

ABOMASAL NEMATODE COMMUNITY IN AN ALPINE CHAMOIS (*RUPICAPRA R. RUPICAPRA*) POPULATION BEFORE AND AFTER A DIE-OFF

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ABSTRACT: Abomasa of 185 chamois shot during 5 consecutive hunting seasons were collected as part of a health monitoring program in an alpine area of Italy and examined for nematodes. The data were obtained during both the preceding period and that following a severe die-off caused by a pneumonia outbreak. Prevalence, mean abundance, mean intensity, and Thul Importance index were consistently high, in particular for *Haemonchus contortus*, having a low host specificity and high pathogenic potential. Species typical of cervids were also consistently detected. The abomasal nematode community showed an isolationist structure, suggesting its composition was primarily determined by external factors such as interspecific interaction among host species and environmental conditions. The effect of different factors (host sex, sampling site, and time) on nematode counts and aggregation were analyzed and discussed considering the peculiarities of the study site and the chamois population crash. In the light of parallel results for health monitoring, abomasal parasitism could represent a predisposing factor for the observed die-off.

It has been shown that macroparasites play a role in regulating wildlife populations (see Tompkins et al., 2002 for review). However, the effect of parasites on free-ranging ruminant populations remains difficult to evaluate under field conditions due to the wide range of factors that can influence the establishment and abundance of parasite species. Host-parasite interactions may not always be clearly evident, thus leading to contradictory interpretations. Furthermore, the use of macroparasites as an index of population health, in particular, counts of gastrointestinal helminths, has often been criticized (Demarais et al., 1983; Waid et al., 1985; Rossi et al., 1997; Pérez et al., 2003). Nevertheless, different studies have demonstrated that parasites can have an impact on health status in natural ruminant populations (e.g., Gulland, 1992; Stien et al., 2002), and further data, both from an ecological perspective and a management point of view, are needed.

If the effect of parasites is considered as the result of various interactions between host, parasite, and environment, studies should ideally focus on (1) the ecological correlates determining the composition and distribution of parasite communities (e.g., climatic conditions and distribution of hosts [Calvete et al., 2003]), (2) the epidemiology and host specificity of the species most likely to exert an impact on hosts (e.g., selected generalist nematodes [Zaffaroni et al., 2000]), and (3) the pathogenic potential of different parasite species and the contributing factors (e.g., food shortage [Gulland, 1992]). Experimental studies are generally unfeasible in wild populations for ethical and logistical reasons. However, evaluation of the parasite community within a host during particular events such as mortality outbreaks or under extreme conditions may provide an opportunity to correlate parasite populations with predisposing factors.

The present study is part of a 5-yr program aimed at monitoring the health status of an alpine chamois (*Rupicapra r. rupicapra*) population.

The aims of the present study were to describe the composition and structure of the abomasal nematode community of the studied population and to examine its changes in relation to a die-off that occurred during the observation period.

MATERIALS AND METHODS

Study area and population

A detailed description of the study site and an analysis of chamois population dynamics and die-off were described previously by Citterio et al. (2003). Briefly, the study was carried out in the mountainous territory of the province of Lecco, Italy (45°59'N, 9°32'E). The climate is intermediate between continental and suboceanic (temperate-subcontinental climate [Gatti, 2004]), and the habitat of the chamois (253 km²) includes a wide range of altitudes (from 500 to >2,000 m above sea level). The study site consisted of 10 contiguous hunting districts with different chamois population densities (e.g., from 7/km² to 17/km² in 2000). In the study area, chamois are hunted by selective culling from October to early December. A stable population of roe deer (*Capreolus capreolus*) is also present in the territory. Moreover, cattle, sheep, and goats share the pastures with wildlife during the grazing season (from late spring to early autumn).

Health monitoring of the chamois in this area began in 1998 in response to an observed decrease in overall body conditions reported by hunters and gamekeepers. Gross findings frequently included lesions related to abomasal nematode infections, with edema and reddening of the mucosa and, in some cases, nodules scattered on the surface. Mucosal hemorrhage was observed in the most severe cases. In one critically affected area (district B2 in Citterio et al., 2003) chamois showed very poor body condition and infections from opportunistic pathogens (Sironi et al., 1999), and food was scarce (Tarantola et al., 2005). Two years after the start of the survey, a pneumonia outbreak occurred in the population from November 2000 to March 2001. In some winter habitats from district B2, pneumonia caused a marked population crash, with mortality of up to 80% of the estimated population.

Abomasal parasite collection

Abomasal nematodes were chosen because they have been shown to affect the health status of alpine wild ruminants (Zaffaroni et al., 1997, 2000), and for ease of organ collection and storage. A total of 185 abomasa were collected in the field by hunters and gamekeepers during the 1998 to 2002 hunting seasons (October–December). An additional 9 abomasa were collected from chamois that died during the pneumonia die-off. The abomasa were frozen upon arrival at game control centers and then thawed in the laboratory. Abomasal nematodes were collected using the technique described in 1986 by the MAFF, and modified as follows: the abomasal content was brought to a volume of 500 ml, mixed thoroughly, and a sample of 50 ml (10%) was taken for parasite collection. Adult worms were collected and counted using a stereomicroscope.

Male nematodes were identified by the morphological criteria described by Skryabin et al. (1961), Drözd (1965), Durette-Desset (1979, 1982), Biocca et al. (1982), and Cabaret et al. (1986). The nomenclature proposed by Durette-Desset (1989) was used for species belonging to Ostertagiinae. Identification was performed to the species level except for *Nematodirus* species. The abomasal nematode count (abundance of male + female nematodes of all species) and the abundance

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of each species (based on male counts) were estimated by multiplying the counts obtained from the 10% aliquot by 10.

Preliminary remarks on data analysis

The following alternative morphologies were considered both as distinct species and as a single species in the analyses: *Teladorsagia circumcincta*/T. *trifurcata*, Suarez and Cabaret, 1992; *Marshallagia marshalli*/M. *occidentalis*, Lichtenfels and Pilitt, 1989; *Ostertagia leptospicularis*/O. *kolchida*, Lancaster et al. 1983; and *Spiculoptera spiculoptera*/Rinadia *mathevossiani*, Drözd et al. 1987.

The structure of the chamois sample by year, sex, and age is reported in Table I, both for the entire study area and for district B2 alone. Because the sample size did not allow the elaboration of an age-intensity curve, two age classes were established in the sample in relation to reproductive competence: juvenile chamois (0 to 3 yr old, not yet considered in the reproductive cohort) and mature chamois (4 to 14 yr old, considered as members of the reproductive cohort). This classification evaluated the additional stress for mature chamois during the hunting season, which takes place at the same time as the rut.

The effect of host age on nematode counts was evaluated within each sex, considering that male mammals often show higher prevalence and intensity for nematode infections compared with females (Wilson et al., 2002).

District B2 was compared with all other districts taken together for an analysis of possible differences in parasitic patterns on the basis of hunting area. Analyses involving district B2 by itself or in comparison with others were performed without considering host sex and age to avoid an excessive reduction of the sample. The same is true for the analyses involving the single nematode species and for parasite aggregation analyses.

Analyses were performed using SPSS 12.0 except where indicated. Statistical significance was established at $P < 0.05$.

Study of nematode community composition and structure

At the component community level, mean abundance, mean intensity (Bush et al., 1997), and range were calculated for the abomasal nematode count and for each nematode species for the entire 5-yr period and for each hunting season. Furthermore, the prevalence and Thul Importance index (Thul et al., 1985) were calculated for each nematode species. For comparative purposes, the same procedures were also performed for district B2 alone.

At the infracommunity level, species richness was calculated; richness was set to 0 in abomasa with no male nematodes, as a rough quantitative measure for statistical analyses. Moreover, the Berger-Parker Dominance index (d [Southwood, 1978]) was calculated in subjects in which at least 1 nematode species was identified ($n = 159$; see Table I).

To detect possible variations among different years, a Kruskal-Wallis test was performed on abomasal nematode counts and single species abundances using the hunting season as a grouping variable. When statistical significance occurred, a Mann-Whitney U -test was then used for the pair-wise comparison between hunting seasons.

To study possible associations, a Spearman correlation test was performed for the entire 5-yr sample to assess pair-wise correlations between the abundance of nematode species. Moreover, cluster analysis using Euclidean distances and a complete linkage method was performed on logarithmically transformed and standardized abundances, to group parasite species on the basis of their patterns of appearance in the chamois.

In the 5-yr sample, the relationship between abomasal nematode population size and species richness was studied by a Spearman correlation test. The same test was used to correlate d with richness values, to evaluate the relationship between the ability of a single species to become dominant, and the number of species in the infracommunity.

It was not possible to fully evaluate abomasal parasitism in the chamois that died during the pneumonia outbreak (194 carcasses were found), because field conditions and decomposition strongly limited the number of the suitable abomasa ($n = 9$) and their reliability for quantitative parasitological analysis. Therefore, only a limited qualitative analysis was carried out.

TABLE I. Structure of the sample of chamois culled during the 5-yr period 1998–2002.*

	Entire study area						District B2					
	Total		Males		Females		Total		Males		Females	
	Juvenile†	Mature‡	Juvenile	Mature	Juvenile	Mature	Juvenile	Mature	Juvenile	Mature	Juvenile	Mature
1998§	32 (24)	16 (15)	19 (19)	7 (7)	13 (5)	9 (8)	3 (3)	2 (2)	2 (2)	2 (2)	1 (1)	1 (1)
1999§	20 (18)	10 (8)	11 (11)	6 (6)	9 (7)	4 (2)	4 (3)	2 (2)	2 (2)	1 (1)	2 (1)	1 (1)
2000§	22 (20)#	25 (22)	9 (7)	12 (12)	12 (12)	13 (10)	3 (3)	11 (10)	2 (2)	4 (4)	1 (1)	7 (6)
2001	15 (14)	18 (17)	10 (10)	8 (8)	5 (4)	10 (9)	1 (1)	8 (8)	1 (1)	4 (4)	—	4 (4)
2002	10 (7)	17 (14)	5 (4)	11 (10)	5 (3)	6 (4)	2 (2)	7 (5)	2 (2)	4 (3)	—	3 (2)

* The number of chamois in which the Berger-Parker Dominance index (d) for abomasal nematodes was calculated is included in parentheses.

† 0–3 yr old.

‡ 4–14 yr old.

§ Premortality period.

|| Postmortality period.

In 1 chamois sex was not determined.

TABLE II. Summary of subgroups compared via BM test. Comparisons between and within age classes were performed within each sex. Analyses comparing districts were performed regardless of sex or age.

	All chamois	Males	Juvenile	Mature	District B2
All chamois	§ **				
Females	—	* † ‡			
Juvenile	—	—	§		
Mature	—	—	* † ‡	§	
District B2	—	—	—	—	§ **
Other districts	—	—	—	—	* † ‡ # ¶

* Abomasal nematode count in all chamois 1998–2002.

† Abomasal nematode count in the premortality period (1998–2000).

‡ Abomasal nematode count in the postmortality period (2001–2002).

§ Abomasal nematode count between the premortality and postmortality period.

|| *Haemonchus contortus* abundance in all chamois 1998–2002.

Haemonchus contortus abundance in the premortality period.

¶ *Haemonchus contortus* abundance in the post-mortality period.

** *Haemonchus contortus* abundance between the premortality and postmortality period.

Study of the relationship between host sex, age, hunting district, and abomasal nematodes in the 5-yr sample

Differences in nematode count due to sex, age, and hunting district were studied by means of the Brunner and Munzel test (BM test) using the SAS program proposed by Neuhäuser and Poulin (2004). Table II shows the subsamples that were compared by the BM test for the abomasal nematode count and for *Haemonchus contortus* abundance, due to the importance of this species at both the intraspecific and interspecific levels (Zaffaroni et al., 2000).

Differences in parasitic richness and *d* were evaluated between the sexes and age classes using a Mann-Whitney *U*-test. Moreover, comparisons for richness and *d* were performed between district B2 and the other districts.

Study of parasitic patterns in relation to the die-off

Differences in the abomasal nematode count and *H. contortus* abundance between premortality and postmortality were analyzed through the BM test (Table II).

Similar differences in richness and *d* between periods were evaluated by a Mann-Whitney *U*-test on the entire sample and subdivided according to host sex and age. The same variations were also evaluated considering only district B2.

Host-parasite interactions were evaluated by monitoring parasite aggregation using negative binomial distribution fitting and estimation of aggregation indices on the abomasal parasitic counts. The indices used (see Wilson et al., 2002) were the parameter *k* and the variance to mean ratio. The distribution fitting and the estimate of *k* (by the maximum likelihood method) were performed using the nb.fit function of S-PLUS 6.1.2. We performed these analyses on the entire 5-yr sample and in the 2 subsamples including the chamois culled before and after the mortality outbreak. The same procedures were performed in district B2 alone.

RESULTS

There was no variation when considering alternative morphs as either a single or distinct species.

Composition and structure of the nematode community

Overall, 12 nematode species and 3 morphs were identified. The prevalence, mean abundance, mean intensity, range, and Importance indices in the quinquennium and for each hunting season are presented in Tables III and IV. Tables V and VI show the same indices for district B2.

In the 5-yr sample, the dominant nematode species ($I \geq 1$) were *H. contortus*, *Teladorsagia circumcincta*, *Trichostrongylus axei*, and *S. spiculoptera*. However, considering that the

dominance status of *S. spiculoptera* was limited to 1999, only *H. contortus*, *Teladorsagia circumcincta*, and *Trichostrongylus axei* were considered as dominant in the community. Most of the species were classified as codominant ($0.01 \leq I < 1$), except *O. ostertagi* and *T. longispicularis*, which were rare and classified as subordinate ($0 < I < 0.01$).

Significant yearly variations in parasitic abundance were detected for *S. spiculoptera*, *Teladorsagia trifurcata*, *Trichostrongylus vitrinus*, and for the abomasal nematode count (Kruskal-Wallis test, $P < 0.05$). The comparison between hunting seasons is presented in Table VII.

Significant Spearman correlation coefficients between species in the 5-yr sample are shown in Table VIII. All significant correlations were positive. Cluster analysis (Fig. 1) revealed an association primarily between *Teladorsagia circumcincta*/*T. trifurcata* and *T. pinnata* and between *S. spiculoptera*/*R. mathevossiani* and *O. leptospicularis*/*O. kolchida*, whereas the dendrogram showed a ladderlike topology for the other species. No relevant association was detectable among the dominant species. The abomasal richness was positively correlated with the abomasal nematode count (Spearman $R = 0.71$, $P < 0.001$) and showed a negative correlation with *d* (Spearman $R = -0.81$, $P < 0.05$).

Qualitative parasitological analysis of chamois that died from November 2000 to March 2001 showed the presence of *H. contortus*, *Teladorsagia circumcincta*, *Trichostrongylus axei*, *S. spiculoptera*, *O. leptospicularis*, and *R. mathevossiani*.

Relationship between host sex, age, hunting district, and abomasal nematodes in the 5-yr sample

Male chamois had higher abomasal nematode counts than females (BM test, $P < 0.001$). All 11 chamois with no abomasal nematodes were female. No significant differences were found between juvenile and mature chamois. The chamois from district B2 had higher abomasal nematode counts (BM test, $P < 0.05$) and *H. contortus* abundances (BM test, $P < 0.01$) than chamois shot in the other districts.

The abomasal richness was significantly higher in male than in female chamois (Mann-Whitney *U*-test, $P < 0.01$), whereas no differences were observed for *d*. No differences were de-

TABLE III. Mean and range of abomasal nematode count, mean abundance (a), mean intensity (i), and ranges for each parasite species in the 5-yr sample 1998–2002, and in each hunting season for the entire study area.

	1998–2002			1998			1999			2000			2001			2002		
	a	i	Range	a	i	Range	a	i	Range	a	i	Range	a	i	Range	a	i	Range
<i>Haemonchus contortus</i>	35.4	50.8	0–350	22.7	37.6	0–120	42	54.8	0–350	40.2	59.1	0–170	38.2	46.7	0–230	38.9	58.3	0–280
<i>Teladorsagia circumcincta</i>	20.4	40.6	0–220	15.2	30.4	0–210	44.3	78.2	0–200	18.3	31.9	0–80	13.6	32.1	0–220	15.2	37.3	0–120
<i>Trichostrongylus axei</i>	20.4	94.3	0–1,600	4.4	30	0–60	3.7	18.3	0–40	13.4	70	0–210	79.7	202.3	0–1,600	7	38	0–100
<i>Spiculoptera</i>	3.2	23.6	0–80	1.3	20	0–30	9.3	25.5	0–80	2.8	32.5	0–50	2.4	16	0–30	1.5	20	0–30
<i>Trichostrongylus vitrinus</i>	1.6	16.7	0–60	1	12.5	0–20	6.3	21.1	0–60	0.2	10	0–10	0.9	15	0–20	0.7	10	0–10
<i>Teladorsagia pinnata</i>	1	13.6	0–20	0.6	10	0–10	2.3	17.5	0–20	1.1	12.5	0–20	0.3	10	0–10	1.1	15	0–20
<i>Ostertagia leptospicularis</i>	1	13.6	0–30	—	—	—	2.7	16	0–30	1.1	12.5	0–20	1.5	12.5	0–20	0.4	10	0–10
<i>Teladorsagia trifurcata</i>	0.9	12.3	0–20	—	—	—	1.7	10	0–10	1.5	14	0–20	1.2	13.3	0–20	—	—	—
<i>Nematodirus</i> spp.	0.8	20	0–80	0.4	10	0–10	—	—	—	0.4	10	0–10	0.6	10	0–10	—	—	—
<i>Rinadia mathevossiani</i>	0.4	10	0–10	0.2	10	0–10	1.3	10	0–10	0.2	10	0–10	3	33.3	0–80	—	—	—
<i>Trichostrongylus colubriformis</i>	0.5	14.3	0–20	0.6	10	0–10	1.7	16.7	0–20	—	—	—	—	—	—	0.7	20	0–20
<i>Ostertagia kolchida</i>	0.4	11.7	0–20	—	—	—	0.3	10	0–10	0.9	13.3	0–20	—	—	—	0.7	10	0–10
<i>Trichostrongylus capricola</i>	0.2	10	0–10	0.2	10	0–10	0.7	10	0–10	0.2	10	0–10	—	—	—	—	—	—
<i>Ostertagia ostertagi</i>	0.3	25	0–40	—	—	—	—	—	—	0.9	40	0–40	0.3	10	0–10	—	—	—
<i>Trichostrongylus longispicularis</i>	0.1	10	0–10	—	—	—	—	—	—	—	—	—	0.3	10	0–10	—	—	—
Abomasal nematode count	214.8	228.8	0–4,840	105.4	115	0–510	269.3	299.3	0–1,080	191.1	191.1	10–900	413.9	413.9	10–4,840	149.3	175.2	0–560

TABLE IV. Prevalence (p) and Thul Importance index (I) for each parasite species in the 5-yr sample 1998–2002, and in each hunting season for the entire study area.

	1998–2002			1998			1999			2000			2001			2002		
	p	I	Range	p	I	Range	p	I	Range	p	I	Range	p	I	Range	p	I	Range
<i>H. contortus</i>	69.7	61.34	60.4	61.7	76.7	49.68	68.1	66.6	81.8	44.96	66.7	76.8						
<i>T. circumcincta</i>	50.3	25.52	50	34.2	56.7	38.76	57.5	25.6	42.4	8.33	40.7	18.33						
<i>T. axei</i>	21.6	10.95	14.6	2.9	20	1.13	19.2	6.2	39.4	45.19	18.5	3.86						
<i>S. spiculoptera</i>	13.5	1.07	6.3	0.4	36.7	5.28	8.5	0.6	15.2	0.53	7.4	0.33						
<i>T. vitrinus</i>	9.7	0.39	8.3	0.4	30	2.93	2.1	0.01	6.1	0.08	7.4	0.16						
<i>T. pinnata</i>	7.6	0.19	6.3	0.2	13.3	0.48	8.5	0.2	3	0.01	7.4	0.24						
<i>O. leptospicularis</i>	8.1	0.16	—	—	16.7	0.69	8.5	0.2	12.1	0.26	3.7	0.04						
<i>T. trifurcata</i>	7	0.15	—	—	16.7	0.43	10.6	0.4	9.1	0.16	—	—						
<i>Nematodirus</i> spp.	3.8	0.07	4.2	0.09	—	—	4.3	0.04	9.1	0.4	—	—						
<i>R. mathevossiani</i>	4.3	0.05	2.1	0.02	13.3	0.27	2.1	0.01	6.1	0.05	—	—						
<i>T. colubriformis</i>	3.8	0.05	6.3	0.2	10	0.26	—	—	—	—	3.7	0.08						
<i>O. kolchida</i>	3.2	0.03	—	—	3.3	0.02	6.4	0.1	—	—	7.4	0.16						
<i>T. capricola</i>	2.2	0.01	2.1	0.02	6.7	0.07	2.1	0.01	—	—	—	—						
<i>O. ostertagi</i>	1.1	0.007	—	—	—	—	2.1	0.04	3	0.01	—	—						
<i>T. longispicularis</i>	0.5	0.0007	—	—	—	—	—	—	3	0.01	—	—						

TABLE V. Mean and range of abomasal nematode count, mean abundance (a), mean intensity (i), and ranges for each parasite species in the 5-yr sample 1998–2002, and in each hunting season for district B2 alone.

	1998–2002			1998			1999			2000			2001			2002		
	a	i	Range	a	i	Range	a	i	Range	a	i	Range	a	i	Range	a	i	Range
<i>H. contortus</i>	54.3	66.4	0–280	55	55	20–100	50	60	0–90	60.7	85	0–170	34.4	38.8	0–140	66.7	85.7	0–280
<i>T. circumcincta</i>	35.2	51.7	0–220	50	100	0–210	58.3	70	0–190	22.1	28.2	0–60	38.9	58.3	0–220	26.7	48	0–120
<i>T. axei</i>	3.4	37.5	0–100	3.3	20	0–20	—	—	—	0.7	10	0–10	2.2	20	0–20	11.1	100	0–100
<i>S. spiculoptera</i>	2	22.5	0–40	1.7	10	0–10	1.7	10	0–10	2.9	40	0–40	—	—	—	3.3	30	0–30
<i>T. vitrinus</i>	0.9	20	0–30	—	—	—	6.7	20	0–30	—	—	—	—	—	—	—	—	—
<i>T. pinnata</i>	1.4	12	0–20	1.7	10	0–10	3.3	20	0–20	1.4	10	0–10	1.1	10	0–10	—	—	—
<i>O. leptospicularis</i>	1.4	12	0–20	—	—	—	—	—	—	2.1	15	0–20	2.2	10	0–10	1.1	10	0–10
<i>T. trifurcata</i>	1.6	14	0–20	—	—	—	1.7	10	0–10	3.6	16.7	0–20	1.1	10	0–10	—	—	—
<i>Nematodirus</i> spp.	0.2	10	0–10	—	—	—	—	—	—	0.7	10	0–10	—	—	—	—	—	—
<i>R. mathewossiani</i>	0.2	10	0–10	—	—	—	—	—	—	0.7	10	0–10	—	—	—	—	—	—
<i>T. colubriformis</i>	0.5	20	0–20	—	—	—	—	—	—	—	—	—	—	—	—	2.2	20	0–20
<i>O. kolchida</i>	0.5	10	0–10	—	—	—	—	—	—	0.7	10	0–10	—	—	—	1.1	10	0–10
<i>T. capricola</i>	0.2	10	0–10	—	—	—	1.7	10	0–10	—	—	—	—	—	—	—	—	—
Abomasal nematode count	236.6	247.9	0–900	211.7	211.7	30–510	258.3	310	0–620	220	220	20–900	258.9	258.9	30–840	242.2	272.5	0–560

ected in richness or *d* either between the age classes or between district B2 and the other districts.

Parasitic patterns in relation to the die-off

Considering the samples of all districts, there was no difference in the abomasal nematode count between chamois examined before and after the die-off, either in the entire sample or subdivided by host sex and age. Likewise, *H. contortus* abundances were not different between the 2 periods examined. The same results were found for district B2 alone.

Considering the results within each period in the whole sample, male chamois were more parasitized than females before the die-off (BM test, *P* < 0.001), whereas this difference was not significant following the outbreak. No differences were observed between the age classes within each period.

Within the premortality period, chamois in district B2 had higher abomasal nematode counts (BM test, *P* < 0.05) and *H. contortus* abundances (BM test, *P* < 0.01) than chamois from the other districts, while after the die-off these differences were no longer significant.

No significant variations were observed in either species richness or *d* between the 2 periods either in the entire study area or in district B2 alone.

Considering all the districts and district B2 alone, the nematode distribution was found to be consistently aggregated (Table IX), showing overdispersion both on the whole and before and after the mortality outbreak. The nematode distribution in the 5-yr sample and within each period did not differ from a negative binomial distribution (*P* = 1). Nonetheless, all indices indicated a higher degree of parasitic aggregation after the die-off.

DISCUSSION

The abomasal community of the studied population showed qualitative differences with respect to other Italian populations of chamois (Balbo et al., 1978; Genchi et al., 1982; Rossi et al., 1989; Lanfranchi et al., 1991; Zaffaroni et al., 1997). With regard to host specificity (Zaffaroni et al., 2000), except for *Teladorsagia circumcincta*, a specialist nematode of bovines typical of chamois, the helminth community was strongly characterized by *H. contortus* and *Trichostrongylus axei*, both of which are considered generalist helminth species. In particular, *H. contortus* peaked in 2001 with the highest prevalence ever recorded in alpine chamois to our knowledge. The presence of specialist nematodes of cervids such as *S. spiculoptera*/*R. mathewossiani* and *O. leptospicularis*/*O. kolchida* was also consistent in the community. *M. marshalli*/*M. occidentalis*, typical in alpine wild bovid populations, was, interestingly, absent in our survey.

Our data are consistent with the results of other surveys performed in alpine wild ruminants (Genchi et al., 1992; Zaffaroni et al., 1996) suggesting that the nematode community tended toward “isolationism” (Holmes and Price, 1986), with no saturation and no inherent equilibrium. This hypothesis is supported by the results of cluster analysis showing independence even between the dominant species, and by the correlations between richness, abomasal nematode count, and *d*. In fact, no competition was detectable and the dominance degree of a single species decreased with the increasing number of species in

TABLE VI. Prevalence (p) and Thul Importance index (I) for each parasite species in the 5-yr sample 1998–2002, and in each hunting season for district B2 alone.

	1998–2002		1998		1999		2000		2001		2002	
	P	I	P	I	P	I	P	I	P	I	P	I
<i>H. contortus</i>	81.8	63.91	100	67.81	83.3	44.38	71.4	69.5	88.9	53.22	77.8	75.4
<i>T. circumcincta</i>	68.2	34.54	50	30.82	83.3	51.78	78.6	27.88	66.7	45.06	55.6	21.54
<i>T. axei</i>	9.1	0.45	16.7	0.68	—	—	7.1	0.08	11.1	0.43	11.1	1.8
<i>S. spiculoptera</i>	9.1	0.27	16.7	0.34	16.7	0.3	7.1	0.33	—	—	11.1	0.54
<i>T. vitrinus</i>	4.5	0.06	—	—	33.3	2.37	—	—	—	—	—	—
<i>T. pinnata</i>	1.1	0.22	16.7	0.34	16.7	0.59	14.3	0.33	11.1	0.21	—	—
<i>O. leptospicularis</i>	11.4	0.22	—	—	—	—	14.3	0.49	22.2	0.86	11.1	0.18
<i>T. trifurcata</i>	11.4	0.26	—	—	16.7	0.3	21.4	1.23	11.1	0.21	—	—
<i>Nematodirus</i> spp.	2.3	0.01	—	—	—	—	7.1	0.08	—	—	—	—
<i>R. mathevossiani</i>	2.3	0.01	—	—	—	—	7.1	0.08	—	—	—	—
<i>T. colubriformis</i>	2.3	0.01	—	—	—	—	—	—	—	—	11.1	0.36
<i>O. kolchida</i>	4.5	0.03	—	—	—	—	7.1	0.08	—	—	11.1	0.18
<i>T. capricola</i>	2.3	0.01	—	—	16.7	0.3	—	—	—	—	—	—

TABLE VII. Significant pair-wise differences (Mann-Whitney *U*-test, *P* < 0.05) in abomasal nematode count and single species abundances between hunting seasons for the entire study area.

	1998	1999	2000	2001	2002
1998	—				
1999	* † ‡ §	—			
2000	† §	* †	—		
2001	† §	* †		—	
2002		* † ‡		§	—

* *S. spiculoptera*.
 † *T. trifurcata*.
 ‡ *T. vitrinus*.
 § Abomasal nematode count.

the community. Interactions among parasite species have a low importance in determining the patterns of such communities, while the major factors are represented by parasite life history (Dobson and Roberts, 1994), host density, behavior (Ezenwa, 2004a; Santín-Durán et al., 2004), seasonality and climatic conditions, host immune capacity, and host specificity (Zaffaroni et al., 1998, 1999, 2000). Therefore, the positive associations between species, the correlation coefficients of which were generally low, were probably not attributable to synergistic interactions but rather to a combination of these factors. In reality, pair-wise correlations were often evident in the case of alternative morphologies or between specialists of the same host groups. Moreover, the dominant species did not reveal important associations, because only *Teladorsagia circumcincta* and *H. contortus* were significantly correlated. Likewise, the yearly variations in abomasal parasitism were probably related to variations of the cited factors, which did not affect the dominant species, but other species or morphs having less regular patterns. Climatic conditions might explain the absence of *M. marshalli/M. occidentalis*, which has been found dominant in both domestic and wild ruminants in areas characterized by cold climates (Cabaret, 1984; Karstein et al., 1987), and which showed a peak during the winter in Swiss Alp ibex (Lanfranchi et al., 1995; Zaffaroni et al., 1999). Actually, the relatively low altitudes in parts of the chamois range and the presence of a warmer and moister component in the climate, compared with other typically alpine areas, could render Lecco Province unsuitable for this parasite species. Moreover, *M. marshalli/M. occidentalis* was never observed, even in the abomasa of the chamois found dead during the pneumonia outbreak (6 out of 9 recovered in the depths of winter, January–February). On the other hand, the same climatic situation may be one of the factors determining the high indices observed for *H. contortus*, considering that larval stages of this nematode are not very resistant to low temperatures (Todd et al., 1976; Jasmer et al., 1986, 1987) and tend to increase in pastures as temperature increases (Krecek et al., 1992).

Interspecific interactions among host species could become a basic factor in determining the composition of the abomasal community, owing to the lack of an inherent equilibrium. This was particularly evident in the studied population in which the consistent presence of generalist and nonspecific parasites could also be explained by the large overlapping of grazing pastures among chamois, roe deer, and sheep and goat flocks often unguarded.

TABLE VIII. Pair-wise significant correlation coefficients (Spearman R , $P < 0.05$) between nematode species in the 5-yr sample 1998–2002 for the entire study area.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>H. contortus</i>	—														
<i>T. circumcincta</i>	0.19	—													
<i>T. axei</i>	0.18	0.21	—												
<i>S. spiculoptera</i>		0.16	0.15	—											
<i>T. vitrinus</i>			0.19	0.19	—										
<i>T. pinnata</i>		0.41	0.33	0.33	0.22	—									
<i>O. leptospicularis</i>		0.26	0.21	0.21	0.32	0.40	—								
<i>T. trifurcata</i>		0.33	0.21	0.21	0.32	0.40	0.25	—							
<i>Nematodirus</i> spp.	0.16	0.19	0.19	0.39	0.16	0.16	0.15	0.19	—						
<i>R. mathevossiani</i>				0.23	0.16	0.16	0.19	0.26		—					
<i>T. colubriformis</i>				0.16	0.16	0.16	0.19	0.26			—				
<i>O. kolchida</i>				0.16	0.16	0.16	0.19	0.26				—			
<i>T. capricola</i>				0.16	0.16	0.16	0.19	0.26					—		
<i>O. ostertagi</i>				0.16	0.16	0.16	0.19	0.26						—	
<i>T. longispicularis</i>				0.17	0.17	0.17	0.19	0.26							—

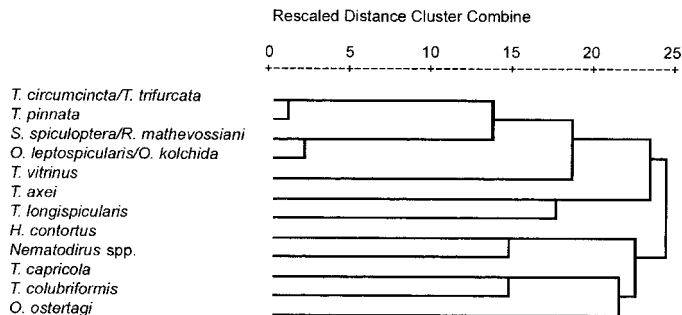


FIGURE 1. Dendrogram based on the abundance of each helminth species in each infracommunity in the 5-yr sample 1998–2002 for the entire study area (Euclidean distances and complete linkage method).

Heterogeneities in nematode counts and richness associated with host gender might be expected, considering the male bias often observed in nematode infections of mammals (Poulin, 1996). According to Zuk and McKean (1996), sex bias could be related to ecological factors such as behavior or morphology, and physiological mechanisms (e.g., stress and hormonal changes). In the present study area, the hunting season takes place at the same time of the chamois breeding season, which implies stress and increasing testosterone levels for mature males. Both of these factors can make males more susceptible to parasites (Folstad et al., 1989). On the contrary, our sample structure did not permit us to evaluate heterogeneity according to host age.

The observed aggregation patterns did not differ from the majority of macroparasitic infections in wildlife for which $k < 1$ (Shaw and Dobson, 1995). Factors determining parasitic aggregation have been summarized by Shaw et al. (1998) and include seasonality, aggregation of infection stages and host behavior, physiology, and immunity. Possible differences in climatic conditions between time and the population decrease due to the pneumonia outbreak presumably influenced the availability and distribution of larval stages in pastures and, consequently, the patterns of parasite abundance and aggregation present in hosts. However, because aggregation tends to stabilize host-parasite dynamics (Møller, 2005) and is generally considered as a positive health index in macroparasitic infections (Rosà et al., 2000), the increase of parasite aggregation after the die-off could also be related to an enhanced ability of the host to control nematode infections. The balance observed in abomasal nematode counts and *H. contortus* abundance between genders and between hunting districts after mortality, failing any significant variation between the 2 periods, suggests

TABLE IX. Aggregation indices in the 5-yr sample 1998–2002, and in the hunting seasons preceding (1998–2000) and following (2001–2002) the die-off.

	k		Variance/mean	
	Entire study area	District B2	Entire study area	District B2
1998–2002	0.65	0.97	759.43	189.45
1998–2000	0.76	1.16	216.33	176.97
2001–2002	0.55	0.79	1423.35	215.40

an improvement in host immunity. This hypothesis is also supported by the parallel results of health monitoring, considering as an example that clinical dermatophilosis, which is favored by immunosuppression, stress, malnutrition, intercurrent infections, and parasites (Gulland, 1992; Ambrose et al., 1999; De Meneghi et al., 2002), was highly spread in the chamois dying in the pneumonia epizootic (Citterio et al., 2003). Considering that pneumonia is a multifactorial disease (Wobeser, 1994), it cannot be excluded that abomasal parasites have acted as a predisposing factor in the studied population, subtracting essential resources for the maintenance of host homeostasis. In favor of this hypothesis it should be stressed that although the abomasal nematode counts observed in the studied population did not differ from the results of other surveys of alpine chamois, the qualitative composition of the abomasal community could imply a different pathogenic potential. In fact, the most important species, *H. contortus*, is considered as one of the most pathogenic abomasal nematodes and has been related to poorer performances and lethal events in both wild bovid and cervid populations, primarily where climatic conditions are not extreme, and where wild and domestic ruminants share a common range (McGhee et al., 1981; Lavín et al., 1997). In this regard, preliminary data revealed a negative correlation between abomasal parasites and blood protein levels of chamois in the study area (Sala et al., 2000). The abovementioned hypotheses are also consistent with data regarding the quality of the diet of chamois in the study area, which appeared poor especially in the critical districts (Tarantola et al., 2005). Actually, nutrition can be a basic factor influencing resistance and resilience to gastrointestinal parasites (Davidson et al., 1980; Coop and Kyriazakis, 1999; Ezenwa, 2004b). Higher parasite counts found in district B2 compared with the other districts, primarily in the premortality period, further support the hypothesis of a role for abomasal nematodes in the population crash.

Finally, the absence of any variation in dominance (*d*) indicates a consistent tendency toward isolationism of the nematode community, apart from the degree of nematode infection and the host condition.

In conclusion, even if confirming that parasitological data per se may be unreliable as population health indices, the results of this survey emphasize the importance of setting the parasitological patterns in the context of wide-range surveillance, to avoid underestimating the importance of parasites (Tompkins et al., 2002). Moreover, from both conservation and management points of view, there is a need to further study the epidemiology, seasonality (including hypobiosis and arrested development), and impact of parasites in alpine ruminant populations. Toward this aim, hypotheses derived from observational studies should be tested by experimental and theoretical studies (Gulland et al., 1993; Damaggio et al., 1996; Stien et al., 2002).

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