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Role of fungi in the trophic niche of the congeneric detritivorous *Asellus aquaticus* and *A. coxalis* (Isopoda)

Loreto Rossi, Anna E. Fano

Rossi, L. and Fano, E. A. 1979. Role of fungi in the trophic niche of the congeneric detritivorous *Asellus aquaticus* and *A. coxalis* (Isopoda) – Oikos 32: 380–385.

The importance of various fungal samples, isolated from plant detritus, and of the plant detritus itself in the trophic niche of *Asellus aquaticus* (L.) and *A. coxalis* Dollf., was studied in the laboratory. We observed that: (1) The fungi and not the plant detritus, from which they are isolated, constitute the energy source for both species. In fact, the animals to whom the sterilized detritus was offered died within a few days. The animals to whom the fungal colonies were given had significantly higher survival and body growth compared to the controls; (2) The various fungal samples, offered as sole source of food, were used with different efficiency, both by animals of the same species and by animals of different species; and (3) The heterogeneous fungal populations, present in nature in the detritus, constitute a food resource mosaic which permits an even distribution of the trophic resources between two ecologically similar, cohabitating detritivorous species.

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Исследовали значение разных грибов, изолированных из растительного детрита, и самого растительного детрита в трофических нишах *Asellus aquaticus* (L.) и *A. coxalis* Dollf. в лабораторных условиях. Наблюдалось: 1. грибы, а не растительный детрит, в котором они развиваются, представляет основной энергетический ресурс для обоих видов. Животные, которых кормили стерилизованным детритом, погибали в течение нескольких дней. Животные, питавшиеся грибным мицелием, имели более высокую выживаемость и размеры в сравнении с контролем; 2. различные группы грибов, предложенные в качестве основной пищи, утилизировались с различной эффективностью, как животными одного вида, так и представителями разных видов; 3. гетерогенные грибные популяции, имеющиеся в детрите в естественных условиях, образуют мозаику пищевых ресурсов, определяющую выровненное распределение пищевых запасов между двумя экологически сходными и соседствующими в одном местообитании детритофагами.

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1. Introduction

The importance of plant detritus as food for the benthic invertebrates has long been known (Jones 1950, Brown 1961, Nelson and Scott 1962, Odum and De la Cruz 1963, Hynes 1963, Minshall 1967), but only recently attention has been given to the role in secondary production of the microbial populations involved in the decaying process of the detritus. An interesting but little known aspect of the problem is constituted by the relationship existing between debris-microflora-detritus feeders. A clear correlation has been observed between:

- (a) the development of fungi populations and the increase in the protein content of the detritus (Kaushik and Hynes 1971);
- (b) type, degree of fungal colonization of the detritus and selection of the detritus by some benthic invertebrates (Bärlocher and Kendrick 1973).

In addition, the ways in which the congeneric species avoid the trophic interaction in the overlapping zones of their range have been studied in many habitats (Brian 1957, Klopfer and MacArthur 1961, Cummins 1964, Mackay 1972). However, little is known of the distribution of resources between ecologically similar species within the same organic substrate in the streams.

These arguments pose interesting problems:

- (1) Does the plant detritus supply the nourishment to the benthic detritus feeders or does it merely constitute the growth substrate of the fungi?
- (2) Do ecologically similar species living in cohabitation use the various colonizing fungi of the detritus in different ways?

Our experiments attempt to respond to these two questions by means of an evaluation of the importance of various fungal samples, isolated from the detritus in the trophic niche of two species of *Asellus*, collected from the same biotope.

2. Materials and methods

The naturally allopatric species *A. aquaticus* (L.) and *A. coxalis* Dollf. have been found for several years in biotopes previously exclusive to *A. aquaticus* (Fano et al. 1977). The samples of both species studied belong to a population of benthic mesofauna of the Sarno River (Naples). In our experiments only larvae born in the laboratory were used: 2762 *A. aquaticus* of 40 broods and 1182 *A. coxalis* of 26 broods.

To avoid contamination of the experimental environment, all the *Asellus* used in the experiment were taken from the maternal pouch in the first embryonic stages and kept in sterile culture until completely developed, according to a previously published technique (Rossi et al. 1975).

The young animals (approximately 1 mm long) of each brood were then distributed 4 or 5 to each of 10

cm diam. glass bowls, each containing 100 ml well water aerated 24 h and sterilized before use.

Ten sets of animals from each species were separated. Each set of *A. aquaticus* contained 250 animals, and each set of *A. coxalis* contained approximately 100 animals.

The diets offered, each to one set of animals of each species, were constituted by (1) 8 types of fungus hyphomycetes in pure culture, each of which was offered to one set of each species; (2) sterilized plant detritus; (3) Plant detritus with live microflora, which served as control for all the experiments. The suitability of each particular diet was evaluated on the basis of survival and rate of body growth (variations in distance from the base of the antenna and the distal part of the telson) registered every three days. The dead animals were removed every day and the water changed every third day. All the experiments were carried out in a thermostatic chamber at 18°C with natural, very low intensity light.

The fungi used, *Alternaria* sp., *Anguillospora* sp., *Aspergillus awamori*, *Aspergillus niger*, *Flagellospora* sp., *Fusarium* sp., *Humicola* sp., *Trichoderma* sp. were previously isolated from decaying leaves taken from the Sarno River. Each of these was cultured in liquid media (malt extract broth). Twenty mm diam. pure colonies were washed with sterile distilled water and offered to the young *Asellus* as their only source of nourishment. Each glass bowl received a single colony replaced every third day.

The plant detritus offered was constituted by dead *Platanus* leaves collected near the Sarno River. The leaves were dried and prepared in 90 mg (dry wt) packs. The leaf packs were then soaked for 4 wk in tap water at 15°C, pH 6.

All packs were then sterilized in an autoclave; a part of these were then offered as they were in complete "asepsis" /Diet (2)/, others, before being offered, were again soaked for 40 d /Diet (3)/.

The sterilization efficiency and the presence of microflora on the soaked leaf packs were verified by submitting 10 packs offered as diet (2) and an equal number of packs offered as Diet (3), to microbiological isolation.

3. Results

The experiments were completed in 60 d. At the end of this period it was evident that the sterilized plant detritus was not suitable to satisfy the energy requirements of the young of any of the two *Asellus* species. All the animals to whom it was offered as the only food source refused to consume it (the leaves did not appear skeletonized) and died within the first 15 d of experiment (Tab. 1). The various fungi offered to the animals as single source of nutrition were suited to this end, but in different ways for the two species. In fact: (1) the *A.*

Tab. 1. Survival and body growth of indifferentiated young *A. aquaticus* and *A. coxalis*, to whom 10 different types of food were offered for 60 d. * – Significance of the difference between the two species (χ^2 -test), ** – Significance of the difference in growth compared to the control animals fed with leaves (t-test) 00 = $p < 0.01$; n.s. = not signif.

Source of food		No. of animals at start	No. Survivors	%		Body length (mm)	
			No.			$\bar{x} \pm 2$ S.E.	
<i>Aspergillus awamori</i>	<i>A.a.</i>	288	256	88.9	00*	4.15±0.103	00**
	<i>A.c.</i>	108	82	75.9		3.95±0.270	00
<i>Anguillospora</i>	<i>A.a.</i>	276	243	88.0	00	4.77±0.110	00
	<i>A.c.</i>	104	26	25.0		3.07±0.302	n.s.
<i>Flagellospora</i>	<i>A.a.</i>	260	223	85.7	00	4.68±0.190	00
	<i>A.c.</i>	104	11	10.6		2.73±0.310	n.s.
<i>Fusarium</i>	<i>A.a.</i>	264	224	84.8	00	4.56±0.198	00
	<i>A.c.</i>	104	0	0.0		–	
<i>Alternaria</i>	<i>A.a.</i>	260	218	83.8	00	3.88±0.152	00
	<i>A.c.</i>	104	16	15.4		3.14±0.290	n.s.
<i>Humicola</i>	<i>A.a.</i>	276	204	73.9	00	3.89±0.104	00
	<i>A.c.</i>	100	0	0.0		–	
<i>Trichoderma</i>	<i>A.a.</i>	266	96	36.1	00	4.23±0.256	00
	<i>A.c.</i>	104	89	85.6		4.33±0.210	00
<i>Aspergillus niger</i>	<i>A.a.</i>	246	77	31.3	00	4.01±0.158	00
	<i>A.c.</i>	108	97	89.8		3.90±0.197	00
Leaves	<i>A.a.</i>	440	318	72.3	n.s.	2.93±0.073	
	<i>A.c.</i>	260	195	75.0		2.63±0.112	
Sterile leaves	<i>A.a.</i>	186	0	0.0		–	
	<i>A.c.</i>	86	0	0.0		–	

Tab. 2. Significance levels in the differences between the number of survivors of the same species on each nutriment resource offered for 60 d to young of *A. aquaticus* and *A. coxalis*. The values in brackets refer to the species *A. coxalis*; the arrows are oriented on the higher value. χ^2 -test, n.s. = not significant, 1% = significant at the 1% level.

	<i>Asperg. awamori</i>	<i>Alter-naria</i>	<i>Fusa-rium</i>	<i>Anguil-lospora</i>	<i>Humico-la</i>	<i>Asperg. niger</i>	<i>Tricho-derma</i>	<i>Falge-lospora</i>
<i>Alternaria</i>	n.s. ↑(1%)							
<i>Fusarium</i>	n.s. ↑(1%)	n.s. ↑(1%)						
<i>Anguillospora</i>	n.s. ↑(1%)	n.s. (n.s.)	n.s. ←(1%)					
<i>Humicola</i>	↑1% ↑(1%)	↑1% ↑(1%)	↑1% (n.s.)	↑1% ↑(1%)				
<i>Aspergillus niger</i>	↑1% ←(1%)	↑1% ←(1%)	↑1% ←(1%)	↑% ←(1%)	↑1% ←(1%)			
<i>Flagellospora</i>	n.s. ↑(1%)	n.s. (n.s.)	n.s. ←(1%)	n.s. ↑(1%)	←1% ←(1%)	←1% ↑(1%)	←1% ↑(1%)	
<i>Flagellospora</i>	n.s. ↑(1%)	n.s. (n.s.)	n.s. ←(1%)	n.s. ↑(1%)	←1% ←(1%)	←1% ↑(1%)	←1% ↑(1%)	
Leaves	↑1% (n.s.)	↑1% ←(1%)	↑1% ←(1%)	↑1% ←(1%)	n.s. ←(1%)	←1% ↑(1%)	←1% ↑(1%)	↑1% ←(1%)

aquaticus to whom the fungi were offered showed compared to the controls (leaves as food), survival rates: (a) significantly higher for 5 of the 8 hyphomycetes offered; (b) similar values for one (*Humicola*); (c) lower values for 2 (*Trichoderma* and *A. niger*) (Tabs 1 and 2). The body growth rates registered for all the animals with

fungi as food were significantly higher than those observed for the control animals (Tab. 1, Fig. 1). (2) the *A. coxalis* showed compared to the controls: (a) significantly higher survival and body growth for two (*Trichoderma* and *A. niger*) of the 8 fungi offered; (b) no significant different survival for one (*A. awamori*)

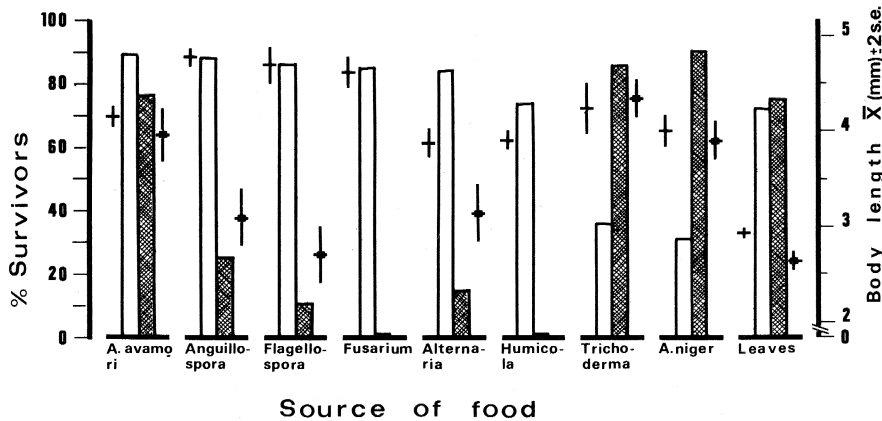


Fig. 1. Percentage survival and body lengths of *A. aquaticus* and *A. coxalis* for each of the 10 types of food offered. Observations on the 60th day of the experiment. Light columns = % *A. aquaticus* surviving; dark columns = % *A. coxalis* surviving. The horizontal bars indicate the average length (projected against the scale to the right) of the species to which the column refers. Vertical bars indicate ± 2 S.E.

where, however, a sharp increase in growth was observed; (c) a much lower survival compared to the controls was noted for the 6 remaining fungal types.

The microbiological analysis of the previously isolated leaf packs revealed a total asepticness of the sterilized leaf packs and a notable microbial development of the soaked ones. Fungi hyphomycetes, belonging to the same orders as those isolated from the detritus taken from nature and offered to the animals, constituted the dominant microorganism class for each of the 10 leaf samples observed. Incipient populations of bacteria and/or protozoa are rapidly repressed by the fungal development.

4. Discussion

From an analysis of the results, essentially two noteworthy points arise: (1) the colonizing fungi of the plant detritus, and not the detritus itself, constitute the energy source for both *Asellus* species; and (2) an accentuated intraspecific variability and a marked interspecific difference in the selection of the fungal resources constitute the bypass to incipient competitive phenomena.

The first point confirms for *A. coxalis*, what we suggested in a previous publication (Rossi and Vitagliano Tadini 1978) and is in agreement with the observations of other authors. We previously demonstrated the suitability of faeces of adult *A. aquaticus* as a nutritive source for the indifferenced larvae of the same species, in as much as it is made up of substantially unabsorbed detritus, rich in microflora (Rossi and Vitagliano Tadini 1978). Williams (1962) described fungal hyphae in the intestinal content of *Asellus meridianus*; Minshall (1967) noted the presence of microflora in the diet of *Asellus brevicaudus*. Bärlocher and Kendrick (1973, 1975) observed the detritivorous animals' preference for leaf areas with high hyphal concentration, and affirm the necessity of the presence of microfungi in plant detritus offered as food, for the survival and growth of *Gammarus pseudolimnaeus* Bousfield.

Mackay and Kalff (1973) confirm these observations for two species of caddis fly larvae and Kostalos and Seymour (1976) for *G. minus*. Furthermore our results do not leave doubts as to the necessity of microbial populations in the detritus, rendering it suitable as the sole food source for both *Asellus* species. We postulate that the fungi, more than the other microbial components, are responsible for the nutritive content of the plant detritus. This is supported because in our experiments: (1) only fungi develop on the soaked plant detritus; (2) colonies of the same fungi are used profitably as food by *Asellus*. The complete inefficiency of the sterile detritus as sole nutritive source cannot be attributed to modifications of the intrinsic proprieties of the plant detritus caused by the sterilization process, since the control group (Diet 3) regularly utilized the same material autoclaved after soaking. The fungi cultured on the analyzed detritus samples constituted the only substantial difference between the soaked and the sterilized detritus.

The development of other microbial elements is, in fact rapidly repressed by the hyphal development. Kaushik and Hynes (1968) and Harley (1971) observed the same phenomenon in various types of decaying leaves both in the laboratory and in nature and affirm that the increase in protein content registered in the microorganism-colonized detritus to a large extent was due to the growth of fungi.

Bärlocher and Kendrick (1975) showed that *G. pseudolimnaeus* assimilated up to 96% of the fungal protein extracted from plant detritus but only 5% of the total content of the newly microorganism-colonized detritus. Similar rates were registered by Hargrave (1970) for the amphipode *Hyaella azteca*.

Furthermore, Kostalos and Seymour (1976) showed the inutility of bacterial diets to *G. minus* survival and development. Our evidence relative to survival and body growth of fungal fed *Asellus* further and unequivocally supports this hypothesis.

The points mentioned above suggest in addition that the fungal substances in the natural diet of benthic in-

vertebrates, and the role of fungi in detritus-recycling have a greater importance than that resulting from the estimates of average microbial biomass per unit weight of decomposing leaves.

The second point arises from the evidence that the various fungi are found in intra- and interspecific degrees of suitability. The different utilization of the various fungi cannot be attributed to age differences among the colonies offered, and therefore their palatability, as has been suggested by some authors (Nikolei 1960, Ulrich 1943, cited by Bärlocher and Kendrick 1973); the colonies were in fact replaced in our experiment every three days by fungal colonies of the same age. Neither can the difference be attributed to the uniformity of the culture medium used, which may not be equally suitable for development of each of the various fungi as is demonstrated by the widespread use of some of these by a fraction, however small, of the animals. We believe it probable that the variability observed derives from the presence of several genotypes in the *Asellus* population, each having different trophic needs, satisfied by the different energetic and vitaminic characteristics of the various types of detritus-colonized fungi (Kaushik and Hynes 1968, Suberkropp and Klug 1976). It seems to be a particular case of polymorphism based on metabolic diversity.

A similar phenomenon, notable also in the results obtained by Bärlocher and Kendrick (1973) has been observed in some species of frugivorous insects. For example in *Ceratitis capitata* Wied, the variability in food selection determines the polyphagy which characterizes the entire population (Cavicchi and Zaccarelli 1974).

We believe that the variability observed in *Asellus* increases the probability of: (1) the population remaining in its own habitat and (2) defense by competitive interactions. It has in fact been demonstrated that the fungal populations present in the detritus fluctuate in quality and quantity according to the season, therefore the contemporary presence in an environment of various genotypes capable of utilizing an equal number of various types of fungi guarantees the persistence of the population and allows an equal distribution of resources between the various individuals. Similarly, the partial but substantial difference in trophic niches of the two cohabitating species constitutes a valid defense mechanism against competition. Food specialization is an ecological isolation strategy often observed in similar and cohabitating species (Klopfer and MacArthur 1961, Piane 1963, Schoener 1965, 1968). Our results show, however, *Asellus*' capacity to detect slight specific differences. Probably in nature the choice is made on the basis of chemical stimuli, as has been suggested by Gajevskaja (1958, in Kaushik and Hynes 1968).

Our results do not allow further speculation of an evolutionary nature as to the alimentary differentiation between the two *Asellus* species. It has been shown however, that the heterogeneous fungal populations, besides providing the indispensable condition for the

realization of turn-over in the detritus, constitute a "coarse-grained" environment, (sensu MacArthur and Wilson 1967) which permits alimentary diversification phenomena in similar and cohabitating detritivorous species. These, on an alimentary resource mosaic, have the possibility of satisfying their nutritional needs in relation to the nutrition disposition, and to the degree and type of antagonistic pressures, factors which notably influence the amplitude of the diet of predator species.

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