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Trophic Niches, Trophic Positions, and Niche Overlaps between Non-Native and Native Fish Species in a Subalpine Lake

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Received: 3 November 2020; Accepted: 7 December 2020; Published: 10 December 2020



Abstract: In the last century, Italian freshwater ecosystems have been invaded by several non-native fish species. In the subalpine Lake Mergozzo (northern Italy), several recently introduced non-native species dramatically expanded their populations. We used carbon and nitrogen stable isotopes to describe the isotopic niches and trophic positions of native and non-native fish species in Lake Mergozzo. We evaluated their trophic niches, trophic diversity, trophic redundancy and trophic evenness utilizing isotopic niche metrics, and estimated asymmetrical niche overlaps. The trophic traits of non-native fish species and *Perca fluviatilis* clearly define them as trophic generalists, in terms of among-individual variability of their isotopic niches. The historical increase in abundance of fish non-native species in this lake, their dominance by numbers and biomass within the assemblage, and their broad asymmetrical niche overlaps suggest that their higher degree of trophic generalism might have been one of the key factors that have promoted the invasion of the recipient community.

Keywords: biological invasions; invasive species; stable isotopes; isotopic niche; food webs; PASE electrofishing; deep lakes; biodiversity; protected areas

1. Introduction

In both terrestrial and aquatic ecosystems, the structural change determined by introduced alien species that become established in a recipient community can have severe ecological and economic impacts [1–3]. The introduction of alien species with unknown invasive potential is a global phenomenon [4,5] that can affect structure, biodiversity and ecosystem functioning [6–11], and alter the evolutionary pathways of populations and communities [12]. One way to characterize biological invasions is to quantify their effects on the recipient food webs, as the result of trophic and non-trophic interactions between native (hereinafter, NS) and non-native species (hereinafter, NNS) [13–16]. Successful NNS invaders frequently have relatively wide trophic niches, or have trophic niches dissimilar than other species in the receiving community (‘vacant niche hypothesis’ [17]; but see [18]), thus being able to use trophic resources unexploited by the NS community [19–21]. Such traits can facilitate the integration of NNS into the food web, increasing both their invasive potential [16], and their resistance to fluctuations in resource availability [22]. Alternatively, NNSs’ trophic niches may overlap with those of NS and compete for the same limiting resources [23–25], with a range of possible outcome scenarios, depending on the synergistic effect of factors such as spatiotemporal variability, presence of predators, number of resources, and environmental conditions [13].

Stable isotope analysis (SIA) has been increasingly used to measure isotopic niches [26], quantify food-web structures and functioning [27,28], and evaluate the impacts of species introductions on the trophic structure of the recipient communities [29–31]. Several metrics and methodological tools were also developed to describe the isotopic niche structure of a group of organisms [32], statistically comparing isotopic niches within and among species and communities [33,34].

In freshwater ecosystems, fishes are frequently introduced alien species, and risk assessments of such introductions are major environmental challenges [5,35–41]. The introduction of fish NNS can drastically change freshwater food-web structures [42,43], and even induce trophic cascades or alter environmental conditions, affecting the whole community [7,8,44–46]. SIA has been increasingly used to investigate these effects [31,47–50].

Lake Mergozzo is a small subalpine lake in northern Italy. Mainly at the end of the 19th century, several fish NNS were introduced in many lakes of the region, which now frequently dominate these fish communities [51–56]. A recent study recorded five fish NNS introduced in this lake before 1950 [*Ameiurus melas* (Rafinesque, 1820), *Coregonus lavaretus* (Linnaeus, 1758), *Lepomis gibbosus* (Linnaeus, 1758), *Micropterus salmoides* (Lacepède, 1802), and *Salvelinus umbla* (Linnaeus, 1758)]; and four fish NNS introduced after 1950 [*Gymnocephalus cernua* (Linnaeus, 1758), *Rhodeus amarus* (Bloch, 1782), *Rutilus rutilus* (Linnaeus, 1758), and *Sander lucioperca* (Linnaeus, 1758)] [56]. According to some authors, *Perca fluviatilis* Linnaeus, 1758 and *Lota lota* (Linnaeus, 1758) might also have been introduced in northern Italy from the Danube system during the Roman Period or the Middle Ages [52,53]; we here consider these species as fish NS.

Within a short temporal frame (October and November 2016), we sampled 15 of the 27 recently recorded fish species in Lake Mergozzo [56], and a range of potential food items from alongshore and offshore environments, conducting SIA ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) to investigate their trophic ecology. Our objectives are to: (i) qualitatively describe and discuss the composition of the selected fish assemblage of Lake Mergozzo, with reference to changes in community structure since the introduction of some fish NNS; (ii) identify groups of potential trophic resources in alongshore and offshore environments and estimate fish trophic positions, discussing these results with known foraging habitats and food ecologies; (iii) estimate pairwise trophic niche overlaps among species; and (iv) discuss the contrasting trophic traits of fish NNS and NS in this assemblage, as possible factors facilitating invasive processes.

2. Materials and Methods

2.1. Study Site

The oligotrophic and relatively deep Lake Mergozzo (total phosphorous concentration $\sim 4 \mu\text{g L}^{-1}$, surface area 1.83 km^2 , maximum depth 73 m; [55]) is in the Ticino River basin (193 m above sea level), in north-western Italy ($45^{\circ}57' \text{ N}$, $8^{\circ}27' \text{ E}$; Figure 1). Historically, the lake was the western branch of the nearby Lake Maggiore. About five centuries ago, the two lakes were divided by the progradation of the Toce River delta, whose detritus conoid eventually reached the opposite bank of Lake Maggiore ([57], Figure 1c).

The two lakes are presently connected by a channel; water typically flows from Lake Mergozzo to Lake Maggiore, and in an opposite direction during floods. Lake Mergozzo is a monomictic water body fed by underwater springs, and has a water residence time of about 6 years. Its basin is mainly composed by granitic and metamorphic rocks. The littoral substrate consists of sand and cobble, with a minor fraction of boulder and gravel. Submerged macrophytes are scarce, and a tract of the lake's southern coast of $\sim 1 \text{ km}$ is colonized by a reed bed [*Phragmites australis* (Cav.) Trin. ex Steud.], near the confluence with the Fondo Toce channel. No commercial fisheries are active in the lake [56], which is included in the protected area 'Lago di Mergozzo and Montorfano' (code IT114000013), within the Natura 2000 European network for biodiversity protection, according to the "Habitat Directive" [58].

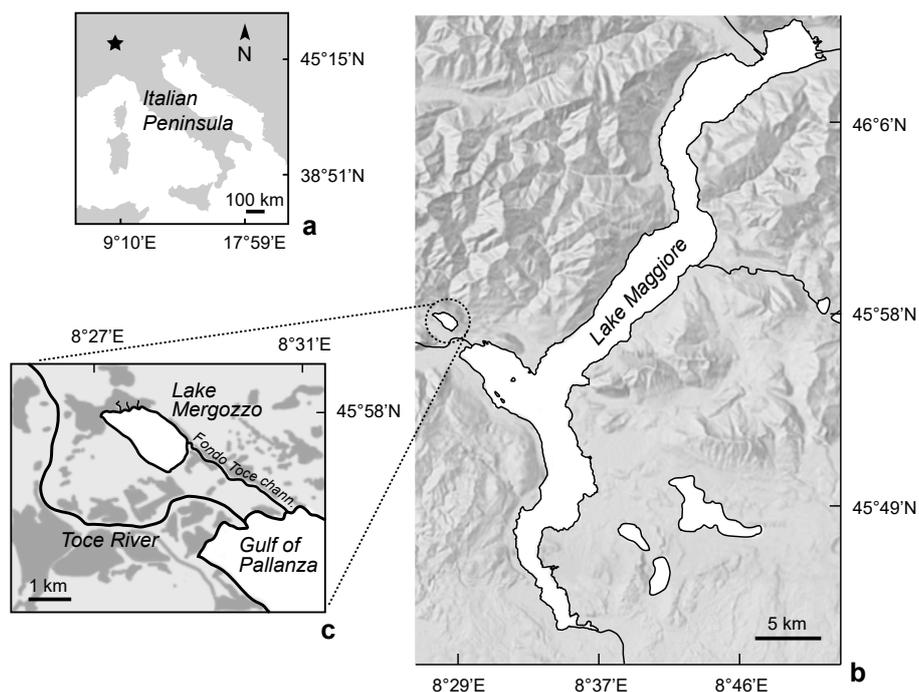


Figure 1. Lake Mergozzo, northern Italy. Inset (a): star = position of Lake Maggiore; inset (b): hydrography and topography of Lake Maggiore; inset (c): hydrography of Lake Mergozzo, dark grey = urban areas.

2.2. Zooplankton, Zoobenthos, and Fish Samples

Carbon sources of lacustrine food webs variably differ from alongshore and offshore environments, due to the differential influence of terrestrial inputs, thus defining littoral and pelagic food webs, respectively [59]. Due to the steep banks and very narrow littoral zone of the lake, we collected zooplankton offshore and zoobenthos alongshore, thus sampling potential fish trophic resources in both littoral and pelagic food webs [60]. Zooplankton was sampled offshore in October 2016, in a single site in the deepest zone of the lake, i.e., at a minimum distance of 500 m from the bank. Two zooplankton samples were collected, using two plankton samplers with a diameter of 59 cm and different filtering efficiency, i.e. with mesh size 450 μm (sample 'Zoo-450') and 850 μm (sample 'Zoo-850') [61,62]. Each net was hauled vertically 15 times in the 0–50 m layer (total volume filtered $\sim 410 \text{ m}^3$). Zoobenthos samples were collected alongshore in October 2016, by kick sampling along a tract of the shore of $\sim 100 \text{ m}$ and at a depth of 0–50 cm, using a hand net with 590 μm mesh size. Fish sample surveys were made on 25–27 October and 9, 10 November 2016. Fishes were sampled both offshore, using benthic and mesopelagic gill nets, and alongshore, using an electrofishing device. Each benthic net was 40 m long and 1.5 m high and was made of 16 panels of equal length, with mesh size 5.5–135 mm. Each mesopelagic gill net included two connected sets, A: 27.5 m long and 6 m high, composed of 11 panels with mesh size 8–55 mm knot to knot; and B: 40 m long and 6 m high, composed of 4 panels with mesh size 75 mm, 95 mm, 115 mm, and 135 mm, respectively. Gill nets were distributed following a depth-stratified sampling design, using a sonar (Echosounder, Lowrance HDS7, transducer 50/200 kHz, 300 W). Benthic nets were distributed in 7 strata, at depths of 1.5–2.9 m (A: $n = 7$), 3.0–5.9 m (B: $n = 7$), 6.0–11.9 m (C: $n = 6$), 12.0–19.9 m (D: $n = 6$), 20.0–34.9 m (E: $n = 6$), 35.0–50.0 m (F: $n = 4$), and $>50.0 \text{ m}$ (G: $n = 8$). Mesopelagic nets were distributed in 4 strata, at depth intervals of 2–7.9 m (A: $n = 4$), 8–13.9 m (B: $n = 4$), 14–19.9 m (C: $n = 4$), 20–26 m (D: $n = 4$). Fishes were sampled alongshore (0–1.49 m [63]) from a boat and during daytime with a built-in-frame EL64GII electrofishing device (Scubla Aquaculture, 7000 W, 600 V, DC current) with a copper cathode (width 2 cm, length 300 cm) and a steel ring anode (thickness 0.8 cm, diameter 50 cm). A point abundance sampling electrofishing

method was adopted, homogeneously distributing the sampling points (dips) along the coast (~1/80 of perimeter length per dip; PASE, number of dips = 74 [56,63]). All the collected items, including fishes that were euthanized with an overdose of an ethanol suspension of eugenol, were transferred to the laboratory in refrigerated plastic bags.

Fish total length (TL, cm) and wet weight were measured to the nearest mm and g, respectively. Fish species were taxonomically discriminated following [64–66]. The taxonomy of the genus *Coregonus* Linnaeus, 1758 is currently in a state of flux. The only species of Lake Mergozzo is morphologically similar to the *Coregonus* sp. ‘lavarello’ of the Lake Maggiore [51], possibly either a hybrid species originated from two species introduced from Swiss hatcheries at the end of the 19th century, or likely one of several species introduced in this lake at different times [64,67–70]). *Coregonus* sp. ‘bondella’, introduced in Lake Maggiore for the first time in 1950 [51,68,69], is apparently absent from Lake Mergozzo. For these reasons, we will refer to the species of Lake Mergozzo as *Coregonus* sp. The taxonomy of the genus *Salvelinus* Richardson, 1836 is also much debated. A species of this genus, often reported in the literature as *S. alpinus* (Linnaeus, 1758), has plausibly been introduced in northern Italy (Trentino Alto Adige) in the 16th century, then being frequently stocked and translocated in many basins throughout this region [71]. Fertilized eggs of *S. alpinus* imported from Munich were introduced in Lake Mergozzo by De Filippi in 1862, and in Lake Maggiore in 1910 [69]. We here refer to these populations as *Salvelinus umbla*, sensu [64]. For electrofishing, sample weights were not available and were inferred using length-weight regressions: *M. salmoides* [72]; *Alburnus arborella* (Bonaparte, 1841), *L. gibbosus*, *P. fluviatilis*, and *R. rutilus* [73]; *Esox cisalpinus* Bianco and Delmastro, 2011, and *Scardinius hesperidicus* Bonaparte, 1845 [74].

Fish abundance was expressed as relative biomass (%b); relative number (%n); biomass (number of individuals) per unit effort, i.e., BPUE (NPUE) = g (n.)/gill nets’ area, or number of electrofishing dips [g (n.) ind. m⁻² or g (n.) dip⁻¹]. To facilitate comparisons with the published literature, ‘dominant’ fish species in the different types of catch (benthic nets, mesopelagic nets, electrofishing) were defined as the species with abundance > 75 percentile of the biomass and number distributions, using both relative abundances and abundances per unit effort; ‘dominant’ fish species in the total catch were defined using relative abundances.

2.3. Stable Isotope Analysis and Trophic Positions

In the laboratory, all the invertebrates were washed to eliminate detritus; macroinvertebrates were also starved for 24 h to empty their guts. Two subsamples from the Zoo-450 and two from the Zoo-850 zooplankton samples ($n = 2$; ~1 mg of dry weight each) were used for stable isotope analyses. Other zooplankton and zoobenthos samples were examined under a dissection microscope, identifying animal organisms to the lowest taxonomic level. For macroinvertebrates, isotopes were analyzed from single individuals, i.e., *Corbicula fluminea* (O.F. Müller, 1774) (Mollusca, Bivalvia; $n = 4$), and ephemeropteran nymphs ($n = 5$). For each of the smaller invertebrate taxa (e.g., cladocerans, cyclopoids), several individuals were combined in two pooled samples, to obtain enough material ($n = 2$; ~1 mg of dry weight each taxon; i.e., ~70–700 individuals) [62]. For fishes, one sample of dorsal muscle was dissected from a subset of the captured individuals ($n = 1–9$) [75–77]. Both invertebrate and fish samples were stored at $-20\text{ }^{\circ}\text{C}$ and subsequently freeze-dried. Before further treatment, exoskeletons, valves, and shells of larger invertebrates were removed under a dissection microscope, while smaller organisms were acidified (HCl 1 M) to remove inorganic carbon, and then re-dried ($60\text{ }^{\circ}\text{C}$, 72 h) before analysis. Both invertebrate and fish samples were then finely powdered and homogenized using a ball mill (Fritsch Mini-Mill Pulverisette 23). Subsamples of 0.15–0.25 mg were transferred into cylindrical tin capsules (5 mm \times 9 mm, Säntis AnalyticalTM) and oven-dried for at least 24 h at $60\text{ }^{\circ}\text{C}$.

The isotopic composition of organic carbon and nitrogen was measured in the Stable Isotope Laboratory of the University of Ottawa (G.G. Hatch Lab; [62,76]), using a CE 1110 Elemental Analyser (Vario EL Cube, Elementar, Germany) and a Delta XP Plus Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Bremen, Germany) coupled to a ConFlo III interface (Thermo Fisher Scientific,

Bremen, Germany). Analytical precision was based on laboratory internal standards, and was usually <0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Isotope ratios were expressed as parts per thousand differences (‰) from a standard reference of PeeDee belemnite for carbon and of atmospheric N_2 for nitrogen, according to the equation:

$$(\delta^{13}\text{C}), (\delta^{15}\text{N}) = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000 \quad (1)$$

where R is the isotopic ratio: $^{13}\text{C}/^{12}\text{C}$, or $^{15}\text{N}/^{14}\text{N}$.

Lacustrine fish consumers typically acquire nitrogen from pelagic and littoral food webs [78], each characterized by a separate set of primary producers. A two-end member mixing model was thus implemented to estimate the fish trophic positions (TP), assuming no trophic fractionation of carbon and linear mixing [59]. The mean $\delta^{15}\text{N}$ signal of the three zooplankton primary consumers *Daphnia* sp. (Cladocera, Daphniidae), *Diaphanosoma brachyurum* (Liévin, 1848) (Cladocera, Sididae) and *Eubosmina longispina* (Leydig, 1860) (Cladocera, Bosminidae) was set as the baseline of the pelagic signal. The mean $\delta^{15}\text{N}$ signal of the benthic primary consumer *C. fluminea*, highly abundant in this system, was set as the baseline of the littoral signal [60]. Although the isotopic signatures of filter-feeding bivalves are generally considered a ‘pelagic’ signature [59,79,80], *C. fluminea* also consumes large amounts of interstitial detritus by pedal feeding [81], and well represents the benthic signature of the alongshore environment, where it was collected. The TP of each fish species in the two-source food web was thus estimated as [59]:

$$TP = \lambda + \left\{ \delta^{15}\text{N}_{\text{consumer}} - \left[\alpha \times \delta^{15}\text{N}_{\text{base-littoral}} + (1 - \alpha) \times \delta^{15}\text{N}_{\text{base-pelagic}} \right] \right\} / \Delta n \quad (2)$$

where λ is the standard trophic level of the baselines [59]; in this case, since our reference organisms are primary consumers, $\lambda = 2$ [60]. $\delta^{15}\text{N}_{\text{consumer}}$ is the mean isotopic signature of each fish species; Δn is the standard average increase in $\delta^{15}\text{N}$ (mean trophic fractionation) from a trophic level to the next one in aquatic food webs (~3.4‰; [59]); α is the proportion of nitrogen in the consumer (fish species) derived from one of the baseline food sources (base-littoral = littoral baseline; base-pelagic = pelagic baseline); assuming similar movements of carbon and nitrogen through the food web, α can be estimated using carbon isotopes as [59]:

$$\alpha = \left(\delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{base-pelagic}} \right) / \left(\delta^{13}\text{C}_{\text{base-littoral}} - \delta^{13}\text{C}_{\text{base-pelagic}} \right) \quad (3)$$

In both animals and plants, lipids are depleted in ^{13}C compared with whole organisms, introducing a bias in the $\delta^{13}\text{C}$ of lipid-rich tissues. The lipid content is positively and linearly correlated to C : N; therefore, the carbon isotopic signature of tissues with C : N > 3.5 (i.e., >5% lipid content for aquatic animals) was normalized as [82]:

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times (\text{C} : \text{N}) \quad (4)$$

2.4. Isotopic Niche Metrics, Asymmetrical Overlaps and Statistical Analyses

The isotopic niches of the studied fish species, i.e., the range of carbon and nitrogen signatures by each group of conspecific individuals, were used to evaluate the among-individual component of their realized trophic niches [32,34,83]. Therefore, for each group of conspecifics we calculated the following isotopic niche metrics (SIBER R package [33]; R v. 4.0.0 [84]): carbon range (CR), nitrogen range (NR), mean distance to centroid (CD), standard ellipse corrected area (SEA_c), standard ellipse Bayesian area (SEA_B), mean nearest neighbor distance (MNND) and its standard deviation (SDNND).

CR is the distance between the lowest and highest $\delta^{13}\text{C}$ values, evaluating the spectrum of trophic sources of each species; NR is the distance between the lowest and highest $\delta^{15}\text{N}$ values, broadly evaluating the range of trophic levels at which each species has been feeding [34]. CD is the average Euclidean distance between the isotopic signature ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ values) of each conspecific and its centroid, i.e., the point whose coordinates are the means of the respective coordinates of all

the points; CD measures the among-individual isotopic diversity of a species, evaluating its trophic diversity. Standard ellipses are in bivariate data the equivalent of SD in univariate data; the standard ellipse area (SEA) is measured as πab , where a and b are the ellipse's semi-major and semi-minor axes, respectively [33]. SEA_c are sample-size insensitive standard ellipse areas (for $n > 3$), i.e., the species' core isotopic niches calculated from the variance and covariance of bivariate isotopic data [34,85,86], evaluating the trophic niche area of a species:

$$SEA_c = SEA(n-1)(n-2) - 1 \quad (5)$$

where n = number of the species' individuals.

SEA_B (standard ellipse Bayesian areas) are obtained from standard ellipses constructed using Bayesian inference. The posterior values of the covariance matrix and means of the sampled isotopic signatures are estimated from a set of iterative draws (20,000 iterations) of a Markov chain Monte Carlo (MCMC) simulation, assigning vague normal priors to the means of the isotopic signatures, and a vague Inverse–Wishart prior to the covariance matrix [33]. We then used the Bayesian credible intervals (CI) of the SEA_B , to compare isotopic niche areas among fish species [34]. Within a species, MNND is the mean of the Euclidean distances to each individual signature's nearest neighbor, i.e., a measure of the density of the individual signatures' packing in the isotopic space. Species with individuals that are on average more isotopically similar, i.e., with higher isotopic redundancy, would have lower MNND values than species with individuals that are on average more dissimilar. SDNND is the standard deviation of the distances to each signature's nearest neighbor, i.e., a measure of the variability of the packing of individual signatures. Species with more even distributions of individual signatures, i.e., with higher isotopic evenness, would have lower SDNND values [32]. Isotopic redundancy and isotopic evenness evaluate trophic redundancy and trophic evenness, respectively.

Percentage pairwise asymmetrical overlaps at α levels 0.025, 0.975 CI, and mean asymmetrical overlaps were estimated between sets of 10 Bayesian niche regions, generated for each of two isotopic niche areas (nicheROVER R package, [87,88]). The asymmetrical overlap is a directional metric estimating the probability that an individual signature of Species A is found in the niche area (a) of Species B (p_{AB}); this probability is different than the probability that an individual signature of Species B is found in the niche area of Species A (p_{BA}), since A and B typically have different niche areas (a_A, a_B). Therefore, if $a_B > a_A$, then $p_{AB} > p_{BA}$. Within the fish subsample used for SIA, fish species with $s < 4$ were eliminated from the analyses of isotopic niche metrics and asymmetrical overlaps.

Mann–Whitney U tests were performed between fish NS and NNS for TP, isotopic niche metrics, and both biomass (BPUE) and number (NPUE) of fishes per unit effort (all sampling methods). These statistical tests were performed in PAST v.4© [89].

3. Results

3.1. Zooplankton, Zoobenthos, and Fish Samples

Zooplankton samples collected offshore contained *Bythotrephes longimanus* Leydig, 1860 (Cladocera, Cercopagididae); Cyclopoida (Copepoda); *Daphnia* sp.; *D. brachyurum*; *E. longispina*; and *Leptodora kindtii* (Focke, 1884) (Cladocera, Leptodoridae). Zoobenthos samples collected alongshore only contained ephemeropteran nymphs (Insecta, Ephemeroptera) and bivalves (*C. fluminea*).

Benthic fish nets collected 72% b and 74% n of the total catch; mesopelagic nets and electrofishing yielded smaller catches (7% b and 4% n ; 22% b and 22% n , respectively) (StotMET, Table 1). A total of 339 fishes were collected, including 7 fish NNS: *Coregonus* sp., *G. cernua*, *L. gibbosus*, *M. salmoides*, *R. rutilus*, *S. umbla*, and *S. lucioperca*; and 8 fish NS: *Alosa agone* (Scopoli, 1786), *A. arborella*, *Cottus gobio* Linnaeus, 1758, *E. cisalpinus*, *L. lota*, *P. fluviatilis*, *S. hesperidicus*, *Squalius squalus* (Bonaparte, 1837) (Table 1). Fish NNS make up most of the total fish sample, both in biomass (23.8·103 g, 73% b) and numbers ($n = 244$, 72% n) (Table 1).

Table 1. Fish catches sampled in Lake Mergozzo in 2016. TL = total length; Fish NNS = fish non-native species; Fish NS = fish native species; RB*b* (*n*) = biomass (number) collected with benthic gill nets; RP*b* (*n*) = biomass (number) collected with mesopelagic gill nets; EF*b* (*n*) = biomass (number) collected with electrofishing; RB%*b* (%*n*), RP%*b* (%*n*), EF%*b* (%*n*) = percentage biomass (number) collected with the different sampling methods, relative to the biomass (number) of all the species collected with the corresponding sampling method; TOT*b* (TOT*n*) = total biomass (number) collected with all sampling methods; TOT%*b* (TOT%*n*) = percentage total biomass (number) relative to the total sample; StotMET = sub-totals of each type of sampling method, and percentages relative to the total sample; in bold: values > 75 percentile of the fish NNS and fish NS corresponding distributions (‘dominant’ species by abundance). See Appendix A, Table A1 for mean TL, and mean BPUE, NPUE.

Species	Common Name	TL (cm)	Biomass							Number of Fish Individuals								
		Range	RB <i>b</i>	RB% <i>b</i>	RP <i>b</i>	RP% <i>b</i>	EF <i>b</i>	EF% <i>b</i>	TOT <i>b</i>	TOT% <i>b</i>	RB <i>n</i>	RB% <i>n</i>	RP <i>n</i>	RP% <i>n</i>	EF <i>n</i>	EF% <i>n</i>	TOT <i>n</i>	TOT% <i>n</i>
Fish NNS §																		
<i>Coregonus</i> sp.	European whitefish	8.4–43.6	29	0.1	2024	93.4	0	0.0	2053	6.3	3	1.2	4	30.8	0	0.0	7	2.1
<i>G. cernua</i>	Ruffe	5.2–17.8	751	3.2	0	0.0	0	0.0	751	2.3	24	9.6	0	0.0	0	0.0	24	7.1
<i>L. gibbosus</i>	Pumpkinseed	4.6–25.0	537	2.3	0	0.0	1380	19.3	1917	5.9	12	4.8	0	0.0	31	40.8	43	12.7
<i>M. salmoides</i>	Largemouth bass	5.4–30.5	537	2.3	0	0.0	2234	31.2	2771	8.5	5	2.0	0	0.0	25	32.9	30	8.8
<i>R. rutilus</i>	Roach	5.8–33.0	10,657	45.7	22	1.0	54	0.8	10,733	32.9	127	50.8	1	7.7	4	5.3	132	38.9
<i>S. umbla</i>	Char	16.3–28.3	520	2.2	0	0.0	0	0.0	520	1.6	5	2.0	0	0.0	0	0.0	5	1.5
<i>S. lucioperca</i>	Pikeperch	37.4–73.0	5080	21.8	0	0.0	0	0.0	5080	15.6	3	1.2	0	0.0	0	0.0	3	0.9
Fish NS																		
<i>A. agone</i>	Shad	10.7–13.0	0	0.0	121	5.6	0	0.0	121	0.4	0	0.0	8	61.5	0	0.0	8	2.4
<i>A. arborella</i>	Bleak	5.0–8.8	19	0.1	0	0.0	4	0.1	23	0.1	5	2.0	0	0.0	2	2.6	7	2.1
<i>C. gobio</i>	Bullhead	4.0–9.7	46	0.2	0	0.0	0	0.0	46	0.1	10	4.0	0	0.0	0	0.0	10	2.9
<i>E. cisalpinus</i>	Southern pike	56.0, 65.0	0	0.0	0	0.0	2975	41.6	2975	9.1	0	0.0	0	0.0	2	2.6	2	0.6
<i>L. lota</i>	Burbot	31.3	161	0.7	0	0.0	0	0.0	161	0.5	1	0.4	0	0.0	0	0.0	1	0.3
<i>P. fluviatilis</i>	Perch	6.5–41.1	3554	15.2	0	0.0	297	4.2	3851	11.8	39	15.6	0	0.0	9	11.8	48	14.2
<i>S. hesperidicus</i>	Italian rudd	15.1–33.0	1304	5.6	0	0.0	205	2.9	1509	4.6	15	6.0	0	0.0	3	3.9	18	5.3
<i>S. squalus</i>	Italian chub	24.6	144	0.6	0	0.0	0	0.0	144	0.4	1	0.4	0	0.0	0	0.0	1	0.3
StotMET			23,339	71.5	2167	6.6	7149	21.9	32,655	100.0	250	73.7	13	3.8	76	22.4	339	100.0

§ biomass of fish NNS = 23,825 g (relative to total biomass = 73.0%*b*). Number of fish NNS = 244 (relative to total number = 72.0%*n*).

Both mean BPUE and NPUE of fish-NNS electrofishing and benthic catches are significantly larger than those of fish NS (Mann–Whitney U tests, $U = 48,524\text{--}145,596, p < 0.001$); the average electrofishing (benthic) catch per unit effort of fish NNS was 1.2 (4) times heavier and 4 (3) times more numerous than that of fish NS (Appendix A, Table A1). Nine fish species dominate different catches. The total catch is dominated in relative biomass by *R. rutilus*, *S. lucioperca*, *P. fluviatilis*, and *E. cisalpinus* (in descending order); and in relative number by *R. rutilus*, *P. fluviatilis*, *L. gibbosus*, and *M. salmoides* (Table 1). Considering both relative abundance and mean catches per unit efforts (BPUE, NPUE), benthic catches are dominated in biomass by *R. rutilus*, *S. lucioperca*, *P. fluviatilis*, and *S. hesperidicus*; and in number by *R. rutilus*, *P. fluviatilis*, *G. cernua*, and *S. hesperidicus*. Mesopelagic catches are dominated in biomass by *Coregonus* sp., *A. agone*, and *R. rutilus*, and in number by *A. agone*, *Coregonus* sp., and *R. rutilus*. Electrofishing catches are dominated in biomass by *E. cisalpinus*, *M. salmoides*, *L. gibbosus*, and *P. fluviatilis*; and in number by *L. gibbosus*, *M. salmoides*, *P. fluviatilis*, and *R. rutilus* (Table 1, Appendix A, Table A1). The only species recorded with all types of sampling methods was *R. rutilus* (Table 1).

The fish depth distribution (relative abundances by depth; Figure 2, Appendix A, Figure A2) provides an overview of the habitat distribution of the fishes sampled alongshore (electrofishing sample); offshore, above the bottom (benthic nets sample); and offshore, in the water column (mesopelagic nets sample).

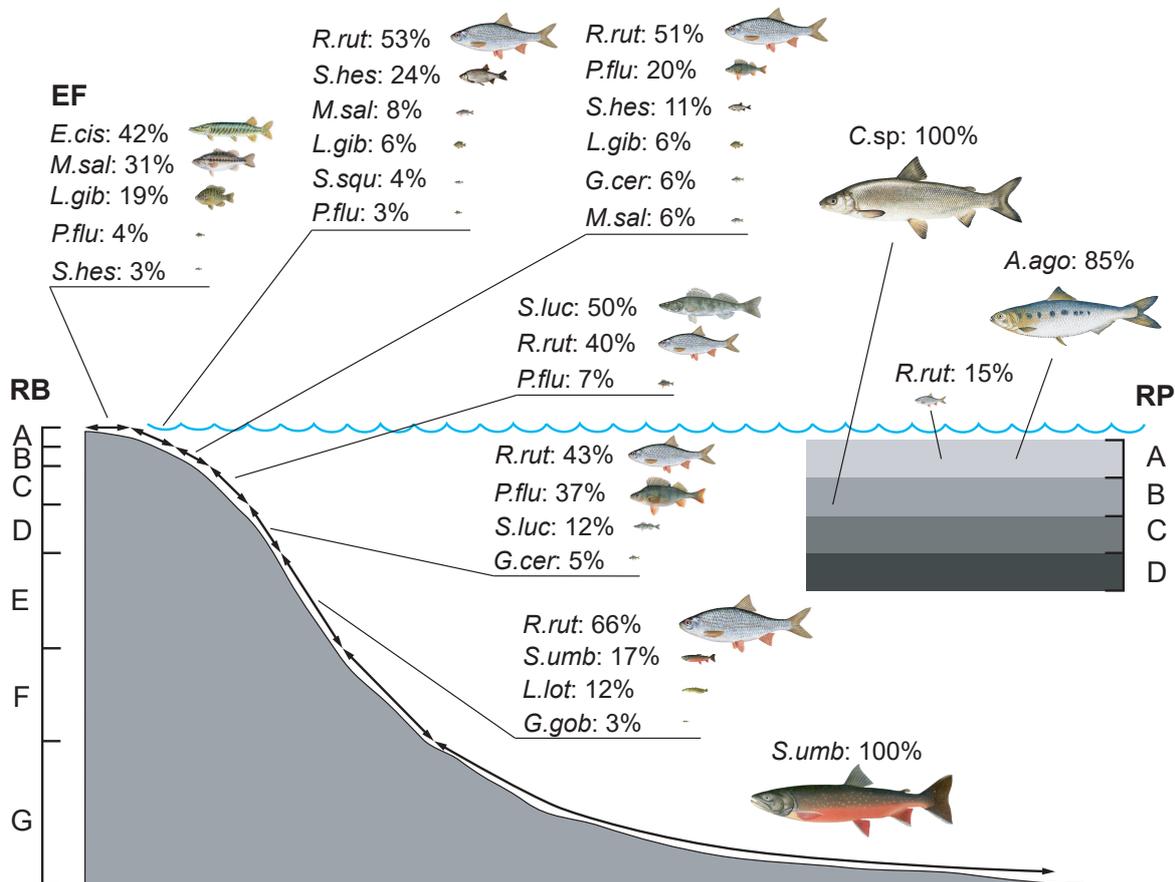


Figure 2. Fish depth distribution; fish relative biomass by depth stratum is indicated for the fishes collected (1) offshore above the bottom (RB = benthic nets, strata A–G), (2) offshore within the water column (RP = mesopelagic nets, strata A–D), and (3) alongshore (EF = electrofishing). Fish images (total length) are proportional to their relative biomass in each depth stratum; only fish species with relative biomass >3% are illustrated. See Figure 3 for species abbreviations.

Table 2. Isotopic signatures of the potential trophic resources of the studied fishes; $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$: mean \pm SD‰; when the number of subsamples < 3, values are reported; AS = alongshore sample (zoobenthos), OS = offshore sample (zooplankton); Zoo-450 = zooplankton sample \geq 450 μm ; Zoo-850 = zooplankton sample \geq 850 μm .

Species	Sample	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Corbicula fluminea</i>	AS	-12.35 ± 1.35	-2.84 ± 1.18
<i>Ephemeroptera</i>	AS	-19.62 ± 0.30	4.01 ± 0.25
<i>Bythotrephes longimanus</i>	OS	$-28.43, -28.29$	3.77, 3.59
<i>Cyclopoida</i>	OS	$-28.73, -28.47$	6.88, 6.54
<i>Daphnia sp.</i>	OS	-31.08	-1.80
<i>Diaphanosoma brachyurum</i>	OS	$-29.47, -29.52$	$-2.64, -2.84$
<i>Eubosmina longispina</i>	OS	$-30.39, -30.37$	$-2.27, -2.26$
<i>Leptodora kindtii</i>	OS	$-28.61, -28.47$	2.45, 2.99
Zoo-450	OS	$-29.33, -29.69$	$-0.07, -1.20$
Zoo-850	OS	$-28.82, -28.63$	3.57, 3.67

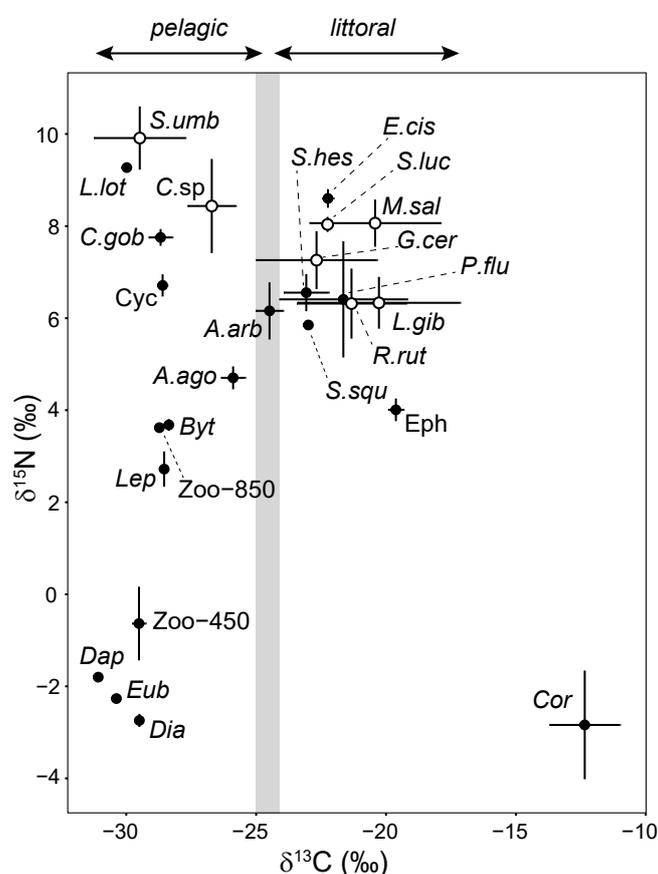


Figure 3. Isotopic biplot illustrating $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of the analyzed organisms (points = means; error bars = standard deviations); grey band: arbitrary 1‰ interval along the $\delta^{13}\text{C}$ axis, approximately separating the pelagic and littoral food webs; white dots: fish non-native species (NNS); black dots: fish native species (NS) and potential food sources. *A.ago*: *Alosa agone*; *A.arb*: *Alburnus arborella*; *Byt*: *Bythotrephes longimanus*; *C.gob*: *Cottus gobio*; *Cor*: *Corbicula fluminea*; *C.sp*: *Coregonus sp.*; *Cyc*: *Cyclopoida*; *Dap*: *Daphnia sp.*; *Dia*: *Diaphanosoma brachyurum*; *E.cis*: *Esox cisalpinus*; *Eph*: *Ephemeroptera*; *Eub*: *Eubosmina longispina*; *G.cer*: *Gymnocephalus cernua*; *Lep*: *Leptodora kindtii*; *L.gib*: *Lepomis gibbosus*; *L.lot*: *Lota*; *M.sal*: *Micropterus salmoides*; *P.flu*: *Perca fluviatilis*; *R.rut*: *Rutilus*; *S.umb*: *Salvelinus umbla*; *S.hes*: *Scardinius hesperidicus*; *S.luc*: *Sander lucioperca*; *S.squ*: *Squalius squalus*; Zoo-450: zooplankton sample, 450 μm ; Zoo-850: zooplankton sample, 850 μm . See also Tables 2 and 3.

Table 3. Isotopic signatures and trophic positions (TP) of the fish species; ss = number of subsamples used for SIA; $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ = mean \pm SD ‰; when ss < 3, values are reported.

Species	ss	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	TP
Fish NNS				
<i>Coregonus sp.</i>	4	8.17 \pm 1.26	−26.56 \pm 0.99	4.94
<i>G. cernua</i>	9	7.26 \pm 0.63	−22.68 \pm 2.32	5.01
<i>L. gibbosus</i>	5	6.33 \pm 0.56	−20.27 \pm 3.13	4.78
<i>M. salmoides</i>	5	8.06 \pm 0.51	−20.42 \pm 2.52	5.22
<i>R. rutilus</i>	8	6.32 \pm 0.76	−21.33 \pm 2.11	4.59
<i>S. umbla</i>	4	9.90 \pm 0.69	−29.48 \pm 1.76	5.75
<i>S. lucioperca</i>	2	7.92, 8.15	−22.24, −22.26	4.92
Fish NS				
<i>A. agone</i>	4	4.49 \pm 0.39	−26.06 \pm 0.22	4.12
<i>A. arborella</i>	4	6.15 \pm 0.62	−24.48 \pm 0.52	2.83
<i>C. gobio</i>	4	7.75 \pm 0.18	−28.68 \pm 0.46	3.29
<i>E. cisalpinus</i>	2	8.46, 8.75	−22.00, −22.30	5.06
<i>L. lota</i>	1	9.67	−29.98	5.15
<i>P. fluviatilis</i>	7	6.40 \pm 1.26	−21.64 \pm 2.46	4.95
<i>S. hesperidicus</i>	5	6.55 \pm 0.40	−23.07 \pm 0.86	4.61
<i>S. squalus</i>	1	5.85	−22.99	4.11

3.2. Stable Isotope Analysis and Trophic Positions

Mean $\delta^{13}\text{C}$ values of the potential trophic sources range from −31.1‰ of *Daphnia sp.* to −12.3‰ of *C. fluminea*; mean $\delta^{15}\text{N}$ values range from −2.8‰ of *C. fluminea* to 6.7‰ of Cyclopoida (Table 2).

Mean $\delta^{13}\text{C}$ values of the fish species range from −29.5‰ of *S. umbla* to −20.3‰ of *L. gibbosus*; mean $\delta^{15}\text{N}$ values range from 4.5‰ of *A. agone* to 9.9‰ of *S. umbla* (Table 3). Along the $\delta^{13}\text{C}$ axis, Zoo-450, Zoo-850, cladocerans and copepods are closer to the pelagic baseline (*Daphnia sp.*, plus *D. brachyurum*, plus *E. longispina*), while ephemeropterans are closer to the littoral baseline (*C. fluminea*) (Section 2.3; Figure 3).

Therefore, potential fish trophic resources form two isotopically distinct groups: those collected in the alongshore environment, with enriched carbon signatures ($\delta^{13}\text{C} > -20\text{‰}$; group A: littoral food web); and those collected in the offshore environment, with depleted carbon signatures ($\delta^{13}\text{C} < -28\text{‰}$; group B: pelagic food web) (Table 2; Figure 3). Along the $\delta^{13}\text{C}$ axis, the signatures of group A are closer to those of fishes with relatively enriched carbon signatures, that likely fed in the littoral food web (*L. gibbosus*, *M. salmoides*, *R. rutilus*, *P. fluviatilis*, *E. cisalpinus*, *S. lucioperca*, *S. squalus*, and *S. hesperidicus*, in order of decreasing $\delta^{13}\text{C}$; mean $\delta^{13}\text{C}$ −20.3‰ to −23.1‰). The signatures of group B are closer to those of fish species with relatively depleted carbon signatures, that likely fed in the pelagic food web (*A. agone*, *Coregonus sp.*, *C. gobio*, *S. umbla*, and *L. lota*; mean $\delta^{13}\text{C}$ −26.1‰ to −30.0‰) (Table 3; Figure 3). *G. cernua* and *A. arborella* apparently fed in both food webs (mean $\delta^{13}\text{C}$ −22.7‰, −24.5‰, respectively). Mean $\delta^{13}\text{C}$ signatures of fish NNS and NS are broadly overlapped, ranging from −29.5‰ (*S. umbla*) to −20.3‰ (*L. gibbosus*) in the former, and from −30.0‰ (*L. lota*) to −21.6‰ (*P. fluviatilis*) in the latter (Table 3; Figure 3).

Mean $\delta^{15}\text{N}$ signatures of potential fish food sources define two distinct groups: (i) ephemeropterans, the pooled larger zooplankton sample (Zoo-850), and the zooplankters *B. longimanus*, Cyclopoida, plus *L. kindtii*, with more enriched $\delta^{15}\text{N}$ signatures; and (ii) *C. fluminea*, the pooled smaller zooplankton sample (Zoo-450), and the zooplankters *E. longispina*, *Daphnia sp.*, plus *D. brachyurum*, with more depleted $\delta^{15}\text{N}$ signatures (Table 2; Figure 3). Mean $\delta^{15}\text{N}$ signatures of fish NNS and NS are broadly overlapped, ranging from 6.3‰ (*R. rutilus*) to 9.9‰ (*S. umbla*) in the former, and from 4.5‰ (*A. agone*) to 9.7‰ (*L. lota*) in the latter (Table 3; Figure 3). The fish trophic positions (TP; Table 3; Appendix A, Figure A1) range from 2.8 of *A. arborella* to 5.7 of *S. umbla*. Fish NNS have non-significantly higher mean TP than fish NS (TP = 5.03 \pm 0.37 SD and TP = 4.27 \pm 0.85 SD, respectively; Mann–Whitney

test, $U = 15$, $p = 0.15$; Table 3; Appendix A, Figure A1). If TP values are divided into three equal intervals, fish NNS include six species with higher TP ($TP \geq 4.80$: *S. umbla*, *M. salmoides*, *G. cernua*, *Coregonus* sp., and *S. lucioperca*, in descending order), and two species with intermediate TP ($4.80 > TP > 3.80$: *L. gibbosus*, *R. rutilus*). Fish NS include three species with higher TP (*L. lota*, *E. cisalpinus*, *P. fluviatilis*), three species with intermediate TP (*S. hesperidicus*, *A. agone*, *S. squalus*), and two species with lower TP ($TP \leq 3.80$: *C. gobio*, *A. arborella*).

3.3. Isotopic Niche Metrics and Overlaps

Fish NNS have significantly higher values of carbon range (CR), mean nearest neighbor distance (MNND) and SD of the nearest neighbor distance (SDNND) than fish NS; and non-significantly higher values of NR, CD, SEA_C and SEA_B (Table 4, Appendix A, Figure A1). The fish NS *P. fluviatilis* has values of the isotopic metrics closer to average fish NNS values (except SDNND; Appendix A, Figure A1), exhibiting the widest nitrogen range (NR), the highest average trophic diversity (CD), and the largest niche areas (SEA_C , SEA_B) of all the fish species (Table 4, Appendix A, Figure A1).

Table 4. Isotopic niche metrics for non-native and native fish species (Fish NNS, Fish NS, respectively): *ss* = number of subsamples used for SIA; CR = carbon range (‰); NR = nitrogen range (‰); CD = mean distance to centroid (‰); SEA_C = standard ellipse corrected area (‰²); SEA_B = standard ellipse Bayesian area (‰²); MNND = mean nearest neighbor distance (‰); SDNND = standard deviation of nearest neighbor distance (‰); Mann–Whitney U tests between fish NNS and NS: * $p < 0.05$; ** $p < 0.01$; fish species with <4 analyzed specimens are not included.

Species	<i>ss</i>	CR *	NR	CD	SEA_C	SEA_B	MNND *	SDNND **
Fish NNS								
<i>Coregonus</i> sp.	4	2.22	2.28	1.02	2.70	2.52	0.94	0.86
<i>G. cernua</i>	9	7.57	2.10	1.98	5.22	5.11	0.90	0.98
<i>L. gibbosus</i>	5	7.88	1.47	2.32	4.86	5.00	1.75	2.00
<i>M. salmoides</i>	5	6.08	1.36	1.85	3.99	4.32	1.48	1.88
<i>R. rutilus</i>	8	6.11	2.37	1.88	5.68	5.56	0.96	0.74
<i>S. umbla</i>	4	4.13	1.47	1.45	5.42	5.79	1.46	0.70
Mean values ± SD		5.67 ± 2.15	1.84 ± 0.46	1.75 ± 0.45	4.64 ± 1.12	4.72 ± 1.19	1.25 ± 0.36	1.19 ± 0.59
Fish NS								
<i>A. agone</i>	4	1.12	0.52	0.42	0.46	1.13	0.53	0.10
<i>A. arborella</i>	4	1.28	1.32	0.68	1.47	2.67	0.76	0.28
<i>C. gobio</i>	4	0.94	0.43	0.41	0.16	0.07	0.26	0.12
<i>P. fluviatilis</i>	7	6.23	3.50	2.40	11.69	12.34	1.20	0.63
<i>S. hesperidicus</i>	5	1.90	0.96	0.81	1.39	1.19	0.62	0.18
Mean values		2.29 ± 2.23	1.35 ± 1.26	0.94 ± 0.83	3.03 ± 4.87	3.48 ± 5.04	0.67 ± 0.35	0.26 ± 0.22

Pairwise mean asymmetrical overlaps provide conservative estimates of trophic niche overlaps ([87]; Table 5). The niches of *A. arborella*, *G. cernua*, *L. gibbosus*, *R. rutilus*, and *S. hesperidicus* are broadly overlapped (arbitrary cut-off $\geq 70\%$) with the niche of the fish NS *P. fluviatilis*; the niches of *A. arborella*, *L. gibbosus*, and *S. hesperidicus* are overlapped with that of *R. rutilus*; and the niche of *S. hesperidicus* is also overlapped with those of *G. cernua* and *L. gibbosus* (Table 5).

Table 5. Credible intervals (0.975, 0.025 CI) and means (Mean) of percentage asymmetrical overlaps (%) between isotopic niche regions of the analyzed fish sample; in each pairwise comparison within a row, the percentage indicates the proportion of the row’s species niche being asymmetrically overlapped with another species’ niche in a column; NA = not assigned; fish species with < 4 analyzed specimens are not included; in *bold*: mean overlaps ≥ 70% (arbitrary cut-off), and grand-mean overlaps of the corresponding species in columns. See Figure 3 for species abbreviations.

		<i>A.arb</i>	<i>A.ago</i>	<i>C.gob</i>	<i>C.sp</i>	<i>G.cer</i>	<i>L.gib</i>	<i>M.sal</i>	<i>P.flu</i>	<i>R.rut</i>	<i>S.umb</i>	<i>S.hes</i>
<i>A.arb</i>	0.025 CI	NA	0.00	0.00	0.00	8.12	0.00	0.00	29.22	5.55	0.00	2.34
	0.975 CI	NA	22.56	0.00	82.45	99.88	86.53	12.12	100.00	100.00	0.00	90.78
	Mean	NA	2.95	0.04	16.94	56.69	32.31	1.82	89.59	75.69	0.26	41.16
<i>A.ago</i>	0.025 CI	0.00	NA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.975 CI	84.87	NA	0.00	15.89	6.0	0.00	0.00	100.00	100.00	0.00	5.38
	Mean	11.08	NA	0.00	1.11	1.04	0.22	0.01	35.02	22.51	0.00	1.05
<i>C.gob</i>	0.025 CI	0.00	0.00	NA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.975 CI	0.00	0.00	NA	19.11	100.00	100.00	0.00	100.00	7.77	94.33	0.00
	Mean	0.05	0.00	NA	2.52	24.48	11.23	0.80	11.07	1.26	5.87	0.03
<i>C.sp</i>	0.025 CI	0.00	0.00	0.00	NA	3.64	0.00	0.00	0.00	0.00	0.00	0.00
	0.975 CI	22.98	22.34	1.13	NA	86.28	53.65	64.87	96.34	46.47	73.81	13.55
	Mean	4.03	0.10	0.08	NA	40.02	11.08	9.82	28.84	6.38	21.62	1.72
<i>G.cer</i>	0.025 CI	1.94	1.00	0.00	1.34	NA	11.89	4.54	56.44	21.32	0.00	7.52
	0.975 CI	39.76	39.56	1.16	27.43	NA	84.34	66.99	100.00	96.77	6.66	58.99
	Mean	11.15	0.05	0.25	10.39	NA	41.60	25.45	85.02	58.91	0.74	24.61
<i>L.gib</i>	0.025 CI	0.00	0.00	0.00	0.00	19.46	NA	0.00	48.55	37.44	0.00	5.03
	0.975 CI	25.8	25.56	1.34	17.34	96.02	NA	33.23	100.00	99.99	2.55	50.05
	Mean	6.39	0.01	0.16	4.07	58.87	NA	2.93	83.26	74.25	0.17	22.12
<i>M.sal</i>	0.025 CI	0.00	0.00	0.00	0.00	7.57	0.00	NA	12.39	0.00	0.00	0.00
	0.975 CI	11.28	0.00	0.00	12.33	97.33	25.71	NA	100.00	90.06	12.25	15.47
	Mean	0.83	0.00	0.01	2.00	57.29	2.66	NA	67.35	28.61	1.29	1.42
<i>P.flu</i>	0.025 CI	1.00	0.00	0.00	0.00	21.56	17.45	2.45	NA	31.27	0.00	6.65
	0.975 CI	27.43	4.65	0.00	16.56	85.33	68.44	40.89	NA	94.84	4.56	46.43
	Mean	8.05	0.58	0.06	3.69	52.23	38.95	14.70	NA	64.60	0.49	18.69
<i>R.rut</i>	0.025 CI	1.00	0.00	0.00	0.00	22.43	26.78	0.00	68.33	NA	0.00	6.77
	0.975 CI	31.85	3.76	0.00	14.88	95.44	86.54	36.55	100.00	NA	0.00	54.72
	Mean	8.72	0.66	0.02	2.25	59.54	54.76	9.58	91.85	NA	0.15	24.67

Table 5. Cont.

		<i>A.arb</i>	<i>A.ago</i>	<i>C.gob</i>	<i>C.sp</i>	<i>G.cer</i>	<i>L.gib</i>	<i>M.sal</i>	<i>P.flu</i>	<i>R.rut</i>	<i>S.umb</i>	<i>S.hes</i>
<i>S.umb</i>	0.025 CI	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	NA	0.00
	0.975 CI	0.00	0.00	1.44	51.22	10.55	3.79	36.72	24.44	0.00	NA	0.00
	Mean	0.02	0.00	0.09	15.19	1.15	0.25	2.24	2.29	0.06	NA	0.01
<i>S.hes</i>	0.025 CI	2.99	0.00	0.00	0.00	47.43	25.11	0.00	88.91	55.38	0.00	NA
	0.975 CI	89.64	1.85	0.00	34.33	100.00	100.00	29.45	100.00	100.00	0.00	NA
	Mean	26.47	0.18	0.01	3.97	88.08	73.53	3.34	98.61	93.84	0.18	NA
Grand-mean overlaps		7.68	0.18	0.08	5.02	42.52	26.03	7.65	55.92	38.94	3.39	10.48

Except *S. umbla*, *P. fluviatilis*, *R. rutilus*, *G. cernua*, and *L. gibbosus* are also the fish species with the largest isotopic niches (Figures 4 and 5); their signatures have the highest average probability to be contained in the niche of another species (grand means: 56%, 39%, 42%, and 26%, respectively; Table 5). In particular, four broad overlaps occurred between the larger niche of a fish NNS and the smaller niche of a fish NS (i.e., *R. rutilus* > *A. arborella*; *G. cernua*, *L. gibbosus*, *R. rutilus* > *S. hesperidicus*); two overlaps between two fish NS (i.e., *P. fluviatilis* > *A. arborella*, *S. hesperidicus*); one overlap between two fish NNS (*R. rutilus* > *L. gibbosus*); and three overlaps between the larger niche of a fish NS and the smaller niche of a fish NNS (*P. fluviatilis* > *G. cernua*, *L. gibbosus*, *R. rutilus*).

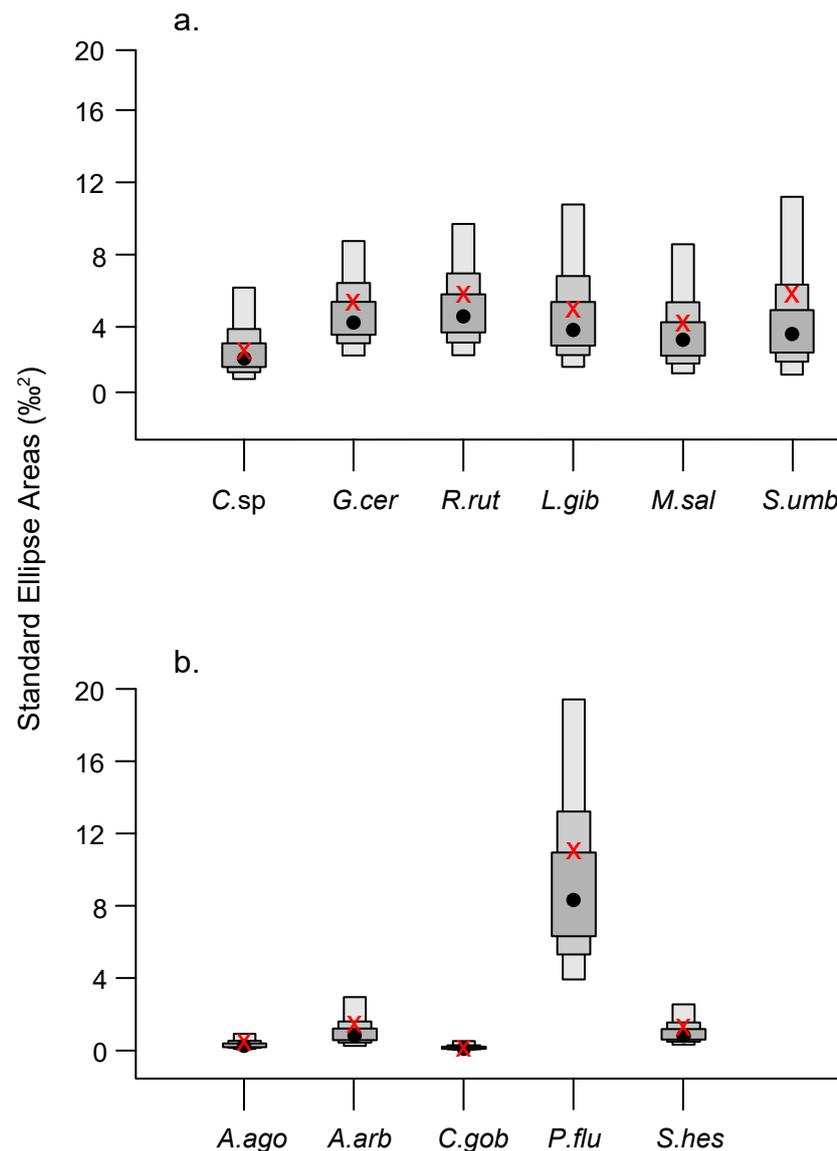


Figure 4. Density plots of Bayesian credible intervals (CI) for the standard ellipse areas of the analyzed fish sample of Lake Mergozzo, including fish non-native ((a) fish NNS) and native ((b) fish NS) species. Black circles: means of SEA_C, red x: means of SEA_B, grey boxes: SEA_B 0.50, 0.75 and 0.95 CI. See Figure 3 for species abbreviations; fish species with <3 analyzed specimens are not included.

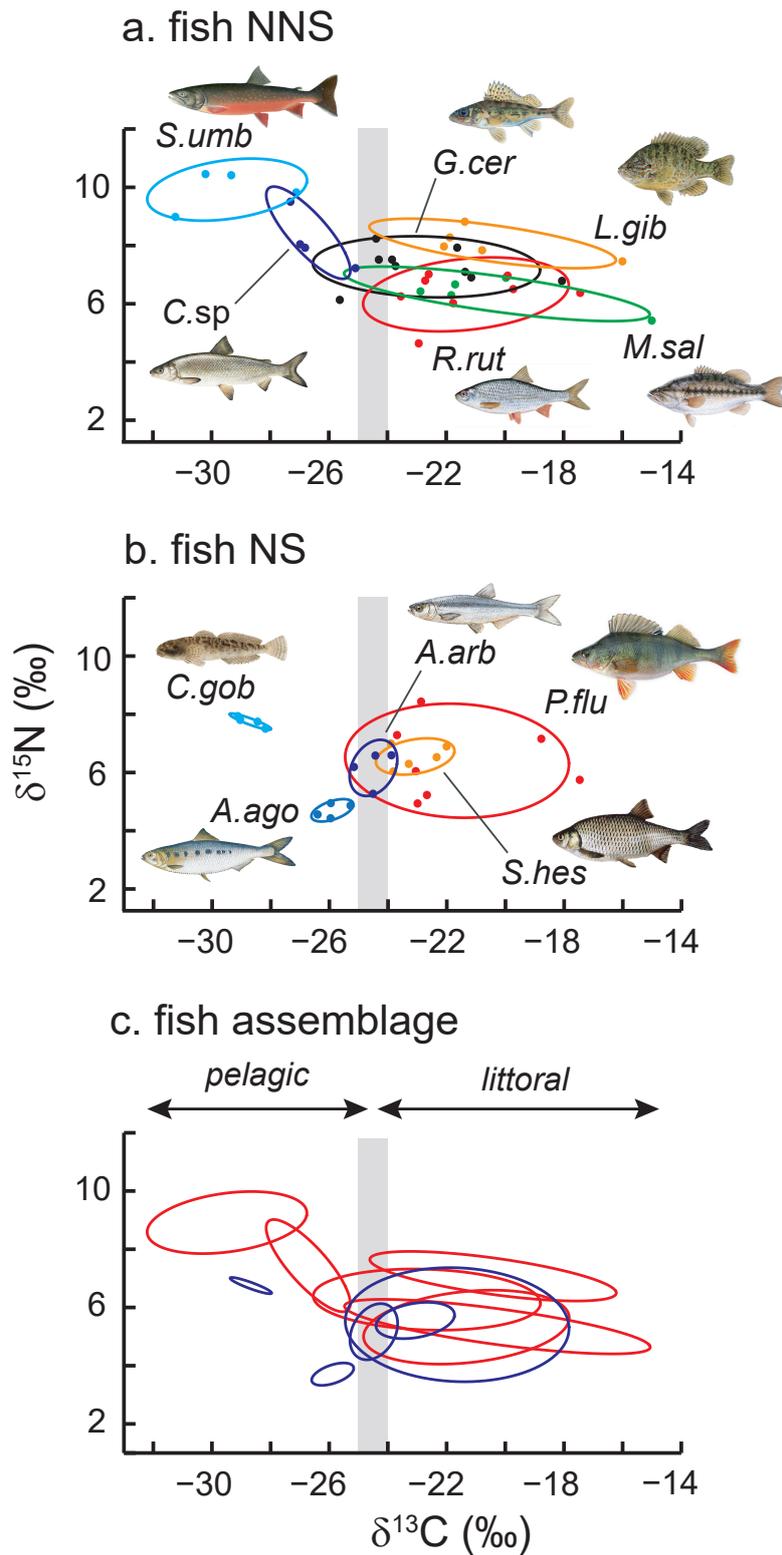


Figure 5. Tropho-chemical graphs of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures with standard ellipse areas (SEA_c) of the analyzed fish sample of Lake Mergozzo; (a) fish non-native species (NNS); (b) fish native species (NS); (c) whole fish assemblage (red ellipses: fish NNS, blue ellipses: fish NS); grey bands: arbitrary 1‰ interval along the $\delta^{13}\text{C}$ axis separating pelagic and littoral food webs (see Figure 3). See Figure 3 for species abbreviations; fish species with <4 analyzed specimens are not included.

4. Discussion

4.1. The Fish Community of Lake Mergozzo

The higher abundance of fish NNS in Lake Mergozzo clearly describes the remarkable change in community structure caused by fish introductions. In a study conducted in 2010 [56] fish NS, fish NNS introduced after 1950, and fish NNS introduced before 1950 made up 40%, 50%, and 10% of the total catch by biomass; and 30%, 61%, 9% by numbers, respectively. In our sample, fish NS, fish NNS introduced after 1950, and fish NNS introduced before 1950 made up 27%, 51%, 22% of the total catch by biomass; and 28%, 47%, 25% by numbers, respectively. This suggests a recent relative increase in the abundance of historically introduced fish NNS (e.g., *M. salmoides*, *L. gibbosus*). Among the fish NNS of this study, *G. cernua*, *R. rutilus* and *S. lucioperca* were first recorded in Lake Mergozzo in 2010 [55] following their appearance in the neighboring Lake Maggiore with a delay of 10–30 years (Volta, unpublished data; [54,90]). All other fish NNS were introduced before 1950, mostly in the 19th century [52,53,56].

In the 2010 survey by Volta et al. [56], the total catch was dominated in relative number by *R. rutilus*, *P. fluviatilis*, *S. hesperidicus*, *G. cernua*, and *M. salmoides*. In the first ichthyological survey of Lake Mergozzo, made only two decades before [51], *G. cernua*, *R. rutilus*, and *S. lucioperca* were not found, and the total catch was dominated in relative number by *S. hesperidicus*, *Rutilus rubilio* (Bonaparte, 1837) [= *Sarmarutilus rubilio* (Bonaparte, 1837)], *P. fluviatilis*, and *Coregonus* species. Within the limitations of sampling biases and different sampling methods, qualitative comparisons between the 1994 survey and both our dataset and the 2010 survey suggest that changes in the relative species abundance in Lake Mergozzo were dramatic. This scenario mirrors other lakes and rivers in northern Italy, once more indicating the rising tide of warm-water tolerant and omnivorous species in the Po River Basin [56,91–94].

4.2. Foraging Habitats and Food Ecology

The large difference in $\delta^{13}\text{C}$ signatures between potential trophic resources sampled alongshore and offshore supports the distinction between a littoral and a pelagic food webs, spatially separated in alongshore and offshore environments, respectively [59,78]. The isotopic signatures of both fish NS and NNS, and of their potential food sources are distributed along this whole $\delta^{13}\text{C}$ gradient. In each environment, isotopic signatures evaluated foraging habitats throughout the entire water column; consistently, carbon signatures suggest that several pelagic (*A. agone*), demersal (*Coregonus* sp., *S. umbla*) and benthic fishes (*C. gobio*, *L. lota*) mainly foraged offshore in Lake Mergozzo, in the pelagic food web. The carbon signatures of other demersal species (e.g., *L. gibbosus*, *M. salmoides*, *R. rutilus*) suggest that these mainly foraged alongshore, along the narrow littoral zone of the lake's steep banks and in the reed bed along its southern bank, in the littoral food web. The epipelagic *A. arborella* and the demersal *G. cernua*, known to perform feeding migrations between habitats at different depths, apparently foraged in both food webs (Appendix A, Table A2). These patterns are consistent with the habitat distribution inferred by the depth distribution of the fish samples, both alongshore and offshore, above the bottom and in the water column.

The $\delta^{15}\text{N}$ signatures of potential fish food sources mirror the known food ecology of the studied fishes. Within the alongshore sample, detritivore and predatory ephemeropteran nymphs have more enriched $\delta^{15}\text{N}$ signatures than the detritus- and filter-feeder *C. fluminea*. Within the offshore sample, the two distinct trophic groups described along the $\delta^{15}\text{N}$ axis clearly include organisms at different trophic levels, i.e., (i) the predatory *B. longimanus*, Cyclopoida, *L. kindtii*, and the pooled sample containing larger zooplankton, with a larger proportion of secondary consumers (Zoo-850); and (ii) the primary consumers *E. longispina*, *Daphnia* sp., *D. brachyurum*, and the pooled sample containing smaller zooplankton, with a larger proportion of primary consumers (Zoo-450). The $\delta^{15}\text{N}$ and computed TP values of the fish species are broadly consistent with their food ecology, taking also into consideration their size ranges (Table 1, Appendix A, Tables A1 and A2). Species with higher TP values include large

piscivores (*S. lucioperca*, *E. cisalpinus*); a flexible predator feeding on fishes and macroinvertebrates (*L. lota*); ontogenetic generalists shifting from zooplanktivory to zoobenthivory to piscivory (*P. fluviatilis*, *M. salmoides*, *S. umbla*); flexible predators ontogenetically shifting from zooplanktivory to zoobenthivory (*Coregonus* sp., *L. gibbosus*); and a zoobenthivore (*G. cernua*). Species with intermediate TP values include a flexible omnivore ontogenetically and seasonally shifting from zooplanktivory to detritivory, zoobenthivory, and algivory (*R. rutilus*); an omnivore ontogenetically shifting from zooplanktivory to herbivory in plant-rich littoral habitats (*S. hesperidicus*); a generalist omnivore feeding on aquatic and terrestrial plants, zoobenthos, and terrestrial epineuston (*S. squalus*); and a zooplanktivore (*A. agone*). Species with lower TP values include a generalist zoobenthivore (*C. gobio*), and a zooplanktivore feeding also on algae (*A. arborella*) (Appendix A, Table A2).

4.3. Trophic Generalism and Niche Overlaps

Two groups of individuals (populations, species) can be defined as more or less ‘generalist’ by comparing either the among-individual variability of their trophic niches, or their within-individual variability, or both. We evaluated the among-individual component of the realized trophic niches of different species, by measuring their isotopic niches and metrics. Several generalist species have a low within-individual and high among-individual diet variation, i.e., they consist of specialists using different resources. Such generalist species typically have a wider spectrum of trophic resources, feed at multiple trophic levels, have lower trophic redundancy, higher trophic evenness, higher trophic diversity, and larger trophic niches. Such traits can boost the invasive potential of introduced species [13,79,95] and reduce their risk of extinction or extirpation in the face of ecological change, by facilitating adaptation in conditions unlikely to have existed in their evolutionary past [96].

The fish NNS of Lake Mergozzo have a significantly higher among-individuals variability of their isotopic niches, using a significantly wider spectrum of trophic resources (CR) and having a significantly lower trophic redundancy (MNND) than fish NS; however, they also have a significantly lower trophic evenness (SDNND). When the fish NS *P. fluviatilis* is not included in this comparison, fish NNS also have a significantly wider range of utilized trophic levels (NR), higher trophic diversity (CD), and larger trophic niches (SEA_c , SEA_B) than fish NS (Mann–Whitney tests, $U = 0.0–0.1$, $p < 0.05$). An exception among fish NS in Lake Mergozzo, *P. fluviatilis* has higher values of CR, MNND, NR, CR, CD, SEA_c and SEA_B than both fish NS and fish NNS, and also has a lower SDNND than fish NNS (Appendix A, Figure A1). This trait would apparently allow this species to more evenly distribute the among-individual diet variation within its population, thus decreasing intraspecific trophic competition and adaptively increasing individual foraging efficiency. The trophic generalism of *P. fluviatilis* has been frequently reported in the literature [97–100], and this trait may have facilitated its wide distribution and high abundance in many European lakes [101], as well as its bioinvasions of several freshwater ecosystems in New Zealand, Australia, and South Africa [102].

The observed higher degree of trophic generalism of only one fish NS (*P. fluviatilis*) and of all fish NNS in Lake Mergozzo, i.e., the higher among-individual variability of their realized trophic niches measured by the isotopic metrics, appears to be caused by non-random mechanisms. Investigations on *P. fluviatilis* and some lacustrine communities showed both an inverse relationship between phenotypic divergence and trophic position, and a higher among-individual diet variation at intermediate trophic levels [103]. Both these observed patterns don’t match some predictions of the trophic cascade hypothesis, i.e., that top predators should be regulated by competition, facilitating their diet and ecomorphological variation, while intermediate predators should be regulated by predation, that would inhibit their diet variation, i.e., by restricting foraging habitat choice. The former observed pattern may be caused by trade-offs between ecomorphological specialization and foraging efficiency, that would constrain among-individual diet variation at higher trophic levels, e.g., in *P. fluviatilis* populations with higher proportions of piscivores [103]. The latter pattern was also observed in lacustrine communities, and can be described by an optimal-foraging model as the occurrence of shifts in foraging-predation risk trade-offs [103]. We hypothesize that the predatory pressure exerted by top

predators on intermediate consumers might have been the ultimate mechanism that selected their high among-individual variation of their realized trophic niches. Any variant that could plastically respond to the presence of a predator in a given habitat type by consuming different prey in different habitat types, would effectively reduce foraging-related mortality risks, thus increasing its fitness [104]. The historical increase in abundance of fish NNS in Lake Mergozzo, their dominance by number and biomass within the assemblage, and the broad asymmetrical niche overlaps suggest that the higher degree of trophic generalism of fish NNS might have been one of the key adaptive traits that have promoted their invasion of the recipient community [46]. In other words, the adaptive capacity of fish NNS to plastically respond to predation by shifting their foraging trade-offs, selected by predatory pressure in their native systems, would have been coopted for another function, i.e., their capacity to plastically respond to trophic competition (invasive potential), after their introduction into the recipient community in a novel selective context [105]. The apparent success of trophic generalists plus piscivores (10 out of 15 species) in Lake Mergozzo might have also been facilitated by the physiography of its littoral zone, its oligotrophic state [55], and the infrequent connection with the neighboring Lake Maggiore, that likely determined relatively low productivity levels. Resultantly, the diets of this fish assemblage would have been characterized by high interspecific competition, that would have penalized both species with scarce trophic opportunism and smaller species, favoring top predators and trophic generalists [51,98,99].

The pattern of asymmetrical overlaps between larger and smaller niches of fish NS and NNS suggests a more complex scenario than depicted in other lentic systems [16,49]. On one hand, the niches of the fish NS *A. arborella* and *S. hesperidicus* are broadly overlapped with larger niches of several fish NNS, but also with the much larger niche of the fish NS *P. fluviatilis*, which is also larger than and overlapped with the niches of several fish NNS; the niches of two fish NNS were also broadly overlapped. Despite having the second-largest isotopic niche area, the niche of *S. umbla* is not broadly overlapped with other species, possibly due to the peculiar habitat of this stenothermal species, that likely feeds on and above the bottom of the lake's deep and cold waters [64]. *L. lota* likely shares this peculiar environment in Lake Mergozzo [106], but was not included in the analyses, since only one individual was captured.

SIA studies have demonstrated variable levels of isotopic niche overlaps between freshwater fish NNS and NS [49,107]. Overlaps between isotopic niches [49,108,109] and diets [14] between animal NNS and NS were associated with reductions in population size or distributional declines of the latter, suggesting trophic competition, e.g., in the presence of limiting or fluctuating resources. Several studies documented decreases in fish NS isotopic niche areas or niche divergence and partitioning, due to competition with sympatric fish NNS [16,34,41,110]. However, the lack of information on resource availability and trophic niches of the fish assemblage of Lake Mergozzo before the fish NNS introductions prevents from speculating about possible trophic reorganizations of the food web and other effects on ecosystem functioning induced by these introductions.

Author Contributions: Conceptualization, P.V., D.C., R.P., and G.P.; methodology—sampling, P.V., R.P.; methodology—SIA analysis: D.C., S.B., S.Z.; methodology—chemical analyses: R.P.; methodology—other statistical analyses: D.C., G.P.; writing—original draft preparation, G.P., D.C.; writing—review and editing, G.P., D.C., R.P., J.R.M., and P.V.; supervision, P.V.; project administration, P.V.; funding acquisition, P.V. All authors have read and agreed to the published version of the manuscript.

Funding: D.C. was funded by the grant LIFE15 NAT/IT/000823 IdroLIFE; G.P., J.R.M. and S.B. were funded by the grant Interreg ITA-CH SHARESALMO. S.Z. was funded by the Cariplo Foundation.

Acknowledgments: The authors wish to thank Igorio Cerutti and Carolina Zellino for their help during the fish sampling campaign, and two anonymous reviewers for their constructive comments and encouragement.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Appendix A

Table A1. Fishes collected in Lake Mergozzo by benthic (RB) gill nets, mesopelagic (BP) gill nets, and electrofishing (EF), in 2016; BPUE (NPUE) = fish biomass (number of individuals) per unit effort; TL (cm) = total length; Fish NS = fish native species; Fish NNS = fish non-native species; all values: mean \pm SD, or values, if $n < 3$. Overall means \pm SD: means \pm SD of the total fish NNS (NS) samples, for each type of sampling method; Grand means: means \pm SD of the total fish sample, for each type of sampling method; in *bold*: values > 75 percentile of the fish NNS and fish NS corresponding distributions ('dominant' species by abundance). See Table 1 for TL ranges, fish numbers and weights.

Fish Species	TL (cm)			BPUE (g ind. m ⁻² or g ind. dip ⁻¹)			NPUE (n. ind. m ⁻² or n. ind. dip ⁻¹)		
	RB	RP	EF	RB	RP	EF	RB	RP	EF
Fish NNS									
<i>Coregonus</i> sp.	11.1 \pm 2.3	39.1 \pm 4.3	-	0.01 \pm 0.05	0.312 \pm 0.863	0.00 \pm 0.00	0.0011 \pm 0.0056	0.0006 \pm 0.0017	0.00 \pm 0.00
<i>G. cernua</i>	12.3 \pm 3.3	-	-	0.26 \pm 0.53	0.000 \pm 0.000	0.00 \pm 0.00	0.0087 \pm 0.0159	0.0000 \pm 0.0000	0.00 \pm 0.00
<i>L. gibbosus</i>	13.2 \pm 2.3	-	11.5 \pm 3.8	0.2 \pm 0.52	0.000 \pm 0.000	18.65 \pm 77.31	0.0045 \pm 0.0104	0.0000 \pm 0.0000	0.42 \pm 1.10
<i>M. salmoides</i>	19.5 \pm 6.2	-	13.9 \pm 7.9	0.20 \pm 0.70	0.000 \pm 0.000	30.19 \pm 104.70	0.0019 \pm 0.0064	0.0000 \pm 0.0000	0.34 \pm 0.69
<i>R. rutilus</i>	17.4 \pm 6.8	13.8	9.7 \pm 3.9	4.04 \pm 6.74	0.003 \pm 0.014	0.73 \pm 4.57	0.0481 \pm 0.0762	0.0002 \pm 0.0006	0.05 \pm 0.23
<i>S. umbla</i>	22.8 \pm 4.4	-	-	0.20 \pm 0.62	0.000 \pm 0.000	0.00 \pm 0.00	0.0019 \pm 0.0054	0.0000 \pm 0.0000	0.00 \pm 0.00
<i>S. lucioperca</i>	56.0, 65.0	-	-	1.92 \pm 11.21	0.000 \pm 0.000	0.00 \pm 0.00	0.0011 \pm 0.0056	0.0000 \pm 0.0000	0.00 \pm 0.00
Overall means \pm SD				0.98 \pm 5.11	0.045 \pm 0.336	7.08 \pm 50.25	0.0096 \pm 0.0337	0.0001 \pm 0.0007	0.12 \pm 0.52
Fish NS									
<i>A. agone</i>	-	11.9 \pm 0.7	-	0.00 \pm 0.00	0.019 \pm 0.035	0.00 \pm 0.00	0.0000 \pm 0.0000	0.0012 \pm 0.0024	0.00 \pm 0.00
<i>A. arborella</i>	8.2 \pm 0.7	-	-	0.01 \pm 0.03	0.000 \pm 0.000	0.05 \pm 0.37	0.0019 \pm 0.0082	0.0000 \pm 0.0000	0.03 \pm 0.16
<i>C. gobio</i>	7.1 \pm 2.0	-	-	0.02 \pm 0.06	0.000 \pm 0.000	0.00 \pm 0.00	0.0038 \pm 0.0134	0.0000 \pm 0.0000	0.00 \pm 0.00
<i>E. cisalpinus</i>	-	-	-	0.00 \pm 0.00	0.000 \pm 0.000	40.2 \pm 248.77	0.0000 \pm 0.0000	0.0000 \pm 0.0000	0.03 \pm 0.16
<i>L. lota</i>	31.3	-	-	0.06 \pm 0.40	0.000 \pm 0.000	0.00 \pm 0.00	0.0004 \pm 0.0025	0.0000 \pm 0.0000	0.00 \pm 0.00
<i>P. fluviatilis</i>	16.1 \pm 8.7	-	12.4 \pm 3.9	1.35 \pm 3.48	0.000 \pm 0.000	4.01 \pm 20.24	0.0148 \pm 0.0292	0.0000 \pm 0.0000	0.12 \pm 0.37
<i>S. hesperidicus</i>	19.1 \pm 4.2	-	16.9 \pm 2.0	0.49 \pm 1.91	0.000 \pm 0.000	2.77 \pm 14.19	0.0057 \pm 0.0262	0.0000 \pm 0.0000	0.04 \pm 0.2.0
<i>S. squalus</i>	24.6	-	-	0.05 \pm 0.36	0.000 \pm 0.000	0.00 \pm 0.00	0.0004 \pm 0.0025	0.0000 \pm 0.0000	0.00 \pm 0.00
Overall means \pm SD				0.25 \pm 1.47	0.002 \pm 0.014	5.88 \pm 88.83	0.0034 \pm 0.0156	0.0002 \pm 0.0009	0.03 \pm 0.17
Grand means				0.59 \pm 3.67	0.022 \pm 0.230	6.44 \pm 73.36	0.0063 \pm 0.0258	0.0001 \pm 0.0008	0.07 \pm 0.38

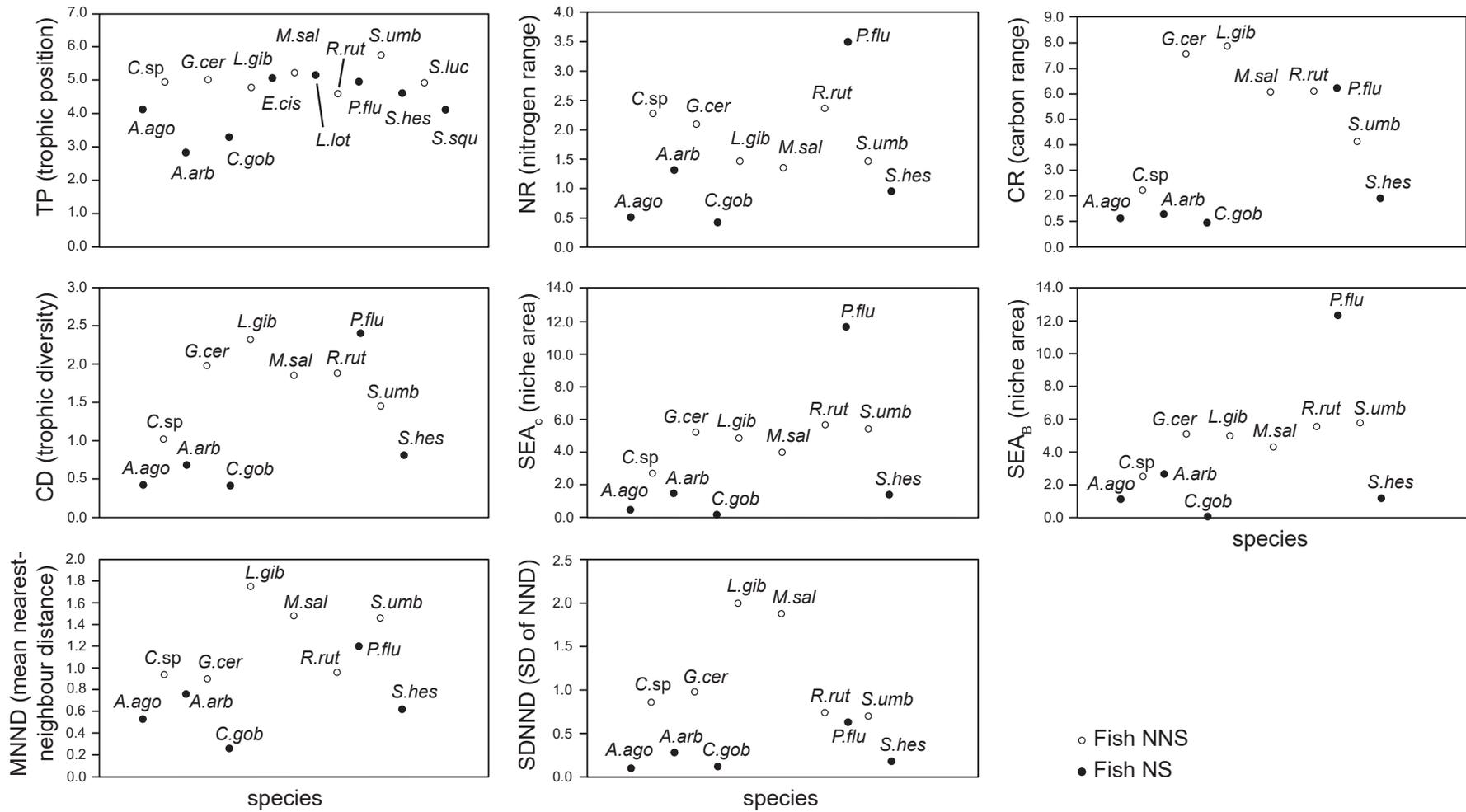


Figure A1. Scatter plots of TP and isotopic niche metrics. For isotopic niche metrics, fish species with <3 analyzed specimens are not included; x axes: fish species; fish NNS (white dots) = fish non-native species; fish NS (black dots) = fish native species. See Table 4 and Figure 3 for abbreviations.

Table A2. Foraging habitats and food ecology of the studied fish species in the literature. Status: NS = fish native species; NNS = fish non-native species in Lake Mergozzo; TL = total length range; *underlined*: main food items, considering the size range and other characteristics of the population of Lake Mergozzo; *in parentheses*: less important food items; see also Table 1, Appendix A, Table A1.

Species	TL (cm)	Status	Common Food Source	Foraging Habitat	References
<i>Coregonus</i> sp.	8–44	NNS	zooplankton, <u>zoobenthos</u>	pelagic, demersal	[51,68,99]
<i>G. cernua</i>	5–18	NNS	zooplankton, <u>zoobenthos</u> , (fishes)	littoral, pelagic, demersal	[55,97,111,112]
<i>L. gibbosus</i>	5–25	NNS	(plant material), zooplankton, <u>zoobenthos</u> , (fishes)	littoral, demersal	[99,113,114]
<i>M. salmoides</i>	5–30	NNS	zooplankton, <u>zoobenthos</u> , <u>macroinvertebrates</u> , <u>fishes</u>	littoral, demersal	[99,115,116]
<i>R. rutilus</i>	6–33	NNS	<u>detritus</u> , <u>plant material</u> , <u>zooplankton</u> , <u>zoobenthos</u>	littoral, pelagic	[54,117]
<i>S. umbla</i>	16–28	NNS	<u>zoobenthos</u> , macroinvertebrates, fishes	pelagic, demersal deep waters	[64]
<i>S. lucioperca</i>	37–73	NNS	(zoobenthos), <u>fishes</u>	littoral, demersal	[118,119]
<i>A. agone</i>	11–13	NS	<u>zooplankton</u>	pelagic	[68,120]
<i>A. arborella</i>	7–9	NS	algae, <u>zooplankton</u>	pelagic	[121,122]
<i>C. gobio</i>	4–10	NS	<u>zoobenthos</u>	benthic	[123]
<i>E. cisalpinus</i>	56, 65	NS	<u>fishes</u>	littoral	[115,124]
<i>L. lota</i>	31	NS	macroinvertebrates, <u>fishes</u>	benthic, deep waters	[106,125]
<i>P. fluviatilis</i>	6–41	NS	zooplankton, <u>zoobenthos</u> , <u>fishes</u>	littoral, pelagic	[97,103]
<i>S. hesperidicus</i>	15–33	NS	<u>detritus</u> , algae, <u>aquatic macrophytes</u> , <u>terrestrial plant matter</u> , <u>zooplankton</u> , (<u>zoobenthos</u>)	littoral	[126]
<i>S. squalus</i>	25	NS	<u>plant material</u> , <u>zoobenthos</u> , <u>terrestrial epineuston</u> , fishes	littoral	[127,128]

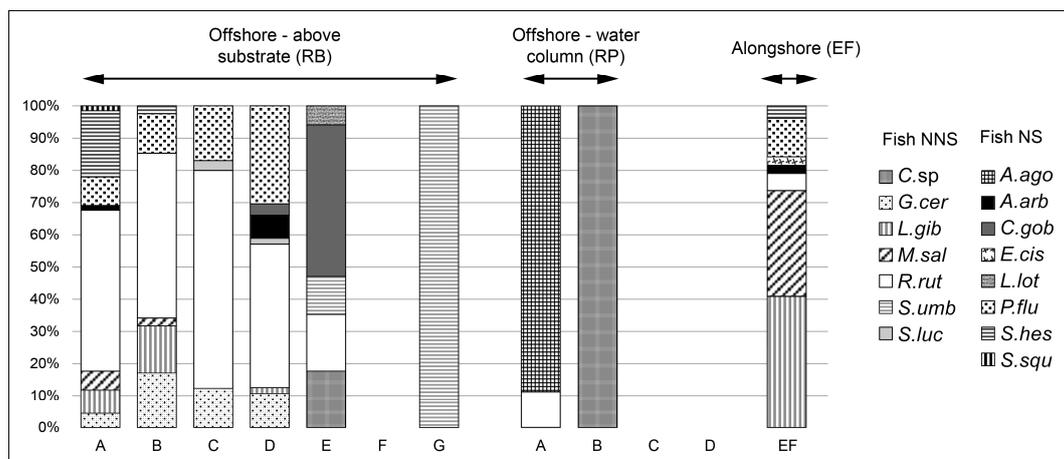


Figure A2. Fish depth distribution: relative number by depth stratum. RB = benthic nets; RP = mesopelagic nets; EF = electrofishing; fish NNS: fish non-native species; fish NS: fish native species. See Figure 3 for species abbreviations.

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