Introduction

The division into “guilds”, defined by Root (1967) as a group of species that exploit the same class of

The diversity of diets in Syllidae (Annelida: Polychaeta)

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Abstract: Results from examination of fecal pellets and gut content of some syllid species (Polychaeta, Annelida) are reported. Specimens were collected from 0 to 20m depths along Apulian coast (Mediterranean Sea). Species collected at shallowest depth showed the presence of microalgae and macroalgae fragments in their guts and were considered herbivores. A prevalence of sediment grains in species from deeper samples together with animal or vegetal detritus, suggest that these are detritivores. Finally some species, collected at different depths, appeared as a mixture of the two previous categories and were considered omnivores. In addition in the omnivores, as well as in the detritivores, spicules of sponges or ascidians (Didemnidae) and bryozoan fragments could be present. Some assumptions were inferred from correlation of feeding structures with feeding categories in syllids. This paper represents a preliminary study, but it intends to warn against broad generalizations. Previous studies of trophic guilds, based on assumptions inferred from a few and old papers relative mainly to the genus Autolytus, considered all the Syllidae as mostly carnivores. Our observations suggest that the syllids are much more various in their diet than previously assumed, and that several of them are not carnivores.

Résumé: La diversité des régimes alimentaires des Syllidae (Annelida: Polychaeta). Les résultats de l’examen des fèces et du contenu intestinal de plusieurs espèces de Syllidae, récoltées à des profondeurs allant de 0 à 20 mètres sur la côte des Pouilles (Méditerranée), sont présentés. Les espèces récoltées dans les eaux peu profondes contenaient des microalgues et des fragments de macroalgues et ont été définies comme herbivores. Par contre, la présence de sédiment chez les espèces d’eaux plus profondes suggère qu’elles sont détrivores. Quelques espèces récoltées à différentes profondeurs représentent un mélange des deux catégories précédentes et ont été nommées omnivores. Dans les omnivores comme dans les détrivores nous avons parfois trouvé des spicules d’éponges ou d’Ascidies Didemnidae et des fragments de Bryozoaires. Des hypothèses sont formulées sur les correlations qui existent entre la morphologie du tractus digestif antérieur et les types de nutrition des Syllidae. Notre étude, bien que préliminaire, permet de mettre en garde contre les généralisations concernant la nutrition de ces polychètes. En effet les études précédentes, basées sur des publications peu abondantes et anciennes, relatives surtout au genre Autolytus, ont considéré tous les Syllidae comme des carnivores. Dans notre contexte cette catégorie est difficile à définir, mais on peut affirmer, d’après notre étude, que beaucoup de Syllidae ne sont pas carnivores.

Keywords: Syllidae, Polychaeta, trophic categories, Mediterranean Sea
environmental resources in a similar way, led to a “feeding guilds” definition based on a joint consideration of food, feeding habits and locomotory patterns (Fauchald and Jumars, 1979). Since trophic analyses may reveal ecological structures not simply attributable to species abundances, as occurred in analysing diversity and abundance of feeding guilds in space or time (Maurer et al, 1979; Bachelet, 1981; Gambi et al. 1982), trophic guilds may be useful in understanding benthic community pattern and processes.

Polychaetes present a broad distribution in benthic marine environment and among macrofaunal taxa they are often dominant both in number of species and individuals (Knox, 1977; Bianchi and Morri, 1985). However, despite their wide employment in studies of benthic marine ecology based on trophic approaches (Maurer and Leathem, 1981; Gambi et al. 1982; Desroziers et al., 1984; Gambi and Giangrande, 1985a, b, c; Giangrande, 1986; Maurer and Williams, 1988; Maurer et al., 1988; De Pavia, 1993; Tena et al., 1993), information about the feeding biology within each polychaete family is scant. This has led to generalization to a whole family or a genus, even if the available data were based on studies conducted on few species or inferred from the correlation of feeding structures with diets. This tendency has been observed particularly within the Syllidae, which is the best represented family on hard substrata.

Very few studies have been conducted to define syllid diet. Katzmann (1972) asserted that in shallow waters syllid species seem to be linked to the epiphytic cover more than associated to a specific algal assemblage and that species living on Cystoseira seem to have no particular trophic requirements.

Fauchald and Jumars (1979) had postulated that all members of the subfamilies Autolytinae and Syllinae were carnivores, while they considered members of Exogoninae and Eusyllinae as herbivore grazers or detritivores. These assumptions were based on few studies (Malaquin, 1893; Allen, 1921; Okada, 1928; Hamond, 1969; Hughes, 1975; Korringa, 1951). In addition, some species such as Haplosyllis spongicola (Grube), Branchiosyllis exilis (Gravier), and Procerea sp., living associated with other invertebrates (from sponges to ophiuroids), can be considered as commensal or parasites, even though they lack specificity (Martin and Britayev, 1998; Britayev et al., 1998). Moreover, the meaning of relationships through benefit-cost analysis have never been investigated. In addition, some species of Exogone have also been found feeding on sponges, suggesting that, also in this case, the relationships could be occasionally parasitic (Pascual et al., 1996). Finally Rasmussen (1973) reports a carnivorous habit for ripe pelagic specimens of Exogone naidina Oersted.

Although the assumptions of Fauchald and Jumars (1979) have never been confirmed by additional experimental observations, they have been widely used even in recent papers concerning feeding guilds of Polychaetes, (Gravina et al., 1995; Chintiroglou, 1996; Porras et al., 1996; Muniz & Pires, 1999), where all the species belonging to the genus Syllis were considered carnivores.

This paper aims to increase the knowledge on syllid feeding habits in their natural environment, including consideration of the feeding apparatus, the features of which may be correlated to feeding strategies.

### Material and methods

Specimens were collected from June 1997 to June 1998 by SCUBA divers on hard substrata in both Adriatic Sea (Otranto, Italy) and Ionian Sea (S. Caterina and Porto Cesareo, Italy) at a depth ranging from 0 to 20 m, on different kind of algal cover. Worms were immediately transferred from sampling sites to laboratory where they were spread out in single jars with fresh filtered sea water (0.45 µm) and kept in air conditioned room ranging from 14 to 24°C according to the temperature at the collection site. Observations on behaviour of 10 syllid species (Tab. 1) were performed with a Leica MZ 12 Stereomicroscope equipped with a videocamera. Worms were kept on different algal substrates such as Cystoseira amentacea Valiante, Halimeda tuna (Hillis & Sol.) Lamouroux, and Peyssonnelia squamaria, (Gmelin) Decaisne, widely colonized by a large number of live epiphytes (encrusting sponges, hydroids, and bryozoans).

Syllid trophic requirements were investigated by examination of gut content and fecal pellets. After collection, 18 species with a variable number of individuals for each species were identified (Tab. 2). Worms were kept in jars in filtered sea water (0.22 µm) without food source

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Syllid species utilized for behavioural observations on different algal substrates colonized by living epiphytes, mainly hydroids and bryozoans.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eusyllis assimilis (Marenzeller, 1875)</td>
<td>Eusyllis lamelligera (Marion &amp; Bobretzky)</td>
</tr>
<tr>
<td>Sphaerosyllis kystrix (Claparède, 1863)</td>
<td>Syllis columbretensis (Campoy, 1982)</td>
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<td>Syllis hylalina (Grube, 1863)</td>
<td>Syllis krohni (Ehlers, 1864)</td>
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<tr>
<td>Syllis prolifer (Krohn, 1852)</td>
<td>Syllis truncata cryptica (Ben-Eliahu, 1977)</td>
</tr>
<tr>
<td>Syllis variegata (Grube, 1860)</td>
<td>Trypanosyllis zebra (Grube, 1860)</td>
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before observation. They began to release fecal pellets after 24 h and the intestines were completely emptied in a week. Fecal pellets were daily collected from the bottoms of jars and analysed. Observations were performed with a Leica fluorescence microscope to identify vegetal matter. The feeding apparatus of individual relaxed with an isotonic solution of MgCl₂ was observed and the lengths of pharynx, proventriculus and teeth were measured with a micrometer. Data were correlated to each other and with feeding strategies. Correlations were performed on the mean obtained within each species after measurement of 5 to 50 specimens. In order to compare intra and interspecific differences, measurements of feeding structures were also taken from available preserved material of Syllis truncata cryptica (50 specimens) and S. variegata (35 specimens).

### Results

Observations on live specimens show that none of the studied species (Tab 1) took an interest either in hydroids or in bryozoans as possible food. Attempts by worms to feed on polyps or zooids were never observed, moreover, worms always recoiled from hydroids when they came in touch. Often they stopped for a long while on algal tissues, and movements of internal feeding apparatus were observed with the stereomicroscope, even though no apparent food particles were observed to move inside the gut. Fecal pellets of 18 different species of Syllidae which had fed in their natural environment have been examined. Gut content was analysed only by fluorescence because its identification with the light microscope never provided good results.
The presence of a large amount of parts of vegetal organisms such as encrusting pluricecellular algae (probably Corallinaceae), partially or totally digested diatoms, and other unidentified unicellular algae, was enhanced only in Syllis armillaris, S. rosea, S. columbretensis, and Sphaerosyllis hystrix. A similar gut content was found in S. gracilis, which showed also the presence of small particles of sediment and crustacean skeletons (Fig. 1a, b). All these species were collected in shallow water from 0 to 3 m, excepting for S. columbretensis, which was collected also from 3 to 6 m depth. In addition, the presence of a large amount of alive ciliate protozoans was observed in the gut of S. rosea.

Sponges spicules, unicellular algae and few sediment grains were found in Syllis prolifera (Fig. 2a, b), S. truncata cryptica, S. hyalina, and Autolytus quindecemdentatus, collected at varying depths. In this last species also crustacean fragments were observed. Syllis prolifera was particularly abundant at shallower sites, while Autolytus quindecemdentatus was collected from 3 to 6 m, and Syllis hyalina, and S. truncata cryptica at deeper depths (6-12 m). A similar fecal pellet composition, but lacking sediment particles, was evidenced also in S. krohnii collected at sites from 0 to 6 m depth (Fig. 3a). Analysis of gut content in S. prolifera, showed the presence also of protozoan skeletons (Fig. 2b). Different food sources were present in specimens from shallow and deeper sites, with a predominance of algae and sediment respectively.

Completely divergent food-habits have been observed for Syllis lutea, S. variegata, Trypanosyllis zebra, Eusyllis lamelligera, E. assimilis, Pionosyllis lamelligera and Syllides fulvus, all collected between 6 and 12 m, which showed mainly sediment grains and unidentified particulate detritus in their fecal pellets (Fig. 3b), even though in some specimens of Pionosyllis lamelligera and S. variegata, sponge spicules and empty bryozoan fragments were also detected.

Fluorescence was particularly high in Syllis gracilis, S. armillaris, S. rosea, Sphaerosyllis hystrix and S. columbretensis, confirming the herbivorous feeding mode, but was also present in S. prolifera, S. truncata cryptica, S. krohnii, and S. hyalina. By contrast, fluorescence was not evidenced in Syllis lutea, S. variegata, Trypanosyllis zebra, Eusyllis lamelligera, E. assimilis, Pionosyllis lamelligera and Syllides fulvus.

Nematocysts were never observed inside fecal pellets of any of the investigated syllid species. The above results are summarized in Tab 2.

According to the presence or absence of vegetal residues, and to the presence or absence of sediment grains and other particulate detritus, species were classified as herbivores, or detritivores. The species whose fecal pellets contained only macroalgal fragments and microalgae and showed high fluorescence were considered herbivores. The species in which a large amount of sediment and unidentified particulate detritus were found, sometimes with few fragments of colonial invertebrates were instead considered detritivores. The species showing both the above mentioned kind of residues, were considered omnivores, even though, based on the present data, the only species which may be really considered omnivorous was S. krohnii, which showed a mixture of micro- and macro-algal fragments and a large amount of well preserved sponge or ascidian spicules.

This first attempt of trophic groups identification is shown in Tab. 2.

High correlation was found between tooth length and feeding strategy (r= 0.74; p<0.01) (Fig. 4a). Herbivore species have the best-developed teeth, reaching the highest value in Syllis gracilis (83.3 µm), while teeth lengths in deposit feeders were very reduced with a mean of only 35.1 µm. A similar pattern resulted by correlation of pharynx lengths with feeding strategies (r=0.6 p<0.05) (Fig. 4b), where herbivores showed higher values than detritivores and omnivores. Correlations related to proventriculus length in which omnivores showed the lowest values, were not significant (r=0.2 p>0.05) (Fig. 4c). The longest proventriculus was 1466.7 µm in S. gracilis, while the longest pharynx was 1433.3 µm in S. armillaris. Fig. 5 shows the difference in pharynx length of two species with different feeding strategies: the herbivorous S. rosea shows longer pharynx and proventriculus (Fig. 5a) compared to the omnivorous S. prolifera (Fig. 5b).

In order to assess the variability of feeding structure with the size of the worm, correlation was performed in Syllis variegata and S. truncata-cryptica, for which a large number of individuals were available. In both species the correlations were always significant. The lower correlation (r = 0.39 p<0.05) was found in S. variegata between tooth length and total worm length (Fig. 6a), while the best correlation resulted for pharynx length (r = 0.77 p<0.01) in the same species (Fig. 6b). However, when values obtained from feeding structure measurements of the two species (Tab. 3) were statistically analysed (T-test), intraspecific variability was found to be significantly lower than interspecific one.

Discussion

Although functional studies based on feeding biology can help to clarify the role of organisms within benthic communities and to explain patterns of distribution, the knowledge on basic biology for most of the benthic organisms is today still too scanty.
Figure 1. Fecal pellets from an omnivorous species Syllis gracilis. a. fragment of a pluricellular alga (incrusting corallinacea Fosliella sp.); b. pennate diatom (1), together with few sediment grains, and a probable crustacean exoskeleton (2).

Figure 1. Fèces de l’espèce Syllis gracilis. a. Fragment d’une algue pluricellulaire (corallinacea incrustante, Fosliella sp.); b. Diatomées penées (1), grains de sable et ce qui semble être un exosquelette de Crustacé (2).
Figure 2. Fecal pellets from the omnivorous *Syllis prolifera*. **a.** Entire fecal pellet showing a large amount of sediment particles; **b.** enlargement of a part of the fecal pellet showing sediment grains, sponge spicules or diatoms (1), silicoflagellate exoskeletons (2) and Dinophyceae (Peridinales, *Podolampas* sp.) (3).

Figure 2. Fèces de l’omnivore *Syllis prolifera*. **a.** contenu intestinal entier montrant une grande quantité de sédiment ; **b.** détail des fèces montrant les grains de sable, les spicules d’éponge ou des diatomées (1) et les exosquelettes de silicoflagellés (2) et des Dinophyceae (Peridinales, *Podolampas* sp.) (3).
Figure 3. a. Fecal pellets from the omnivorous *Syllis khronii*, showing an agglomerate of pluricellular algae and a large amount of sponge or ascidian (Didemnidae) spicules (1); b. the fecal pellet from the detritivorous *Syllis variegata* from a deeper sample, showing the large amount of sediment.

Figure 3. a. Fèces de l’omnivore *Syllis khronii* montrant un agglomérat d’algues pluricellulaires et une grande quantité de spicules d’éponges ou d’ascidies (Didemnidae) ; b. fèces du détritivore *Syllis variegata* provenant d’un échantillon plus profond, montrant une grande quantité de sédiment.
Since syllids live in dense assemblages on colonial organisms such as hydroids or bryozoans, it was supposed that most of the syllid species could feed on them, as reported in the observations of Okada (1928), relative to the Autolytinae. Species belonging to this subfamily can feed on polyps, sucking up their gastric fluid, as species of the genus *Procerastea* do, or eating tentacles and upper portion of the hydrants as do *Autolytus* spp.

This work was started to investigate the possibility of predation on hydroids and bryozoan by Syllidae other than Autolytinae. However, observations on the species behaviour indicated that they were not interested in hydroids as food source, on the contrary they seemed to be disturbed by their presence. Specimens were observed to remain quiet on algal surfaces, moving their internal feeding apparatus: they were probably grazing on algal epiphytes, even though food was not observed moving inside, nor was the feeding apparatus observed extruded from the mouth. It must also be stressed that generally all the examined syllid species moved towards crevices to avoid light because they were disturbed by the microscope light.

Until now, only Autolytinae are proved to be carnivorous, even though this is established only by direct observations (Allen, 1921; Okada, 1928; Hamond, 1969). Autolytinae are often strictly associated to hydroids, sometimes building mucous tubes along the colonies (Hughes, 1975), and it is probable that this habit can be extended to the whole subfamily. Within the Autolytinae, *Proceraea* sp., infesting up to 33% of the hydrothecae of *Abietinaria turgida*, is considered to be a parasitic form (Britayev et al., 1998). This species seems to feed on the polyps as demonstrated by the presence, in the gut, of pigmented granules which are characteristic of the hydroid tissues.

The searching for nematocysts within fecal pellets or gut contents gave always negative results. However, since the carnivorous syllids seem to be eating mostly the internal fluid of animals, the difficulty in founding rests of hydroids and bryozoans inside the fecal pellets is evident. In general, it is difficult to identify carnivores, except in the case of predation on hydroid fragments leaving nematocysts as traces.

Examination of gut content and fecal pellets in 18 species, led to hypothesize the existence of different trophic categories especially within the genus *Syllis*. These categories have been preliminary indicated as herbivores, omnivores and detritivores.

As far as the detritivores are concerned, a better definition of the detritus quality ingested (vegetal detritus, sediment particles, diatoms, bacteria etc.), is needed to assess the category. In the present paper identification was based mainly on the presence of sediment within fecal pellets, where a large amount of particulate and often unidentified detritus was also evidenced. It was supposed that fragmented sponge or ascidian spicules, as well as fragments of colonial animals like bryozoans skeletons,
found within fecal pellets of species considered detritivores, derived mostly from the action of pharynx sucking the detritus surface layer, rather than by real predation. Some bryozoan species form encrusted colonies and, on considering the feeding apparatus morphology, it is not possible that syllids can feed on such material. Moreover, sponge spicules were large and broken just like that generally found within detritus.

By contrast, the spicules found in *S. krohnii* fecal pellets, probably derive from grazing on sponge or ascidian tissues, since they were very abundant and well preserved. The absence of sediments and of a large amount of microalgae in this species can support this hypothesis. Syllids feeding on sponge tissues are already well known (Tsurumi and Reiswig, 1997).

A better definition of the category here named omnivores, is also required, because omnivores ought to include also the food derived through carnivory, whilst vegetal and animal rests as microalgae and sponge or ascidian spicules, without sediment, were found only in *S. krohnii*.

Finally *S. prolifera*, the only species where also protozoan residual were found, could be better considered opportunistic than omnivorous, because its feeding habit varied according to the depth at which specimens were collected.

These conclusions are supported by the correlation between feeding apparatus morphology and feeding strategies, where detritivores are the forms with the less developed teeth. These forms probably do not need the presence of such structure, mainly sucking available detritus from the surface directly through the pharynx. By contrast, the best developed teeth are found in herbivores, also showing the highest value in pharynx length; they probably have to graze vegetal epiphytes from the substrate, before sucking them. Lastly, in the omnivores the length of pharynx and proventriculus was similar to those in detritivores, but with a tooth length similar to that of herbivorous species. Even though more data from other species and additional specimens of the same species are needed to confirm this trend, comparison between the omnivorous *S. truncata cryptica* and the detritivorous *S. variegata* shows that intraspecific variability of teeth, pharynx and proventriculus sizes, is lower than variability observed between the two species.
The function of each structure within the syllid feeding apparatus was firstly studied by Okada (1928) in Autolytus edwarsi (Autolytinae), who asserted that the proventriculus creates a negative pressure by the pumping action of the pharynx, which can be extruded and oriented acting as a sucking device, while the toothed crown (trepan) was used to cut hydroid tentacles or to pierce the surface of the prey. The feeding apparatus of Autolytinae is quite different from that of other subfamilies, presenting a very long pharynx, used in sucking out the content of colonial invertebrates after piercing their surface with the pharyngeal teeth.

More information is needed especially to better define the categories to which the species here investigated belong, and to increase our knowledge to other species so far not investigated. Moreover, for a better definition of trophic requirements, studies on digestive enzymes should also be done. It was particularly interesting to find ciliate Protozoa inside the intestine of an herbivorous form, which could be symbiotic mutualists similar to those occurring in most herbivores. Unicellular organisms, looking like zooxantelle were also observed inside the gut of Exogone dispar, which was found living inside a sponge, showing how complex and specialized the syllid feeding strategies could be. Further studies are needed to clarify the above observations.

The present work represents a first attempt to define syllid feeding strategies and a warning about dangerous generalizations from a few data. Up to now, representatives of this polychaete family were considered mostly carnivores, leading to wrong conclusions, for example in examining the distribution of species along environmental gradients (Giangrande, 1986). Even though this study is preliminary, it demonstrates that carnivorous habits are not a widespread strategy within the Syllidae; on the contrary syllids seems to have different feeding strategies perhaps related to the most abundant energy source. In our study, herbivores or grazers were collected always in shallower samples, detritivores in deeper samples, and omnivores were present at all depths.

Table 3: Measurements and variability of different parts of anterior gut in Syllis variegata and S. truncata cryptica

<table>
<thead>
<tr>
<th>Species</th>
<th>Pharynx</th>
<th>Proventriculus</th>
<th>Tooth</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>mean length</td>
<td>coefficient of variation</td>
<td>mean length</td>
</tr>
<tr>
<td>Syllis variegata</td>
<td>951±5</td>
<td>27</td>
<td>886±5</td>
</tr>
<tr>
<td>Syllis truncata cryptica</td>
<td>648±2</td>
<td>18</td>
<td>347±8</td>
</tr>
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</table>
References


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