

Biology and status of whitefishes from Lake Santa Croce (Dolomites, Italy)

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with 3 figures and 7 tables

Abstract: The biology and status of European whitefish (*Coregonus* sp.) was studied in Lake Santa Croce, a small (7.8 km², maximum depth 41 m) Alpine lake in northeastern Italy. The species was established through introductions probably from Switzerland. These whitefish, never commercially exploited, have not been the focus of much attention. The present paper describes the biological status of the Lake Santa Croce whitefish (i.e., morphology, growth, age, and feeding) together with zooplankton and benthic invertebrate communities as part of studies conducted from December 1996 to September 1997. Whitefish from Santa Croce Lake ranged in age from 0+ to 7+. At the age 0+ fish reached 191.5 mm in length and 51 g in average, at age 6+ – 452.1 and 760 g, respectively. Stomach contents analysis revealed that the whitefish mainly ate *Daphnia* and copepods being the overall most important food source. The gill-raker number of the whitefish from Santa Croce Lake was similar as in other Alpine whitefish slow-growing populations. Preliminary genetic analysis suggests that, as in other Alpine lakes in northern Italy, the whitefish may be the “lavarello” form, originating from hybridization among the introduced forms.

Introduction

Some of the Alpine lakes in northern Italy currently contain coregonid populations as the result of introductions that occurred as early as 1861. According to SOLA et al. (1989), in the last century three recognized whitefishes (*Coregonus wartmanni coeruleus*, *C. schinzi helveticus* and *C. macrophthalmus*) were successively introduced from Switzerland into several lakes of Northern Italy. [Editors note: nomenclature for the European whitefish has proven to be difficult to resolve and is inconsistent among researchers due to uncertain phylogeny that

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stems from extensive polymorphism. This inconsistency is recognized and HEESE (1992) recommended that all European whitefish be treated as a complex, and the Alpine whitefish or (Bloch) be renamed *forma* (Bloch) in recognition of the lack of diagnostic differences in this complex of fishes. To date, however, no single nomenclature convention for these fish is universally accepted.] A few years after the introduction, the original forms interbred and produced a new form termed "lavarello" (DOTTRENS 1955). By further introductions, this form was spread into several lakes in northern and central Italy. Apart from few large lakes in the Lombardia region (e.g., Lakes Maggiore, Garda, Iseo and Como), coregonids were not commercially exploited. Because of this inattention, the biological and taxonomical status of the introduced coregonids has not been sufficiently studied, especially in several smaller lakes. LORO et al. (1991) and ZANETTI et al. (1993) carried out preliminary limnological and ichthyological investigations in one of these lakes: Lake Santa Croce. ZANETTI et al. (1993) reported that the first whitefish introduction into Lake Santa Croce was carried out in 1901–1902, when *Coregonus schinzi helveticus* was stocked from the Brescia fishery station. The second introduction was made in 1945, when *Coregonus wartmanni coeruleus* was stocked into the lake (FOSSA 1988). The aim of the present study was to describe particular elements of the biological and taxonomical status of the whitefishes occurring in Lake Santa Croce.

Methods

Study area

Lake Santa Croce (Fig. 1) is located in northeastern Italy (Veneto region, Dolomite Mountains) along the Alpage river system, in the Piave river drainage. Lake Santa Croce is of moderate area and depth, and has a drainage area of 154 km² (Table 1). The lake was formed by the natural blockade of a valley with stone from recent mountain glacial activity. In 1928, surface

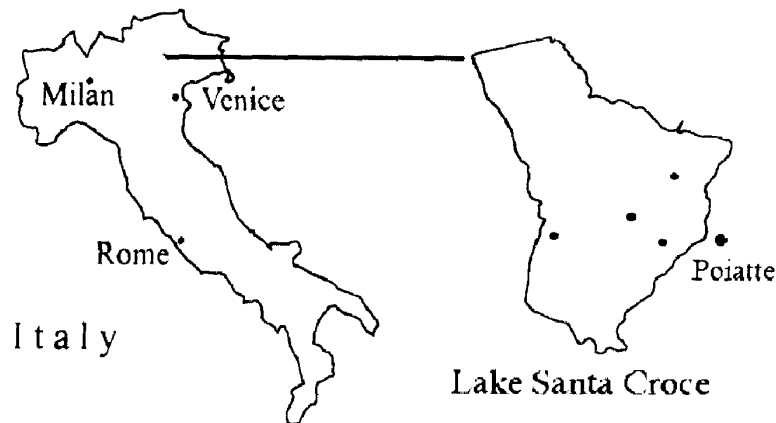


Fig. 1. Study area in northeastern Italy. Black circles are sampling sites in Santa Croce Lake.

Table 1. Limnological characteristics of Lake Santa Croce (after ZANETTI et al. 1993).

Parameter	Value
Altitude [m a.s.l.]	386
Maximal length [km]	4.75
Maximal width [km]	2.4
Lake surface [km ²]	7.8
Maximal depth [m]	41.0
Mean depth [m]	19.0
Length of shoreline [km]	12.9
Catchment area [km ²]	154
Volume [m ³]	150,160·10 ⁶
Theoretical water renewal time [yr]	0.117
Number of fish species	26

area was enlarged by damming of the outflow for hydroelectric power. The original fish community consisted of pike (*Esox lucius* L.), perch (*Perca fluviatilis* L.), various cyprinid fishes (*Rutilus pigus* Lacepede, *Leuciscus cephalus* L., *Scardinius erythrophthalmus* L., *Alburnus alburnus alborella* De Filippi) and salmonid fishes (*Salmo trutta trutta* L. and *Salmo marmoratus* Cuv.). There is no commercial fishery, only a recreational fishery. *Coregonus lavaretus* has been sporadically caught by anglers in the lake.

Survey and analysis methods

Fish population surveys were conducted from December 1996 – September 1997 to determine basic biological data. European whitefish were caught using sets of gill nets at four sampling sites (Fig. 1). Each gang of gill net consisted of 13 nets (two nets 30 x 2 m, two nets 30 x 4 m, four nets 50 x 4 m, two nets 20 x 5 m, and three nets 30 x 5, 50 x 5 and 50 x 6 m, respectively). The mesh size (stretch measure) of nets ranged from 10 to 60 mm by sequential 5-mm intervals. Gill nets were fished overnight and fish were removed in the early morning. Length (mm) and mass (g) were measured for all specimens, and sex and maturity were determined for each fish. Ages were determined from scales. For morphometric comparisons, live specimens were measured and body parameters were expressed as percentage value relative to total length and head length. For genetic characterization, allele frequencies (AAT, ADH, CK, G3PDH, GPI, IDDH, IDHP, LDH, MEP, MDH, PGDH, PGM, SOD) were derived from electrophoretic separation of the enzyme products of 34 genetic loci from 50 fishes. Conditions for electrophoresis as well as locus and allele nomenclature followed BODALY et al. (1991).

The stomach contents of the whitefishes were analyzed monthly during the study period. The number of prey of each species or animal group in each of the stomachs collected was counted in the laboratory.

Benthic and pelagic invertebrates were sampled monthly with the sampling of fish for food habit analysis. The benthic samples were taken by a Petersen sampler, strained with a 0.2-mm

mesh sieve and fixed in 4% formalin. Zooplankton were also sampled monthly using a standard plankton net of 1 m length and 20 cm mouth diameter with a 50 μm mesh netting. Vertical hauls were taken on each sample date from water depth of 5 to 11.5 m (2.5 x Secchi disk depth). All samples were preserved in 4% formalin and examined under microscope.

Results

Zooplankton resources

Rotatoria in Santa Croce Lake were represented by *Kellikottia*, *Asplanchna* and *Synchaeta* spp. mainly in summer and autumn. The percentage presence of rotifers ranged from 0 in April to over 77% in November (Table 2). *Daphnia longispina* and *Leptodora kindti* comprised the majority of the Cladocerans. Development of *Daphnia* populations was observed from May (46% of total zooplankton) to September (22% of total zooplankton). *Leptodora* was found in samples in early August, but this species is probably not fully represented in our samples due to net avoidance. Prevalence of cladocerans in the lake ranged from 3% in November to 46% in May. Copepoda was represented by *Cyclops strenuus*, *Mesocyclops leuckarti* and sporadically by *Thermocyclops* and *Eudiaptomus* spp. Young stages of cyclopoids (nauplii and copepodites) were abundant all year long, in densities ranging 0.3–36 individuals·dm⁻³ in late autumn. Prevalence of copepods in zooplankton ranged from 19% in November to 65–67% in April and September. Copepods were the most abundant and consistent crustacean zooplankton, typical of cold, oligotrophic Alpine lakes. In general, zooplankton was not abundant in Lake Santa Croce. Densities of organisms ranged from 5 individuals·dm⁻³ in December-January to 250 individuals·dm⁻³ in late autumn. During winter and early spring (to April), zooplankton densities were extremely low (less than 100 individuals per cubic decimeter).

The benthic invertebrate densities were more consistent throughout the study period, but some differences occurred. The maximum density of benthic organisms in total exceeded 20,000 individuals·dm⁻² in the summer (Table 2). The prevalence of Chironomidae and *Pisidium* increased to 5.9% and 32.1% in summer, respectively. Tubificidae, Lumbriculidae and Naididae (Oligochaeta) were the most abundant group of benthic organisms for whole year.

Lake Santa Croce European whitefish

Whitefish from Lake Santa Croce ranged in age from 0+ to 7+, with most fish in our collections ages 2+ and 3+. Fish ranged 150–510 mm in length and 22–1190 g in weight (Table 3). Size comparison by sex, with the males ranging 200–500 mm and 54–1130 g and females ranging 200–525 mm and 57–1190 g, show no apparent gender differences. According to SZCZERBOWSKI'S (1978) criterion, growth in weight of these whitefish was slow (Fig. 2). Fish reached on average 191.5 mm in length and 51 g at first year of life, 230.2 mm and 105.1 g at second year of life, 313.8 mm and 268.3g at third year of life, 389.1 mm and 502.2 g at fourth year of life, 429.7 mm and 629.7 g at fifth year of life, 439.2 and 658.8 g at sixth year of life, and 452.1 and 760 g at seventh year of life. The greatest annual incremental growth was found through the second year of life, when the fish reach a total length greater than 270 mm. The

Table 2. Zooplankton and benthos composition in Lake Santa Croce. Percent total number of each group in parentheses.

<i>Taxa</i>	<i>Oct</i> <i>1996</i>	<i>Nov</i> <i>1996</i>	<i>Dec</i> <i>1996</i>	<i>Jan</i> <i>1997</i>	<i>Mar</i> <i>1997</i>	<i>Apr</i> <i>1997</i>	<i>May</i> <i>1997</i>	<i>Jun</i> <i>1997</i>	<i>Jul</i> <i>1997</i>	<i>Aug</i> <i>1997</i>	<i>Sept</i> <i>1997</i>
	Zooplankton (numbers per dm ⁻³)										
Rotifera	19.05 (33.76)	193.81 (77.69)	2.30 (49.68)	2.56 (50.10)	1.98 (38.37)		4.62 (16.92)	39.42 (47.48)	15.36 (34.78)	20.49 (61.29)	8.89 (11.39)
Cladocera	8.81 (15.62)	8.01 (3.21)	1.00 (21.60)	1.11 (21.72)	1.06 (20.54)	3.68 (32.31)	12.72 (46.59)	28.91 (34.82)	7.52 (17.03)	4.81 (14.39)	17.34 (22.22)
Copepoda	28.56 (50.62)	47.64 (19.10)	1.33 (28.72)	1.44 (28.18)	2.12 (41.09)	7.71 (67.69)	9.96 (36.48)	14.69 (17.69)	21.28 (48.18)	8.13 (24.31)	51.81 (66.39)
ZooplanktonTotal	56.42	249.46	4.63	5.11	5.16	11.39	27.30	83.02	44.16	33.43	78.04
	Benthos (numbers per dm ⁻²)										
Pisidium	972 (16.6)	1736 (17.9)		1667 (21.6)	139 (8.0)	1111 (18.4)	1181 (28.3)	556 (13.6)	10417 (32.1)	5625 (24.0)	486 (20.0)
Musculium	69 (1.1)										
Chironomidae		69 (0.7)		69 (0.9)			69 (1.7)	208 (5.1)	972 (3.0)	1389 (5.9)	69 (2.8)
Ceratopogonidae		69 (1.0)							139 (0.4)	208 (0.9)	69 (2.8)
Simuliidae	69 (1.1)										
Tubificidae	4861 (77.8)	4792 (49.3)		2917 (37.8)	1111 (64.0)	4306 (71.3)	1875 (45.0)	1944 (47.5)	15903 (49.0)	8125 (34.6)	486 (20.0)
Lumbriculidae		2222 (22.9)		1667 (21.6)	486 (28.0)		556 (13.3)	972 (23.7)		3889 (16.6)	1042 (42.8)
Naididae	208 (3.3)	833 (8.6)		1389 (18.0)		347 (5.7)	486 (11.7)	347 (8.5)	4444 (13.7)	3472 (14.8)	278 (11.4)
Helobdella								69 (1.7)	208 (0.6)	694 (3.0)	
Valvata									139 (0.4)	69 (0.3)	
Nudibranchio	69 (1.0)										
Nematoda						278 (4.6)			139 (0.4)		
Aracnidae									69 (0.2)		
BenthosTotal	6250	9722		7708	1736	6042	4167	4097	32431	23472	2431

size increments subsequently decreased with age of fish. The relationship between weight (W) in grams and total length (L) in centimeters of the studied population is described by the function: $W = 10.974 e^{(0.0096 L)}$.

Table 3. General size characteristics of Lake Santa Croce whitefish.

Parameter	Range	Mean	SD
Body weight (g)	22–1190	447.6	264.3
Total length (mm)	150–510	351.4	82.8
Males' body weight (g)	54–1130	424.1	208.5
Males' body length (mm)	200–500	366.3	63.6
Females' body weight (g)	57–1190	444.9	220.2
Females' body length (mm)	200–525	369.7	66.8

The morphometric measures, described as proportion of total length (TL) for 15 body measures and as proportion of head length for 6 cranial measures, is shown in Table 4. The head of the European whitefish ranged from 15.4% to 19.5% of TL, averaging 17.3%. Our measurements indicate that the body is elongated with a maximum height of only 17.3% to 23.9% of TL, averaging 21.4%.

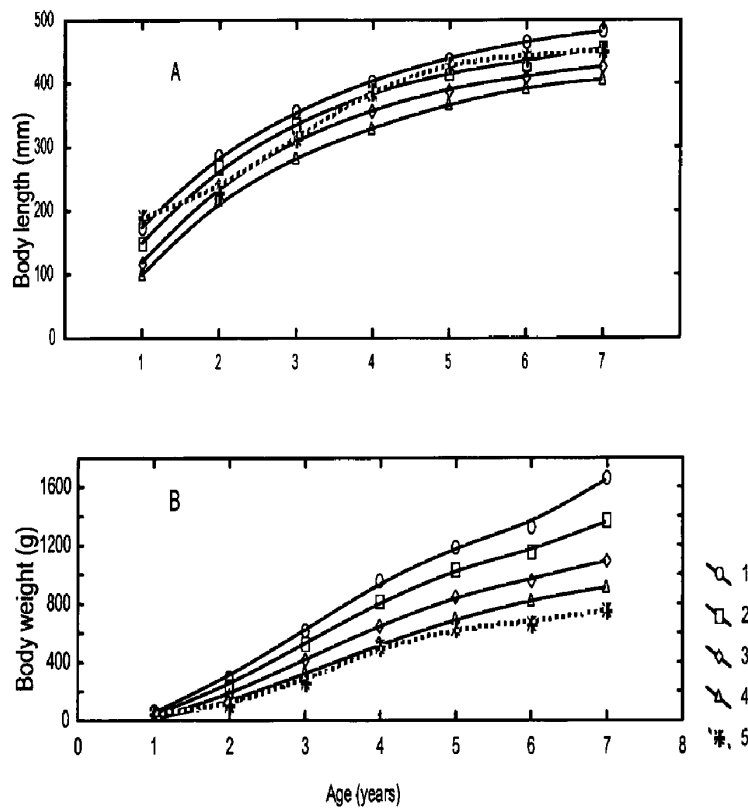


Fig. 2. Growth rate in length (A) and weight (B) of whitefish from Santa Croce Lake comparing to Szczerbowski's scale (1978). Explanations: 1 – very fast, 2 – fast, 3 – moderate, 4 – slow, 5 – Santa Croce Lake.

Table 4. Morphological characteristics of *Coregonus lavaretus* L. from Lake Santa Croce (n = 94).

Parameter	Range	Mean	SD
Total length (mm)	185–514	351.43	82.85
Body weight (g)	52–1025	447.64	264.32
	Percent of total length		
Body length	85.0–90.6	87.67	1.32
Predorsal length	38.2–43.4	40.65	1.17
Postdorsal length	36.0–41.8	39.13	1.21
Greatest body height	17.3–23.9	21.36	1.29
Smallest body height	4.6–7.0	6.18	0.34
Pre-anal distance	62.1–69.5	65.20	1.62
P-V distance	25.3–31.2	27.68	1.11
V-A distance	21.1–26.7	23.66	1.17
Dorsal fin length	9.0–12.9	10.91	0.62
Dorsal fin height	12.6–17.7	15.01	1.01
Pectoral fin length	11.6–16.9	13.25	0.84
Ventral fin length	10.8–15.4	13.24	0.83
Anal fin length	9.1–13.5	11.27	0.91
Anal fin height	8.5–11.8	10.05	0.68
Head length	15.4–19.5	17.28	0.80
	Percent of head length		
Pre-eye distance	21.5–32.1	28.17	1.99
Eye diameter	19.4–30.1	24.17	2.11
Posteye distance	44.0–59.5	52.65	2.26
Head height	57.1–77.3	65.77	3.79
Head width	35.9–51.5	44.17	2.82
Length of lower jaw	23.5–32.1	28.09	1.66

All alleles found in the European whitefish from Lake Santa Croce were typical for this species (BODALY et al. 1991). The only exception was locus *sMEP-4** at which the two alleles, *100 and *135, were segregated, where *Coregonus lavaretus* is typically homozygous for *135 at *sMEP-4** (Table 5). This finding suggests that, as in other north Italian lakes, the whitefish form in Lake Santa Croce may be the "lavarello", the result of hybridization between the original introduced forms (DOTTRENS 1955).

The whitefish preyed mainly on zooplankton. Though abundant, rotifers were not important food items. *Daphnia*, *Leptodora*, and copepods together were the dominant food items for all age classes of whitefish (Table 6). *Daphnia longispina* and *Leptodora kindti* were especially important as prey items for the older age groups (Table 6). *Alona*, chironomidae larvae, and insect pupae were only occasionally found in the whitefish stomachs. *Pisidium* and nematodes were seasonally important. These benthic organisms were found in stomachs during early spring when other food was scarce. In March, many specimens had empty stomachs (Fig. 3).

Table 5. Alleles with their electrophoretic mobility (in parentheses), frequencies of the alleles, percentage of polymorphic loci (P, 99% criterion) and mean heterozygosity (H) in the examined whitefish sample. P and H based on 34 loci. The following loci were monomorphic for 100 allele (unless other electrophoretic mobility stated): *sAAT-1**, *sAAT-2**, *ADH** (-100), *CK-A2**, *CK-B**, *G3PDH-1* (0), *GPI-A1** (112), *GPI-A2**, *GPI-B1**, *GPI-B2**, *mLDHP-1**, *mLDHP-2*, *slDHP-3*, *slDHP-4**, *LDH-A2**, *LDH-B1**, *LDH-B2**, *LDH-C**, *sMDH-A1**, *sMDH-A2**, *mMEP-1**, *mMEP-2**, *sMEP-3**, *PGDH**, *PGM-1** (-100), *sSOD** (125). Standard error of heterozygosity (H) shown in parenthesis.

Locus	Allele	Frequency
<i>G3PDH-2*</i>	<i>a</i> (100)	0.935
	<i>e</i> (50)	0.065
<i>G3PDH-3*</i>	<i>a</i> (100)	0.211
	<i>e</i> (65)	0.133
	<i>f</i> (70)	0.656
<i>LDH-A1*</i>	<i>a</i> (100)	0.957
	<i>c</i> (65)	0.043
<i>sMDH-B1,2*</i>	<i>a</i> (120)	0.886
	<i>b</i> (100)	0.114
<i>sMEP-4*</i>	<i>a</i> (100)	0.424
	<i>b</i> (135)	0.576
<i>PGM-2*</i>	<i>a</i> (-100)	0.989
	<i>c</i> (-155)	0.011
P (%)		20.6
H (%)		3.9 (0.017)

Some younger individuals consumed whitefish eggs in December and March (up to 2.6 eggs per fish); the presence of *Pisidium* in the stomachs of these fish was also noted. Larger specimens (over 300 mm in length and age 3+) preyed on *Pisidium* (up to 43 individuals per fish). The greatest incidence of empty stomachs in March was found in the larger fish, a potential signal of stronger competition for food among the larger whitefish. Seasonal feeding activity of the whitefish, measured as number of prey items per fish, was the lowest in early spring and was consistent with the pattern of number of empty stomachs (Fig. 3).

Comparison with other Alpine whitefish populations

The gillraker count in Lake Santa Croce whitefish corresponds to that of the "lavarello" form from Lake Maggiore. ZANETTI et al. (1993) concluded that the unimodal gillraker-count distribution in the Lake Santa Croce whitefish population indicated the existence of only one ecological form. The mean number of gillrakers was 32.02 (± 0.35), whereas in the Lake Maggiore whitefish this value was 31.34 (± 0.12) (BERG & GRIMALDI 1965). In comparing another meristic, ZANETTI et al. (1993) reported the lateral line scale count in Lake Santa Croce whitefish was 84.9 (± 1.28) and 84.06 (± 1.26) in males and females, respectively. In Lake Maggiore, the number of scales was 90.5 (± 0.96) in the "lavarello" form, whereas the "bondella" form has 85.3 (± 0.28) scales (BERG & GRIMALDI 1965). It appears the gillraker number com-

Table 6. Food composition (numbers per fish) by age class of the Lake Santa Croce whitefish. N is the number of fish studied and Ne indicates number of empty stomachs for each age class.

Age class	1996			1997							
	Oct	Nov	Dec	Mar	Apr	May	Jun	Jul	Aug	Sept	
0+	N	3	14	5							
	Ne	0	2	2							
	Cyclops	1.3	20.7	3967.0							
	Daphnia	29.3	443.6								
	Alona		0.2								
	Leptodora		0.3								
	Pisidium		2.1	3.0							
Chironomid larvae		1.7									
1+	N	22	23	11	24	1	21	3	27	2	
	Ne	1	6	6	22	1	3	0	1	1	
	Asplanchna							1.1			
	Cyclops	3.3	16.4	10.2			34.6	25.0	93.1		
	Daphnia	604.7	283.0	6.2			1649.0	810.0	2659.8	258.0	
	Alona		0.04							18.0	
	Leptodora		0.5					34.2			
	Pisidium		3.4	0.8	7.0						
	Chironomid larvae								3.1		
	Coregonid eggs			2.6							
2+	N	52	37	29	26	30	29	8	28	14	22
	Ne	11	3	10	21	5	8	1	5	2	7
	Cyclops	85.9	21.9	6.3		228.1	22.9	18.6	52.3	4.1	13.0
	Eudiaptomus			0.6							
	Mesocyclops							0.4			
	Daphnia	2212.5	372.7	290.7		40.5	888.5	804.0	1131.3	310.7	353.5
	Leptodora	1.7	0.3						7.8	3.7	0.1
	Pisidium	0.2	0.1		22.6	0.1	0.3				
	Chironomid larvae					0.04					
	Diptera pupae					1.2					
	Insecta		0.03								
Nematoda				12.0							
3+	N	28	28	18	27	30	30	32	30	26	25
	Ne	7	4	13	16	6	4	8	5	7	12
	Asplanchna								0.04		
	Cyclops	69.1	16.3		294.5	312.6	38.1	19.5	65.6	21.8	199.6
	Eudiaptomus	0.9		0.6							
	Mesocyclops								0.4		
	Daphnia	1507.2	174.4	370		64.4	1585.1	923.2	1356.8	908.9	751.1
	Leptodora	4.3	0.2						6.2	6.8	
	Pisidium				42.8						
	Chironomid larvae	0.05							0.04		0.1
	Nematoda				43.6						
Diptera pupae					0.8						
Coregonid eggs				1.3							
4+	N	2	3	12	30	25	27	24	3	10	24
	Ne	0	0	1	20	4	5	5	0	2	8
	Cyclops	30	14.3	10	924	394.9	45.2	53.1		67.9	975.1
	Eudiaptomus	0.9									
	Mesocyclops									0.5	
	Daphnia	1298	92.7	1105	10	26.8	1496.3	1869.5	17	1016.1	1491.8
	Leptodora									26.3	3.2
	Pisidium				14.8	2.6					
	Chironomid larvae				48.9	20.2					
	Nematoda					4.8					
Culex larvae						0.04					
5+ to 7+	N				6	5	3	4	27	23	8
	Ne				6	2	2	1	5	5	1
	Asplanchna								0.9		
	Cyclops					27.7	12	49.3	56.7	109.2	20.4
	Daphnia					3.7	366	2290.7	709.4	1557.2	177.6
	Leptodora								5.0	63.1	
	Pisidium								25.5		
Chironomid larvae					0.3			0.1			

compares to that of original Swiss whitefish populations, which is common to slow-growing populations (Table 7).

The level of genetic polymorphism (expressed as percentage of polymorphic loci) and mean heterozygosity in Lake Santa Croce whitefish were similar to values observed in a variety of European whitefish populations. The polymorphic locus *sMEP-4** was segregated for two alleles (**100* and **135*), which has been reported from *Coregonus lavaretus* populations in Switzerland (JANKUN et al. 1998) and in Austria (M. LUCZYNSKI, unpubl. data). Some Austrian populations exhibited frequencies of the allele *sMEP-4*100* as high as reported here. This finding is corroborated by the genetic distance of only 0.002 and 0.009 (NEI 1978) estimated between the Italian whitefish samples and those from Attersee "Reinenke" and "Kröpfling" forms, respectively. However, this study does not allow definitive conclusions regarding genetic relatedness of the Lake Santa Croce whitefish to those inhabiting other Alpine lakes. Considering gillraker number and genetic polymorphism suggest that the whitefish from Lake Santa Croce are of the "lavarello" form, as found many other north Italian populations.

Aside from genetics, the Lake Santa Croce whitefish fecundity was comparable with those of some local forms in Polish lakes (KAJ 1955) and similar as in the "bondella" and the "lavarello" forms from Lake Maggiore (SPREAFICO et al. 1974, GANDOLFI et al. 1991). Absolute fecundity of whitefish ranged from 16,010 to 35,272 eggs (ZANETTI et al. 1993). These fish mature at age 1+, however about 8% of specimens stay immature (ZANETTI et al. 1993). The food habits of

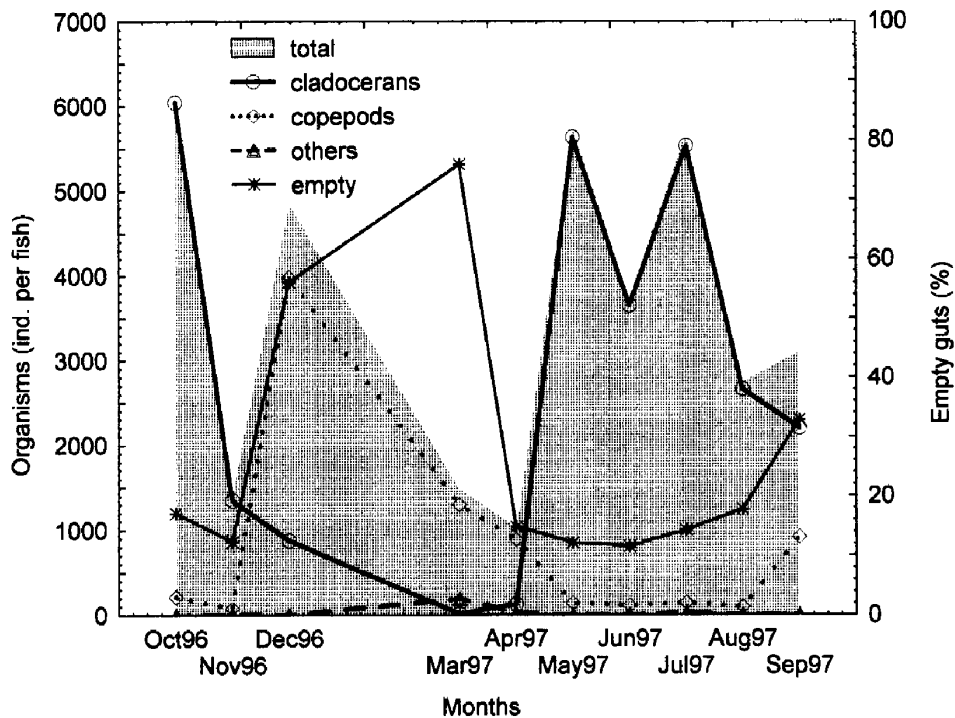


Fig. 3. Seasonal feeding activity of whitefish from Santa Croce Lake.

Table 7. Comparison of the Santa Croce whitefish population with other Alpine lake populations.

Lake and local form	Gill-raker Count		Growth	Source
	Range	Mean		
Lake Santa Croce	28–39	32.02	Slow	ZANETTI et al. (1993)
Lake Maggiore				
Lavarello	23–38	31.34	Fast	BERG & GRIMALDI (1965)
Lake Brienz				
Felchen	26–44		Fast	KIRCHHOFER (1995)
Brienzzlig	33–49		Slow	KIRCHHOFER (1995)
Winter-Brienzzlig	33–49		Slow	KIRCHHOFER (1995)
Lake Thun				
Albock	25–40		Fast	KIRCHHOFER & TSCHUMI (1986)
Brienzzlig	33–50		Slow	KIRCHHOFER & TSCHUMI (1986)
Lake Biel				
Palée	22–35		Fast	RUFLI (1978)
Bondelle	30–40		Slow	RUFLI (1978)
Lake Alpnach				
Albeli	29–47	40.50	Slow	SVARVAR & MÜLLER (1982)
Felchen	24–45	33.20	Fast	SVARVAR & MÜLLER (1982)
Lake Vierwaldstätt				
Albeli	36–45	40.80	Slow	SVARVAR & MÜLLER (1982)
Felchen	27–39	34.3	Fast	SVARVAR & MÜLLER (1982)
Edelfisch	32–41	35.5	?	BIRRRER & SCHWEIZER (1936)
Lake Constance				
Blaufelchen	29–46	36.2	Fast	STEINMANN (1950)
Lake Sempach				
Felchen	26–38	33.5	?	STEINMANN (1950)

whitefish from Lake Santa Croce were similar to whitefishes in other lakes in northern Italy (GIUSSANI 1974, GIUSSANI & GRIMALDI 1975) and in Switzerland (RUFLI 1979, PONTON & GERDEAUX 1988, RUHLE 1988). Probably strong competition among different age groups of whitefish occurs there. Whitefish may be an important competitor for other fish feeding on zooplankton, however, there was no direct pressure of whitefish on small specimens of other fishes observed. During winter and early spring most of fishes starved or preyed on their own eggs and benthic organisms (*Pisidium*, Nematoda). Similarly, RUFLI (1979) reported that in Lake Biel during the spawning period of the "bondelle" form, the majority of pre-spawners and spawned "palée" prey on the eggs of the "bondelle" form. As in Lake Walenstadt (RUHLE 1988), most of the mature fish from Santa Croce Lake were found to have empty stomachs.

The growth of the Lake Santa Croce whitefish was similar to some slow-growing forms (brienzzlig, winter-brienzzlig, bondelle) from Swiss Alpine lakes (RUFLI 1978, KIRCHHOFER & TSCHUMI 1986, KIRCHHOFER 1995). Fast growth of whitefish during the first year of life is only possible if metabolic needs are compensated by adequate amounts of zooplankton. For older fish these amounts are probably too small and growth in weight is slow. This is a signal of poorer feeding conditions and strong competition for food. Older whitefish have to change their foraging habits to benthic organisms. They probably move from the pelagic feeding places to the deeper parts of the lake when the zooplankton is temporarily scarce. However, some

authors (RUFLI 1979, LAPPALAINEN & LEHTONEN 1996, LEHTONEN & NIEMELÄ 1998) suggest other possible reasons for whitefish growth differences in mountain lakes. They point out that differentiation in annual temperature sums or the higher altitude of the lake above sea level cause a notable change in growth rate of whitefish.

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