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Mass loss and macroinvertebrate colonisation of fish carcasses in riffles and pools of a NW Italian stream

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Abstract

In this study, we analysed the decomposition of trout carcasses in a low-order Apennine stream, with the aim to investigate the mass loss rate in a Mediterranean lotic system, and to examine the influence of microhabitats on the invertebrates colonising fish carcasses. In May 2003, we put 56 dead rainbow trout (*Oncorhynchus mykiss*) in the stream, placing seven sets (four trout each) in both riffle and pool habitats. At four dates, we removed one trout per set to measure its dry mass and determine the associated macroinvertebrate assemblage. Fifty-eight macroinvertebrate taxa colonised the carcasses, with significant differences between the erosive and depositional microhabitats. Riffle trouts hosted richer and denser colonist communities than pool trouts. Chironomidae, *Serratella ignita*, *Habrophlebia* sp., *Dugesia* sp. and *Protonemura* sp. were the five most abundant taxa. Decomposition was initially very rapid in both environments and then tapered off over time. The mass loss rate was higher ($k = -0.057$ day^{-1}) than that found in other studies. Higher Mediterranean temperatures probably increase the process. Although we found no significant difference between riffles and pools, mass loss was more regular in erosive habitats, underlining the importance of local, small-scale conditions. In small, low-order, heterotrophic streams, fish carcasses represent an important resource and shelter for rich and diversified invertebrate assemblages.

Introduction

Much of the energy support of lotic food webs derives from non-living sources of organic matter. Thus rivers and streams are partly heterotrophic systems (Cummins, 1979; Vannote et al., 1980). Heterotrophic pathways are of greatest importance where the opportunities for primary production are scarce, such as in running water. The recycling of nutrients during organic matter decomposition has long been recognised as an important component of lotic ecosystems. Therefore, the pathways and processes by which plant material is decomposed in streams have been thoroughly investigated (e.g., Iron et al., 1988; Cummins et al., 1989; Murphy et al., 1998). However, recent studies and reviews of nutrient dynamics in aquatic systems have noted that relatively little is known about the decomposition of animal remains in freshwater bodies, even though animals can significantly influence nutrient cycling processes (Andersson et al., 1988; Merritt & Wallace, 2000). Freshwater invertebrates are usually essential agents in the breakdown of organic material, nutrient cycling and energy flow within stream food webs (Vannote et al., 1980; Rosi-Marshall & Wallace, 2000). Hence these organisms likely play an important role in carrion decomposition.

Most data on this topic has come from studies conducted in Nearctic rivers, in which spawning migrations of anadromous salmonids are a significant source of organic material and inorganic nutrients to freshwater systems (Gende et al., 2002; Wipfli et al., 2003). Ecologists have recognised the importance of this allochthonous input since the 1930s (Juday et al., 1932), which may involve tons of marine-produced biomass each year: for example, the pacific salmons sequester marine nutrients while maturing at sea and transfer this biomass to lotic systems where they spawn and die (Mathisen et al., 1988; Wipfli et al., 1998; Jonsson & Jonsson, 2003). Isotope approaches have reported that marine C and N from salmon carcasses are incorporated into stream biota at various trophic levels (Bilby et al., 1996; Bilby et al., 1998) and recent studies have reported that the nature of salmon-derived material entering the food web varies at different stages in the decomposition cycle of the fish (Gende et al., 2002). Salmon carcasses are utilised at every level of the lotic food chain (Wilson et al., 1998). The presence and density of spawning salmons: (a) affect stream productivity, increasing the standing crop of periphyton (Wipfli et al., 1998; Fisher Wold & Hershey, 1999; Wipfli et al., 1999), (b) influence macroinvertebrate communities, enhancing individual growth rates (Ito, 2003) and local abundance (Minakawa et al., 2002), and (c) increase the growth rate of resident salmonids (Wipfli et al., 2003).

Macroinvertebrates certainly play a key role in the decomposition of carrion in stream systems (Chaloner et al., 2002). The abundance, richness and species composition of invertebrate communities are probably important elements in this context, but the taxa involved in decomposition and the rate of mass loss could change in different stream microhabitats. A few studies have underlined the importance of microhabitat conditions in the decomposition of carcasses. In particular, Kline et al. (1997) observed more rapid salmon carcass decomposition close to shore and in nearby streams than on the bottom of the Alaskan Lake Iliamna, where anoxia and negligible water flow are expected. Chaloner et al. (2002) noticed that mass loss differed little among streams but there was considerable variation within different logjams, suggesting that small-scale local conditions may influence the carrion decomposition.

Also if fish decomposition could be considered as a key factor only in the trophic webs of streams and rivers where a huge number of anadromous fish terminate their life more or less simultaneously and with a clear seasonality, the presence of fish carcasses in the streambed represent a discrete source of organic matter, whose importance in European streams is until now neglected.

Our objectives in this study were (a) to measure the rate of fish carcass decomposition (i.e. mass loss) in a NW Italian stream, a Mediterranean inland freshwater system with considerably higher mean temperatures than those of previously studied sites, and (b) to examine the influence of different river microhabitats on the invertebrates colonising fish carcasses by testing whether or not macroinvertebrate abundance, taxa diversity and indicator species differ between riffle and pool microhabitats.

Methods

Study site

The study took place in the Visone River, a small tributary of the Bormida River, NW Italy (44° 37′ N, 8° 30′ E; Fig. 1). This lotic system presents a good environmental quality, reaching First Class in the Italian E.B.I. system (Ghetti, 1997), corresponding to an environment without or negligible human alteration. The stream contains brown trout (*Salmo trutta* L.) and rainbow trout (*Oncorhynchus mykiss*), partly derived from human release. We selected seven pools and seven riffles in a 5 km section (altitudinal range: 365–400 m asl). These two type of microhabitats differ in some abiotic parameters (Table 1), as measured by Eijkelkamp 13.14 and 18.28 portable instruments.

Mass loss

Fifty-six rainbow trout females were placed in the Visone River on 9 May 2003 (Fig. 1, bottom). Trouts were selected and obtained the day before placement from a local fish farm. The freshly dead fish were weighted and positioned individually in numbered 10 mm mesh envelopes. The envelopes were fixed with stones and nylon cords. Fourteen

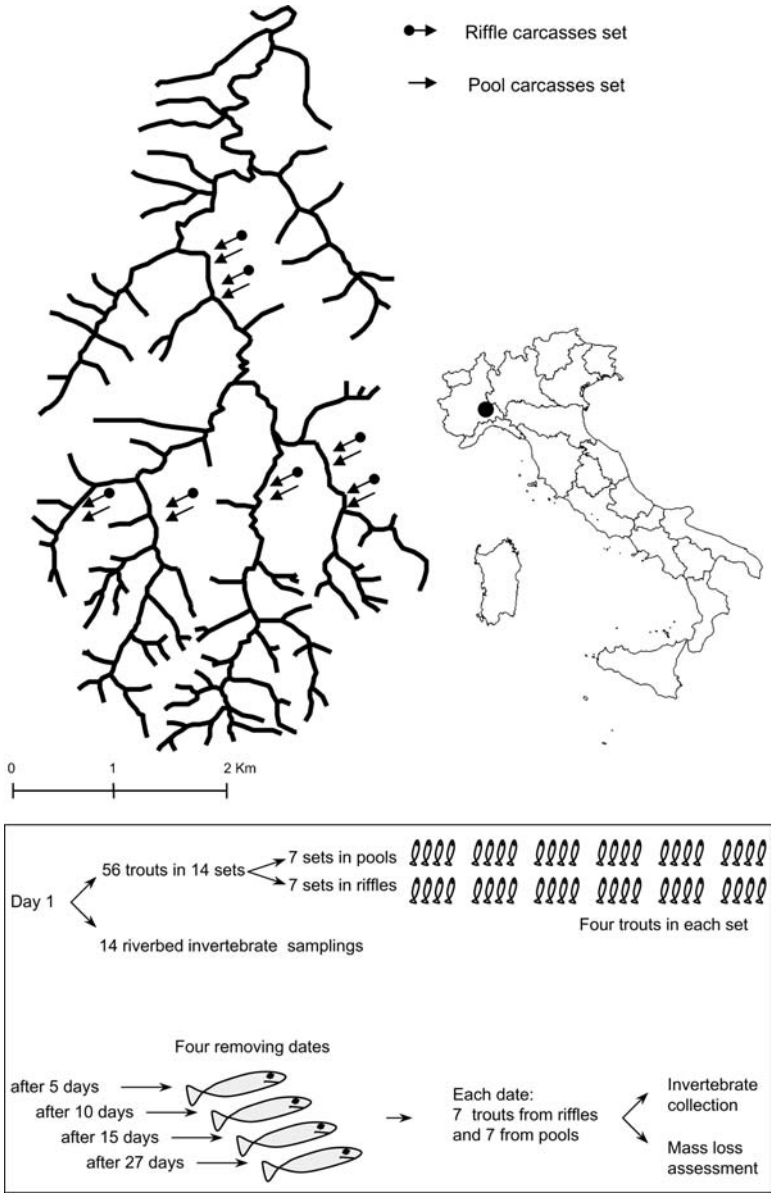

Figure 1. Location of the sampling stations on the Visone River, NW Italy (top), and experimental design (bottom).

Table 1. Conductivity, temperature, dissolved oxygen, pH and flow velocity (mean ± SD, range) of riffle and pool environments measured during the sampling period

	Riffles	Pools
Conductivity (μS cm^{-1})	350.0 ± 38.2 (302–383)	383.0 ± 5.50 (370–387)
Temperature (°C)	15.4 ± 2.10 (14.0–18.2)	16.8 ± 1.60 (14.5–18.6)
Dissolved oxygen (mg l^{-1})	8.30 ± 0.18 (8.20–8.35)	7.90 ± 0.25 (7.60–8.20)
pH	8.59 ± 0.23 (8.36–8.89)	8.57 ± 0.16 (8.35–8.72)
Flow velocity (m s^{-1})	0.60 ± 0.22 (0.35–0.95)	0.15 ± 0.07 (0.10–0.29)

sets of four carcasses each were used: seven sets were placed in riffle environments and seven in pools. The water was 15–30 cm deep in riffles and 40–60 cm in pools. The carcasses were left in place for a maximum of 27 days. This period was long enough to allow macroinvertebrates to reach their maximum abundance, as reported in the literature (Hauer & Lamberti, 1996) and observed in a previous experiment carried out in this lotic system (Fenoglio et al., 2002), and short enough to avoid floods. After 5, 10, 15 and 27 days, at each date 14 carcasses (one per pool and riffle set) were randomly selected and removed from the stream. The sample size decreased on the last date because one of the riffle carcasses was lost.

The initial mean mass of the trouts was 78.8 g ± 4.6 SE and did not differ between the riffle and pool habitats ($F_{1,54} = 0.85$; $p = 0.36$ ns). The initial dry mass of each fish was estimated by multiplying the original wet mass by 0.28, as indicated in Wipfli et al. (1998). When removed, the carcasses were immediately transported to the laboratory and dried to a constant mass at 80 °C to determine the remaining mass. Carcass mass loss was quantitatively modelled using percentage remaining mass.

Macroinvertebrate colonisation

Once removed from the riverbed, each carcass was placed in a white plastic tray. Macroinvertebrates were carefully collected with forceps from the mouth, interiors, gills and external surface and stored in 70% ethanol. The macroinvertebrates dislodged from each trout when its body was moved were collected with a 250 μm mesh net and added to the sample. In the laboratory, all organisms were counted and identified to the genus, except for Chironomidae, Simuliidae and early instars of some Trichoptera and Diptera, which were identified to the family. Each taxon was also assigned to a Functional Feeding Group (FFG: scrapers, shredders, collector–gatherers, filterers and predators) (Merritt & Cummins, 1996). To compare the abundances of invertebrates from the carcasses with the densities of natural populations of macroinvertebrates in the riverbed, we collected a sample from each of the 14 sites using a 0.25 m^2 surber. The surber sampling was conducted at the beginning of the experiment, on the same day in which the carcasses were placed.

The total number of macroinvertebrates and species richness of samples collected in pools and riffles were compared by ANOVA performed on log-transformed data, by using the SYSTAT 8.0 package (Wilkinson, 1992). Richness accumulation curves, generated with Estimates 6.0 software (Colwell, 1997), were used to compare the sampling dates and the cumulative taxa numbers for all samples from each habitat type.

To compare the community composition among the 27 riffle and 28 pool samples, we used Correspondence Analysis, an ordination technique that has been shown to be suitable for count datasets (Gauch, 1982; Legendre & Legendre, 1983).

The habitat preference of individual taxa was evaluated using indicator species analysis computed by the INDVAL 2.0 software (Dufrêne, 1998). Indicator species analysis is a randomisation-based test that compares the relative abundance and relative frequency of taxa occurrence to find indicator species assemblages characterising groups of samples. A taxon's affinity for a sampling group is expressed as a percentage (Dufrêne & Legendre, 1997).

Results

Mass loss

Carcasses changed in appearance over time. Muscles became paste-like, while eyes, gills and skin persisted throughout the experiment. After 10 days, the riffle carcasses developed a furry, 2–4 mm mould-like fungal coating that gradually was covered by silt and fine particulate organic matter. This layer was very thin or absent in pool carcasses.

The carcasses exhibited an exponential mass loss over time. The decrease was very rapid in the first few days in both pool and riffle carcasses. There was no significant difference in mass loss rate between riffle and pool trout at each removal date (day 5: Mann–Whitney $U = 22.0$, $n = 14$, $p =$ n.s.; day 10: $U = 25.0$, $n = 14$, $p =$ n.s.; day 15: $U = 26.0$, $n = 14$, $p =$ n.s.; day 27: $U = 25.0$, $n = 13$, $p =$ n.s.), but the pool trouts showed a

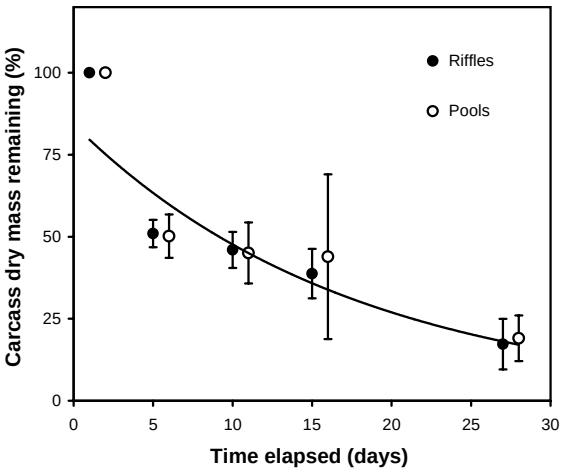

Figure 2. Mean remaining mass (percentage of original dry mass ± SD) of trout carcasses placed in two natural stream habitats.

greater dispersion of mass loss values (Fig. 2). For example, after 15 days, the mean percentage remaining mass was almost equal in the two microhabitats (≈38%), but there was a much higher variability in lost mass of the pool carcasses (from 13 to 93% of remaining mass, compared with 33–54% in the riffle carcasses).

Macroinvertebrate colonisation

In total, we collected 6965 macroinvertebrates belonging to 58 taxa in the trout carcasses, and 6242 macroinvertebrates belonging to 76 taxa in the natural riverbed (Table 2). Invertebrates were found mainly on the external surface but also in the gills, mouth and visceral cavity. Diptera of the family Chironomidae and the Ephemeroptera *Serratella ignita* (Ephemerellidae) and *Habrophlebia* sp. (Leptophlebiidae) were the most abundant taxa, constituting respectively 29, 27 and 10% of total mean abundance; the flatworm *Dugesia* sp. and the stonefly *Protonemura* sp. were also abundant (Table 2).

The total abundance of macroinvertebrates did not vary significantly over time (Fig. 3 top), either in riffle carcasses ($F_{3,23} = 0.103$, $p = 0.96$ n.s.) or in pool carcasses ($F_{3,24} = 2.02$, $p = 0.14$ n.s.). The mean number of invertebrates found in all carcasses was 124.4 ± 94.9 SD ($n = 55$), with 187.4 ± 81.0 SD in riffles (n = 27) and 61.3 ± 13.2 SD in pools ($n = 28$). The mean invertebrate abundance in riffle carcasses was significantly higher than in pool carcasses ($F_{1,53} = 65.6$, $p < 0.001$).

Community richness significantly increased over time in carcasses placed in the riffle habitats (Fig. 3 bottom; $F_{3,23} = 4.83$, $p < 0.009$), but did not differ among the four sampling periods in carcasses placed in the pool habitats ($F_{3,24} = 1.28$, $p = 0.30$ n.s.). When taxa richness of riffle vs. pool carcasses was compared separately for the four sampling periods, the number of taxa was always significantly higher in riffle samples (Table 3). Species accumulation curves showed that few additional taxa were likely to be found with additional sampling (Fig. 4).

Correspondence Analysis showed clear differences (ordination axis 1 and axis 2) between the macroinvertebrate assemblages in the riffle and pool carcasses (Fig. 5).

The composition of the macroinvertebrate communities colonising pool and riffle trouts was quite different: in riffles, the five most abundant taxa were *Serratella ignita*, Chironomidae, *Dugesia* sp., *Protonemura* sp. and *Baetis* sp.; in pools, *Habrophlebia* sp., Chironomidae, *Serratella ignita*, Polycentropodidae and *Lymnaea* sp. were most abundant. Fifteen taxa with strong habitat affinities were identified by indicator species analysis (Table 4). Twelve of them showed a strong affinity for riffle carcasses, while three showed a strong affinity for pool carcasses. When we analysed the chronological succession of the carcass fauna (focusing only on the abundant taxa with a high indicator value), we found that some groups were early colonisers: initially (day 5 samples) they showed a very high abundance and frequency of occurrence but then progressively decreased. This tendency was exemplified by Chironomidae and *Dugesia* sp. in riffles, but not in pools. Other groups were late colonisers, with highest abundance on the last sampling date (day 27): Polycentropodidae, Leptoceridae, *Wormaldia* sp., *Helicus substriatus*, Helodidae, *Boyeria irene* and Hydracarina in the riffle habitat, and *Leuctra* sp., *Habroleptoides* sp., Chironomidae and *Helicus substriatus* in the pool habitat. Some taxa were intermediate colonisers, with peak abundance on the second and third sampling dates (day 10 and day 15): representative taxa were *Serratella ignita*, *Habrophlebia* sp. and *Hydropsyche* sp. in riffles,

Table 2. Percent relative abundance for macroinvertebrates collected in the natural riverbed, and from fish carcasses, and significant ANOVA results for taxa collected in fish placed in riffles vs. pools

Taxon	FFG[a]	Riverbed		Fish carcasses		ANOVA	
		Riffle (relative abund.)	Pool (relative abund.)	Riffle (relative abund.)	Pool (relative abund.)	*F*	*P*
Plecoptera							
Leuctra sp.	Sh	2.23	1.09	1.62	1.86	5.13	0.028
Protonemura sp.	Sh	1.59	0.72	7.63	0.11		
Isoperla sp.	P	1.27	0.70	0.26	–		
Nemoura sp.	Sh	0.64	0.69	0.08	0.06		
Amphinemura sp.	Sh	0.60	1.45	0.02	–		
Chloroperla sp.	P	0.32	0.36	0.15	0.06		
Ephemeroptera							
Baetis sp.	Cg	4.78	3.26	3.83	0.64	15.4	0.001
Serratella ignita	Cg	3.18	2.54	31.67	10.71	21.7	0.001
Habrophlebia sp.	Cg	0.65	1.81	1.22	38.15	7.07	0.01
Habroleptoides sp.	Cg	0.59	1.45	0.02	–		
Electrogena sp.	Sc	1.27	–	0.02	0.11		
Caenis sp.	Cg	0.96	0.72	–	0.06		
Ecdyonurus sp.	Sc	2.55	–	0.1	0.35		
Paraleptophlebia sp.	Cg	0.64	0.36	0.02	–		
Centroptilum luteolum	Cg	0.32	1.09	0.23	–		
Torleya major	Cg	0.29	0.36	0.08	–		
Trichoptera							
Hydroptilidae	Sc	0.60	0.35	0.02	–		
Polycentropodidae	F	0.58	1.20	1.22	5.53		
Leptoceridae	Cg	0.32	0.34	0.89	0.41		
Beraeidae	Cg	0.29	0.32	0.02	0.17		
Wormaldia sp.	F	1.91	–	1.45	0.06	9.27	0.004
Chimarra sp.	F	1.27	0.35	0.02	–		
Philopotamus sp.	F	0.60	0.24	0.34	–		
Hydropsyche sp.	F	1.27	0.30	1.16	–		
Rhyacophila sp.	P	0.63	0.29	0.17	–		
Halesus sp.	Sh	1.32	0.27	0.76	0.06		
Micropterna sp.	Sh	0.58	–	0.02	–		
Stenophilax sp.	Sh	0.96	0.36	0.02	–		
Allogamus sp.	Sh	0.98	0.38	0.13	0.06		
Glossosomatidae	Sc	2.23	–	0.21	0.11		
Sericostoma pedemontanum	Sh	0.64	–	0.06	2.38		
Lepidostomatidae	Sh	0.27	0.74	1.27	0.12		
Diptera							
Chironomidae	Cg	28.03	36.59	28.62	30.05	28.5	0.001
Tipulidae	Sh	0.65	1.09	0.02	–		
Athericidae	P	0.62	1.20	0.08	0.11		
Limoniidae	P	0.34	0.75	–	0.06		
Culicidae	Cg	0.21	0.75	0.01	–		

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Table 2. (Continued)

Taxon	FFG[a]	Riverbed		Fish carcasses		ANOVA	
		Riffle (relative abund.)	Pool (relative abund.)	Riffle (relative abund.)	Pool (relative abund.)	*F*	*P*
Stratiomydae	P	0.31	0.37	0.02	–		
Ceratopogonidae	P	0.65	1.12	0.08	0.17		
Simuliidae	F	2.55	0.36	1.41	0.06		
Coleoptera							
Helicus substriatus	Sh	1.28	0.36	3.54	0.81		
Helodidae	Sh	0.62	0.32	0.11	–		
Elminthidae	Cg	1.27	0.35	0.28	0.17	6.27	0.015
Hydraenidae	Sc	1.59	–	0.23	–		
Dytiscidae	P	0.34	1.81	0.02	0.12		
Girynidae (larvae)	P	–	1.09	–	–		
Odonata							
Calopteryx virgo	P	0.32	1.10	–	0.23		
Onychogonphus sp.	P	0.64	0.36	0.02	0.23		
Boyeria irene	P	–	0.72	0.04	0.12		
Chalcolestes viridis	P	–	0.69	–	0.06		
Anellida							
Naididae	Cg	0.96	1.80	0.43	0.60		
Eiseniella tetraedra	Cg	0.60	1.09	0.02	–		
Lumbriculidae	Cg	0.63	1.79	–	0.06		
Lumbricidae	Cg	0.32	0.73	–	0.04		
Tricladida							
Dugesia sp.	P	2.23	1.45	10.06	2.04	17.7	0.001
Arachnida							
Hydracarina	P	6.37	7.97	0.45	0.69		
Gasteropoda							
Ancylus fluviatilis	Sc	4.46	1.81	0.04	0.06		
Lymnaea sp.	Sc	0.96	1.45	0.40	3.32		
Other taxa[b]		7.32	10.87	–	–		
All taxa (%)		100	100	100	100		
(N)		4948	1294	5248	1717		

[a] FFG: functional feeding groups (Cg = collectors–gatherers; F = filterers; P = predators; Sc = scrapers; Sh = shredders).
[b] Taxa found only in natural riverbed: Asellidae, Blephariceridae, *Choroterpes pictetii*, *Cordulegaster boltoni*, *Dina* sp., *Echinogammarus* sp., *Ephemera danica*, *Gyraulus* sp., Haliplidae, *Micronecta* sp., *Nepa* sp., *Orthetrum* sp., *Osmylus fulvicephalus*, *Perla* sp., *Phyrrosoma nimphula*, *Potamophylax cingulatus*, *Sialis* sp., Tabanidae.

and *Serratella ignita,* Polycentropodidae and *Lymnaea* sp. in pools.

The density of the natural macroinvertebrate assemblages found in the streambed was significantly higher in riffles (surber samples mean = 2828 ± 696 ind./m^2) than in pools (mean = 740 ± 404 ind./m^2) ($F_{1,12} = 47.1$; $p < 0.001$). Interestingly, although some groups were abundant and widespread on the river bottom, they were nearly absent on the trout carcasses: in particular, the mayflies *Ecdyonurus* sp. were abundant in riffle habitats, with densities up to 87 ind./m^2 in

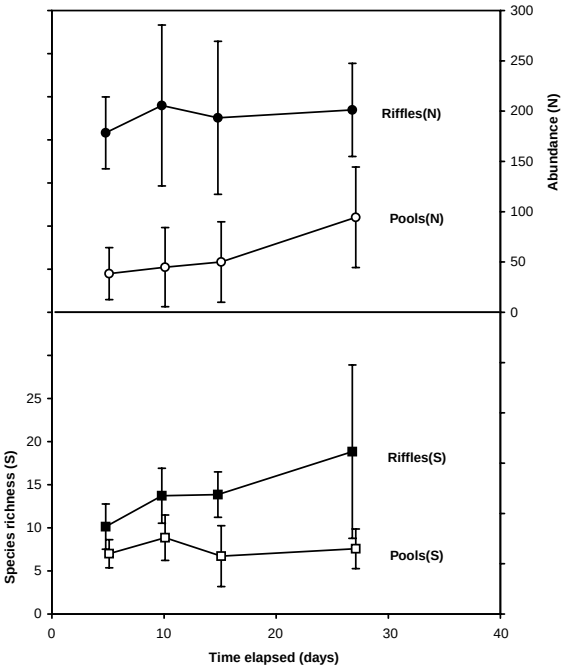

Figure 3. Time-related variation of mean abundance and community richness of macroinvertebrates found on trout carcasses placed in two natural stream habitats. Error bars represent ± 1 SD.

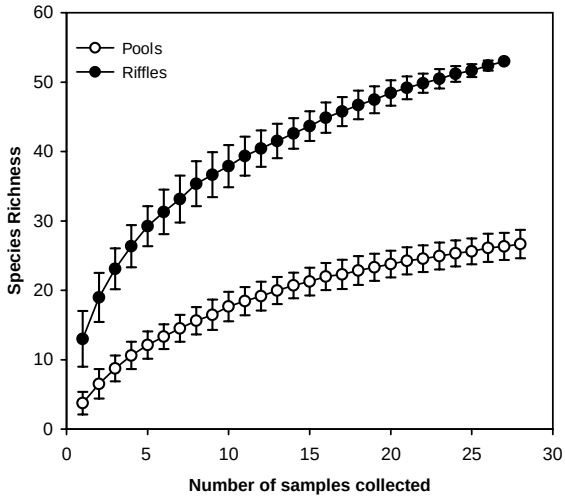

Figure 4. Taxa accumulation curves for invertebrates in trout carcasses in riffle and pool habitats.

some riffle stations, but almost absent in the carrions. Moreover, in pool habitats the mayfly *Ephemera danica* reached up to 12 ind./m^2 but was absent in carcasses. A similar pattern was observed for water Heteroptera (Corixidae, Nepidae and Notonectidae), Diptera (Tabanidae) and alderflies *Sialis* sp., all present in the riverbed but not in the carrion. In contrast, other groups seemed to be attracted by carrions, reaching densities higher than in the riverbed: this was the case of *Dugesia* sp., *Serratella ignita*, Chironomidae and *Habrophlebia* sp.

Collector–gatherers was the most abundant FFG in the trout carcasses (70.7% of total number, 81.0% in pools and 67.4% in riffles), followed by shredders (9.5% of total number, 4.6% in pools and 11.0% in riffles) and predators (9.5% of total number, 3.9% in pools and 11.4% in riffles), while filterers and scrapers were usually scarce. Shredders ($F_{1,53} = 5.3$, $p < 0.05$) and filterers ($F_{1,53} = 27.9$, $p < 0.001$) were significantly more abundant in riffles than in pools, whilst collector–gatherers were significantly less abundant ($F_{1,53} = 4.0$, $p < 0.05$). No significant differences for scrapers ($F_{1,53} = 1.8$, $p = 0.60$ n.s.) or predators FFG ($F_{1,53} = 0.62$, $p = 0.6$ n.s.) were found.

Table 3. Comparison (mean ± SD, ANOVA tests) of abundance and taxonomical richness in the trout carcasses in riffles and pools

Date	Parameret	Habitat		Statistics	
		Riffles	Pools	*F*-value	*p*
Day 5	Abundance (*N*)	178.4 ± 35.6	36.7 ± 27.2	49.0	0.001
	Richness (*S*)	10.1 ± 2.7	7.0 ± 1.6	23.3	0.001
Day 10	Abundance (*N*)	205.6 ± 118.9	46.6 ± 37.9	19.3	0.002
	Richness (*S*)	13.7 ± 3.3	8.8 ± 2.4	5.6	0.045
Day 15	Abundance (*N*)	193.3 ± 76.1	67.6 ± 78.8	4.1	0.050
	Richness (*S*)	13.8 ± 2.7	6.7 ± 3.6	7.3	0.027
Day 27	Abundance (*N*)	201.2 ± 46.3	94.4 ± 72.6	8.0	0.002
	Richness (*S*)	18.8 ± 9.0	7.6 ± 2.3	14.4	0.005

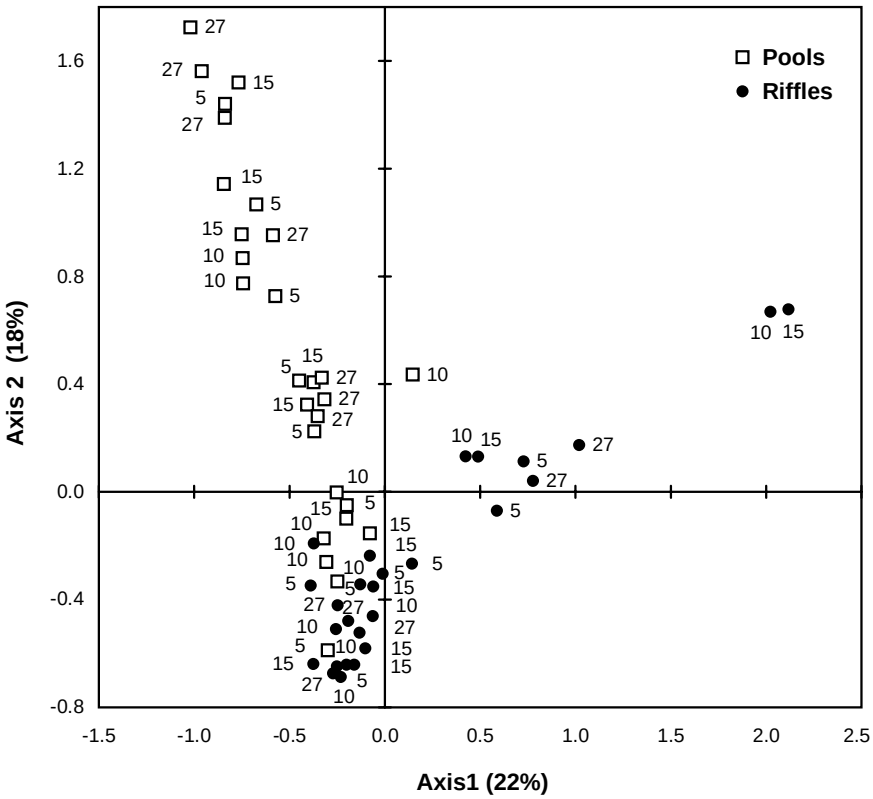

Figure 5. Correspondence Analysis ordination of 55 samples of trout carcasses based on 58 macroinvertebrate taxa; differences in invertebrate assemblages between riffle and pool habitats are depicted. Data labels report the time elapsed (days) from placing the trouts in the riverbed.

The analysis of the temporal evolution of the FFG abundances revealed that only the scrapers differed significantly in abundance among the four dates, increasing over time in riffle carcasses ($F_{3,23} = 3.2$, $p < 0.05$).

The functional composition of the macroinvertebrate community in the natural riverbed was somewhat similar to that of the carcasses. Collector–gatherers was the most abundant FFG (44.1% of individuals in riffles, 55.4% in pools), followed by predators (14.1% in riffles, 20.0% in pools) and shredders (12.4% in riffles, 7.5% in pools). However, the natural riverbed also contained many scrapers and filterers, which were found in low densities in the carcasses.

Discussion

In this study of decomposition of fish carcasses in two natural stream microhabitats (pools and riffles), we found that the colonising faunal assemblages clearly differed in both density and taxonomic composition.

The trout carcasses exhibited an exponential mass loss over time and attracted a rich community of macroinvertebrate colonists. Our study shows that microhabitat conditions are very important in the decomposition process, as recently suggested by Chaloner et al. (2002). However, the main influence was on the macroinvertebrate community, whereas there was little effect on mass loss. The decomposition rate was almost the same in the two microhabitats, although the process was more variable in the pools. Previous studies have underlined that abiotic parameters, such as pH, temperature, dissolved oxygen and running water speed, affect the decomposition of vertebrate carcasses in aquatic systems (Smith et al., 1989; Parmenter & Lamarra, 1991). In particular, water temperature plays a key role in the development and growth of saprobic

Table 4. Indicator values, habitat abundance and fidelity for macroinvertebrates collected from trout carcasses in riffles and pools

Taxa	FFG[a]	Indicator Value (%)	Habitat	
			Riffle (*n*/27 sites)	Pool (*n*/28 sites)
Riffle taxa				
Leuctra sp.	Sh	57.1	85[b]/21	32/12
Protonemura sp.	Sh	40.6	400/11	2/2
Baetis sp.	Cg	84.4	201/24	11/8
Serratella ignita	Cg	87.0	1662/26	184/19
Wormaldia sp.	F	47.5	76/13	1/1
Hydropsychidae	F	66.7	61/78	0/0
Lepidostomatidae	Sh	54.0	67/15	2/2
Chironomidae	Cg	75.1	1502/27	516/28
Simuliidae	F	43.9	74/12	1/1
Helichus substriatus	Sh	58.7	186/17	14/7
Elminthidae	Cg	31.1	15/10	3/3
Dugesia sp.	P	90.5	528/26	35/10
Pool taxa				
Habrophlebia sp.	Cg	81.1	64/13	655/25
Polycentropodidae	F	50.5	64/20	95/24
Lymnaea sp.	Sc	31.0	21/8	57/12

[a] FFG: functional feeding groups as in Table 2.
[b] Habitat data show the total number of individuals collected and the number of sites where each single taxon was found.

microbial and fungal communities, a prime force in decomposition. The fact that we found no difference in the decomposition rate between pools and riffles could be due to the small differences in the abiotic parameters (conductivity, temperature, dissolved oxygen, pH), even though the flow was 2.5 times faster in riffles than in pools. However, we believe that our data support the hypothesis that the similar decomposition rates were due to similar consumption by the two different macroinvertebrate assemblages eating the carcasses.

The mean decomposition rate in our study ($k = -0.057$ day^{-1} from a single exponential regression) is similar to that found by Parmenter & Lamarra (1991) but higher than those reported in other studies of carrion decomposition ($k = -0.048$ day^{-1}: Minshall et al., 1991; $k = -0.033$ day^{-1}: Chaloner et al., 2002). In general, carrion decomposition is much faster than for most non-woody and woody plants (from $k = -0.001$ to -0.005 day^{-1}, Webster & Benfield, 1986), suggesting greater palatability of dead animal matter.

The macroinvertebrate assemblages clearly differed between pool and riffle carcasses. The taxa richness was almost constant in riffles, while it increased slightly over time in pool carcasses. However, in the four sampling periods the number of sampled individuals and the taxa richness were always higher in riffles than in pools. The greater richness in riffle carcasses could be explained by several factors. For example, it might be a direct expression of the greater natural abundance of erosive microhabitats. We hypothesise that the different consistency of the fungal (oomycetes) layer covering the carcasses also plays an important role. We found a greater growth of the fungal layer in riffle trout than in pool ones: this could be an important factor in the colonisation by stream invertebrates, allowing transfer of material from vertebrate carrion to the lotic food web. The fungal layer could be a good refuge and excellent substratum for many invertebrate species, acting as a filter that traps fine organic matter transported in the flow. Moreover, it is also important to consider the functional composition of the carrion assemblages: many filterers (genera *Wormaldia*, *Chimarra*, *Philopotamus*, *Hydropsyche*, and the family Simuliidae) were found only or

mainly in riffle trout, where they can shelter in the carcasse and use rapidly flowing water to feed. As suggested in other studies (Minakawa & Gara, 1999), filterers can also collect fine particulate organic matter deriving directly from the carcasses, so that their abundance is significantly greater in riffle trout than in pool ones. In contrast to the findings of other studies (Wipfli et al., 1998; Chaloner et al., 2002), Chironomidae midges were abundant but did not constitute the dominant taxon in either the pool or riffle habitats. In riffle carcasses, *Serratella ignita* was the most common invertebrate, while the most abundant one in pools was another mayfly, *Habrophlebia* sp. Both mayflies are collector–gatherers that feed on organic particles detaching from the carcass. Perhaps the lower abundance of Chironomidae is related to the faunal characterization of Mediterranean streams.

The impact of macroinvertebrate colonists is diversified and that decomposition is the result of many processes involving various agents. Macroinvertebrates can use carrion as a source of food and/or shelter: shredders can chew and burrow into dead material, producing large amounts of fine animal particles and faeces. Their activity provides refuge and food for other taxa, including many collectors. The collector–gatherers FFG was dominant in both riffle and pool environments: this is consistent with previous studies showing the importance of these organisms in transferring energy and material from carrion to the rest of the lotic food web (Haskell et al., 1989; Chaloner & Wipfli, 2002). Moreover, many flatworms appeared suddenly on the surface of the carrion: they find their food by olfaction (Reynoldson & Young, 2000), so they can rapidly make contact with freshly dead fish. It is well known (Bellamy, pers. comm.) that many species of triclad flatworms scavenge on animal bodies. They could play a role in the decomposition of fish carcasses, mainly by secreting enzymes (proteases) through their eversible pharynx onto the flesh of the trout, making it more soluble in water.

The spatial heterogeneity of the riverbed, the unaltered environmental conditions and the presence of retention structures (Cederholm & Peterson, 1985) increase the recycling capacity of a lotic system. Although the quantitative importance of vertebrate carrion in nutrient cycles could be site-specific and extremely variable, fish carcasses in Apennine rivers are an important resource for macroinvertebrates, representing abundance and biodiversity hotspots.

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