wellingtonensis					19		19																		
Doris verrucosa						14																			
Archidoris stellifera												13													
Ctenodoris flabellifera					19		19																		
Archidoris odhneri				05											05										
Doriopsis granulosa														22											
Doriopsis pecten																22									
Doriopsis viridis								22																	
Hypselodoris sp.																									
Hypselodoris peasei		22																							
Hypselodoris kayae																									
Glossodoris macfarlandi																									
Cadlina luteomarginata				05													05								
Chromodoris lilacina																									
Hypselodoris vibrata																									
Glossodoris tricolor																					14				
Glossodoris amoena																						19			
Chromodoris californiensis																									
Halgerda rubra																									

	Mycale maunakea	Aplysilla glacialis	Microciona coccinea	Stelletta estrella	Gellius sp.	Microciona atrasanguinea	Myxilla agennes	Myxilla incrustans	Desmacidon sp.	Haliclona permollis	Haliclona sp.	Kaneohea poni	Reniera japonica	Reniera okadai	Microciona haematodes	Toxadocia violacea	Microciona seriata	Isociona lithophoenix	Ophlitaspongia pennata	Hoplocamia neozelanicum	Plocamia karykina	Zygerherpe hyaloderma	Esperiopsis originalis	Petrosia dura	Callyspongia diffusa	Mycale lingua	Mycale psila	Mycale adhaerens	Caecate
Hexabranchus marginatus																													Hexabranchidae
Jorunna tomentosa										22																			Kentodoridinae
Archidoris montereyensis																													Archidoridinae
Archidoris pseudoargus																													
Archidoris flammea									14																				
Archidoris wellingtonensis																													
Doris verrucosa																													
Archidoris stellifera																													
Ctenodoris flabellifera																													
Archidoris odhneri								05																					
Doriopsis granulosa																													Doridinae
Doriopsis pecten																													
Doriopsis viridis																													
Hypselodoris sp.		22																	22										Chromodoridinae
Hypselodoris peasei																													
Hypselodoris kayae		23																											
Glossodoris macfarlandi					16						16																		
Cadlina luteomarginata								05																					
Chromodoris lilacina	22																												
Hypselodoris vibrata												22																	
Glossodoris tricolor																													
Glossodoris amoena																													
Chromodoris californiensis				16							16																		
Halgerda rubra															22														Halgerdinae

Trippa scabriuscula									22			Trippinae ?
Discodoris heathi	05						05				05 05	Discodoridinae
Discodoris fragilis										22		
Aldisia sanguinea									14			Aldisinae
Austrodoris macmurdensis				08 08 08								
Rostanga pulchra						09			09 28	32 28		
Rostanga arbutus								04 04				Acaecate
Rostanga rufescens							29					
Rostanga rubicunda						31			03 31			
Diaulula sandiegensis	05						05 05					Diaululinae
Peltodoris atromaculata										14		
Anisodoris nobilis		16	16			05	16 05			30	16 05	
Dendrodoris nigra	22											Dendrodorididae
Doriopsilla albopunctata		16	16			16						

Easy —— Gradient of ease of fragmentation of the sponge skeleton —— Difficult

1-Abeloos & Abeloos, 1932
2-Anderson, 1971
3-Ayling, 1968
4-Baba (in MacFarland, 1966)
5-Bloom[1]
6-Carefoot, 1967
7-Cook, 1962
8-Dayton et al., 1970[1]
9-de Laubenfels, 1927
10-Doran, 1951 (in Cook, 1966)
11-Fisher, 1937 (McMillian, 1942)
12-Flattely, 1922 (in Cook, 1966)
13-Forrest, 1953
14-Fournier, 1969
15-Garstang, 1889
16-McBeth, 1970
17-Miller, 1961
18-Millott, 1937
19-Morton & Miller, 1968
20-Rose, 1971
21-Thompson, 1964
22-Young, 1966
23-Young, 1967
24-6, 17, 18
25-5, 7
26-6, 13, 17, 20, 21
27-1, 15
28-2, 7, 9, 10
29-12, 14
30-5, 16
31-3, 19
32-2, 9

[1]species representing less than 10% of diets omitted

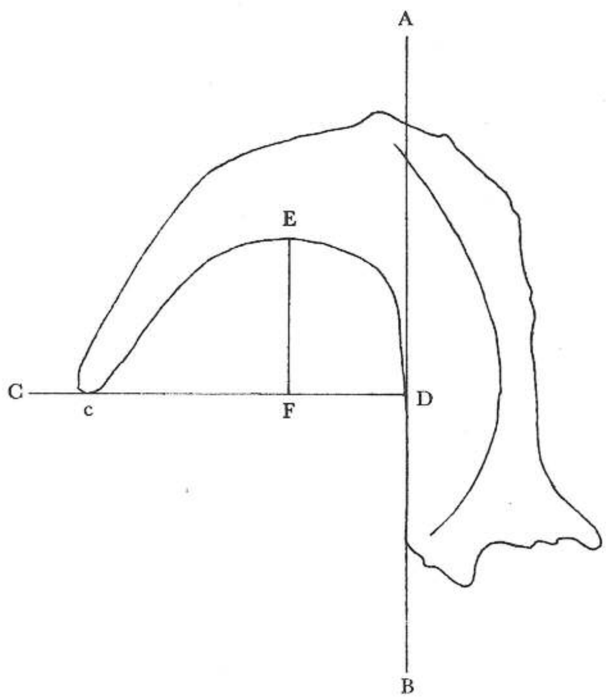

Figure 1

Procedure for estimation of radular tooth curvature

Construct a line (AB) parallel to the shaft; construct a line (CD) perpendicular to AB and touching the tooth tip; construct a line (EF) perpendicular to CD such that the distance between E and F is the maximum possible. The curvature index is:

$$\frac{\text{(distance between E and F)}}{\text{(distance between C and D)}}$$

per radula for all specimens prepared by the author. Curvature for other species was based on a similar analysis of published tooth drawings.

Preference experiments were done as follows: In the laboratory, food mosaics consisting of pieces (approximately 1 cm³) of *Halichondria panicea* (Pallas, 1766), *Haliclona permollis* (Bowerbank, 1866), *Myxilla incrustans* (Esper, 1805 - 1814) and *Mycale adhaerens* (Lambe, 1894) (1 : 1 : 1 : 1 by volume) were made available to 3 specimens each of *Archidoris montereyensis*, *A. odhneri* and *Anisodoris nobilis*, and to 2 specimens of *Diaulula sandiegensis*. Each dorid species was presented with its own mosaic to eliminate interspecific behavioral effects. Water entered the experimental chambers centrally at a flow rate of approximately 100 ml/minute. All dorids were starved for 7 days prior to the start of the experiment (sufficient time for all spicules from previous feedings to be voided from the dorids' digestive tracts). After 5 hours, the dorids were removed from the chambers. They were then cleaned and isolated in clean one-liter capacity plastic containers. Feces were collected, processed and examined as described above. Several random samples were taken from the mosaics and were similarly processed to form a comparison control for density of sponge spicules.

The relative percentage of the characteristic spicule types for each sponge in each fecal sample was estimated. Similarly, the percentage of each spicule type in the controls was estimated. Within the sampling error of the estimation procedure, the amounts of whole sponge available and the amounts of the characteristic spicule types in the controls were identical and exhibited a ratio of 1:1:1:1. The mean percent for each sponge for each dorid species was then calculated.

RESULTS

The taxonomy and skeletal characteristics of sponges known to occur in dorid nudibranch diets are presented in Table 1. Radular characteristics and the presence or absence of a caecum for dorids known to consume sponges are presented in Table 2.

The species of sponges occurring at frequencies of 10% or more in the feces of the dorids mentioned previously, along with an extensive review of dorid-sponge interactions, are presented in Table 3. The taxonomic arrangement of the genera in Table 1 is primarily based on that given by Bergquist *et al.* (1971), Bergquist & Hartman (1969) and Bakus (1966, personal communication).

The statistical analyses of the distribution of points in Table 3 is given in Table 4. *Diaulula sandiegensis* failed to feed during the course of the preference experiments and therefore will be omitted from further mention. The results of the preference experiments are presented in Table 5.

DISCUSSION

Diets are the result of complex interactions between predator abilities and preferences and prey availability (Emlen, 1966, 1968; Menge, 1972; Paine & Vadas, 1969). There are two underlying assumptions in demonstrating a correlation of predator-to-prey morphologies from diets in nature. The current concept of optimal food selection is that, through the process of evolution acting on the predator, the food that maximizes fitness will become the preferred prey (EMLEN, 1968). If the supply of food is sufficient and historically stable, specialization is the predicted outcome of natural selection. Furthermore, the specialization is usually reflected in predator morphology (see CODY, 1968). If the supply or stability of the food is low, exploitation of a range of similar foods, *i. e.*, generalization, is predicted. The assumption is then that the most preferred prey will be that prey for which the predator is morphologically adapted.

The second assumption relates to prey availability. If the predator is forced to expand its diet to compensate for scarce resources (MACARTHUR & PIANKA, 1966), diet expansion could act to obscure any correlations of predator-to-prey morphologies. If a correlation of predator-to-prey morphologies can be demonstrated, altering resource availability from the actual (but unknown) quantities to lower levels of availability might destroy the correlation due to generalization of the predator's diet, but an increase in resource availability can only improve the correlation. The same logic holds with regard to misidentifications of species and erroneous dietary information. These effects would more likely contribute "noise" than information content. Thus a demonstration of the correlation utilizing dietary data from nature would support the hypothesis, while failure to demonstrate the correlation does not necessarily imply negation of the hypothesis, but would cast doubt on the concept of specializations in the sponge-rasping dorid nudibranchs.

The radular anatomy of dorids has been critically examined (YOUNG, 1966, 1969; ROSE, 1971) and the great variance in radula tooth morphology has given rise to the speculation that there might be a correlation to the sponge prey (THOMPSON & BEBBINGTON, 1973). The digestive morphologies of many dorids have been described (HANCOCK & EMBLETON, 1852; BERGH, 1879, 1880; MARCUS, 1961; MORSE, 1968; ROSE, 1971; YOUNG, 1966) and are of 2 types: either the animal possesses a caecum, a spicule-compacting organ of the stomach (MILLOTT, 1937; FOR-

Table 4

Statistical analyses of point distributions in Table 3 (null hypothesis is randomness). The axes in Table 4 were divided as indicated and the number of symbols per cell were totaled.

Sponge skeletons	Species	Caecate dorids	Acaecate dorids	Chi-Square	Degrees of freedom	Probability
non-reticulated	*Leucetta solida* to *Myxilla incrustans*	32	19	5.66	1	<0.025
reticulated	*Desmacidon* sp. to *Mycale adhaerens*	6	15			
non-reticulated	*Leucetta solida* to *Higginsia* sp.	22	8	17.81	4	<0.001
bundled	*Rossella racovitzae* to *Myxilla incrustans*	10	11			
isodictyal	*Desmacidon* sp. to *Isocliona lithophoenix*	6	4			
ladder-like	*Ophlitaspongia pennata* to *Plocamia karykina*	0	4			
reticulated	*Zygerherpe hyaloderma* to *Mycale adhaerens*	0	7			

Table 5

Food preferences of dorid nudibranchs in the laboratory.
The relative amount of any sponge eaten by one nudibranch was estimated by the proportion of the characteristic spicule types in a well-mixed sample of the feces of that animal (see text for further details).

Dorid species	Sample size	Caecate or acaecate	Percent appearing in feces			
			Halichondria panicea non-reticulate	*Myxilla incrustans* semi-reticulate	*Haliclona permollis* isodictyal	*Mycale adhaerens* highly reticulate
Archidoris montereyensis	3	C	83	17	0	0
Archidoris odhneri	3	C	53	30	0	17
Anisodoris nobilis	3	A	2	20	5	73
random samples of mosaic	6		27	25	23	25

REST, 1953), or it does not (FOURNIER, 1969; BLOOM, 1974). Unfortunately, the digestive morphology of dorids is rarely mentioned in the taxonomic literature and the presence or absence of a caecum must be inferred from other dorids within a given subfamily.

Sponge skeletal morphology is also quite diverse, but tends to be similar within a given order. The order Halichondrida is characterized by spicules and spongin "intermingled without definite localization" (HYMAN, 1940). Bundled megascleres characterize the order Hadromerida while an isodictyal pattern (a pattern in which a 3-dimensional lattice is formed by spicules interconnected at their tips by spongin) characterizes the order Haplosclerida. The large order Poecilosclerida has a variety of skeletal types but is, in general, characterized by a reticulate network of interconnected spicules and spongin (HYMAN, *op. cit.*). Sponges, then, can be arranged to form a discontinuous resource gradient with regard to increasing difficulty of fragmentation. In other words, the first sponges would be the non-reticulated sponges (Halichondrida), followed by the bundled sponges (Hadromerida), then the semi-reticulated sponges (Haplosclerida) and ending with the highly reticulated sponges (Poecilosclerida). There are exceptions to these generalities and the actual descriptions of the skeletons of sponges which appear in dorid diets are given in Table 1 and their ranking is presented in Table 3.

The presence of a caecum appears to be a critical factor in dorid digestive strategies. A dorid with a caecum can handle large quantities of large and usually sharply-pointed spicules released by digestion of an unorganized or non-reticulated sponge. However, modifications of the radula and the intestine to handle non-reticulated sponge tissue and fecal-spicule ropes respectively appear to exact an energetic disadvantage when feeding on a more-reticulated sponge (the data supporting these generalities will be presented in a forthcoming paper).

Conversely, the absence of the caecum, paired with a more robust radula and a more muscular intestine, appear to be adaptations to a more-reticulated prey. Utilizing caecal and radular characteristics, the prediction is that animals with a caecum should preferentially consume non-reticulated sponges while animals without a caecum should preferentially consume reticulated sponge prey. Animals with more robust radulae, *i. e.*, fewer but larger and more strongly-hooked teeth, should preferentially consume more-reticulated sponges than animals sharing the same caecal characteristics but having less robust radulae. Due to lack of information on the size of radulae relative to the size of the animals, the only consistent measure of radular robustness readily available is the degree of "hook" or curvature of the radular teeth (Figure 1).

These predictions can be tested by regarding the data presented in Table 3 as points plotted on a Cartesian coordinate system and statistically analyzing the point distribution for randomness and correlation between the axes. The horizontal axis is the discontinuous resource gradient of sponges mentioned earlier, with non-reticulated sponges on the left. The vertical, or dorid, axis is arranged with all caecate animals as a group placed above all acaecate animals. Within these 2 categories, the subfamilies and the species within the subfamilies are arranged by mean radular tooth-curvature with the degree of hook increasing from top to bottom.

Given the arrangement of these axes, the prediction made above would imply a diagonal cluster from upper left (caecate, non-reticulated) to lower right (acaecate, reticulated). Visually, there does appear to be such a cluster (Table 3).

These data were analyzed statistically by regarding the table as a contingency table and testing for randomness. The results of such testing are presented in Table 4. When Table 3 is regarded as a 2×2 contingency table (caecate vs. acaecate; non-reticulated vs. reticulated), the chi-square statistic is sufficiently large to allow rejection of the null hypothesis of a random point distribution at the 0.025 level.

Further subdivision of the sponge axis results in an even more significant rejection ($p < 0.001$). This increase in the confidence that there is a relation between the axes may well be due to the addition of radular hook information. The correlation of the 2 axes is 0.45 (Contingency Coefficient) and the correlation is significant at the 0.001 level (SIEGEL, 1956).

Laboratory food preferences demonstrate the same pattern. The experimental design was such that the dorids were exposed to equal quantities of 4 sponges of widely varying skeletal complexity by placing the animals on a well-mixed sponge mosaic. If the ratio of characteristic spicule type in the feces for the 4 sponges was approximately equal to the ratio of those spicules in the control samples, the dorid producing the feces would have treated the mosaic in a generalized manner. If the ratio in the feces differed markedly from the ratio in the controls, the animal preferentially selected only certain grain-types in the mosaic. As shown in Table 5, caecate animals preferentially consumed non-reticulated sponges while acaecate animals preferentially consumed reticulated sponges.

The demonstration that there is a correlation between sponge and dorid morphologies may help to explain some of the puzzling variations in dorid morphology and is proof that there are specializations within the category of sponge-rasping dorid nudibranchs.

SUMMARY

1. Dorid digestive morphology is reviewed and the hypothesis that there are specializations within the category of sponge-rasping dorid nudibranchs as shown by a correlation of dorid morphology to sponge skeletal morphology is advanced.

2. Information on dorid diets is collected from a large number of fecal samples of 6 species of dorids found in the San Juan Archipelago, Washington, and from the literature, and is summarized to allow testing of the hypothesis.

3. There is a statistically significant correlation of dorid-to-sponge morphologies as shown by an analysis of dorid diets in nature.

4. Laboratory feeding-preference experiments support the conclusions reached through correlative means.

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