FEEDING ECOLOGY OF SOME COMMON INTERTIDAL NEOGASTROPODS AT DJERBA, TUNISIA

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RÉSUMÉ. — L'alimentation de certains Gastéropodes prédateurs communs de l'étage littoral de Djerba (Tunisie) est étudiée par l'analyse du contenu de l'appareil digestif. *Conus ventricosus* mange 14 espèces de Polychètes et 1 de Gastéropode, des espèces de Nereididae étant sa nourriture la plus courante. Le Buccin *Buccinulum corneum* se nourrit principalement de Polychètes euniciens et sabelliens, mais mange quelques Gastéropodes, particulièrement *Cerithium vulgatum*. *Cantharus dorbignyana* et *Engina bicolo* se nourrissent tous deux de Gastéropodes et de Polychètes, alors que *Mitrella scripta* se nourrit de Gastéropodes et de leurs œufs. *Columbella rustica* semble être herbivore. Une comparaison faite avec d'autres études menées en différents endroits suggère que les espèces de *Conus* venant de localités ayant une température hivernale de l'eau de mer plus basse, tendent à avoir une alimentation plus variée et étendue.

PREDATORY GASTROPOD
FEEDING ECOLOGY
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ABSTRACT. — The diets of some common predatory gastropods from intertidal habitats at Djerba, Tunisia, were investigated by gut content analysis. *Conus ventricosus* eats fourteen species of polychaete and a gastropod, with species of Nereididae the most common food items. The whelk *Buccinulum corneum* feeds mainly upon sabellid and eunicid polychaetes, but eats some gastropods. *Pisania striata* and *Phyllonotus trunculus* both eat gastropods, particularly the abundant *Cerithium vulgatum*. *Cantharus dorbignyana* and *Engina bicolor* both eat polychaetes and gastropods, whilst *Mitrella scripta* eats gastropods and their eggs. *Columbella rustica* appears to be herbivorous. A comparison with studies elsewhere suggests that *Conus* species from localities with cooler winter seawater temperatures tend to have broader diets.

INTRODUCTION

Recent empirical and theoretical models concerning the response of organisms to seasonal environments (Boyce, 1979, Valentine, 1983, 1984) suggest that one of the trophic responses is for animals to increase the *per capita* resources available by feeding upon a wider range of food items. Another response is to feed at lower trophic levels, thereby shortening the food chain and increasing efficiency. These responses result in a tendency for animals in seasonal environments to be trophic generalists.

Amongst predatory gastropods there is some evidence of broad latitudinal patterns in the degree of food specialisation (Taylor & Taylor, 1978). At high latitudes, species of a number of gastropod genera are known to have catholic diets, including as prey several animal phyla. These broad diets are often coupled with scavenging habits. Particular examples are members of the family Buccinidae including *Buccinum*, *Neptunea* (Pearce & Thorson,

Table I. — Common intertidal and shallow sublittoral Neogastropods at Djerba, Tunisia. Size expressed as mean shell length (mm), with standard deviation.

Gastropods	Habitat	Size
Muricidae		
Phyllonotus trunculus (Linnaeus, 1758)	sublittoral, thin sand on rock; rock	43.5 (5.8), n = 49
Muricopsis cristatus (Brocchi, 1814)	low intertidal and sublittoral rock and boulders.	19.9 (5.6), n = 51
Columbellidae		
Mitrella scripta (Linnaeus 1758)	sublittoral fringe, beneath boulders	13.6 (3.3), n = 17
Columbella rustica (Linnaeus, 1758)	sublittoral fringe, beneath boulders	16.1 (1.9) n = 14
Nassariidae		
Amyclina corniculum (Olivi 1792)	intertidal silt on rock	14.8 (1.4), n 30
Buccinidae		
Pisania striata (Gmelin 1791)	intertidal rocks, boulders and crevices	19.5 (4.2), n = 37 (Tourgueness) 23.3 (2.1), n = 78 (Bordjili)
Engina bicolor (Contraine 1835)	sublittoral fringe, beneath blocks	7.9 (0.5), n = 6
Cantharus dorbigynana (Payraudeau 1826)	low intertidal boulders	15.4 (3.3), n = 38
Buccinulum corneum (Linnaeus 1758)	sublittoral silty-sand, on rock	32.6 (7.8), n = 60
Fasciolariidae		
Fasciolaria lignaria (Linnaeus 1758)	sublittoral fringe, beneath boulders	14.1 (2.6), n = 15
Colubrariidae		
Colubraria reticulata (Blainville 1826)	sublittoral fringe, beneath blocks	18.8 (2.7), n = 15
Mitridae		
Mitra ebenus (Lamarck, 1811)	intertidal and sublittoral rock crevices	14.3 (1.5), n = 5
Conidae		
Conus ventricosus Gmelin 1791	intertidal rocky shore, beneath boulders boulders and silty sand on rock	18.8 (5.1), n = 128 Bordjili 22.2 (3.3), n = 98 Tourgueness

1967; Taylor, 1978; Shimek 1984) and *Searlesia* (Louda, 1979). In addition to their well-known scavenging activities upon dead and moribund prey, species of Nassariidae from temperate areas, for example, *Nassarius reticulatus* and *Ilyanassa obsoletus* are known to feed extensively upon organic detritus (Scheltema, 1964; Curtis & Hurd, 1979; Hurd, 1985; Tallmark, 1980).

By contrast, many tropical predatory gastropods have rather narrow diets usually including only a few species from a major prey class (Taylor, 1984). Good examples are the highly stenophagic species of *Conus* inhabiting coral reefs, which feed upon relatively few species of polychaetes (Kohn 1959, 1968, 1981, Kohn & Nybakken 1975). A further example of the specialised diets of tropical gastropods is amongst species of the family Mitridae, each of which feed upon just one or two species of sipunculans (Kohn, 1970; Fukuyama & Nybakken, 1983; Taylor, 1984, 1986).

One problem with latitudinal comparisons of diet is that the higher and lower latitude predators which have been studied to date, are taxonomically unrelated. As yet, there is little evidence of any intraspecific or intrageneric change in diet breadth with latitude. Although the data were collected for a different purpose, Kohn (1966) showed that *Conus californicus* from southern California feeds upon a much wider range of prey than its tropical congenors. At Hong Kong the muricid *Cronia margariticola* appears to have a broader diet than in the more equatorial parts of its range (Taylor, 1980). Additionally, there is some evidence that the temperate species in the largely tropical family Cymatidae, such as *Fusitrition oregonense* from the N.E. Pacific (Eaton in Kohn, 1983) and other species in Australia and New Zealand (Laxton, 1971) may have broader diets than their tropical relatives. However, despite these few examples there is very little quantitative data concerning this phenomenon.

The gastropod fauna of the Mediterranean Sea supports a number of common predatory gastropod species which belong to genera with largely tropical distributional ranges. Notable amongst these are *Conus ventricosus* (= *C. mediterraneanus*), and species of *Mitra, Pisania, Cantharus, Engina, Colubraria, Mitrella, Columbella, Phyllonotus* and *Muricopsis*. Apart from the observations of Alpers (1932) of *Conus ventricosus* feeding upon the polychaete *Perinereis cultrifera,* the diets of these gastropods are unknown.

This study of intertidal predatory gastropods around Djerba, Tunisia was initiated with the objective of establishing the food of these common shore animals in order to compare them with congenors or close relatives elsewhere. These data might then be used to test the hypothesis that diets tend to be broader in seasonal environments.

STUDY SITES

Collections were made in September 1984 from sites on the island of Djerba, situated at the southern end of the Gulf of Gabes, Tunisia (Lat. 34° N, 10° 40' E). The Gulf of Gabes is unusual in the Mediterranean in having a large tidal range of around 2.2 m at Gabes and around 1 m at Djerba. Mean winter temperatures in the gulf are 14.6°C and in the summer 25.4 °C (Ktari-Chakroun & Abderrazak, 1971).

Collections were made at two main sites :

1. Ras Tourgueness; this site consists of low rocky sandstone outcrops about 1 km west of the headland of Ras Tourgueness. The intertidal rock is eroded into irregular gullies and pools with the lower portions covered by a turf of red and green algae. The gastropod fauna includes *Conus ventricosus, Pisania striatus, Gibbula umbilicaris,* and *Monodonta turbinata.*

2. Bordjili : this site is situated about 200 m south of the Lighthouse at Bordjili at the NW tip of Djerba and consists of a ramp-shaped, low, cliff about 2 m high. The cliff is heavily dissected into pools and gullies with a step at the base on to a broad and shallow, sublittoral platform. Nearshore, this is covered by a variable thickness of sediment with patches of *Zostera* and *Posidonia,* with sponges embedded into the sediment. Loose boulders are common at the base of the cliff and sporadically scattered amongst the seagrasses. The intertidal gastropod fauna includes *Littorina neritoides* in the littoral fringe. Occurring lower on the shore are *Gibbula umbilicaris, Monodonta turbinata, Pisania striata* and *Conus ventricosus,* and in the tidal pools, *Cerithium vulgatum.* At the margins of the sublittoral platform *Cerithium vulgatum* is extremely abundant on open sandy substrates, along with *Phyllonotus trunculus, Buccinulum corneum,* and *Conus ventricosus.* On the undersides of boulders there is a diverse gastropod fauna including *Pisania striatus, Conus ventricosus, Mitrella scripta, Columbella rustica, Colubraria reticulata, Muricopsis cristata* and *Haliotis lamellosa.*

Additional samples of the nassariid *Amyclina corniculum* were collected from a muddy-silt habitat about 1 km N of Adjim on the southwest corner of Djerba.

METHODS

The predatory gastropods for dietary analysis were, after cracking the shells, preserved in 8 % formalin as soon as possible after collection. Food remains from the oesophagous, stomach and rectum were mounted on slides in Aquamount and identified by microscopic examination.

RESULTS

The prey identified from the gut content analysis and by field observation of predatory gastropods are shown in Table II. Polychaetes and gastropods are the main prey organisms eaten.

The diet of *Conus ventricosus* differed at the two localities sampled. At Bordjili the remains of 14 species of polychaete and a gastropod were recovered. Polychaete species from nine different families were eaten; 39 % of the remains were of the family Nereididae, with the eunicid *Palola siciliensis* and the capitellid *Capitella capitata* also quite common. Additionally, a single individual contained the operculum of the gastropod *Cerithium vulgatum.* By contrast, in *Conus* specimens from the rocky shore near Ras Tourgueness only one species of polychaete *Perinereis cultrifera* was recorded. The differences between the two localities may be due to variations in prey availability between the two sites, but this was not investigated.

Eighty-six per cent for of the food items from the sublittoral whelk *Buccinulum corneum* consisted of polychaetes and 12 % of gastropods. The sabellid *Branchiomma lucullana* forms 67 % of the polychaete remains with *Palola siciliensis* also important. The gastropods eaten include *Cerithium vulgatum* and *Columbella rustica.*

Although the results are based upon rather small samples the other buccinids *Cantharus dorbignyana* and *Engina bicolor* both feed mainly upon polychaetes. *Cantharus* eats *Palola siciliensis* and *Sabellaria spinulosa* and species of Maldanidae. The remains of the polychaetes *Dodecaceria* and *Vermilia* and gastropod radulae from juvenile *Cerithium vulgatum* were recovered from *Engina bicolor.*

The nassariid *Amyclina corniculum* has a diet which includes polychaetes and Crustacea. Most of the polychaete remains were of the dorvelleine, *Ophyrotrocha puerilis* and 26 separate jaws were recovered from one gastropod. The variety of crustacean remains recovered probably result from the scavenging activities of this snail upon dead and moribund material. In addition to the animal remains, quantities of blue-green algal filaments were found in the stomach of *A. corniculum.*

Only one specimen of *Fasciolaria lignaria* contained food remains; these consisted of setae from the capitellid polychaete *Notomastus.*

The common intertidal whelk *Pisania striata* feeds mainly upon gastropods. In particular, *Cerithium vulgatum* but also *Gibbula* and *Monodonta* have been recognised from radula and jaw remains. The prey are held in the foot and the proboscis inserted through the aperture. Three individuals of *Pisania* also contained fragments of barnacles and two others the setae of the polychaete *Polydora antennata.*

Table II. — Food items recovered from Djerba neogastropods. Polychaete classification after Fauchald (1977).

Prey items	*Conus ventricosus*		*Pisania striata*	*Buccinulum corneum*	*Cantharus dorbignyana*	*Engina bicolor*	*Mitrella scripta*	*Phyllonotus trunculus*	*Amyclina corniculum*
POLYCHAETA	a	b							
Spionidae									
Polydora antennata Clapérade	1		2						9
Polydora sp.									3
Cirratulidae									
Cirratula cirratus (Müller)	4								
Dodecaria concharum Oersted						2			
Capitellidae									
Capitella capitata (Fabricius)	5								
Maldanidae									
Clymene lumbricoides (Quatrefages)	1								
Johnstonia clymenoides (Quatrefages)	2								
Maldanid sp. A					2				
Maldanid sp. B					1				
Maldanid sp. C							1		
Syllidae									
Syllis amica Quatrefages	3								
Nereididae									
Perinereis cultrifera (Grube)	8	63							
Perinereis sp.	1	1							
Nereis caudata (Delle Chiaje)	8								
Nereis sp.		1							1
Eunicidae									
Palola siciliensis (Grube)	5			13	5	1			
Lumbrinereidae									
Lumbrineris coccinea Renieri	2			13	5	1			
Lumbrineris sp.	1								
Dorvilleidae									
Ophyrotrocha puerilis Clap. & Mecz.									14
Sabellariidae									
Sabellaria spinulosa Leuckart					3				
Terebellidae									
Terebella lapidaria Kahler	3				2				
Sabellidae									
Branchiomma lucullana (Delle Chiaje)			1	29					
Serpulidae									
Vermilia multicristata Philippi)						2			3
Polychaete setae indeterminate				1	3				
GASTROPODA									
Monodonta sp.			2						
Gibbula sp.			3				2		
Cerithium vulgatum Bruguière	1	40		2		3		47	
Columbella rustica (Linnaeus)				1					
gastropod tissue undet.			7	3	1		7		
gastropod eggs							6		
BIVALVIA									
Modiolus barbatus (Linnaeus)								2	
CIRRIPEDIA			3						
CRUSTACEA					1				10
Number examined	94	85	103	82	22	18	30	*	53
Number of identified prey	46	64	58	51	13	11	16	49	41
% food items = polychaetes	98.8	100	3.5	86.3	92.3	72.7	6.3		75.6
% food items = molluscs	2.2		89.7	11.8	7.8	27.3	93.7	100	

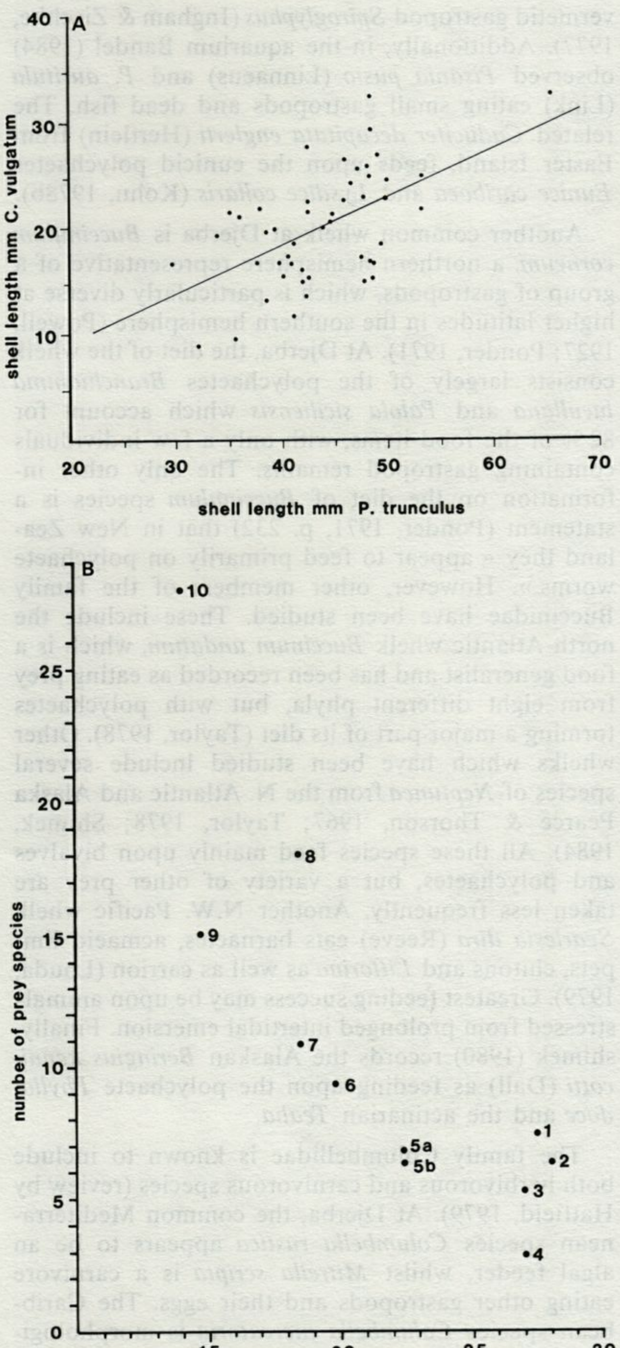

Fig. 1. — A, Relationship between the sizes of *Cerithium vulgatum* prey and the predator *Phyllonotus trunculus* at Bordjili, Djerba; B, Relationship between the number of prey species in the diet and winter seawater temperature for *Conus* species at various localities. Points for localities 1-7 represent means for several *Conus* species. Localities 8-10 are for single species. Except for Djerba, the data are from Kohn 1959, 1966, 1968, 978, 1981; Kohn and Nybakken 1975; and Nybakken 1978, 1979. Key to localities : 1. Indonesia 2. Maldives 3. Chagos 4. Enewetak 5. Hawaii 6. Gulf of California and W. Mexico 7. Galapagos Islands 8. Easter Island 9. Djerba 10. San Diego.

The sublittoral muricid *Phyllonotus truncatus* also feeds mainly upon *Cerithium vulgatum,* which are not drilled, as is the habit of most other muricids, but held in the foot and attacked through the aperture. Additionally, two individuals were observed eating small individuals of the bivalve *Modiolus barbatus.* Figure 1,A shows the relationship between the sizes of predator and prey for *P. truncatus* feeding upon *Cerithium vulgatum.* It is apparent that the mean prey size increases with predator size, as do both the largest and smallest prey taken. These data are consistent with the results that would be expected if the predators were conforming to optimal prey selection models (Leviten, 1976). However, as Hughes (1980) has pointed out, similar predictions would be expected for purely mechanical reasons, if the power and dexterity in handling prey are functions of predator size.

Out of the two species of Columbellidae examined, *Mitrella scripta* is a carnivore. Nine individuals contained gastropod tissue and in two cases, the remains of the radula identified this as a *Gibbula* species. The stomach remains from a further six individuals consisted of eggs, probably from an opisthobranch gastropod. One further specimen contained setae of a maldanid polychaete.

Six specimens of the other columbellid *Columbella rustica* all contained abundant algal filaments, diatoms and sediment. This species is apparently herbivorous.

No identifiable food remains were recovered from the 20 specimens examined of *Colubraria reticulata.* Faecal material in the rectum consisted solely of small brown granules. These are similar to brown granules seen in the digestive gland. The lack of material in the stomach, supports the suggestion of Ponder (1971) that some *Colubraria* species may feed suctorially.

No food remains were recovered or feeding observations were made upon *Muricopsis cristatus* and *Mitra ebenus.*

DISCUSSION AND CONCLUSIONS

The diets of *Conus* species have been intensively studied in other parts of the world by Kohn and his associates (Kohn, 1959, 1966, 1968, 1971, 1978a, 1981; Kohn & Nybakken 1975; Nybakken 1978, 1979) and these studies provide much the best data for latitudinal comparisons of diet.

Conus species in the tropical Indo-Pacific are known for their relatively specialized diets and in general amongst those taxa from coral-reef habitats, relatively few species of prey (largely polychaetes) are eaten. However, *Conus* inhabiting the Galapagos

Islands and the Gulf of California eat more prey species (Nybakken, 1978, 1979) and *Conus miliaris*, the single species on Easter Island, consumes eighteen prey species (Kohn, 1978a). Additionally, *Conus californicus* the single species inhabiting the Californian coast, has been recorded at San Diego as eating 28 different prey items from 4 phyla, including bivalves, gastropods, cephalopods, polychaetes, crustacea and fish (Kohn, 1966).

The broad diets of the solitary *Conus* species at Easter Island and southern California have been interpreted as perhaps resulting from ecological release in the absence of other potentially competing *Conus* species (Kohn, 1966, 1978). However, if the view is taken that increased diet breadth is an adaptational response to seasonal environments, then the higher latitude *Conus* species would be expected to have broader diets than their tropical congenors. There is a broad correlation of diet breadth with latitude, but certain faunas like the *Conus* species from the Galapagos Islands, have broader diets than might be expected from their equatorial location. However, the Galapagos are washed by cool upwelling currents, with for the latitude, a large seasonal range in sea surface temperatures (Abbott, 1966). If the diet breadth of *Conus* as measured by the number of prey species eaten, is plotted against seasonal temperature variation, then *Conus* species at localities experiencing 5° C or more seasonal temperature variation have broader diets. However, a much better correlation is obtained if diet breadth is plotted against mean winter sea surface temperature (Fig. 1,B). A clear trend in diet breadth shows that those species from localities experiencing cooler winter temperatures have considerably broader diets than those species from warmer waters. A similar relationship is seen by plotting the number of polychaete families eaten; this gives an indication of the morphological diversity of the prey taken. The correlation of water temperatures and food diversity affords an alternative explanation to the ecological release hypothesis.

Out of the other gastropod species at Djerba, the buccinids *Cantharus dorbigynana* and *Engina bicolor* are both northerly species of genera with otherwise, largely tropical distributions. Species in these genera which have been examined elsewhere include *Cantharus undosus* and *C. fumosus* which are both food generalists eating a variety of polychaetes as well as other gastropods (Taylor 1984). The tropical *Engina* species which have been examined (*E. mendicaria, E. alveolata, E. lineata, E. zonalis*), apparently feed entirely upon polychaetes, and gastropod remains have not been found in any of these tropical species (Taylor, unpub). *Pisania striata*, the common intertidal buccinid at Djerba, feeds mainly upon gastropods, particularly *Cerithium vulgatum*, with only a few polychaetes and barnacles in the diet. Other *Pisania* studied for diet include *Pisania tincta* (Conrad) from Florida, which feeds mainly upon the vermetid gastropod *Spiroglyphus* (Ingham & Zischke, 1977). Additionally, in the aquarium Bandel (1984) observed *Pisania pusio* (Linnaeus) and *P. auritula* (Link) eating small gastropods and dead fish. The related *Caducifer decapitata englerti* (Hertlein) from Easter Island, feeds upon the eunicid polychaetes *Eunice cariboea* and *Lysdice collaris* (Kohn, 1978b).

Another common whelk at Djerba is *Buccinulum corneum*, a northern hemisphere representative of a group of gastropods, which is particularly diverse at higher latitudes in the southern hemisphere (Powell, 1927; Ponder, 1971). At Djerba, the diet of the whelk consists largely of the polychaetes *Branchiomma lucullana* and *Palola siciliensis* which account for 82 % of the food items, with only a few individuals containing gastropod remains. The only other information on the diet of *Buccinulum* species is a statement (Ponder, 1971, p. 232) that in New Zealand they « appear to feed primarily on polychaete worms ». However, other members of the family Buccinidae have been studied. These include the north Atlantic whelk *Buccinum undatum*, which is a food generalist and has been recorded as eating prey from eight different phyla, but with polychaetes forming a major part of its diet (Taylor, 1978). Other whelks which have been studied include several species of *Neptunea* from the N. Atlantic and Alaska Pearce & Thorson, 1967; Taylor, 1978; Shimek, 1984). All these species feed mainly upon bivalves and polychaetes, but a variety of other prey are taken less frequently. Another N.W. Pacific whelk *Searlesia dira* (Reeve) eats barnacles, acmaeid limpets, chitons and *Littorina* as well as carrion (Louda, 1979). Greatest feeding success may be upon animals stressed from prolonged intertidal emersion. Finally, shimek (1980) records the Alaskan *Beringius kennicotti* (Dall) as feeding upon the polychaete *Phyllodoce* and the actinarian *Tealia*.

The family Columbellidae is known to include both herbivorous and carnivorous species (review by Hatfield, 1979). At Djerba, the common Mediterranean species *Columbella rustica* appears to be an algal feeder, whilst *Mitrella scripta* is a carnivore eating other gastropods and their eggs. The Caribbean species *Columbella mercatoria* is morphologically similar to *C. rustica* and has also been recorded as eating algae (Bandel, 1984). Additionally, two species of Caribbean *Mitrella* feed on hydroids (Bandel, 1984).

This study has provided new data on the diets of some common Mediterranean predatory gastropods. This information should help in determining the role of these gastropods in the trophic organisation of intertidal and shallow-water communities of which they are such an abundant component.

In conclusion, there is good evidence amongst *Conus* species that the diversity of prey eaten is correlated with the mainly latitudinal variations in minimum seawater temperatures. However, for other predatory gastropods there are insufficient data from different localities, for any possible broad-scale patterns in dietary diversity to be determined.

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