# ORIGINAL ARTICLE

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# Trophic relationships of polychaetes associated with different algal growth forms

Received: 3 December 2004 / Revised: 25 August 2005 / Accepted: 26 August 2005 / Published online: 18 October 2005 © Springer-Verlag and AWI 2005

Abstract The trophic relations of the polychaete species associated with four different algal growth forms (filamentous, fan-shaped, bush-like and encrusting) were studied in the North Aegean Sea. Samples for the spatial analysis were collected in summer with a quadrate sampler (400 cm<sup>2</sup>) at a depth range of 15-40 m. Filamentous and encrusting forms were also seasonally sampled in order to detect the temporal changes. A total of 5,494 individuals belonging to 79 species were classified to 12 feeding guilds, considering the type of food, the feeding apparatus and the motility patterns involved. Carnivores dominated, followed by herbivores and filter-feeders, among all the algal forms studied, excepting the fan-shaped form where filter-feeders prevailed mainly due to a massive recruitment of spirorbids. With respect to the abundance of the various feeding guilds, filamentous and fan-shaped forms discriminated, whereas bush-like and encrusting forms showed high similarity. The occurrence of polychaete feeding guilds among both filamentous and encrusting forms showed seasonal changes, with summer and spring samples, respectively, discriminating. The results of the trophic group analysis conformed to previous information provided by a taxon composition analysis of the dominated by the same algae communities. However, a functional study can give additional information and is thus a useful tool for the study of hard bottom communities.

Keywords Polychaeta · Feeding guilds · Hard substrate · Aegean Sea

Communicated by H.-D. Franke

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#### Introduction

The upper sublittoral zone of Mediterranean hard bottoms is dominated by macroalgae, while deeper zones are dominated by zoobenthos (Bellan-Santini et al. 1994; Garrabou et al. 2002). Algal communities with their high structural complexity are important biotopes for zoobenthos, and the form of the pilot alga directly influences the macrobenthic community structure (Abbiati et al. 1987; Giangrande 1988; Krapp-Schickel 1993; Chemello and Milazzo 2002; Fraschetti et al. 2002; Antoniadou et al. 2004). Polychaetes are among the most abundant taxa on hard bottoms, usually comprising over one-third of the richness both the species and the numerical abundance (Giangrande et al. 2003; Chintiroglou et al. 2004; Antoniadou et al. 2004).

Fauchald and Jumars (1979) presented a detailed analysis of the feeding biology of polychaetes, using the concept of feeding guilds. There are many ways to create functional groups, i.e. with respect to reproductive behavior, the degree of opportunism, etc., but it seems that trophic relationships are most important to assess the function of communities (Bremner et al. 2003). According to these authors, feeding guilds should reflect differences in the particle size of the food and its composition (microphages and macrophages), in the mechanism of food intake (herbivores, carnivores, filterfeeders, surface-deposit feeders and burrowers) and in the motility patterns associated with feeding (sessile, discretely motile and motile). In this sense, feeding guilds do represent more than mere feeding interactions.

Considering the importance of polychaetes for the structure and function of the communities, we studied the trophic relationships of polychaetes associated with different algal-growth forms as well as possible seasonal changes in these relationships. The results were compared with those from a taxonomic composition analysis of the same community in order to evaluate the implications of these two approaches in assessing the functional diversity.

## Methods

# Study area

Seven coastal sites were sampled in the northern Aegean Sea (Fig. 1). According to the vertical extension of the hard substrate, one to three depth levels (15, 30 and 40 m) were set at each site, covering the local depth range of the sciaphilic algae community (Antoniadou and Chintiroglou 2005). Four different algal-growth forms were distinguished: (1) filamentous algae (FA), recorded at St 1 and S 3 at the depth level of 15 m and also at St 1-4 at the depth level of 30 m; (2) fan-shaped algae (FanA), recorded at St 2 and St 4 at the depth level of 15 m; (3) filamentous and bush-like algae (FBA), recorded at St 7 at depth levels of 15 and 30 m; and (4) encrusting algae (EA), recorded at St 1 and St 3 at depth level of 40 m and also at St 5 at 18 m depth (for details, see Antoniadou 2004). For a spatial analysis, all algal forms were sampled in summer 1998 (stations 1-6) or summer 1999 (station 7); FA and EA forms were also sampled (from summer 1997 to summer 1998) for a seasonal analysis.

## Data collection

Sampling was carried out by SCUBA diving, using a quadrate sampler (Bellan-Santini 1969) covering a surface of 400 cm<sup>2</sup> (Weinberg 1978; Karalis et al. 2003), by totally scraping off the rocks in order to collect both the motile and sessile fauna (Antoniadou and Chintiroglou

2005). Five replicates were collected per depth level and site, thus a total of 75 and 65 samples were available for the study of spatial and seasonal variations, respectively. All samples were sieved (0.5 - mm mesh size) and preserved in a 10% formalin solution. After sorting, all the polychaetes were counted, identified down to species level and the wet weight of the specimens was measured. The classification of the polychaete species to different feeding guilds followed Fauchald and Jumars (1979).

### **Statistics**

The null hypotheses tested in this study were that the abundance or the biomass of the various polychaete feeding guilds was equally distributed (1) among the four algal forms and (2) among the four seasons for the FA and EA facies. A one-way ANOVA test was applied on logarithmically transformed (log +1) data, to normalize the variance of numerical abundances and biomasses (Zar 1984; Clarke and Green 1988). The Fisher PLSD test was also used in order to examine partial differentiations.

The data obtained for the different algal forms were analysed by multivariate techniques (hierarchical cluster analysis and non-metric multidimensional scaling), based on the Bray–Curtis semi-metric distance index, calculated from: (1) presence/absence records and (2) log-transformed numerical abundances, using PRIMER package (Clarke and Warwick 1994). SIMPER analysis was applied to identify the percentage contribution of each feeding guild to the overall dissimilarity among

Fig. 1 Map of the study area indicating sampling sites



Table 1 Classification of the polychaete species recorded to various feeding guilds according to Fauchald and Jumars (1979)

Carnivores	Herbivores	Surface-deposit feeder	Burrowers	Filter-feeders
CMJ: motile, jawed pharynx	HMJ: motile, jawed pharynx	SDJ: discretely motile, jawed pharynx	BMX: motile, unarmed	FDT: discretely motile, tentaculated
Arabella iricolor	Dorvillea rubrovittata	Aponuphis bilineata	Heteromastus filiformis	Pherusa sp.
(Montagu, 1804) Dorvillea rubrovittatus	(Grube, 1855) Exogone naidina (Orteod, 1845)	(Baird, 1870) Onuphis sp.	(Claparede, 1864) Polyopthalmus pictus	FST: sessile, tentaculated
(Stimpson, 1854)	<i>Grubeosyllis limbata</i> (Claparede, 1868)	SDT: discretely motile, tentaculated	(Dujardin, 1839) Sclerocheilus minutus (Grube, 1863)	Amphiglena mediterranea (Leyding, 1851)
Eunice torquata (Quatrefages, 1865)	Lysidice ninetta (Audouin and MilneEdwars, 1833)	Laonice cirrata (Sars, 1851)	BSX: sessile, unarmed pharynx	Branchiomma bombyx (Dalyell, 1853)
Eunice vittata (DelleChiaje, 1929) Eusyllis blomstrandi (Malmgren, 1867) Haplosyllis spongicola (Grube, 1865) Harmothoe areolata (Grube, 1860) Harmothoe ljungmani (Malmgren, 1867) Harmothoe spinifera (Ehlers, 1864) Kefersteinia cirrata (Kefferstein, 1862) Laetmonice hystrix (Savignyi, 1820) Lumbrineris coccinea (Renier, 1804) Palola siciliensis (Grube, 1840) Pholoe minuta (Fabricius, 1780) Pionosyllis lamelligera (SaintJoseph, 1856) Pterosyllis formosa (Claparede, 1863) Scalisetosus fragilis (Claparede, 1863) Scalisetosus fragilis (Claparede, 1868) Spermosyllis torulosa (Claparede, 1865) Syllis amica (Quatrefages, 1865) Syllis cirropunctata (Michel, 1909) Syllis cornuta (Rathke, 1843) Syllis gracilis (Grube, 1840 Syllis gracilis (Grube, 1863) Syllis krohvii	MilneEdwars, 1833) Marphysa fallax (Marion & Bobretzky, 1875) Nematonereis unicornis (Grube, 1840) Platynereis dumerilii (Audouin & MilneEdwars, 1833) Scoletoma funchalensis (Kinberg, 1865) Sphaerosyllis pirifera (Claparede, 1868)	Polydora caeca (Orsted, 1843) Polycirrus aurianticus (Grube, 1860) Theostoma oerstedi (Claparede, 1864) SST: sessile, tentaculated Amphitrite variabilis (Risso, 1826) Dodecaceria concharum (Orsted, 1843) Terebella lapidaria (Linnaeus, 1767) Terebellides stroemi (Sars, 1835) SMX: motile, unarmed pharynx Capitella capitata (Fabricius, 1780)	Euclymene oerstedii (Claparede, 1836)	Ficopomatus enigmaticus (Fauvel, 1923) Hydroides pseudouncinata (Zibrowius, 1968) Janita fimbriata (DelleChiaje, 1822) Jasmineira candela (Grube, 1863) Placostegus crystallinus (Zibrowius, 1968) Pomatoceros lamarckii (Quatrefages, 1865) Pomatoceros triqueter (Linnaeus, 1865) Protula sp. Sabella fabricii (Kroyer, 1856) Sabella pavonina (Savignyi, 1820) Serpula concharum (Langerhans, 1880) Serpula vermicularis (Linnaeus, 1767) Spirorbidae Vermilliopsis infundibulum (Gmelin, 1788) Vermilliopsis labiata (Costa, 1861)
(Éhlers, 1864) Syllis prolifera (Krohn, 1852)				
Syllis vittata (Grube, 1840) Trypanosyllis coeliaca				
(Claparede, 1868)				

#### Table 1 (Contd.)

Carnivores	Herbivores	Surface-deposit feeder	Burrowers	Filter-feeders
Carnivores Trypanosyllis zebra (Grube, 1860) Xenosyllis scabra (Ehlers, 1864) CDJ: discretely motile, jawed pharynx Ceratonereis costae (Grube, 1840) Glycera tesselata (Grube, 1863) Glycinde nordmanni (Malmgren, 1865) Goniada maculata (Ortsed, 1843)	Herbivores	Surface-deposit feeder	Burrowers	Filter-feeders
Nereis rava (Ehlers, 1868) Nereis zonata (Malmgren, 1867) CMX: motile, unarmed pharynx Chrysopetalum debile (Grube, 1855) Euphrosine foliosa (Audouin and MilneEdwars, 1833) Phyllodoce madeirensis (Langerhans, 1880)				

groups (Clarke and Warwick 1994). All the above techniques were employed in both the spatial and temporal analyses.

## Results

Composition, abundance and biomass of polychaete feeding guilds

Eleven feeding guilds were identified among the 79 species of polychaetes associated with the four algal facies studied for the spatial analysis: four guilds of surface-deposit feeders (SDJ, SDT, SST and SMX), three guilds of carnivores (CMJ, CDJ and CMX), two guilds of burrowers (BSX and BMX) and one guild each of herbivores (HMJ) and filter-feeders (FST) (Table 1). Most of these guilds were found also among the 66 species collected during the seasonal sampling of FA and EA algal forms; however, SMX and BSX were missing while FDT appeared in addition (total: ten feeding guilds; Table 1).

The number and dry weight of polychaetes of the different feeding guilds differed significantly (Fig. 2). CMJ, CDJ, HMJ and FST showed the highest abundance in all algal facies, whereas the numbers of burrowers and surface-deposit feeders were very low. The high abundance of FST in FanA was due to the large number of spirorbids found settled on the thalli of the algae (i.e. *Padina pavonica*). The same results were recorded with respect to biomass, with some variation depending on the algal facies. Remarkable differences between the feeding guilds were also observed in the seasonal study of the FA and EA facies (Fig. 3). CMJ,

CDJ, HMJ and FST dominated; still their contribution differed with season, especially in the EA facies.

The dominant feeding guilds showed significant differences in their distribution to the four algal facies (see ANOVA results in Table 2; and details as to significantly different pair of samples in Table 3), with two exceptions: (1) the CMJ guild was equally distributed in terms of abundance and (2) the HMJ guild was equally distributed in terms of biomass. Concerning the temporal analysis, the abundance of the CMJ guild showed significant changes in both the FA and EA facies, and the abundance of the HMJ guild only in the EA facies. No significant changes were found for any of the guilds with respect to biomass (Table. 2, 3).

### Similarity analyses

Hierarchical cluster analysis (Fig. 4), based on presence/ absence data, showed a high similarity of the four facies of the sciaphilic algae community. However, the same analysis and also the multidimensional scaling technique based on numerical abundance data discriminated three groups of samples on about 65% similarity level: the samples from the FA facies; the samples from the FanA facies; and the samples from the EA ; and FBA facies which were placed close together (group A) on about 80% similarity level (Fig. 4). As SIMPER analysis showed (Table 4), the CMJ and CDJ guilds were mainly responsible for the discrimination of the FA facies, while the FST guild highly contributed to the discrimination of FanA facies. Finally, the CMJ, FST and CDJ contributed to the discrimination of group A (FBA and EA facies).



Fig. 2 Mean abundance (left) and mean biomass as wet weight (right) of polychaete feeding guilds associated with the four different algal growth forms

The temporal analysis of the FA facies on the basis of presence/absence data (Fig. 5) showed high similarity of two groups of samples: (1) summer and winter and (2) autumn and spring. Concerning numerical abundance data, cluster analysis revealed the discrimination of summer samples on about 55% similarity level (Fig. 5). As indicated by SIMPER analysis (Table 4), this was mainly due to the abundance of the CMJ and HMJ guilds. The temporal analysis of the EA facies led to the discrimination of the spring samples, both on the basis of presence/absence and numerical abundance data

(Fig. 6); mainly on the score of the CMJ and CDJ guilds (see SIMPER results in Table 4).

#### Discussion

Algae-dominated communities are characterized by a high biodiversity and complexity, hosting a large number of ecologically diverse zoobenthic species (Antoniadou 2004; Antoniadou and Chintiroglou 2005), among which polychaetes are the second major taxon at least in

Filamentous algae (FA)





Fig. 3 Seasonal analysis of mean abundance and mean biomass (wet weight) of polychaete feeding guilds associated with filamentous (left) and encrusting (right) algal forms

the sciaphilic algae community (Antoniadou et al. 2004). This community seems to conserve its diversity when the analysis proceeds from a structural (species composition) to a functional level (trophic relations), since 12 feeding guilds were found in this study. Most polychaete species recorded were carnivores followed by herbivores or filter-feeders, depending on the facies considered. The prevalence of carnivores has also been reported for *Posidonia oceanica* meadows (Gambi et al. 1992, 1995) and for other hard substrate communities such as the photophilic algae community (Bianchi and Morri 1985; Desrosiers et al. 1986; Antoniadou and Chintiroglou

1997) and the *Cladocora caespitosa* assemblage (Chintiroglou 1996); carnivores also predominate among the macrophagous polychaetes in the *Mytilus galloprovincialis* assemblage (Damianidis and Cintiroglou 1998, 2000). In the present study, carnivores were represented mostly by species of the families Syllidae, Eunicidae and Glyceridae, which preferably feed on colonial or other small invertebrates (Fauchald and Jumars 1979). As to the other two dominant guilds, herbivores were mainly represented by the nereid *Platynereis dumerilii*, some members of the subfamily Exogoninae (i.e. *Grubeosyllis limbata*, *Sphaerosyllis pirifera*) and by the eunicids

Feeding guilds	Spatial		Temporal F	FA	Temporal E	ĒΑ
	F	Р	F	Р	F	Р
Abundance						
CMJ	1.94	0.131	3.11	0.003	5.77	0.008
CDJ	4.77	0.004	1.48	0.235	0.81	0.473
HMJ	8.05	0.001	2.69	0.058	2.94	0.085
FST	25.44	0.001	0.82	0.490	1.12	0.374
Biomass (dry weight	t)					
CMJ	2.96	0.037	2.02	0.126	2.09	0.145
CDJ	3.41	0.022	0.75	0.529	1.64	0.247
HMJ	0.58	0.630	1.02	0.392	1.13	0.382
FST	6.34	0.001	1.35	0.273	1.39	0.289

Bold indicates statistically significant differences

Table 3 Fisher PLSD results

Feeding guild	Abundance	Biomass
Significant differences of polyc	chaete feeding guilds associated with the four differer	nt algal growth forms
CĎJ	EA and FanA, FA	FBA and FA, FanA
	FanA and FBA	
СМЈ		EA and FA, FB
HMJ	FA and EA, FBA	
	EA and FanA	
FST	FA and EA	FA and FBA
	FanA and FA, FBA, EA	FanA and FA, FBA, EA
	FA	EA
Significant differences of polyc	haete feeding guilds associated with filamentous (FA)	) and encrusting (EA) algal forms on a seasonal basis
СМЈ	Autumn and summer, spring	Spring and summer, autumn, winter
HMJ		Spring and summer, winter

Lysidice ninetta and Scoletoma funchalensis, which mostly feed on epiphytes (Jania sp., Ceramium sp., etc.); filter-feeders, on the other hand, were represented by Serpulidae and Spirorbidae. Serpulids settle among the thalli of the algae and the rocks, while spirorbids mostly settle on the surface of the thalli of FanA. Serpulids were constantly present in the four facies studied, whereas spirorbids were found only in the FanA facies. The fairly low abundance of burrowers and surface-deposit feeders may result from the presence of various predators (carnivorous polychaetes, gastropods, crustaceans, etc.), which inhibit their settlement in microhabitats provided by the algae (Chintiroglou 1996).

The locomotory patterns of polychaetes are directly connected with their feeding habits (Damianidis and Chintiroglou 2000). Thus, motile macrophagous species dominated the sciaphilic algae community, followed by sessile microphagous species. Motile species seem to be well adapted as they are able to benefit from the increased animal biomass in vegetated habitats (Vizzini et al. 2002).

The spatial analyses showed a high similarity of the four algal facies studied, as, overall, the same feeding guilds were present. However, with respect to the abundance data of the different feeding guilds, the FanA and the FA facies were clearly distinct, whereas the FBA and EA facies did not differ from each other. The discrimination of the FanA facies was due to the large number of filter-feeders (FST guild). Spirorbids made the highest contribution in both abundance and biomass to this facies. However, due to their very small size, their effect is much stronger in terms of abundance (Antoniadou et al. 2004). Spirorbids are typically multiannual (Fauchald 1983), capable to settle immediately after release from the parental tubes. However, their presence should not be considered as stable, as most of them probably perish when the thalli of *P. pavonica* decay after mid-September (Diapoulis and Koussouris 1988).

The discrimination of the FA facies is probably more complicated, as more feeding guilds are involved. Carnivores showed an increased abundance in the FA facies as opposed to FBA and EA, whereas the differences with the FanA facies were insignificant. On the other hand, the abundance of herbivores was increased in the FA facies in comparison with the three others. Turf -forming algae seem to create a highly suitable environment for many zoobenthic species (Antoniadou 2004; Antoniadou and Chintiroglou 2005). The densely entangled axes of the dominant alga *Womersleyella setacea* form a complex mesh that provides refuge to small invertebrates, while a large amount of sediment is captured among the thalli, increasing the available microhabitats (Pavia et al. 1999; Piazzi and Cinelli 2000; Kelaher et al.



**Fig. 4** Affinity of polychaete feeding guilds associated with different algal growth forms (FA: filamentous algae, EA: encrusting algae, FanA: fan-shaped algae, FBA: filamentous bush-like algae). Results of cluster analysis based on presence/absence data (above) and on numerical abundances (below) calculated from the total of summer samples; and results of MDS analysis based on numerical abundances calculated from different sites (stations 1–7) and depths (15, 30 and 40 m)

2001; Hata and Nishihira 2002; Gorgula and Connell 2004). Additionally, a wealth of food particles, including benthic diatoms, is entrapped, ensuring the nutrition of many small-sized grazers such as the members of the subfamily Exogoninae. On the other hand, large-sized grazers such as P. dumerili and several eunicids may use the algal thalli or the associated epiphytes as a food source. The FA facies also host the highest biomass of carnivores, both free motile and discretely motile species, whereas herbivores showed similar values in biomass among the studied facies, in contrast with their abundance. This particular pattern can be explained by the high numbers of Exogoninae recorded in the FA facies; due to the small body-size of these polychaetes, an increase in their abundance has only little influence on biomass.



Fig. 5 Affinity of polychaete feeding guilds associated with filamentous algal forms (FA) on a seasonal basis. Results of cluster analysis based on presence/absence data (above) and numerical abundances (below) calculated from the total number of samples per season; Sp spring, S summer, A autumn, W winter



Fig. 6 Affinity of polychaete feeding guilds associated with encrusting algal forms (EA) on a seasonal basis. Results of cluster analysis based on presence/absence data (above) and numerical abundances (below) calculated from the total number of samples per season; Sp spring, S summer, A autumn, W winter

The qualitative analyses of the FA showed that overall the same feeding guilds were present throughout the year. Yet, considering their abundance, the summer samples were clearly distinct. During summer, the dominance of carnivores increased, especially that of motile species. This may be attributed to the reproductive cycles of some species, rather than to an actual increase in food supply, since their biomass remained

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Feeding guilds	FA - FBA (77%)	FA - FanA (65.8%)	FA - EA (76.8%)	FBA - FanA (84.8%)	FBA - EA (19.6%)	FanA - EA (84.5%)	FA - FBA + EA $(77\%)$	FanA - FBA + EA (84.7%)
Spatial analys CMJ CDJ FST HMJ SDT	sis 25.76 22.35 19.52	13.74 9.7 66.05 9.08	27.74 26.55 24.24 19.31	91.14	38.75 11.25 30.00 10.00	92.65	28.83 26.15 23.29 19.42	91.89
	Grou	p A (spring, autumn,	, winter); similarity:	76%		Group A (summer);	dissimilarity: 47.9%	
Temporal and CMJ HMJ CDJ FST	alysis of the FA fa 31.30 29.77 24.74 13.37	cies				31.06 28.18 16.94 19.09		
	Grou	p A (summer, autum	m, winter); similarity	y: 81.4%		Group A (spring); di	issimilarity: 56%	
Temporal ané CMJ CDJ HMJ FST	ulysis of the EA fa 45.83 21.08 15.64 15.64	cies				43.39 28.44 11.47 10.65		

Table 4 Simper results

The temporal pattern of the EA showed an unusual division, as spring samples were split-off. Spring samples showed minimal abundance and also diverged quantitatively with only four feeding guilds being present: CMJ, HMJ, BMX and FST. Both carnivores and herbivores showed a marked decline in abundance, whereas there were no significant changes in the filter-feeders. Concerning carnivores, a similar decrease was also observed in biomass. At this time of the year, surface waters in the North Aegean start to warm up and also the recruitment of macroalgae in shallow zones begins. As a result, an increased amount of food is provided to many herbivorous benthic invertebrates, which in turn attracts several predators, including carnivorous polychaetes. Apart from the implications of their life cycles, the low abundance of free motile polychaetes in spring samples may result from vertical migration towards shallower and more favourable biotopes (Antoniadou et al. 2004), whereas at the same time the populations of the sedentary species remain in a good status.

Several authors reported that the seasonality on sublittoral rocky bottoms is mainly due to a summer distinction, which is achieved by the massive recruitment of a few species (Cardell and Gilli 1988; Damianidis and Chintiroglou 2000; Fraschetti et al. 2002; Karalis et al. 2003). This is in accordance with the results of the functional analysis of the FA facies in the upper sublittoral zone, whereas in the case of the EA facies that occur in deeper waters, a different process seems to be also involved. Hence, the locomotory patterns of polychaetes may have a key role for the assessment of the seasonal pattern in the deeper sublittoral zone. Besides, the distribution of polychaetes in both time and space seems to be influenced by biotic interactions (Antoniadou et al. 2004).

In conclusion, the results provided by the structural (i.e. taxon composition) and the functional (i.e. trophic group) analysis of the algae-dominated communities (Antoniadou et al. 2004) are in strong agreement, a fact already reported by several authors (Desrosiers et al. 1986; Damianidis and Chintiroglou 2000; Karalis et al. 2003). However, a consideration of trophic group relations provides additional information (Chintiroglou 1996; Bremner et al. 2003). An analysis of feeding guilds reveals stable characteristics of benthic communities, and thus it represents a robust method for studying their ecology.

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