The feeding habits of three Mediterranean sea anemone species, *Anemonia viridis* (Forskål), *Actinia equina* (Linnaeus) and *Cereus pedunculatus* (Pennant)

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ABSTRACT: The feeding habits of the Mediterranean sea anemones *Cereus pedunculatus, Actinia equina* and *Anemonia viridis* were examined mainly by analysing their coelenteron contents. The three species are opportunistic omnivorous suspension feeders. Main source of food for *A. viridis* and *C. pedunculatus* are crustaceans (mainly amphipods and decapods, respectively), while for the midlittoral species *A. equina,* it is organic detritus. Using the same method, the temporal and spatial changes in the diet of *A. viridis* were examined. During the whole year, crustaceans seem to be the main source of food for *A. viridis.* The diet composition of this species, however, differs remarkably in space, possibly reflecting the different composition of the macrobenthic organismic assemblages in different areas. The data collected are compared with the limited bibliographical information.

INTRODUCTION

Since Aristotle's time, it has been known that sea anemones can capture and feed on small fish, although it is only recently that information on their feeding habits has begun to emerge. Our understanding of their nutrition has changed considerably in recent years (Van Praët, 1985).

Studies of the coelenteron contents of *Anthopleura elegantissima, A. xanthogram-mica, Metridium senile, Anemonia viridis* (= *A. sulcata*), *Actinia equina, Edwardsia longicornis, E. danica, Phymactis clematis, Bunodactis marplatensis, Calliactis parasitica,* and *Urticina eques* have contributed to the knowledge of the prey composition of these anemones (Ellehauge, 1978; Möller, 1978; Zamponi, 1980; Sebens, 1981; Van Praët, 1983; Den Hartog, 1986; Chintiroglou & Koukouras, 1991). Schlichter (1975a, 1975b, 1978) demonstrated the ability of *Anemonia viridis* to take up glucose and aminoacids at concentrations found in natural water. It is also known that sea anemones can, by pinocytosis and phagocytosis, satisfy to a great extent their energetic demands using soluble macromolecules or particulates from their environment (Van Praët, 1978, 1980, 1983). The feeding advantages of the sea anemones *Phyllactis flosculifera* and *Anemonia viridis* resulting from their symbiosis with unicellular algae (zooxanthellae) were reported by Steele & Goreau (1977) and Janssen & Möller (1981). There is evidence that species previously thought to be carnivorous, also feed on plant remains and that there may be a seasonal change in the relative importance of these two feeding methods (Van Praët, 1982).

However, there is no information available on the temporal and spatial variations of the anemones' diet, neither at the intraspecific nor at the interspecific level. The goal of this study is to examine the feeding habits of·three common anemones of the Mediterranean Sea (*Anemonia viridis, Actinia equina* and *Cereus pedunculatus*) and to study the seasonal and spatial changes in *A. viridis* diet.

MATERIAL AND METHODS

160 individuals of *Anemonia viridis*, 60 of *Actinia equina* and 61 of *Cereus pedunculatus* were collected by diving, in different areas of the infralittoral and circalittoral zones of Thermaikos Gulf, during summer. Specimens of the two former species were collected from hard substrata, while those of the third from soft substrata of this area. After their removal from the substrate, the specimens were kept, each one separately, in a 10 % Formalin solution. In the laboratory, their coelenteron content was extracted under a stereoscope. The various food remains were identified to the lowest taxonomic level allowed by their condition, or they were characterized as unidentified. During the sampling period, observations on anemone feeding reactions were made. Some individuals were kept in aquaria for further observations.

The study of the seasonal diet composition of *A. viridis* was based on 840 individuals (group I), and the study of the changes in diet composition with depth on 648 individuals (group II). The samples were collected from two unpolluted, neighbouring and typical biotopes of the infralittoral zone, located in the eastern part of Thermaikos Gulf, where the populations of *A. viridis* form a "carpet" (e.g. Rossi, 1949). Other data on the two biotopes are given in the "Results". The wet weight of each sea anemone, in "crude units of biomass" (Crisp, 1984), was calculated after its gastrovascular cavity had been emptied of food.

During the seasonal samplings, temperature, salinity and dissolved O_2 values of the water near the bottom were measured.

The treatment of the data related with food remains of the sea anemones was made according to the methods of Deniel (1975) and Le Mao (1985). These methods are usually applied to the study of the qualitative and quantitative diet composition of fishes. The following parameters were calculated:

$$\text{Vacuity coefficient } V = Ev \cdot 100/N$$

$$\text{Percentage of a prey } Cn = n \cdot 100/Np$$

where: Ev, the number of empty coelenterons,
      N, the total number of coelenterons examined,
      n, the total number of individuals of a certain prey species, and
      Np, the total number of prey individuals

The various prey species can be distinguished according to the Cn value as being preferential (Cn > 50 %), secondary (10 % < Cn < 50 %) or accidental (Cn < 10 %).

A *t*-test was used to compare the observed diet frequencies. Values of *t* were calculated as
$$t = (P_1 - P_2) / \sqrt{(P \cdot Q/N_1 + P \cdot Q/N_2)}$$

where P_1 and P_2 are the percentages of the observed N_1 and N_2, $P = N_1/(N_1 + N_2)$ and $Q = N_2/(N_1 + N_2)$.

RESULTS

Qualitative composition of the diet

A n e m o n i a   v i r i d i s . Of the 160 anemone coelenterons examined, only 37 were found to contain food remains, giving a vacuity coefficient of approximately 77 % (Fig. 1). 88 food particles corresponding to 36 prey species were found (Table 1). As shown by Cn values, none of the prey species can be characterized as preferential, since Cn is always lower than 50 %. However, the amphipod *Corophium acutum* (Cn = 31.82 %) can be characterized as secondary prey, while the remaining should be included in the category of accidental prey (Cn < 10 %). Among higher groups (Fig. 1), crustaceans are characterized as preferential (Cn = 57.95 %) and molluscs as secondary prey (Cn = 20.45 %).

A c t i n i a   e q u i n a . Of the 60 coelenterons examined, only 18 contained food remains. Consequently, the vacuity coefficient was 70 %. 44 food remains were found, corresponding to 16 prey species (Table 2). According to the Cn values, none of the prey species can be characterized as preferential, although organic detritus is not far from this. Organic detritus, as well as insects, crustaceans and molluscs belong to the secondary prey category (Fig. 1).

C e r e u s   p e d u n c u l a t u s . Of the 61 examined specimens, only 12 contained food remains (V = 80.33 %). The 70 food remains found correspond to 12 prey species (Table 3). None can be characterized as preferential prey. The amphipod *Corophium acutum* and mainly the decapods *Athanas nitescens* and *Pisidia longimana* can be characterized as secondary prey. All the remaining prey species should be characterized as accidental prey (Table 3). Among higher taxa (Fig. 1), crustaceans (94 %) are almost the exclusive source of food.

Feeding reactions of sea anemones

Observations made during this study showed that *A. viridis* moved its tentacles actively when feeding on crushed mussels or artificial food, while *A. equina* and *C. pedunculatus* waited for the food particles to fall on their oral discs. In many cases, *A. viridis* tentacles searched the substrate for food particles, a fact not observed in the other two anemone species. In contrast to the tentacles' reaction, the columns and the oral discs of *A. equina* and *C. pedunculatus* were more active than those of *A. viridis*. The reactions to food of the oral discs and columns of the latter were only of short duration, while there was a constant effort to cover food particles with its tentacles. The persistent contraction of the columns and oral discs of *A. equina* and *C. pedunculatus* was very evident. However, there was a difference between the two species in the speed of the oral disc contraction. In the former it occurred within about 20 seconds, while in the latter within less than 10 seconds.

Changes in the *Anemonia viridis* diet

Seasonal changes

A. viridis populations are often very dense and form extensive "carpets" on the shallow rocky bottoms of the infralittoral zone. The organisms associated with these
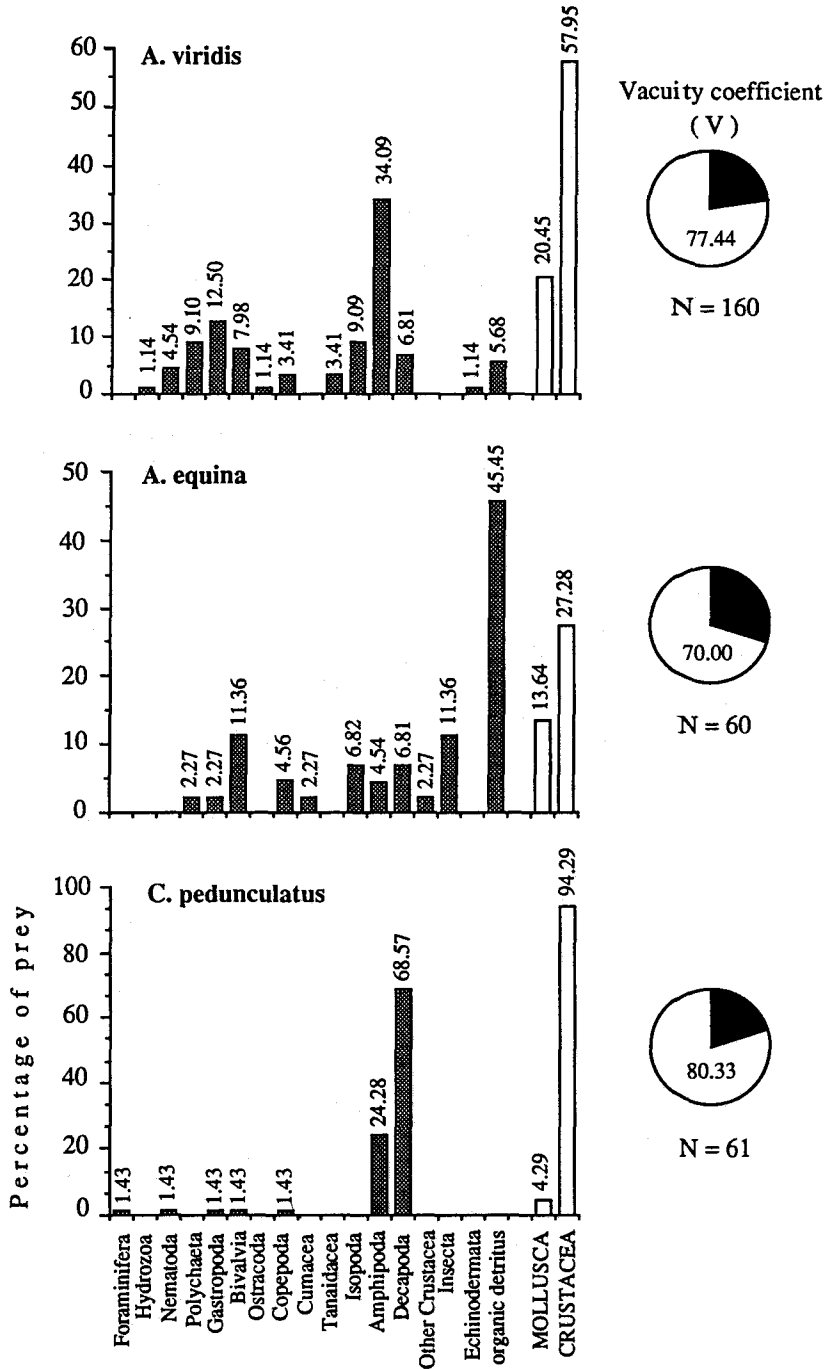
Fig. 1. Composition of the diet of *Anemonia viridis*, *Actinia equina* and *Cereus pedunculatus*. The white columns represent the total percentages of Mollusca and Crustacea

Table 1. Analysis of the coelenteron content of 160 *A. viridis* individuals

				n	Cn
Hydrozoa		*Aglaophenia* sp.		1	1.14
Nematoda				4	4.54
Polychaeta		*Ceratonereis hircinicola*		1	1.14
		Platynereis sp.		1	1.14
		Nereidae		1	1.14
		Amphitrite sp.		1	1.14
		Spirorbidae		1	1.14
		Others		3	3.42
Mollusca	Gastropoda	*Tricolia pontica*		1	1.14
		Rissoa parva		3	3.40
		Apicularia lia		1	1.14
		Bittium reticulatum		3	3.40
		Others		3	3.40
	Bivalvia	*Mytilus galloprovincialis*		3	3.40
		Musculus costulatus		2	2.27
		Chlamys varia		1	1.14
		Others		1	1.14
Crustacea	Ostracoda			1	1.14
	Copepoda			3	3.40
	Tanaidacea	*Leptochelia* sp.		1	1.14
		Tanais sp.		2	2.27
	Isopoda	*Gnathia* sp.		3	3.40
		Cymodoce truncata		1	1.14
		Cymodoce sp.		1	1.14
		Bagatus sp.		3	3.40
	Amphipoda	*Corophium acutum*		28	31.82
		Dexamine spiniventris		1	1.14
		Haustoriidae		1	1.14
	Decapoda	*Pilumnus spinifer*		1	1.14
		Pisa tetraodon		1	1.14
		Pisidia longimana		1	1.14
		Diogenes pugilator		1	1.14
		Xantho granulicarpus		1	1.14
		Others		1	1.14
Echinodermata		*Holothuria* sp.		1	1.14
Organic detritus				5	5.68

populations form characteristic assemblages. The specimens used to study the changes in the diet of *A. viridis* were collected from such an assemblage, in which the anemone mean density reached approximately 650 individuals/m^2. This assemblage was settled on a rocky substrate, in depths between 0.30 m and 1.70 m, and covered a total area of approximately 15 m^2. The water temperature during sampling was 18.5 °C in autumn (12th October), 13.5 °C in winter (14th February), 20.6 °C in spring (22nd May) and 25.1 °C in summer (20th July). Salinity and dissolved O_2 values were 30.0–33.5 ‰, and 6.3–7.1 ppm, respectively.

The analysis of the 16 seasonal samples (4 × 4), each covering an area of 625 cm^2,

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Table 2. Analysis of the coelenteron content of 60 *A. equina* individuals

			n	Cn
Polychaeta			1	2.27
Moll.	Gastropoda		1	2.27
	Bivalvia	*Mytilus galloprovincialis*	4	9.10
		unidentified	1	2.27
Crustacea	Copepoda		2	4.56
	Cumacea	Nannastacidae	1	2.27
	Isopoda	*Gnathia* sp.	2	4.56
		Cymodoce sp.	1	2.27
	Amphipoda	*Hyale dollfusi*	1	2.27
		unidentified	1	2.27
	Decapoda	*Acanthonyx lunulatus*	1	2.27
		Pilumnus spinifer	1	2.27
		unidentified	1	2.27
	Other		1	2.27
Insecta			5	11.36
Organic detritus			20	45.45

Table 3. Analysis of the coelenteron content of 61 *C. pedunculatus* individuals

			n	Cn
Foraminifera			1	1.43
Nematoda			1	1.43
Moll.	Gastropoda	*Philippia* sp.	1	1.43
	Bivalvia		1	1.43
Crustacea	Copepoda		1	1.43
	Amphipoda	*Liljeborgia dellavallei*	1	1.43
		Corophium acutum	15	21.42
		Ericthonius sp.	1	1.43
	Decapoda	*Thoralus cranchii*	3	4.29
		Athanas nitescens	20	28.57
		Pisidia longimana	24	34.28
		Pilumnus spinifer	1	1.43

collected from the above assemblage, revealed the presence of 78 species. The most abundant species in order of frequency were the following: the sea anemone *A. viridis*, the alga *Halimeda tuna*, the mollusc *Coralliophilla meyendorffi*, the polychaete *Nereis zonata*, and the algae *Cladophora albida* and *Laurencia obtusa*. A detailed description of this assemblage has been given by Chintiroglou & Koukouras (in press). The total number of individuals of the assemblage, as well as that of *A. viridis* itself, was highest during summer. During autumn and winter, polychaetes were the most dominant group of the assemblage, while during summer and spring molluscs were predominant (*A. viridis* not taken into consideration).

Although an important number of individuals was collected during seasonal samplings, very few of them contained food particles in their coelenteron. The vacuity coefficient had the following very high values: autumn, V = 99.15 % (N = 118); winter, V = 97.87 % (N = 141); spring, V = 85.64 % (N = 195); and summer, V = 91.98 % (N = 237). The t-test to compare the observed vacuity frequencies shows significant differences, at the 95 % confidence level for all comparisons except between winter and autumn.

In autumn, only two amphipod individuals (one of which was *Maera inaequipes*) were found in the coelenteron of *A. viridis* individuals. In winter, only organic detritus, one individual of the tanaid *Heterotanais* sp. and one individual of the gastropod *Alvania* sp. were found. The food composition in spring and summer is given in Table 4 and in Figure 2. In spring, the food of *A. viridis* consisted mainly of crustaceans (Cn = 70.83 %), which are characterized as preferential prey, while polychaetes (12.5 %) are secondary prey. In summer, crustaceans were again the preferential prey, but with a lower percentage (Cn = 50.02 %) while the number of consumed polychaetes was almost twice as high as in spring (Cn = 22.22 %). Organic detritus make up 22.20 % of the diet, and molluscs 5.56 %. Certainly, amphipods constituted the most prominent part of the consumed food in both spring and summer.
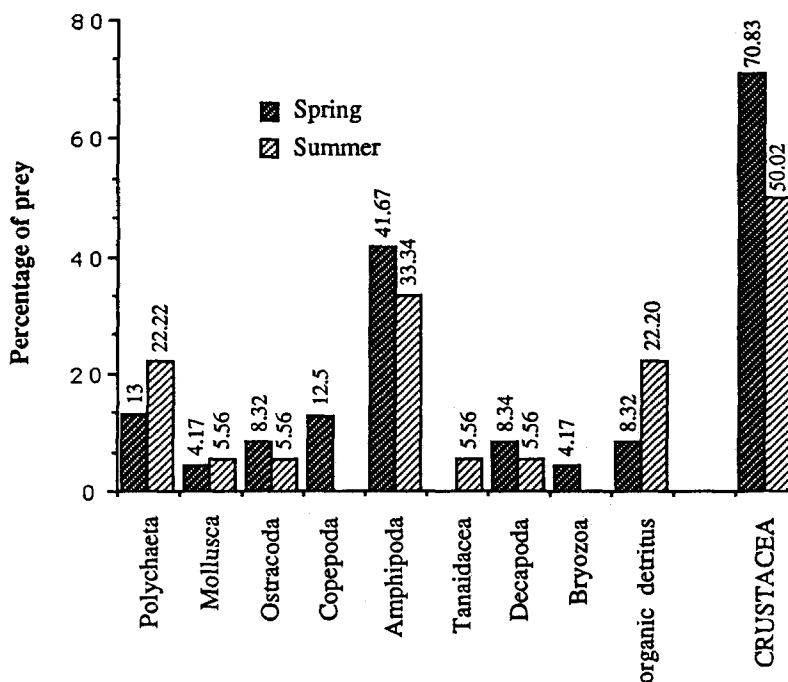

Fig. 2. Composition of the diet of *A. viridis* in spring and summer. The columns on the right represent the total percentage of Crustacea

Table 4. Analysis of the coelenteron content of 195 and 237 *A. viridis* individuals collected in spring (2. 5. 1981) and summer (20. 7. 1981), respectively

			Spring n	Spring Cn	Summer n	Summer Cn
Polychaeta		*Laetmonice hystrix*	–	–	1	5.56
		Typosyllis variegata	1	4.17	2	11.10
		Nereis zonata	–	–	1	5.56
		Nereidae	1	4.17	–	–
		Branchiomma bombyx	1	4.17	–	–
Moll.	Bivalvia	Tellinidae	1	4.17	–	–
		unidentified	–	–	1	5.56
Crustacea	Ostracoda		2	8.32	1	5.56
	Copepoda		3	12.50	–	–
	Amphipoda	*Leucothoe spinicarpa*	1	4.17	–	–
		Hyale dollfusi	1	4.17	–	–
		Elasmopus rapax	2	8.32	–	–
		Elasmopus sp.	–	–	1	5.56
		Maera inaequipes	–	–	1	5.56
		Dexamine spiniventris	–	–	1	5.56
		Atylus sp.	1	4.17	–	–
		Amphithoe ramondi	1	4.17	1	5.56
		Lembos websteri	–	–	2	11.10
		unidentified	4	16.67	–	–
	Tanaidacea	*Tanais* sp.	–	–	1	5.56
	Decapoda	*Xantho poressa*	–	–	1	5.56
		Alpheus dentipes	1	4.17	–	–
		unidentified	1	4.17	–	–
Bryozoa			1	4.17	–	–
Organic detritus			2	8.32	4	22.20

Depth-related changes

For the study of the depth-related changes in the diet of *A. viridis*, samples were collected along a transect of about 150 metres, located very near the area in which the seasonal samples were taken. This transect extended vertically from the coast to the midlittoral zone to a depth of 3 m. The samples were collected randomly from three zones, defined mainly according to the substrate type (Fig. 3).

The assemblage of zone A is that of the infralittoral pebbles (Pérès & Picard, 1964; Pérès, 1967) and extends from the coast to a distance of approximately 60 m (depth 0–1 m). The characteristic macrofaunal species in this zone was the crab *Xantho poressa*. 147 individuals of *A. viridis* were collected in zone A, in which the population density of this species was approximately 24 individuals/m². The mean wet weight of the individuals in this zone was 0.97 ± 0.45 g.

Zone B extends approximately from 60 to 100 m from the coast (depth 1–2 m). The assemblage settled in this area is that of the soft photophilic algae (Pérès, 1982), although the substrate consists of phanerogamic rhizomes, pebbles and sand (Fig. 3). Dominant
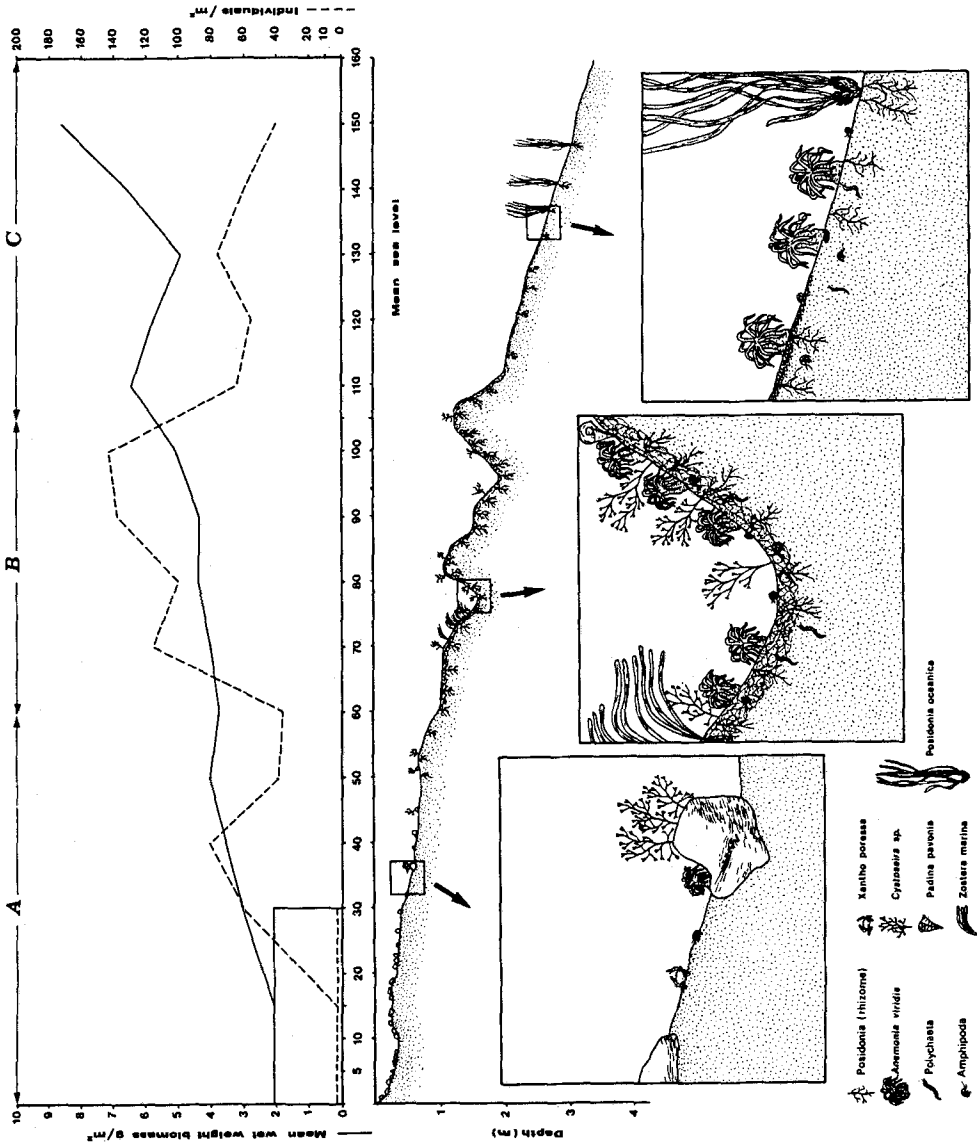
Fig. 3. Above: Fluctuation of the mean value of wet biomass and the abundance of *A. viridis* population along the transect. Below: General view of the transect and its three zones

Table 5. Analysis of the coelenteron content of 147 *A. viridis* individuals collected from zone A, 427 from zone B, and 74 from zone C (July 10, 1981)

			Zone A		Zone B		Zone C	
			n	Cn	n	Cn	n	Cn
Foraminifera			–	–	1	0.56	–	–
Polychaeta		Harmothoe areolata	–	–	1	0.56	1	1.56
		Harmothoe sp.	–	–	1	0.56	–	–
		Typosyllis variegata	–	–	6	3.38	5	7.81
		Syllidae	–	–	–	–	2	3.13
		Nereis rava	–	–	1	0.56	1	1.56
		Nereis zonata	–	–	7	3.93	2	3.13
		Nereis sp.	–	–	–	–	5	7.81
		Nereis sp. 1	–	–	5	2.81	–	–
		Nereis sp. 2	–	–	3	1.69	–	–
		Platynereis dumerilii	1	6.25	–	–	–	–
		Nereidae	–	–	4	2.25	–	–
		Marphysa fallax	–	–	1	0.56	–	–
		Lumbrineris gracilis	–	–	1	0.56	–	–
		Eunicidae	–	–	1	0.56	–	–
		Polydora sp.	–	–	–	–	1	1.56
		Notomastus sp.	–	–	1	0.56		
		Capitellidae	–	–	–	–	1	1.56
		Maldanidae	–	–	2	1.12		
		Ampharetidae	–	–	–	–	1	1.56
		Eupolymnia nebulosa	–	–	1	0.56	–	–
		Terebellidae	–	–	2	1.12	–	–
		Branchiomma lucullana	–	–	1	0.56	–	–
		Spirographis sp.	–	–	1	0.56	–	–
		Chone collaris	–	–	–	–	1	1.56
		Chone sp.	–	–	2	1.12	–	–
		Jasmineira elegans	–	–	–	–	1	1.56
		Sabellidae	–	–	3	1.69	–	–
		various unidentified	–	–	10	5.63	5	7.81
Sipuncula		Aspidosiphon muelleri	–	–	1	0.56	–	–
Mollusca	Gastropoda	Mangelia sp.	–	–	1	0.56	–	–
		Bittium sp.	–	–	–	–	1	1.56
		various unidentified	1	6.25	1	0.56	3	4.69
	Bivalvia	Musculus costulatus	–	–	3	1.69	3	4.69
		Tellinidae	–	–	2	1.12	–	–
		Hiatella arctica	–	–	1	0.56	–	–
		unidentified	–	–	1	0.56	–	–
Crustacea	Ostracoda		–	–	1	0.56	1	1.56
	Copepoda		1	6.25	11	6.19	5	7.81
	Amphipoda	Stenothoe tergestina			2	1.12	–	–
		Elasmopus rapax			2	1.12	–	–
		Elasmopus sp.	1	6.25	–	–	–	–
		Ceradocus sp.	1	6.25	–	–	–	–
		Maera inaequipes	–	–	2	1.12	–	–
		Apherusa sp.	–	–	1	0.56	–	–
		Dexamine spiniventris	–	–	2	1.12	1	1.56
		Amphithoe ramondi	–	–	5	2.81	2	3.13

Table 5 (contd)

			Zone A		Zone B		Zone C	
			n	Cn	n	Cn	n	Cn
Crustacea	Amphipoda	*Amphithoe* sp.	1	6.25	1	0.56	1	1.56
		Lembos websteri	2	12.5	7	3.93	4	6.25
		Ericthonius brasiliensis	–	–	1	0.56	–	–
		Corophium acutum	–	–	1	0.56	–	–
		Corophium sp.	–	–	1	0.56	–	–
		various unidentified	1	6.25	25	14.06	2	3.13
	Tanaidacea	*Tanais dulongii*	2	12.5	–	–	1	1.56
		Tanais grimaldii	–	–	1	0.56	–	–
		Tanais sp.	–	–	13	7.31	3	4.69
		Heterotanais sp.	1	6.25	3	1.69	–	–
		Apseudes sp.	–	–	2	1.12	1	1.56
		unidentified	–	–	–	–	1	1.56
	Decapoda	*Thoralus cranchii*	–	–	4	2.25	–	–
		Alpheus dentipes	–	–	5	2.81	4	6.26
		Athanas nitescens	–	–	2	1.12	2	3.13
		unidentified	1	6.25	–	–	–	–
	various unidentified		2	12.5	9	5.06	2	3.13
Echin.	Ophiuroidea		–	–	2	1.12	1	1.56
Organic detritus			1	6.25	10	5.62	–	–

species were the algae *Jania rubens, Cystoseira crinita, C.' spinosa, Padina pavonica* and the phanerogamous plant *Z. nana*. In this zone, 427 individuals of *A. viridis* were collected. Population density was 132 individuals/m², which had a mean wet biomass of 1.17 ± 0.51 g.

Zone C is located at the end of the transect (depth 2–4 m). The substrate was coarse sand in which the phanerogame *Posidonia oceanica* grew in patches. The anemone population density was approximately 59 individuals/m², with a mean wet biomass of 1.57 ± 0.71 (sd) g. 74 individuals were collected from this zone.

The diet composition of the anemones in each zone, resulting from the analysis of the coelenteron content of the individuals, is given in Table 5 and Figure 4. The vacuity coefficient (V) decreases from zone A to zone C (zone A: V = 89.8 %, N = 147; zone B: V = 70.0 %, N = 427; zone C: V = 56.8 %, N = 74). The *t*-test shows significant differences, at the 95 % confidence level, for all comparisons.

Among the various prey species found in the coelentera of the examined individuals, none can be characterized as preferential. Two prey species, the amphipod *Lembos websteri* and the tanaid *Tanais dulongii*, were characterized as secondary prey, and all the remaining prey species belong to the category of accidental prey.

Crustaceans are the main food source in the three zones (Fig. 4), and especially in zone A, where they represent 81.25 % of the total prey individuals. However, their relative importance decreases gradually from zone A to zone C. In contrast, the polychaete percentage increases from 6.25 % in zone A to 30.34 % in zone B and 40.61 % in zone C.
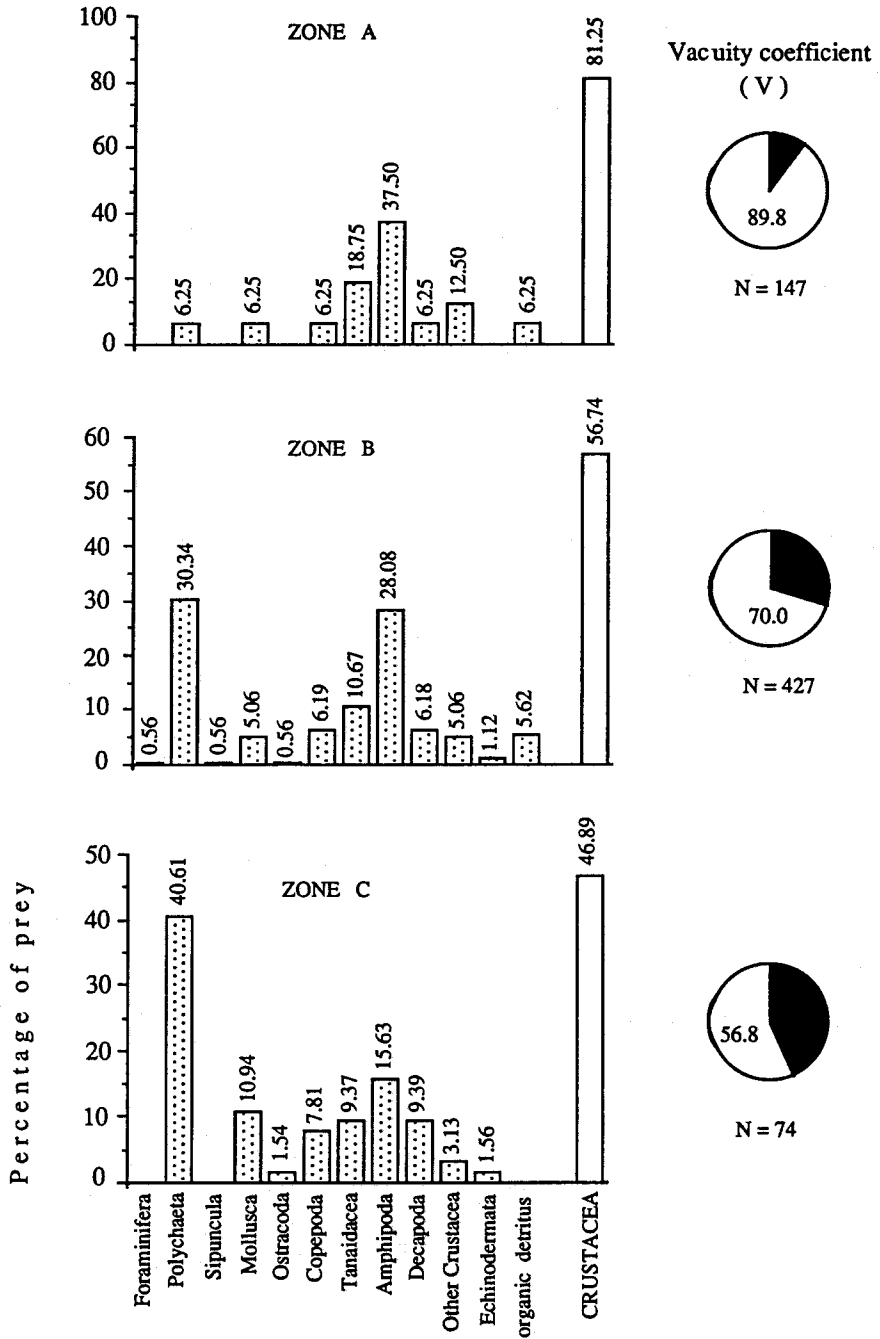
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Fig. 4. Composition of *A. viridis* diet in the zones A, B, and C. The white column represents the percentage of Crustacea

DISCUSSION

Diet and feeding reactions

The only information concerning the macrofeeding habits of *Anemonia viridis* is given by Möller (1978). He examined the coelenteron contents of 160 individuals of this species from the English Channel, and found that, as in Thermaikos Gulf, the most important prey organisms are crustaceans (62 %, against 58 % in Thermaikos Gulf) and molluscs (28 %, against 20 %). In contrast, the vacuity coefficients of the two areas differ considerably: 12.5 % in the English Channel against 77.4 % in Thermaikos Gulf. This difference may be attributed to differences in food deposits between the two areas.

The restricted information on the feeding habits of *Actinia equina*, and the absence of information on *Cereus pedunculatus* make comparisons difficult. From culture experiments, Ormond & Caldwell (1982) reported that *A. equina* was frequently observed with its tentacles expanded and its mouth open, but the response to food offered to the tentacles was slow or absent. In these experiments, molluscs (*Mytilus edulis*), small crustaceans and organic detritus were found to be a potential food source of this anemone, a behaviour characterized by Ormond & Caldwell (1982) as opportunistic feeding. However, the most important food source for *Actinia equina* seems to be organic detritus.

Sebens (1981) recognized three basic ways of macro-feeding in the species *Anthopleura elegantissima*, *A. xanthogrammica* and *Metridium senile*: (a) Prey suspended in the water column, usually zooplankton, is intercepted by one or more tentacles and transferred to the mouth. (b) Sessile prey dislodged by wave action or by foraging predators is washed into the tentacle crown. (c) Motile prey, such as sea urchins, crustaceans, and fish, blunder into the anemone's tentacles and is then captured. Turbid or turbulent water conditions may facilitate this type of capture.

Generally, the qualitative composition of *Anemonia viridis*, *Actinia equina* and *Cereus pedunculatus* food seems to reflect the above described feeding methods as well as the food deposits of the biotopes in which they live.

A. viridis also captures its food actively. The tentacles of this species are longer than its column and able to search for food by "sweeping" the substrate. Consequently, meiofaunal-microfaunal and microfloral elements can be included in its diet. Eleftheriou & Basford (1983) also observed an active search for food in the species *Cerianthus lloydi*. *C. pedunculatus* and *A. equina* with their relatively short tentacles are not able to search actively for prey. They feed on organisms or organic detritus that fall onto their oral disc. *C. pedunculatus*, which is an inhabitant of the infralittoral zone, seems to feed almost exclusively on crustaceans, which it catches easily owing to its rapid oral disc contraction. Actually, in the coelentera of the examined *C. pedunculatus* specimens, whole individuals of macrobenthic species such as the amphipod *C. acutum* and the decapods *P. longimana* and *A. nitescens* were found. This means that *C. pedunculatus* feeds mainly by the third method, described above under (c). The main food source of *A. equina*, which lives on the midlittoral hard substrates, is organic detritus, abundant in these biotopes because of the vigorous water movement. Similar observations on anemone species of the genera *Anthopleura* and *Metridium* were made by Sebens (1981).

Therefore, the sea anemones *A. viridis*, *C. pedunculatus* and *A. equina* should be considered as opportunistic omnivorous suspension feeders. *A. viridis* can also behave

like a predator. *A. viridis* and *C. pedunculatus* basically feed on crustaceans, while *A. equina* is detritivore. Their diets may also include meiofaunal (nematodes, copepods, ostracods) and macrofaunal (decapods, polychaetes, molluscs) organisms. The role of these sea anemones in the benthic food web seems to be quite important and they should be considered as both primary and secondary consumers.

Changes in the diet of *A. viridis*

A. viridis is possibly the most well known representative of sea anemones that live symbiotically with unicellular zooxanthellae (Steele & Goreau, 1977). The ability of *A. viridis* to take up glucose and aminoacids at concentrations found in natural waters was demonstrated by Schlichter (1975, 1978). Tiffon & Daireaux (1974) and Tiffon (1976) showed that *Cerianthus lloydi* captures and phagocytoses fine detrital particles and bacteria. Furthermore, there is evidence that species previously thought to be carnivorous also feed on plant remains and that there may be a seasonal change in the relative importance of these two feeding methods (Van Praët, 1982).

The data of the present study show that *A. viridis* feeds both on species of its own assemblage and, occasionally, on species of neighbouring assemblages. The restricted presence of gastropods in its diet, although their abundance in the assemblage is high all over the year, indicates a resistance of these animals to the anemone's toxic nematocysts (Salvini-Plawen, 1972). Crustaceans (mainly amphipods) contribute to its food during the whole year, while polychaetes contribute in considerable amounts only during spring and summer. However, the quality and quantity of macrofood does not seem to depend directly on the quality and quantity of the food available in the assemblage, but is controlled by the opportunities and the ability of the anemone to capture it.

Concerning the changes in diet composition of *A. viridis* along a transect, the following remarks can be made: In zone A, in which the substrate is instable since it consists mainly of pebbles that can easily be moved by wave action, the density of *A. viridis* population is low and the assemblage consists mainly of actively moving crustaceans able to withstand the peculiar conditions prevailing in this area. For this reason, the diet of *A. viridis* in this zone is composed to a high percentage of such crustaceans. Nevertheless, the available food in zone A is very restricted and, consequently, the vacuity coefficient is much higher than in the other two zones.

In the somewhat deeper zone B, a typical photophilic soft algae assemblage exists, in which the number of species and individuals is remarkably high. In this zone, the population density of *A. viridis* was highest and the number of the prey species found in the coelenteron of the examined individuals was also much higher than that found in the other two zones. The vacuity coefficient was lower than that in zone A, but was still high (70 %), indicating that the ability to gain food is restricted, although potential food is abundant. It may be suggested that, mainly due to the presence of many algae, the motile organisms can easily avoid the anemone tentacles.

In zone C, where patches of the phanerogame *Posidonia oceanica* are present and depth is down to 4 m, the *A. viridis* population (with an intermediate density, in comparison to that in the other two zones) consists of the biggest individuals. The fact that the biggest individuals of *A. viridis* live in greater depths has already been mentioned by Pax & Müller (1962) and Schmidt (1972). The same has been observed for

other sea anemone species, too, as for example for *Anthopleura xanthogrammica* and *Metridium senile* (Sebens, 1981). The reasons for this are not clear. A first reason may be that the biggest individuals migrate to greater depths in order to avoid competition. According to Sebens (1980, 1984), *Anthopleura elegantissima* and *A. xanthogrammica*, which compete for space, may behave in two basic ways when they confront difficulties in feeding: They either increase the ,frequency of asexual breeding or they migrate to other areas. Ottaway (1978) reports for *Actinia tenebrosa* that young individuals are the winners in infraspecific competition. The above mentioned behaviour has also been observed in *Anemonia viridis,* which either breeds asexually by longitudinal fission or it migrates (Stephenson, 1935; Pax, 1936; Schmidt, 1972). In greater depths, although the available food is often restricted here, the biggest individuals can nevertheless cover their trophical needs, as is obvious from their low vacuity coefficient. This may be due to the fact that they can exploit a greater space, both because of reduced competition and a larger feeding area (oral disc and tentacles). A second reason for the occurrence of the bigger individuals in greater depths may be the following: Because this species has a reduced ability of attachment to the substrate (Pax & Müller, 1962) when it grows above a certain size, it faces the danger of becoming detached and washed away by the waves (Koehl, 1977). In greater depths, however, hydrodynamism is restricted.

As the data suggest, the main food source along the transect are crustaceans (motile organisms), and especially amphipods, the two reasons for this being (1) this group of animals is more likely to be captured by the anemone tentacles, and (2) amphipods are the more abundant group in the assemblages along the transect.

From the more shallow to the deepest areas of the transect, the participation of crustaceans in the food composition of *A. viridis,* although it is always first in order, decreases gradually by approximately 50 %, while the' participation of polychaetes increases six-fold. These local changes in diet composition reflect the changes in the composition of the macrofauna along the transect, which in turn are a result of the change in the substrate from pebbles to sand.

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