Fungal parasitism in freshwater calanoid population: ecological consequences and possible mechanisms involved in the infection process

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Abstract

This paper reports the results of a study on a zoosporic fungus (Saprolegniaceae) parasitizing populations of *Eudiaptomus intermedius* (Copepoda, Calanoida) in mountain lakes located in the Northern Apennines, Italy. The dynamics of this infectious process was previously described in one of the lakes of the study area. The virulence is particularly high at the end of the calanoid reproductive phase, when the fungal hyphae penetrate the host eggs provoking their degeneration. Here new data are presented and the phenology of the host–parasite interaction is comparatively analyzed in different years and in different sites. The occurrence of the parasite was assessed at a regional scale. Possible mechanisms involved in the pathogen dispersal and in the host recognition are proposed, and the ecological impact of the fungal parasitism on the calanoid populations is discussed.

Introduction

Traditionally, theoretical and applied ecology greatly benefited from insights and hypotheses derived from the study of plankton communities (Lampert & Sommer, 1997). However, in plankton ecology the role of parasitism was ignored or remained relegated to a subordinate position for a long time, due to the overwhelming attention paid to competition and predation as main biotic factors influencing the composition and the successional stages of plankton assemblages.

This picture has significantly changed over the last decades. Parasites have been investigated in a number of planktonic taxa (Green, 1974), and host–pathogen relationships are currently recognized as important determinants in population and community dynamics (Bruning et al., 1992; Chiavelli et al., 1993; Holfeld, 2000; Gorbunov, 2001;

Ibelings et al., 2004). Furthermore, plankton organisms result to be particularly suitable for investigations on microevolution processes driven by parasites (Capaul & Ebert, 2003; Schmid-Hempel & Ebert, 2003).

This is the report of the results of a study on a parasitic fungus found in populations of the calanoid copepod *Eudiaptomus intermedius* (Steuer, 1897) inhabiting Northern Apennine lakes (Italy). The host–parasite dynamics in one of these lakes was previously described by Rossetti et al. (2002) on the basis of four-year observations. So far, there have been few documented accounts of freshwater calanoids affected by fungal parasites, and all of these are circumscribed to three genera: *Boeckella* in New Zealand (Burns, 1980, 1985a, b, 1989), *Leptodiaptomus* in Northern America (Redfield & Vincent, 1979), and *Eudiaptomus* in Europe (Gicklhorn, 1923; Unestam, 1973; Miao & Nauwerck, 1999).

The aims of this paper are to assess the incidence of parasitized *E. intermedius* populations at a regional scale, and to compare the phenology of the fungal infection in different copepod populations and in different years. Moreover, the possible mechanisms involved in the host–parasite interaction are suggested and the ecological impact of the fungal pathogen is discussed.

Distribution and ecology of *E. intermedius* in the Northern Apennines

Eudiaptomus intermedius is an Eastern Alpine – Illyric species and the study area is the western limit of its distribution (Stella, 1984; Dussart & Defaye, 2002). In the Northern Apennines, it is mostly found in permanent, oligotrophic water bodies located at altitudes over 1000 m a.s.l. and with a distinct pelagial zone and low solute concentrations (Tavernini et al., 2003). In deeper and larger lakes, *E. intermedius* is generally univoltine and is the dominant zooplankton species in terms of biomass (Ferrari & Ascolini, 1975; Ascolini et al., 1979; Rossetti et al., 1995); reproductive activity of overwintering adults usually starts in April–May, immediately before ice thawing, and lasts until July–August; occasionally, a second generation may occur in autumn, but with negligible increase in the population density (Rossetti et al., 1995). Each female may lay several egg clutches; the number of eggs per sac gradually decreases with the progression of the reproductive phase (Rossetti et al., 1995). In shallower or more productive permanent water bodies and in astatic habitats, the number of generations per year is less predictable; diapausing eggs, in variable proportion, are produced both in permanent lakes and temporary habitats (Tavernini et al., 2003). In deeper lakes, during summer thermal stratification, copepodites and adults tend to occupy the deeper layers with low tendency to migrate through the water column (Cattadori, 1993; Rossetti, 1994; Rossetti & Viglioli, 2001).

Characteristics of the fungal infection in *E. intermedius*

The phenology of the fungal infection was described for the population of *E. intermedius* of Lake Scuro Parmense by Rossetti et al. (2002) from samples collected weekly or fortnightly in the open-water season of 4 years. In that study, the presence of the same parasite was also occasionally reported in other 4 populations of *E. intermedius* sampled in Northern Apennine water bodies (Gemio Superiore, Gemio Inferiore, Ballano and Verdarolo) out of a total of 26 (Table 1).

The watermold was tentatively identified as *Aphanomyces* sp. (Saprolegniaceae), due to its similarity with fungal infections on calanoids reported in the literature (e.g., *A. ovidestruens* in Gicklhorn, 1923 and *Aphanomyces* sp. in Burns, 1980 and following papers). Indeed, the recent taxonomic revision of the genus *Aphanomyces* led to exclude *A. ovidestruens* as valid species and to synonymize it with *A. scaber*; although their taxonomic position has not been accurately determined yet, the fungal parasites described by Burns (loc. cit.) likely belong to other species of the genus *Aphanomyces* (Johnson et al., 2002). Kiziewicz (pers. comm.) confirmed that the watermold found in Northern Apennine lakes must be ascribed to *Aphanomyces*, a genus which is known to grow on living and dead freshwater crustaceans (Czeczuga et al., 2002). Watermolds have never been observed in the two other calanoid species (*Mixodiaptomus kupelwieseri* and *M. tatricus*) present in the study area (Tavernini et al., 2003).

The following consistencies were observed in the infection process occurring at Lake Scuro Parmense in 1992–1994 and 1998 (Rossetti et al., 2002):

1. Only adult females are attacked by the parasite and exclusively during the reproductive phase.
2. The parasite is not found at the very beginning of the recruitment period, but its virulence significantly increases at the end of the reproductive phase (peaks of 40–89% of parasitized adult females).
3. Fungal hyphae are first located on the female abdomen and then also develop on the egg clutches.
4. The presence of hyphae do not hamper mating and the spermatophore attachment.
5. The watermold is not lethal for adult calanoids; other effects on host survivorship due to hyphae attachment (e.g., reduced

Table 1. Location and habitat features of Northern Apennine water bodies in which populations of *Eudiaptomus intermedius* have been found during different limnological surveys (Rossetti et al., 2002; Tavernini et al., 2003; Bartoli, 2004)

Lake	H (m)	S (ha)	Z_{max} (m)	Lat N	Long E	Habitat type	Thermal regime	Trophic state	Fungal parasites
Scuro Parmense	1527	1.16	10.4	44° 23′ 53″	09° 56′ 42″	Natural, Permanent	Usually dimictic	Oligotrophic	Yes
Santo Parmense	1507	8.16	22.5	44° 24′ 06″	10° 00′ 38″	Natural, Permanent	Dimictic	Oligo-mesotrophic	Yes
Gemio Superiore	1355	3.57	5.6	44° 23′ 20″	10° 02′ 49″	Natural, Permanent	Polymictic	Eutrophic	Yes
Gemio Inferiore	1339	3.25	7.4	44° 23′ 08″	10° 02′ 58″	Natural, Permanent	Polymictic	Eutrophic-hypereutrophic	Yes
Ballano	1341	7.34	19.0	44° 22′ 07″	10° 06′ 01″	Reservoir, Permanent	Irregular	Oligo-mesotrophic	Yes
Verdarolo	1390	1.13	3.0	44° 21′ 31″	10° 07′ 22″	Natural, Permanent	Polymictic	Eutrophic	Yes
Riondo	1328	0.12	2.5	44° 29′ 25″	09° 25′ 01″	Natural, Permanent	Polymictic	Meso-eutrophic	No
Bino Minore	1299	0.05	2.5	44° 37′ 05″	09° 32′ 59″	Natural, Permanent	Polymictic	Oligo-mesotrophic	No
Moo	1106	0.30	2.0	44° 37′ 35″	09° 32′ 27″	Natural, Permanent	Polymictic	Meso-eutrophic	No
Nero	1540	0.65	2.5	44° 33′ 42″	09° 30′ 06″	Natural, Permanent	Polymictic	Mesotrophic	No
Buono	1140	0.20	2.0	44° 33′ 14″	09° 47′ 54″	Natural, Permanent	Polymictic	Meso-eutrophic	No
Pozza N.O. Buono	1135	<0.01	0.2	44° 33′ 20″	09° 47′ 54″	Natural, Temporary	–	–	No
Pozza S.O. Buono	1156	<0.01	0.2	44° 33′ 12″	09° 47′ 54″	Natural, Temporary	–	–	No
Pradaccio	1430	2.69	3.0	44° 23′ 35″	10° 01′ 18″	Dammed, Permanent	Polymictic	Mesotrophic	No
Monte Acuto	1576	0.80	8.1	44° 19′ 25″	10° 10′ 58″	Natural, Temporary	Usually dimictic	Oligo-mesotrophic	No
Pozza Monte Acuto	1251	<0.01	0.3	44° 28′ 16″	10° 09′ 08″	Natural, Temporary	–	–	No
Paduli	1160	38.68	19.0	44° 20′ 57″	10° 08′ 16″	Reservoir, Permanent	Irregular	Mesotrophic	No
Palude Lago Verde	1508	<0.01	1.5	44° 21′ 43″	10° 05′ 34″	Natural, Semi-permanent	–	–	No
Frasconi	1606	0.20	1.5	44° 22′ 01″	10° 04′ 40″	Natural, Permanent	Polymictic	Oligo-mesotrophic	No
Sillara Superiore	1732	1.14	10.8	44° 21′ 49″	10° 04′ 08″	Natural, Permanent	Dimictic	Oligotrophic	No
Sillara Inferiore	1731	1.14	10.0	44° 21′ 45″	10° 04′ 02″	Natural, Permanent	Dimictic	Oligotrophic	No
Martini	1714	0.08	1.6	44° 21′ 22″	10° 05′ 04″	Natural, Semi-permanent	–	–	No
Compione Superiore	1686	0.18	2.0	44° 21′ 40″	10° 04′ 30″	Natural, Permanent	Polymictic	Oligo-mesotrophic	No
Compione Inferiore	1674	0.47	2.9	44° 21′ 44″	10° 04′ 33″	Natural, Permanent	Polymictic	Oligo-mesotrophic	No
Palo	1508	0.87	5.6	44° 21′ 22″	10° 06′ 50″	Natural, Permanent	Polymictic	Oligo-mesotrophic	No
Scuro di Rigoso	1392	0.40	3.0	44° 21′ 33″	10° 07′ 38″	Natural, Semi-permanent	–	–	No

H, height above sea level; *S*, surface area; Z_{max}: maximum depth.

swimming ability or increased vulnerability to visual predators) are probably negligible.

6. Fungal hyphae eventually penetrate the host eggs which quickly degenerate, followed by the appearance of spherical oogonia.

7. No relationship can be established between total density of the calanoid population and incidence of infected adult females (Fig. 1).

8. The density of adult calanoids at the end of the open water period, i.e. those that will overwinter and reproduce the next year, was relatively constant over the years (from 0.5 to 2 ind. l^{-1}) and not dependent on the amount of parasitized females.

9. Parasitized females do not seem to recover from the fungal infection.

Materials and methods

Samplings were carried out at monthly intervals during the ice-free period, in 2001 and 2003 at Lake Santo Parmense, and in 2003 at Lake Scuro Parmense and Lake Gemio Inferiore. The sampling stations were located in the deepest part of each lake. On each survey, temperature was measured and water samples for chemical analysis were collected at different layers over a depth profile. The complete database containing detailed information on physical and chemical analyses is available on request from the author. Zooplankton was sampled with a 50 μm mesh conical net hauled vertically through the water column; samples were immediately preserved in a 4% buffered formalin solution. Developmental stages of
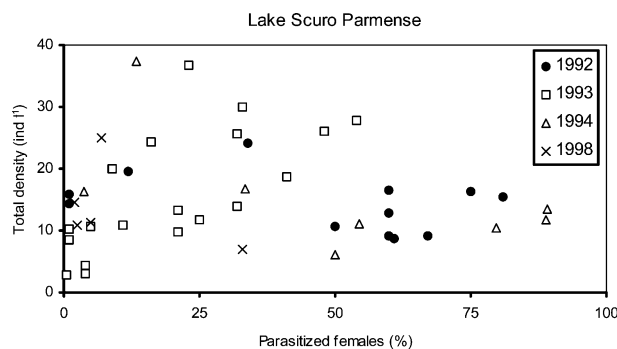
E. intermedius were counted separately (nauplii, CI-CV, adult males and females), and the animals were carefully examined for the presence of fungal parasites under a compound microscope.

In spring and autumn 2003, 11 other lakes (located between 1341 and 1732 m a.s.l. in neighbouring Apennine valleys) were sampled as populations of *E. intermedius* had been reported in earlier limnological surveys (Tavernini et al., 2003), and the occurrence of fungal epibionts was assessed (Bartoli, 2004). This group of lakes included Gemio Superiore, Ballano, and Verdarolo, where calanoids occasionally parasitized by watermolds had been found in previous years, but also Scuro di Rigoso, Palo, Martini, Sillara Superiore, Sillara Inferiore, Compione Superiore, Compione Inferiore, and Pradaccio (Table 1).

Results

Lake Santo Parmense

The presence of a fungal parasite (Figs. 2 and 3) in this lake in 2001 (75% and 63% of parasitized adult females in June and July, respectively) and then again in 2003 (20% of parasitized adult females in June) was rather unexpected, since it had never been reported in extensive samplings carried out in previous decades (Moroni, 1962; Ferrari & Ascolini, 1975; Cattadori, 1993). The infection mechanism is identical to that described by Rossetti et al. (2002) in Lake Scuro Parmense (see above). In 2001, the population of *E. intermedius* showed only one reproductive period in late
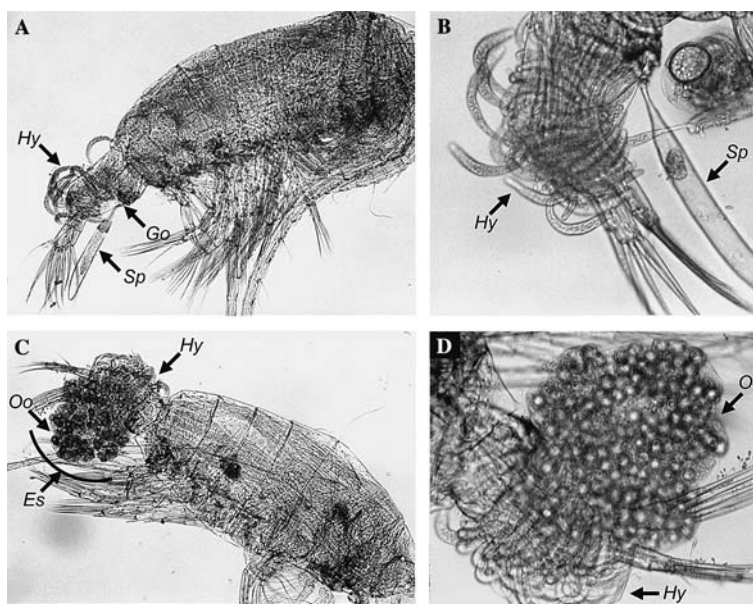

Figure 1. Relationship between total density of the *Eudiaptomus intermedius* population and percentage of infected adult females in Lake Scuro Parmense (pooled data 1992–1994 and 1998). Only sampling dates in which the parasite was present were considered.

Figure 2. Infective stages in adult females of *Eudiaptomus intermedius* (Lake Santo Parmense, June 15, 2001). (A, B): Females with hyphae attached to the abdomen. (C, D): Aspects of egg sacs after the development of oogonia. *Go*: gonopore; *Sp*: spermatophore; *Hy*: fungal hyphae; *Es*: egg sac; *Oo*: oogonia with oospores.

spring-early summer, while in 2003 ovigerous females and larval stages were also observed in October (Fig. 3), probably due to the unusually protracted thermal stratification and the delayed onset of the autumn mixing.

Lake Scuro Parmense

The peculiar meteorological conditions observed in summer–autumn 2003, with scarce precipitations and high air temperatures, greatly influenced the trends of hydrochemical variables and the seasonal succession of the plankton community in this small lake. In September, the lake volume was reduced by approximately 35% compared to the beginning of the open water period. For the first time during the long-term monitoring of this lake, which started in 1986, a dense bed of Characeae, probably belonging to the genus *Tolypella* (Maria Luigia Borghi, pers. comm.), covered the lake bottom completely from May to September, with a depression of the phytoplankton compartment accompanied by negligible values of dissolved nutrients and high water transparency. These conditions, along with a prolonged summer thermal stability, led to completely different successional events in the

zooplankton community from those previously observed. In particular, the density peak of *E. intermedius* occurred in September, i.e. 2–3 months later than in other years (Rossetti et al., 2002); moreover, juvenile stages were present on all the sampling dates, except for July, indicating an overlap of different reproductive cohorts (Fig. 4). Infected adult females were found in July (75%) and, to a much lesser extent, also in September and October (Fig. 4).

Lake Gemio Inferiore

This lake has undergone intensive fish stocking for several decades and shown a dramatic decrease in water quality in the last few years. In 2003, the water transparency ranged between 0.5 and 2.1 m. Chlorophyll-*a* reached punctual maxima exceeding 80 μg l^{-1} in July and August, and in September concentrations of more than 70 μg l^{-1} were measured throughout the water column. Rare calanoid copepodites were collected only in July and August, probably coming from sporadic hatching of resting eggs released in the sediments when a well-structured population of *E. intermedius* was still present in this lake.
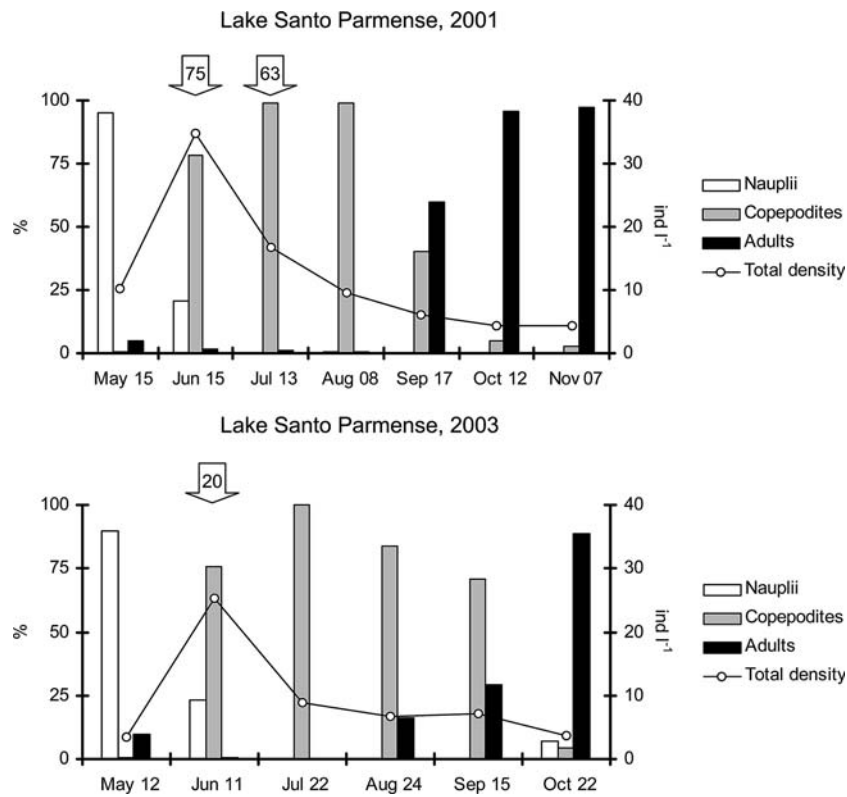
Figure 3. Percentage of nauplii, copepodites and adults, and total density of the *Eudiaptomus intermedius* population in Lake Santo Parmense in 2001 (upper) and 2003 (below). Arrows indicate the presence of fungal parasites and the enclosed figures the percentage of infected adult females.
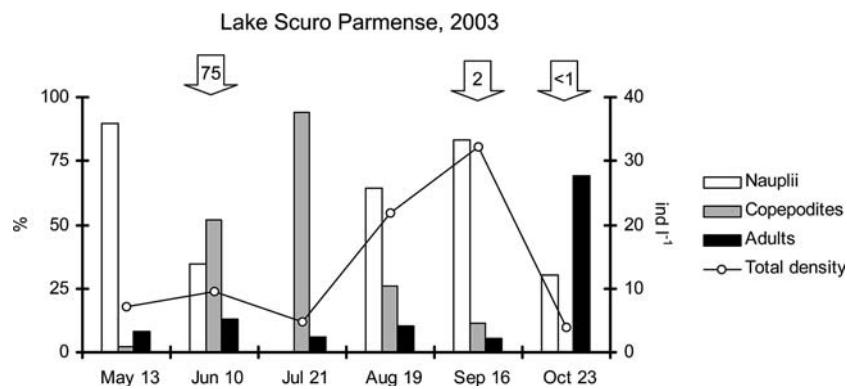

Figure 4. Percentage of nauplii, copepodites and adults, and total density of the *Eudiaptomus intermedius* population in Lake Scuro Parmense in 2003. Arrows indicate the presence of fungal parasites and the enclosed figures the percentage of infected adult females.

Other lakes of the study area

Fungal parasites infecting *E. intermedius* were seen only in Lake Verdarolo. In this shallow water body, ovigerous females and larval stages were present in both spring and autumn samples, but parasitized adult females (approximately 40%) were observed in October only. In Lake Ballano, the other lake in which the fungal infection had been previously reported (Rossetti et al., 2002), only nauplii and copepodites were encountered in the analyzed samples.

Discussion

Acquisition of new information on the occurrence of fungal parasites in Apennine populations of *E. intermedius* and the extension of data series collected over several years allowed to delineate some definite patterns and to draw preliminary hypotheses on possible factors involved in the infection process.

Eudiaptomus populations attacked by watermolds resulted to be fairly few at a regional scale, namely 6 out of 26, and only in rare occasions the pathogen seems to have an effective impact on the host dynamics (Fig. 1). The occurrence of the parasite was recorded in lakes with contrasting trophic characteristics, but the rate of parasitism was far higher in less productive water bodies. The parasite was not observed in any of the *E. intermedius* populations colonizing temporary or semi-permanent habitats (Table 1). The permanent lakes in which the fungus appeared are naturally fishless, but all of them have been stocked with fish, although with different intensity and duration. The parasite could have as primary target the fish populations and only in some cases could infect other animal hosts. In fact, many Saprolegniaceae are considered opportunistic facultative parasites, and the same species may infect a number of different hosts (Neish, 1977; Czeczuga et al., 2002). The virulence towards *Eudiaptomus* may thus depend on the abundance of fish hosts. This finding is congruent with the low fish density observed in Lake Scuro Parmense, resulting only from few trouts illegally introduced on several occasions and not from regular stocking programs. Furthermore, the occurrence of fungal parasites in Lake Santo Parmense shortly followed the suspension of trout stocking dating back to the late 1990s (Maldini et al., 2004). Interestingly, no other microcrustacean species (cyclopoid copepods and cladocerans) were found to be infected by the fungal parasite in these two lakes.

The temporal phenology of the parasite shows regular trends in lakes Scuro Parmense and Santo Parmense. The highest presence of infected females was constantly seen in June–July, when a clear thermal stratification takes place with up to 10 °C of difference between surface and deep waters. However, the temperature range is narrower (usually between 5–6 and 10 °C) in metalimnic and hypolimnic layers, where adults of *E. intermedius* are preferentially situated. During autumn mixing, parasitized females were found only occasionally and in low densities. In Lake Verdarolo, infected females were abundant in October 2003, when the water temperature was approximately 9 °C. Miao & Nauwerck (1999) reported a positive relationship between temperature and infection rate in females of *E. gracilis* attacked by *Aphanomyces* sp. From the data collected in Apennine lakes, the proportion of infected females observed in different years does not seem to be related to water temperature. Actually, temperature changes may be less important than concomitant physico-chemical variation in explaining the seasonal appearance of watermolds (Johnson et al., 2002). The dispersal of infective stages and the actual virulence of the parasite may also be affected by biotic factors, such as a top-down control. For example, Kagami et al. (2004) demonstrated that the grazing on fungal zoospores by *Daphnia* could significantly decrease the impact of parasites on the diatom *Asterionella formosa*.

The occurrence of the parasite infecting *E. intermedius* is not triggered by a density-dependent mechanism. This was evident from annual series collected in Lake Scuro Parmense in the 1990s, but especially in 2003, when unusual meteoclimatic conditions caused a marked shift in the seasonal peak of *E. intermedius* compared to previous years. In fact, a high incidence of parasitized females was found in June, whilst few individuals carrying hyphae were observed in coincidence with the density maximum of September.

There is a strict coupling between appearance of infective stages and presence of calanoid adult females available for mating or in reproductive phase. Although egg clutches are the final ''target'' of the parasite, the dynamics of the epidemic process suggests that other signals are involved in the host identification. Release of infectious zoospores could be cued by infochemicals produced for mate location by sexually receptive females. The use of diffusible, probably not species-specific sex pheromones to detect mating females has been proven in copepods (Watras, 1983; Winsor & Innes, 2002). Instead, recognition of the attachment site by the fungal parasite could be mediated by compounds located on the host body. For example, surface glycoproteins used by

males to determine the developmental or reproductive state of females and as markers of regions important in copulation and spermatophore placement have been found on representatives of the three free-living orders of copepods (Kelly et al., 1998). Five major sites associated with glycoproteins have been described for copepods by Snell & Carmona (1994), including the lateral margin of the genital segment, the urosome segment junctions and the gonopore: these sites also represent the elective positions for hyphae attachment in the studied host–parasite association. Moreover, these assumptions are coherent with the findings that immature stages or adult males of *E. intermedius* are not affected by the fungal parasite.

The occurrence of the parasite only at the end of the reproductive period of *Eudiaptomus* has important consequences. The parasite does not have lethal effects on infected females, which are usually doomed to die after several cycles of egg laying also in populations immune to fungal diseases. It is thus possible that the protraction of the reproductive period and the associated physiological debilitation lead to a gradual decrease in the host immunocompetence, and consequently in its resistance against pathogens, determining the observed exponential increase in infected females. The culmination of the fungal infection generally coincides with a decrease in the host fecundity, measured as mean number of eggs per sac. On the other hand, even though the parasite acts as a powerful factor in controlling the calanoid population density, the timing of emergence actually weakens the potential virulence of the watermold and suggests a tradeoff between parasite transmission and parasite-induced host mortality (Day, 2003). In Lake Scuro Parmense, in spite of a considerable interannual variability in water physico-chemical features and in biotic factors (including different frequencies of the fungal parasites), *Eudiaptomus* showed little changes in its demographic parameters, as can be seen from the relative constancy of the population density peaks and abundance of adults sustaining the reproductive activity. Internal regulatory mechanisms, e.g. the hatching of resting eggs (Tavernini et al., 2003), are likely to play an important role in coping with the impact of disturbing factors. The almost complete disappearance of *Eudiaptomus* from Lake Gemio Inferiore must be related to the dramatic worsening of the trophic conditions occurred in the last years (Bartoli, 2004) rather than to the effect of fungal parasitism.

Conclusions

Parasite–host interactions are often overlooked (Minchella & Scott, 1991; Green, 1999), although they are recognized as key factors in the functioning of ecological systems (Dobson & Hudson, 1986) and in driving evolutionary processes (Haag & Ebert, 2004). The present contribution identifies an infection caused by zoosporic fungi as one of the major constraints in controlling the population dynamics of calanoids in mountain lakes, but it especially raises some relevant points to which future investigations should be directed through a combination of field and laboratory experiments, also in order to test some hypotheses introduced here in a rather speculative way. For example, the precise taxonomic identification of the fungal parasite and the accurate description of its life cycle and other potential hosts in the studied lakes are necessary to understand the infectious process and its causal mechanisms. In addition, the analysis of demographic and behavioural traits as compensatory strategies used by calanoids to mitigate the impact of the parasite is of great interest, as well as the assessment of the hosts' susceptibility to the fungal infection in relation to the physiological adaptations (Mucklow et al., 2004) and to the differences in genetic characteristics of the microcrustacean populations (Little & Ebert, 2001).

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