Food Web Topology in High Mountain Lakes

Javier Sánchez-Hernández1,2, Fernando Cobo2,3, Per-Arne Amundsen1*

1 Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Tromsø, Norway, 2 Department of Zoology and Physical Anthropology, Faculty of Biology, University of Santiago de Compostela, Santiago de Compostela, Spain, 3 Station of Hydrobiology “Encoro do Con”, Castroagudín s/n, 36617 Vilagarcía de Arousa, Pontevedra, Spain

* per-arne.amundsen@uit.no

Abstract

Although diversity and limnology of alpine lake systems are well studied, their food web structure and properties have rarely been addressed. Here, the topological food webs of three high mountain lakes in Central Spain were examined. We first addressed the pelagic networks of the lakes, and then we explored how food web topology changed when benthic biota was included to establish complete trophic networks. We conducted a literature search to compare our alpine lacustrine food webs and their structural metrics with those of 18 published lentic webs using a meta-analytic approach. The comparison revealed that the food webs in alpine lakes are relatively simple, in terms of structural network properties (linkage density and connectance), in comparison with lowland lakes, but no great differences were found among pelagic networks. The studied high mountain food webs were dominated by a high proportion of omnivores and species at intermediate trophic levels. Omnivores can exploit resources at multiple trophic levels, and this characteristic might reduce competition among interacting species. Accordingly, the trophic overlap, measured as trophic similarity, was very low in all three systems. Thus, these alpine networks are characterized by many omnivorous consumers with numerous prey species and few consumers with a single or few prey and with low competitive interactions among species. The present study emphasizes the ecological significance of omnivores in high mountain lakes as promoters of network stability and as central players in energy flow pathways via food partitioning and enabling energy mobility among trophic levels.

Introduction

Ever since the concepts of food chains and food webs were introduced in the in the late 1800s, many studies on feeding relationships have been carried out to address food web complexity and functioning [1]. The importance of omnivorous species as promoters of stability [2–4] has been recognised as a result of their ability to use different food resources leading to reduced inter- and intraspecific competition [4]. In addition, the prevalence of omnivores in food webs may be related to two other important features: firstly, omnivores can have an important impact on energy flows and nutrient cycling [5] and secondly, omnivores can increase the number of links (usually measured as linkage density or the average number of links per
species) and hence the food web connectance (i.e., the realized number of links as a proportion of the potential number of links) [3].

Fish are usually at the top of freshwater food chains [6–9]. In lakes, a major pathway of energy transfer is often through pelagic food chains [10], but also benthic prey can be important resources for fish [11,12]. Fish, via their foraging behaviour, are able to modify important food web properties such as for example linkage density, connectance and omnivory [13]. Food web topology in lakes has received attention [14–19], but the majority of the studies have focused on the pelagic zone [15,17–19], and relatively few have included the macroinvertebrates from the littoral and profundal zones [14,16]. The inclusion of the benthic biota in food web analysis allows a broader perspective of ecosystem functioning, especially when it is considered that the pelagic, littoral and profundal zones may be coupled through fish [12,20].

High mountain lakes that are present across the world constitute simple systems due to low species diversity [21–23] and low primary production [24,25]. Originally fish-free alpine lakes have frequently been stocked with salmonid species for recreational purposes, and food webs can be affected by fish introductions because fish are able to modify the structure and composition of both the zooplankton and littoral macroinvertebrate communities [26–28]. To understand the ecosystem functioning of such high mountain lakes, their food web topology has to be explored, but there are still several issues relating to food web structure, prevalence of omnivory and trophic level about which little is known. A notable exception is the study by Harper-Smith et al. [16], which demonstrated that the structural complexity of the food web in high elevation lakes in Sierra Nevada (2870–3600 m) is greatest in those that are fish-free. In the present study, we have constructed trophic webs for three high elevation lake systems of Central Spain (lakes Caballeros, Cimera and Grande de Gredos) to include all relevant trophic levels (littoral vegetation, phytoplankton, zooplankton, macroinvertebrates, amphibians and fish). The main objective was to provide, analyse and compare high-resolution topological food webs for the three systems; one lake without fish, one with introduced brook charr Salvelinus fontinalis (Mitchill, 1814) (henceforth simply charr) and one with native brown trout Salmo trutta Linnaeus, 1758 (henceforth simply trout). More specifically, this study aimed to: (i) quantify important structural network properties of alpine lakes such as food web connectance, number of trophic levels and prevalence of omnivory, (ii) investigate how the structural network properties change when benthic biota are added to complement the pelagic web and complete the lacustrine food web, and (iii) compare the food web topology of these alpine lakes with published information from other lentic systems using a meta-analytic approach. We hypothesised that (i) connectance would be higher in lakes with fish than those without, (ii) structural network properties should be more complex when benthic biota are incorporated, and (iii) food webs in alpine lakes are relatively simple in terms of linkage density and connectance, in comparison with lowland lakes.

Methods

Ethics statements

The Servicio Territorial de Medio Ambiente de Ávila (Junta de Castilla y León) granted permission for sampling and protocols were approved by the Institutional Animal Care and Use Committee of the University of Santiago de Compostela (Spain). All procedures conformed to European Union (86/609/EEC) and Spanish (Royal Decree 223/1998) guidelines on animal care and experimentation. All efforts were made to minimize animal stress and suffering during this study. Fish were euthanized by cerebral concussion followed by cervical dislocation to ensure the cessation of life. None of the sampled species were endangered or protected.
Study area

The study area is located in the Gredos Mountains (Ávila, Central Spain) within the Sierra de Gredos Natural Park, which is part of the Natura 2000 network (Council Directive 92/43/EEC). The topography has origin in tectonic developments during the Alpine Orogeny (Cenozoic), and landscape changes during the Last Glacial Period (Late Pleistocene), when glaciers formed the lakes of the Gredos Mountains [29]. The study involves three high mountain lakes (Caballeros, Cimera and Grande de Gredos) on the northern slope of the Gredos Mountains at altitudes between 1935 and 2140 m.a.s.l. (Fig 1). The lakes are oligotrophic, with conductivities generally below 10 \( \mu \text{S/cm} \) [30,31]. The bottom of these lakes is mainly silty with relatively low organic matter content, but in the shoreline area the amounts of sandy bottom and block material are higher [30]. The lakes are ice-covered for 6–7 months from November/December to April/May, with ice cover durations of approximately 185 days for the Grande de Gredos lake and 220 days for Cimera lake [30]. Ice phenology is under the influence of climate change via precipitation and air temperature changes [32]. The three lakes are monomictic with winter inverse stratification during the ice-covered period, whereas after the ice-melt periods, water column mixing predominate [30,31].

Caballeros lake (40°13’N, 5°35’W) with a maximum depth of 5.2 m and a surface area of 14027 m\(^2\) [30,31], is located in a small granite catchment at 2025 m.a.s.l. [30,31]. The catchment is dominated by \textit{Nardus stricta} grasslands and psicroxerophytic meadows, but with alpine shrub vegetation on the less steep slopes [30,31]. Macrophytes are scarce in the lake, but small areas of \textit{Antinoria agrostidea}, \textit{Isoetes boryana}, \textit{Sparganium angustifolium}, \textit{Callitriche palustris} and \textit{Carex} spp. exist in the littoral zone [33,34]. There are no fish species in the lake.

Cimera lake (40°15’N, 5°18’W) is within a small granite catchment at 2140 m.a.s.l. with exposed rock, i.e. mostly without developed soils but with small \textit{Nardus stricta} grasslands and psicroxerophytic meadows [35]. The lake has a maximum depth of 9.4 m and a surface area of 44900 m\(^2\) [30,35]. There are no submerged macrophytes, but small areas of water-mosses, mainly \textit{Drepanocladus exannulatus} and \textit{Fontinalis squamosa}, are present in the littoral zone [31]. The levels of polycyclic aromatic hydrocarbons in the superficial sediments of the lake are lower than in lakes in France, Austria, Poland, Slovakia, Ireland and Norway, indicating low contamination by persistent organic pollutants [36]. The only fish present is the charr, which was introduced between 1940 and 1960 and currently has a stable population [35].

Grande de Gredos lake (40°15’N, 5°16’W) is located at 1935 m.a.s.l. The catchment area is mainly rocky with small \textit{Nardus stricta} grassland and psychroxerophytic meadows [37]. The lake has a maximum depth of 6.5 m and a surface area of 63076 m\(^2\) [31]. The littoral zone is predominantly shallow and there is abundant aquatic vegetation, mainly \textit{Subularia aquatica}, \textit{Isoetes velaturn}, \textit{Isoetes boryana}, \textit{Juncus bulbosus}, \textit{Juncus tanageia}, \textit{Callitriche palustris}, \textit{Antinoria agrostidea}, \textit{Ranunculus peltatus}, \textit{Carex nigra}, \textit{Drepanocladus exannulatus}, \textit{Fontinalis squamosa}, \textit{Sphagnum denticulatum} and \textit{Sparganium angustifolium} [30,33,34]. The main anthropogenic impact is from a mountain refuge built in 1971 [37,38]. Native trout are the only fish present in the lake.

Species compositions

The two primary sources for the data were surveys of macroinvertebrates, amphibians and fish conducted in all three lakes during the summers of 2006 and 2008, and retrieved from publications containing relevant information about the three lakes. Macroinvertebrates were collected from the littoral zone with a pond net by kicking and sweeping (10 samples in each lake), standardised by kicking for 5 minutes. Macroinvertebrates were separated from silt, sand and vegetation and preserved in 96% ethanol for later identification in the laboratory. Species lists were
supplemented with information from published studies [30,31,39,40] to establish the final macroinvertebrate data set. Amphibians were monitored by searching for hidden individuals in cavities, soil cracks and under rocks both during daylight and at night (with flashlights). Two anurans (Bufo spinosus Daudin, 1803 and Rana iberica Boulenger, 1879) and an urodelan, Salmandra salamandra (L), were found in the three lakes. Fish were captured by fishing using spinning lures; a total of 49 charr (11–27.2 cm) and ten trout (21–26 cm) were collected. Stomachs were removed and preserved in 96% ethanol for later analysis of stomach contents. Information about phytoplankton and zooplankton compositions were taken from Toro et al. [30] and Toro and Granados [31]. The species compositions of each group (phytoplankton, zooplankton, macroinvertebrates, amphibians and fish) in each lake are given as supporting information (S1 File). To study the macroinvertebrate trophic structure, each taxon was assigned to a functional feeding group (FFG) based on information from relevant literature [41]. The groups used are based on Merritt and Cummins [42], and species were classified according to Sánchez-Carmona et al. [3] as: 1) collectors (feed on fine detritus deposited on the substrate), 2) filterers (feed on fine detritus suspended in the water column), 3) shredders (feed on coarse organic material, such as leaves or wood), 4) predators (feed on other macroinvertebrates) and, 5) scrapers (feed on algae). This study is based on presence-absence data for species in each lake (i.e. the species composition) and does not include considerations of abundance.

**Food web construction**

The establishment of feeding links between the species present in the lakes was performed on the basis of our stomach contents analyses (macroinvertebrates and fish) together with information from the literature. Literature searches were conducted using databases (e.g., Web of Science, Dialnet and IngentaConnect) to find information about the feeding habits of the zooplankton, macroinvertebrate, amphibian and fish species present in the lakes. The diets of charr and trout in high mountain lakes are well documented [43–46]. Diet compositions of the amphibian species present in the lakes are also known [47–49]. For the diets of zooplankton
and macroinvertebrates [41,53,54], studies from a broad geographical range had to be used (see full reference list used in this study for establishing the feeding links between the species in S2 File). Due to a lack of information about whether the phytoplankton species present are unicellular, filamentous, colonial or other forms, most phytoplankton species are considered as being unicellular except for some Chlorophyta (Pediastrum tetras, Scenedesmus sp., Dictyosphaerium sp., Dictyosphaerium enrenberqianum, Dictyosphaerium subsolitarius, Hya-lotheca dissiliens, Sphaerocystis schroeteri and Spirogyra sp.), some Bacillariophyceae (Aulaco-seira distans, Asterionella formosa, Navicula cryptocephala, Navicula sp., Fragilaria crotonensis and Tabellaria flocculosa), some Cyanophyta (Anabaena sp., Pseudanabaena sp., Lyngbya sp. and Bicosoeca alaskana) and some Chrysophyceae (Dinobryon bavaricum, Dinobryon sertu-laria, Salpingoeca sp. and Synura sp.) that are mainly filamentous or colonial species [55,56]. We assumed that filamentous and colonial forms of phytoplankton species cannot be utilized as food by zooplankton because of their size [57], whereas zooplankton could graze on unicel-lular species. Rotifers have only been recorded in Caballeros lake (Keratella quadrata and Con-ochilus sp.) [31]. The trophic base in the benthic habitats were aggregated into the following groups: coarse organic material (leaves, wood), fine detritus, macrophytes, water-moss and periphyton. Fungi or bacteria are able to break down coarse organic material and fine detritus [58], but microorganisms have not been included in this study.

The topological food webs of the three lakes were established according to Amundsen et al. [18], consisting of an \( n \times n \) matrix on \( n \) species, with predators as columns and prey as rows, and with binary entries (0 or 1) in the matrix indicating whether a predator eats a prey species. Then, food web images were produced with FoodWeb3D software developed by the Pacific Ecoinformatics and Computational Ecology Lab [59,60] and available at http://www.foodwebs.org/. The trophic link matrices used for food web construction are given as supporting information (S1–S3 Datasets). To characterise food web topology, a suite of 23 properties was calculated (Table 1). We calculated the number of trophic levels, linkage density and connectance using previously described methods [18,19]. We paid attention to generalization (\( \text{GenSD} \), “average number of prey eaten per predator in the web”) and vulnerability (\( \text{VulSD} \), “average number of predators per prey in the web”) [61], that are widely-reported [3,62,63]. When \( \text{GenSD} \) is higher than \( \text{VulSD} \), it means that there are few consumers with numerous prey and many consumers with a single prey [3]. In line with other studies, trophic similarity (\( \text{Sim} \)) was calculated to address the trophic overlap of food webs [3,63]. The measurement of trophic overlap using a similarity index between every pair of taxa in a food web was proposed by Martínez [14]; index values vary from zero (when two taxa have no common predators or common prey) to one (when two taxa have the same set of predators and prey) [14]. Williams and Martínez [64] recommended the combination of traditional food web properties with analyses of mean short-weighted trophic level (\( \text{MeanSWTL} \)) and mean shortest chain to a basal species (\( \text{MeanShortChn} \)), because these parameters can provide valuable information about energy flow. \( \text{MeanSWTL} \) can indicate how many steps energy must take to get from an energy source to a consumer [1] and \( \text{MeanSWTL} \) has been used to calculate the trophic level averaged across taxa in food webs [62,63]. To calculate \( \text{MeanSWTL} \), the FoodWeb3D software assigns a value for basal taxa as one, obligate herbivores have trophic level two, and higher level consumers have a value based on their feeding relationships to other levels; more detail about how this index is calculated can be found in previous works [63,64]. Topological food webs were established separately for the pelagic zone and the complete system (pelagic and benthic biota), which allowed us to compare network complexity between the pelagic and complete networks. In addition, topological food webs for Cimera and Grande de Gredos lakes were also constructed without fish species in order to make their structure compatible and comparable with...
Caballeros lake (fishless lake). This approach allowed us to examine whether fish predation could modify the structure of the food webs in high mountain lakes.

**Meta-analytic approach**

Meta-analysis refers to a set of methods used to analyse or compare results from different studies [65]. The data from the three lakes were compared to food web statistics gathered from 18 published food webs from lentic systems [14–19]. The meta-analysis was carried out separately for complete food webs [14,16], and pelagic food webs [15,17–19], and was implemented by using common food web properties presented in all the 18 published food webs: species richness (S), number of links (L), linkage density (D) and connectance (C). The data used are provided as supporting information (S1 Table). A principal component analysis (PCA) was used to explore differences in the food web properties among systems. In addition, data matrices were analysed using between-class analysis in order to explore the affinity of the systems in the PCA. Between-class analysis is a method used to enhance the understanding of similarities between grouped classes [66,67]. The data analysis involved in three steps: (i) the dudi.pca function was employed to perform a principal component analysis of a data frame, (ii) the

---

**Table 1. Food web properties.**

| Metric                        | Definition                                                                 |
|-------------------------------|---------------------------------------------------------------------------|
| Richness (S)                  | Taxonomic richness of the food web                                         |
| Lower trophic taxa (Sl)       | Fraction of species that are lower trophic taxa (terrestrial organic material, fine detritus, periphyton, macrophytes and water-moss) |
| Phytoplankton richness (Sp)   | Fraction of species that are phytoplankton                                  |
| Zooplankton richness (Sz)     | Fraction of species that are zooplankton                                   |
| Macroinvertebrate richness (Sm)| Fraction of species that are macroinvertebrate                             |
| Amphibian richness (Sa)       | Fraction of species that are amphibian                                     |
| Fishes richness (Sf)          | Fraction of species that are fishes                                        |
| Links (L)                     | Number of links between individuals                                        |
| Linkage density (D)           | \( D = \frac{L}{S} \)                                                      |
| The potential number of links (Lp) | \( Lp = \frac{S^2}{2} \)                                    |
| Directed connectance (C)      | \( C = \frac{L}{S^2} \)                                                    |
| Top species (T)               | Fraction of species that have no predators                                  |
| Intermediate species (I)      | Fraction of species that have both predators and prey                       |
| Basal species (B)             | Fraction of species that are not consumers                                  |
| Omnivory (Omn)                | Fraction of species that are omnivores (consume prey from more than one trophic level) |
| Herbivores (Herb)             | Fraction of species that are herbivores (only consume basal species)       |
| Cannibalism (Can)             | Fraction of species that are canibals                                      |
| MeanSWTL                      | Mean short-weighted trophic level [64]                                     |
| MeanShortChn                  | Mean shortest chain to a basal species                                     |
| GenSD                         | Generality standard deviation (standard deviation of the number of resources per species) |
| VulSD                         | Vulnerability standard deviation (standard deviation of the number of consumers per species) |
| Trophic similarity (Sim)      | Mean Jaccardian similarity [14]                                            |
| MaxSim                        | Maximum Jaccardian similarity [14]                                         |

Definition of the 23 food web properties calculated for the three high mountain lakes.

doi:10.1371/journal.pone.0143016.t001
scatter function was used for plotting the food web properties axes, the position of lakes and the eigenvalues of the PCA, and (iii) the s.class function was used to test for differences in the projection of the food web properties with ellipses and gravity centers grouped by study. In order to explore the statistical significance of the between-group analysis, a permutation test (Monte-Carlo test) was used [68]; the test was considered statistically significant at \( P < 0.05 \). Graphical outputs and permutation analysis were computed with the ADE4 library implemented in R freeware [69]. The ADE4 library [70] is at http://cran.es.r-project.org/.

**Results**

**Food web topology**

The combination of benthic biota with the pelagic network to give the complete food web increased the number of links (by 4.9 and 14.3 times in Caballeros and Cimera, respectively) and resulted in an increase in food-web characteristics such as linkage density and GenSD (Table 2). In addition, when fishless topologies were constructed for the three lakes, GenSD and VulSD values were lower in the fishless condition, whereas there were no marked differences in connectance (Table 2). The remainder of this section refers to the complete networks, but information about the pelagic and fishless food-web metrics can be obtained from Table 2.

Taxonomic richness of the food webs varied from 64 to 96 (Table 2), of which the majority were macroinvertebrates (48% in Caballeros and 67% in Cimera) and phytoplankton (41% in Grande de Gredos). In all three lakes, Chironimidae dominated the taxonomic richness of the macroinvertebrate community with 19.4%, 40.6% and 56.1% of the total number of taxa in the respective lakes (Caballeros, Grande de Gredos and Cimera). Collectors and predators were proportionally the most abundant functional feeding groups, while filter feeders were scarce and were only represented by *Pisidium casertanum* (Poli, 1791) (Fig 2).

Structural network properties (number of links, connectance and linkage density) were always higher in Cimera (charr-lake) than in the other two lakes (Table 2). The food webs had from 4096 to 9216 potential links, of which only 5.8–8.9% were observed. In all lakes, the food webs included a large proportion of species that are both predators and prey, i.e. that are intermediate species (>45%, Table 2). The proportion of basal species was high in Grande de Gredos (52%), but much lower in the other two lakes (16% and 34% in Cimera and Caballeros, respectively), and the percentage of top species was higher in fishless Caballeros (9%) than in the two lakes where fish are present (2% and 1% in Grande de Gredos and Cimera, respectively). The species at the highest trophic levels in the food webs were amphibians in Caballeros, and charr and trout in Cimera and Grande de Gredos, respectively (red balls in the Fig 3).

Six trophic levels were identified in lakes with fish species; basal level (terrestrial organic material, fine detritus, periphyton, macrophytes and water-moss), phytoplankton, zooplankton, macroinvertebrates, amphibians and fish. Five trophic levels were recognised in the fishless lake (Caballeros). Interestingly the studied high mountain food webs were characterised by high proportions of omnivores regardless of lake type (Table 2), and the prevalence of omnivores was always above 80%. The fraction of species that were cannibals was low, and never above 0.10 (Table 2).

Measures of trophic level characteristics (*MeanSWTL* and *MeanShortChn*) were similar, but there were some differences (Table 2). The lakes with fish (Grande de Gredos and Cimera) had the highest *MeanSWTL*-values, and Cimera tended to have shorter food chains (lowest *MeanShortChn*-value) than the other two lakes (Table 2). The average number of prey species eaten per predator species (*GenSD*) and the mean number of predators per prey (*VulSD*) were highest in Cimera and lowest in Caballeros (Table 2). Values of *VulSD* were higher than those for *GenSD* in all the food webs. Some taxa such as colonial phytoplankton, nematodes and *Gordius*
sp. were not consumed by predators. With regard to trophic similarity ($Sim$), numerical values were closer to 0 than to 1 in all three lakes (values between 0.14 to 0.26), meaning that many taxa did not have common predators or common prey. The maximum trophic similarity ($MaxSim$) was the same in the three lakes (Table 2).

### Meta-analytic approach

Food web properties of the networks addressed in the present study were compared to published data for 18 food webs from lentic systems (Fig 4). The first two axes of the PCA explained 97.8 and 99% of the total variability of the pelagic and complete food webs, respectively (Table 3). The interpretation of the axes in the PCA, i.e. position of lakes, and position of food web properties and eigenvalues, are shown in the upper parts of (Fig 4A and 4C). The permutation test confirmed that the difference among groups was significant among the complete food webs (Fig 4D, $P = 0.004$), but not among the pelagic food webs (Fig 4B, $P = 0.168$). Thus, the comparison among pelagic food webs shows that our networks were similar to those in other systems. For the complete food webs, our webs differ from those recorded for other systems (Fig 4D). The estimated food web properties (i.e., richness, number of links, linkage density and connectance) are low in comparison with values reported by Martinez [14]; but in

### Table 2. Food web topology.

|                     | Caballeros Pelagic | Caballeros Complete | Cimera Pelagic | Cimera Fishless | Cimera Complete | Grande de Gredos Pelagic | Grande de Gredos Fishless | Grande de Gredos Complete |
|---------------------|--------------------|---------------------|---------------|----------------|-----------------|--------------------------|---------------------------|---------------------------|
| Richness ($S$)      | 21                 | 64                  | 17            | 84             | 85              | 43                       | 95                        | 96                        |
| Lower trophic taxa ($S_l$)* | 0                 | 0.13                | 0             | 0.06           | 0.06            | 0                        | 0.17                      | 0.17                      |
| Phytoplankton richness ($S_p$) | 0.76              | 0.27                | 0.59          | 0.15           | 0.15            | 0.86                     | 0.41                      | 0.41                      |
| Zooplankton richness ($S_z$) | 0.24              | 0.08                | 0.35          | 0.07           | 0.07            | 0.12                     | 0.05                      | 0.05                      |
| Macroinvertebrate richness ($S_m$) | 0                 | 0.48                | 0             | 0.68           | 0.67            | 0                        | 0.34                      | 0.33                      |
| Amphibian richness ($S_a$) | 0                 | 0.05                | 0             | 0.04           | 0.04            | 0                        | 0.03                      | 0.03                      |
| Fishes richness ($S_f$) | 0                 | 0                   | 0.06          | 0              | 0.01            | 0.02                     | 0                         | 0.01                      |
| Links ($L$)         | 70                 | 344                 | 45            | 580            | 645             | 101                      | 498                       | 534                       |
| Linkage density ($D$) | 3.3                | 5.4                 | 2.6           | 6.9            | 7.6             | 2.3                      | 5.2                       | 5.6                       |
| The potential number of links ($L_p$) | 441               | 4096                | 289           | 7056           | 7225            | 1849                     | 9025                      | 9216                      |
| Directed connectance ($C_d$) | 0.16              | 0.08                | 0.16          | 0.08           | 0.09            | 0.05                     | 0.06                      | 0.06                      |
| Top species ($T$)   | 0                  | 0.09                | 0.06          | 0.06           | 0.01            | 0.02                     | 0.06                      | 0.02                      |
| Intermediate species ($I$) | 0.24              | 0.57                | 0.24          | 0.77           | 0.82            | 0.07                     | 0.42                      | 0.46                      |
| Basal species ($B$) | 0.76               | 0.34                | 0.75          | 0.17           | 0.16            | 0.91                     | 0.52                      | 0.52                      |
| Herbivores (Herb)   | 0                  | 0.18                | 0             | 0.08           | 0.06            | 0                        | 0.10                      | 0.05                      |
| Omnivory (Omn)      | 0.64               | 0.84                | 0.64          | 0.90           | 0.91            | 0.72                     | 0.90                      | 0.93                      |
| Cannibalism (Can)   | 0.09               | 0.09                | 0.12          | 0.06           | 0.06            | 0.02                     | 0.04                      | 0.04                      |
| MeanSWTL            | 2.60               | 2.71                | 3.58          | 2.76           | 2.89            | 3.37                     | 2.94                      | 3.17                      |
| MeanShortChn        | 2.43               | 2.25                | 2.64          | 2.23           | 2.15            | 2.88                     | 2.44                      | 2.51                      |
| GenSD               | 0.53               | 0.65                | 0.53          | 0.93           | 0.84            | 0.39                     | 0.76                      | 0.73                      |
| VulSD               | 1.88               | 1.13                | 1.76          | 1.78           | 1.79            | 3.61                     | 1.52                      | 1.52                      |
| Trophic similarity ($Sim$) | 0.43              | 0.14                | 0.37          | 0.25           | 0.26            | 0.59                     | 0.19                      | 0.19                      |
| MaxSim              | 1                  | 1                   | 1             | 1              | 1               | 1                        | 1                         | 1                         |

Values of structural properties food webs for the three high mountain lakes. See Table 1 for definitions of each property.

*Lower trophic taxa includes organic material, detritus, periphyton and littoral vegetation.

doi:10.1371/journal.pone.0143016.t002
contrast, the richness, number of links between individuals and linkage density were higher than values reported by Harper-Smith et al. [16] (values are shown in S1 Table).

**Discussion**

**Food web topology**

Our study confirms that the food web topology of alpine lakes may be relatively simple in terms of structural network properties like linkage density and connectance in comparison with lowland lakes, but our findings also demonstrate that the studied mountain lakes clearly were dominated by a high proportion of omnivores and species at intermediate trophic levels. Food webs often have between four and six trophic levels [18,19,71]. In our case, six trophic levels were revealed in two out of the three lakes addressed in the study, whereas five trophic levels were identified in fishless Caballeros. **MeanSWTL** was lower in the fishless system than in the lakes with fish. This could be related to the high predation capacity of fish as generalistic and opportunistic foragers, here represented by trout and charr, that are able to feed on a large variety of taxa and increase the number of feeding links in a food web [8,44,72,73]. Our **MeanSWTL**-values were relatively high compared to those previously reported for lakes, streams, estuaries, marine habitats and terrestrial systems [3,62]. For example, Dunne et al.
**Fig 3. Alpine food webs.** Three-dimensional visualization of the complexity of food webs from the three studied lakes in Central Spain. Image produced with software Foodweb3D available from the Pacific Ecoinformatics and Computational Ecology Lab (http://www.foodwebs.org/), and written by RJ Williams [59,60]. Balls are nodes that represent species and sticks are the links that connect balls through consumption. The vertical axis corresponds to trophic level, basal trophic levels (yellow) are on the bottom; upper trophic levels are on the top (red).

doi:10.1371/journal.pone.0143016.g003

**Fig 4. Meta-analytic approach.** Principal component analysis (PCA) plot based on four food web properties. This is a composed plot, made of: A and C parts- a plot of food web properties axes, position of lakes and eigenvalues projected into PCA, B and D parts- the projection of the food webs with ellipses and gravity center grouped by study.

doi:10.1371/journal.pone.0143016.g004
MeanSWTL-values for food webs in lakes in the range 2–2.7, but our MeanSWTL-values were higher than this. For the Iberian Peninsula, the only comparable information is from food webs in streams [3], and our MeanSWTL-values were higher than for the lotic webs. These differences could relate to the high proportion of omnivores and species at intermediate trophic levels identified in our study.

The food webs in our high mountain lakes were characterized by a high proportion of omnivores and intermediate trophic level species, suggesting that these taxa may play an important role in ecosystem functioning of alpine lakes. In general, omnivory is common in food webs [64], and high levels of omnivory have been observed in temperate lakes [74]. Thompson et al. [75] reviewed the prevalence of omnivory in different ecosystems (streams, lakes, terrestrial and marine systems), and found that lakes in general have intermediate prevalence of omnivory relative to marine systems (higher) and streams (lower). The present study demonstrates that omnivory in alpine lakes can be very important with values always above 80% in the complete networks. Our values were higher than those for Mediterranean shallow-oligohaline lakes [76], subtropical lakes [77], Mediterranean streams [3], North American zooplankton food webs of lakes [78] and some marine food webs from USA and UK [64], but similar to some temperate lakes [74] and marine food webs [62,79]. Several researchers have claimed that a high prevalence of omnivorous species in a food web likely has ecological significance because a high predation capacity increases linkage density and promotes the stability and persistence of webs [3,76,80,81]. Omnivorous species exploit resources at multiple trophic levels, and this might be important to reduce inter- and intraspecific competition, enhance the partitioning of food and promote the mobility of energy transfer. Taking the opposite point of view, omnivory could also increase competition by increasing the potential for species to share prey [82,83]. However, it seems more reasonable to posit that omnivory reduces competition for food in the studied lakes; a conclusion supported by the trophic similarity index, which revealed that trophic overlap was low in all three lakes. The high prevalence of intermediate and omnivorous species could reflect an important role in energy flow in high mountain food webs with them acting as important vectors for transferring energy inputs from both allochthonous and autochthonous sources into the lake food webs.

Contrary to our expectations, the food web complexity in the Caballeros network (fishless system), measured as directed connectance, was similar to Cimera lake (charr system), but higher than Grande de Gredos lake (trout system). Food web complexity in lakes has previously been related to the presence or absence of fish species [16,84]. Harper-Smith et al. [16] pointed out that the connectance in high mountain lakes with fish was 24% lower than in fishless systems. On the other hand, Parker and Huryn [84] have shown that fish are able to increase food chain length and network complexity. Recent studies have also demonstrated that when fish were introduced into freshwater ecosystems, they are able to alter the topology

### Table 3. Scores of eigenvalues.

|                      | Model 1 (pelagic zone) | Model 2 (pelagic and benthic zones) |
|----------------------|------------------------|------------------------------------|
| Eigenvalue of axis 1 | 2.974                  | 2.954                              |
| Eigenvalue of axis 2 | 0.936                  | 1.007                              |
| Eigenvalue of axis 3 | 0.087                  | 0.032                              |
| Eigenvalue of axis 4 | 0.003                  | 0.008                              |

Scores of eigenvalues extracted by principal component analysis for each model. Two models are shown; firstly including literature from the pelagic zone (model 1) and secondly including literature using both pelagic and benthic zones (model 2).

doi:10.1371/journal.pone.0143016.003
of food webs, increasing linkage density, connectivity and complexity [19,85]. Thus, it is reasonable to posit that food webs might differ between fishless lakes and lakes with fish. In our case, some differences were found in the number of links and linkage density among networks (always Cimera > Grande de Gredos > Caballeros), but when the food topology was constructed without the fish species, linkage density was higher in Caballeros than in Grande de Gredos (Cimera > Caballeros > Grande de Gredos). These findings differ somewhat from the higher linkage density found in fishless systems in North-American alpine lakes [16]. Therefore, our study highlights that fish predation may modify the structure of the food web. Trout is a native species in Grande de Gredos and charr was introduced in Cimera, and our results indicate that the top-down effects may be higher in alpine lake systems with trout as the top predator than those in which charr have been introduced. However, this conclusion should be treated with caution, and more studies would be needed to corroborate or refute this.

When fish are present, vulnerability and generality of food webs tend to be higher. Our results are consistent with Schoener [61]'s conclusion that standard deviations for generalization distributions (GenSD) are lower than those for vulnerability distributions (VulSD). This conclusion was arrived by following the study of terrestrial, marine benthic, marine pelagic, marine estuarine, intermediate estuarine, and lotic and lentic freshwater systems. By contrast, some researchers have found that GenSD values exceeded VulSD values in high mountain lake [16] and stream food webs [3]. It has been considered that when this occurs (i.e., GenSD > VulSD), it means that there are few consumers with numerous prey and many consumers with a single prey [3]. Our study revealed the opposite, as in all three lakes there were many consumers with numerous prey and few consumers with a single prey (Fig 3). Also, comparing our GenSD and VulSD values with published data from alpine lakes, our GenSD and VulSD values were lower and higher, respectively, than reported by Harper-Smith et al. [16]. Trophic similarity (Sim) gives us valuable information about whether or not taxa in food webs have common predators and prey [14]. In our case, the mean value of this metric was lowest in the fishless lake, but was low (below 0.30) for all three lakes, indicating that trophic overlap between taxa tended to be low in all three studied lakes.

Although we have gained some knowledge about high-altitude lake systems, several ecological aspects are still left unexplored. In particular, limited information is available about the topology of alpine lacustrine food webs, including both the pelagic and benthic compartments [16]. Our study aimed to assist in filling this knowledge gap and enhance the understanding of alpine ecosystems. It is noteworthy that the results of our study highlight the important role of omnivores for the functioning of high mountain lake food webs. How projected changes in climate will influence such food-web structure is not certain, but food chain lengths of modern lakes seem to be shorter than in ancient lakes as a consequence of the prevalence of omnivores and herbivores [86]. Increases in water temperature are likely to lead to increases in eutrophication and stratification with a reduction of oxygen in the hypolimnion; such changes may result in the extirpation of salmonids [87]. Therefore, knowledge about food web topology and functioning in high mountain lakes is required in order to allow predictions to be made about how energy flow and food-web interactions could be affected by ongoing climate change.

**Meta-analytic approach**

The outcome of the meta-analysis indicated that the studied lakes had structural food web properties that differed from several North American lakes. The complete food webs in the high mountain lakes were simple compared to those in Little Rock Lake, a mesotrophic and low altitude lake in northern Wisconsin [14], but more complex than those of high mountain lakes in central Sierra Nevada, which had lower richness, linkage density and number of
feeding links between species [15]. On the other hand, the multivariate PCA demonstrated that our pelagic networks were similar to other pelagic systems [15,17–19]. Although our meta-analysis revealed some similarities and dissimilarities in structural network properties between pelagic and complete food webs, the results of the analyses should be taken with some caution because they are focused around a small number of topology metrics based on the number of links and species richness. Future studies might extend the present work to investigate homogeneity among food webs, including observations from more alpine lakes and more metrics. Our findings revealed that when the biota and trophic interactions in the benthic zone are combined with the pelagic food web to provide the complete food web for a lake system, the network properties change. It should, however, be kept in mind that the topology of these alpine lakes was constructed by combining observational data and published literature. Consequently, some of the feeding links between species might not have taken place in the studied lakes. Thus, by including theoretical links from a number of different studies, the number of links and thereby other food web properties (e.g., connectance, linkage density, omnivory, etc) might be overestimated, but our topologies could be used as an initial reference for temperate high-mountain lakes.

Supporting Information
S1 Dataset. Data links of Caballeros food web. Refer to S1 File for food web naming conventions.
(TXT)
S2 Dataset. Data links of Cimera food web. Refer to S1 File for food web naming conventions.
(TXT)
S3 Dataset. Data links of Grande de Gredos food web. Refer to S1 File for food web naming conventions.
(TXT)
S1 File. Data nodes of complete food webs, including list of species and basic information about each nodes.
(XLS)
S2 File. Full reference list used in this study for the food web construction.
(DOCX)
S1 Table. Food web properties used for the comparative study. Richness (S), links (L), linkage density (D) and connectance (C). When the reference includes several values for the same lake, food web properties are shown as average values with the range in parenthesis.
(DOCX)

Acknowledgments
We are very grateful to Ricardo Sánchez Grande, Gustavo de la Fuente Bragado, Manuel Martín Jiménez, Emilio Álvarez Álvarez and María del Carmen Cobo for their field assistance. The authors would like to thank Rosa San Segundo and Félix López (Junta de Castilla y León). Thanks also to Dr. Malcolm Jobling for constructive suggestions and English corrections. We appreciate constructive comments from one anonymous referee, which considerably improved the quality of the manuscript.
Author Contributions
Conceived and designed the experiments: JSH. Performed the experiments: JSH. Analyzed the data: JSH. Contributed reagents/materials/analysis tools: JSH. Wrote the paper: JSH P-AA FC.

References
1. Dunne JA (2009) Food webs. In: Meyers RA editor. Complex Networks and Graph Theory section of the Encyclopedia of Complexity and Systems Science. New York: Springer. pp. 3661–3682.
2. Fagan WF (1997) Omnivory as a stabilizing feature in natural communities. Am Nat 150: 554–567. doi: 10.1086/286081 PMID: 18811300
3. Sánchez-Carmona R, Encina L, Rodríguez-Ruiz A, Rodríguez-Sánchez MV, Granado-Lorencio C (2012) Food web structure in Mediterranean streams: exploring stabilizing forces in these ecosystems. Aquat Ecol 46: 311–324. doi: 10.1007/s10452-012-9400-5
4. Kratina P, LeCraw RM, Ingram T, Anholt BR (2012) Stability and persistence of food webs with omnivory: Is there a general pattern? Ecosphere 3: 50. doi: 10.1890/ES12-00121.1
5. Covich AP, Palmer MA, Crowl TA (1999) The role of benthic invertebrate species in freshwater ecosystems. Bioscience 49: 119–128. doi: 10.1371/journal.pone.0117630 PMID: 25714337
6. Byström P, Karlsson J, Nilsson P, Van Kooten T, Ask J, Olofsson F (2007) Substitution of top predators: effects of pike invasion in a subarctic lake. Freshwat Biol 52: 1271–1280. doi: 10.1111/j.1365-2427.2007.01763.x
7. Rush SA, Paterson G, Johnson TB, Drouillard KG, Haffner GD, Hebert CE, et al. (2012) Long-term impacts of invasive species on a native top predator in a large lake system. Freshwat Biol 57: 2342–2355. doi: 10.1111/fwb.12014
8. Eloranta AP, Kahilainen KK, Amundsen P-A, Knudsen R, Harrold C, Jones RI (2015) Lake size and fish species richness determine resource use by top consumers in subarctic lakes. Ecol Evol 5: 1664–1671.
9. Rodriguez-Lozano P, Verkaik I, Rieradevall M, Prat N (2015) Small but Powerful: Top Predator Local Extinction Affects Ecosystem Structure and Function in an Intermittent Stream. PLoS ONE 10(2): e0117630. doi: 10.1371/journal.pone.0117630 PMID: 25714337
10. Lampman G, Makarewicz JC (1999) The Phytoplankton Zooplankton Link in the Lake Ontario Food Web. J Great Lakes Res 25: 239–249. doi: 10.1016/S0380-1330(99)70733-1
11. Vadeboncoeur Y, Vander Zanden MJ, Lodge DM (2002) Putting the lake back together: Reintegrating benthic pathways into lake food web models. BioScience 52: 44–54. doi: 10.1641/0006-3568(2002)052[0044:PTLBTR]2.0.CO;2
12. Vander Zanden MJ, Vadeboncoeur Y (2002) Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83: 2152–2161. doi: 10.1890/0012-9658(2002)083[2152:FIAIBP]2.0.CO;2
13. Lazzaro X, Lacroix G, Gauzens B, Gignoux J, Legendre S (2009) Predator foraging behaviour drives food-web topological structure. J Anim Ecol 78: 1307–1317. doi: 10.1111/j.1365-2656.2009.01588.x PMID: 19619219
14. Martinez ND (1991) Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. Ecol Monogr 61: 367–392. doi: 10.2307/2897047
15. Havens K (1992) Scale and structure in natural food webs. Science 257: 1107–1109. doi: 10.1126/science.257.5073.1107 PMID: 17840281
16. Harper-Smith S, Berlow E, Knapp R, Williams R, Martinez ND (2005) Communicating ecology through food webs: Visualizing and quantifying the effects of stocking alpine lakes with fish. In: de Ruiter PC, Wolters V, Moore JC editors. Dynamic Food Webs: Multispecies assemblages, ecosystem development and environmental change. San Diego: Academic Press. pp. 407–423.
17. Jonsson T, Cohen JE, Carpenter SR (2005) Food webs, body size, and species abundance in ecological community description. Advan Ecol Res 36: 1–84. doi: 10.1016/S0065-2504(05)36001-6
18. Amundsen P-A, Lafferty KD, Knudsen R, Primicerio R, Klemetsen A, Kuris AM (2009) Food web topology and parasites in the pelagic zone of a subarctic lake. J Anim Ecol 78: 563–572. doi: 10.1111/j.1365-2656.2008.01518.x PMID: 19175443
19. Amundsen P-A, Lafferty KD, Knudsen R, Primicerio R, Kristoffersen R, Klemetsen A, Kuris AM (2013) New parasites and predators follow the introduction of two fish species to a subarctic lake: implications for food-web structure and functioning. Oecologia 171: 993–1002. doi: 10.1007/s00442-012-2461-2 PMID: 23053223
20. Eloranta AP, Knudsen R, Amundsen P-A (2013) Niche segregation of coexisting Arctic charr (Salvelinus alpinus) and brown trout (Salmo trutta) constrains food web coupling in subarctic lakes. Freshwat Biol 58: 207–221. doi: 10.1111/fwb.12052
21. Morales-Baquero R, Carrillo P, Cruz-Pizarro L, Sánchez-Castillo P (1992) Southernmost high mountain lakes in Europe (Sierra Nevada) as reference sites for pollution and climate change monitoring. Limnetica 8: 39–47.
22. Modenutti BE, Balseiro EG, Queimaliños CP, Añón Suárez DA, Diéguez MC, Albariño RJ (1998) Structure and dynamics of food webs in Andean lakes. Lakes & Reservoirs: Res Manage 3: 179–186. doi: 10.1046/j.1440-1770.1998.00071.x
23. Tiberti R (2011) Ecology of Alpine lakes in Gran Paradiso National Park. Ph.D. Thesis, The University of Pavia.
24. Strakařová V, Callieri C, Carrillo P, Cruz-Pizarro L, Fott J, Hartman P, et al. (1999) Investigations on pelagic food webs in mountain lakes—aims and methods. J Limnol 58: 77–87. doi: 10.4081/jlimnol.1999.77
25. Strakařová V, Fott J, Hartman P, Macek M, Nedoma J, Šimek K, et al. (2000) Structure of pelagic food webs in low-alkalinity lakes—forested and alpine catchments. Silva Gabreta 4: 199–212.
26. McNaught AS, Schindler DW, Parker BR, Paul AJ, Anderson RS, Donald DB, et al. (1999) Restoration of the food web of an alpine lake following fish stocking. Limnol Oceanogr 44: 127–136. doi: 10.4319/lo.1999.44.1.0127
27. Tiberti R, Brighenti S, Iacobuzio R, Rolla M, Pasquini G (2014a) Behind the impact of introduced trout in high altitude lakes: adult, not juvenile fish are responsible of the selective predation on crustacean zooplankton. J Limnol 73: 593–597. doi: 10.4081/jlimnol.2014.969
28. Tiberti R, von Hardenberg A, Bogliani G (2014b) Ecological impact of introduced fish in high altitude lakes: a case of study from the European Alps. Hydrobiologia 724: 1–19. doi: 10.1007/s10750-013-1696-1
29. Pedraza J, Carrasco RM, Domínguez-Villar D, Villa J (2013) Late Pleistocene glacial evolutionary stages in the Gredos Mountains (Iberian Central System). Quat Int 302: 88–100.
30. Toro M, Granados I, Robles S, Montes C (2006) High mountain lakes of the Central Range (Iberian Peninsula): Regional limnology & environmental changes. Limnetica 25: 217–252.
31. Toro M, Granados I (2001) Las lagunas de la Sierra de Gredos. Monografías de la Red de Espacios Naturales de Castilla y León. Valladolid: Junta de Castilla y León. (In Spanish)
32. Sánchez-López G, Hernández A, Pla-Rabés S, Toro M, Granados I, Sigó J, et al. (2015) The effects of the NAO on the ice phenology of Spanish alpine lakes. Clim Change 130: 101–113. doi: 10.1007/s10584-015-1353-y
33. Aldasoro J, de Hoyos C, Vega JC, Vicuña BG (1984) Comunidades de plantas macrófitas y de crustáceos en las lagunas de Montaña del NW de España Limnetica 1: 111–115. (In Spanish with abstract in English)
34. Aldasoro JJ, Toro M (2001) La vegetación acuática de las lagunas de la Sierra de Gredos. In: Toro M, Granados I editors. Las lagunas de la Sierra de Gredos. Monografías de la red de espacios naturales de Castilla y León. Valladolid: Junta de Castilla y León. pp. 67–77. (In Spanish)
35. Granados I, Toro M (2000) Recent warming in a high mountain lake (Laguna Cúmera, Central Spain) inferred by means of fossil chironomids. J Limnol 59: 109–119. doi: 10.4081/jlimnol.2000.s1.109
36. Fernández-P, Vilanova RM, Grimault JO (1999) Sediment fluxes of polycyclic aromatic hydrocarbons in European high altitude mountain lakes. Environ Sci Technol 33: 3716–3722. doi: 10.1021/es9904639
37. Robles S, Rodríguez JM, Granados I, Guerrero MC (2000) Sulphite-reducing clostridia in the sediment of a high mountain lake (Laguna Grande, Gredos, Spain) as indicators of faecal pollution. Internati Microbiol 3: 187–191.
38. Toro M, Flower RJ, Rose N, Stevenson AC (1993) The sedimentary record of the recent history in a high mountain lake in Central Spain. Verh Internat Verein Limnol 25: 1108–1112.
39. Martínez-Sanz C, Fernández-Aláez C, García-Criado F (2012) Richness of littoral macroinvertebrate communities in mountain ponds from NW Spain: what factors does it depend on? J Limnol 71: 154–163. doi: 10.4081/jlimnol.2012.e16
40. Sánchez-Hernández J (2009) Nuevas aportaciones a la comunidad bentónica de las lagunas de la Sierra de Gredos. Cuadernos Abulenses 38: 197–203. (In Spanish with abstract in English)
41. Tachet H, Richoux P, Bourmaud M, Usseglio-Polatera P (2002) Invertebratébrés d'eau douce. Systématique, biologie, écologie. Paris: CNRS Editions. (In French)
42. Merritt RW, Cummins KW (1996) An introduction to the aquatic insects of North America. Dubuque: Kendall/Hunt Publishing Company.
43. Lacasse S, Magnan P (1992) Biotic and abiotic determinants of the diet of the brook trout, Salvelinus fontinalis, in lakes of the Laurentian Shield. Can J Fish Aquat Sci 49: 1001–1009. doi: 10.1139/f92-112
44. Cavalli L, Chappaz R, Bouchard P, Brun G (1997) Food availability and growth of the brook trout, *Salvelinus fontinalis* (Mitchill), in a French alpine lake. Fisheries Manag Ecol 4: 167–177. doi: 10.1046/j.1365-2400.1997.00116.x

45. Cavalli L, Chappaz R, Gilles A (1998) Diet of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) in sympatry in two high altitude alpine lakes. Hydrobiologia 86: 9–17. doi: 10.1023/A:1003466725314

46. Sánchez-Hernández J, Cobo F, González MA (2007) Biología y la alimentación del salvelino, *Salvelinus fontinalis* (Mitchill, 1914), en cinco lagunas glaciares de la sierra de Gredos (Ávila, España). NACC 16: 129–144. (In Spanish with abstract in English)

47. Lizana M, Ciudad MJ, Pérez-Mellado V (1986) Uso de los recursos tróficos en una comunidad ibérica de anfibios. Rev Esp Herpetol 1: 207–211. (In Spanish)

48. Guerrero F, Perez-Mellado V, Gil MJ, Lizana M (1990) Food habits and trophic availability in the high mountain population of the spotted salamander from Spain (*Salamandra salamandra almanzor*) (Caudata: Salamandridae). Fol Zool 89: 841–853.

49. Lizana M (1990) Ecología de Bufo bufo en la Sierra de Gredos. Ph.D. Thesis, The University of Salamanca. (In Spanish)

50. Barrabin JM (2000) The rotifers of Spanish reservoirs: Ecological, systematical and zoogeographical remarks. Limnetica 19: 91–167.

51. Gulati RD, Bronkhorst M, van Donk E (2001) Feeding in *Daphnia galeata* on Oscillatoria limnetica and detritus derived from it. J Plankton Res 23: 705–718. doi: 10.1093/plankt/23.7.705

52. García-Chicote J, Rojo C, Rodrigo MA (2007) Alimentación de Acanthocylops robustus: Un caso de canibalismo. Limnetica 26: 265–276. (In Spanish with abstract in English)

53. Sutton MF (1951) On the food, feeding mechanism and alimentary canal of Corixidae (Hemiptera, Heteroptera). Proc Zool Soc Lond. 121: 465–499. doi: 10.1111/j.1096-3647.1951.tb00749.x

54. López-Rodríguez MJ, Tiemo de Figueroa JM (2006) Estudio de la dieta ontogénesis de la ninfa de *Protonemura meyeri* (Piclet, 1842) (Pieoptera, Nemouridae) en Río Blanco (Granada, España). Acta Granatense 4/5: 41–44. (In Spanish with abstract in English)

55. Wehr JD, Sheath RG (2003) Freshwater Algae of North America, Ecology and Classification. San Diego: Academic Press.

56. Guiry MD, Guiry GM (2014) AlgaeBase. World-wide electronic publication. Galway: National University of Ireland. Available: http://www.algaebase.org

57. Kampe H, König-Rinke M, Petzoldt T, Benndorf J (2007) Direct effects of *Daphnia*-grazing, not informational, mediate a shift towards large inedible colonies of the gelatinous green alga *Sphaerocystis schroeteri*. Limnologica 37: 137–145. doi: 10.1016/j.limno.2007.01.001

58. Romani AM, Fischer H, Mille Lindblom C, Tranvik LJ (2006) Interactions of bacteria and fungi on decomposing litter: differential extracellular enzyme activities. Ecology 87: 2559–2569. doi: 10.1890/0012-9658(2006)87[2559:IOBAFO]2.0.CO;2 PMID: 17089664

59. Williams RJ (2010) Network3D [computer program]. Cambridge: Microsoft Research.

60. Yoon I, Williams RJ, Levine E, Yoon S, Dunne JA, Martinez ND (2004) Webs on the Web (WoW): 3D visualization of ecological networks on the WWW for collaborative research and education. Proc. SPIE 5295, Visualization and Data Analysis 5295: 124–132. doi: 10.1117/12.526956

61. Yoon I, Williams RJ, Levine E, Yoon S, Dunne JA, Martinez ND (2004) Webs on the Web (WoW): 3D visualization of ecological networks on the WWW for collaborative research and education. Proc. SPIE 5295, Visualization and Data Analysis 5295: 124–132. doi: 10.1117/12.526956

62. Yoon I, Williams RJ, Levine E, Yoon S, Dunne JA, Martinez ND (2004) Webs on the Web (WoW): 3D visualization of ecological networks on the WWW for collaborative research and education. Proc. SPIE 5295, Visualization and Data Analysis 5295: 124–132. doi: 10.1117/12.526956

63. Yoon I, Williams RJ, Levine E, Yoon S, Dunne JA, Martinez ND (2004) Webs on the Web (WoW): 3D visualization of ecological networks on the WWW for collaborative research and education. Proc. SPIE 5295, Visualization and Data Analysis 5295: 124–132. doi: 10.1117/12.526956

64. Yoon I, Williams RJ, Levine E, Yoon S, Dunne JA, Martinez ND (2004) Webs on the Web (WoW): 3D visualization of ecological networks on the WWW for collaborative research and education. Proc. SPIE 5295, Visualization and Data Analysis 5295: 124–132. doi: 10.1117/12.526956

65. Yoon I, Williams RJ, Levine E, Yoon S, Dunne JA, Martinez ND (2004) Webs on the Web (WoW): 3D visualization of ecological networks on the WWW for collaborative research and education. Proc. SPIE 5295, Visualization and Data Analysis 5295: 124–132. doi: 10.1117/12.526956

66. Yoon I, Williams RJ, Levine E, Yoon S, Dunne JA, Martinez ND (2004) Webs on the Web (WoW): 3D visualization of ecological networks on the WWW for collaborative research and education. Proc. SPIE 5295, Visualization and Data Analysis 5295: 124–132. doi: 10.1117/12.526956

67. Clesse D, Dufour AB, Thioulouze J (2004) The ade4 package—a: One-table methods. R News 4: 5–10.

68. Thioulouze J, Prin Y, Duponnois R (2012) Multivariate analyses in soil microbial ecology: a new paradigm. Environ. Ecol Stat 19: 490–499. doi: 10.1007/s10651-012-0198-z
69. Ihaka R, Gentleman R (1996) R: a language for data analysis and graphics. J Comput Graph Stat 5: 299–314. doi: 10.1080/10618600.1996.10474713
70. Thioloule J, Chessel D, Dolédec S, Olivier J-M (1997) ADE-4: a multivariate analysis and graphical display software. Statist Comput 7: 75–83. doi: 10.1023/A:10185135.0268
71. Tronstad L, Hall RO, Koel TM Jr, Gerow KG (2010) Introduced Lake Trout Produced a Four-Level Trophic Cascade in Yellowstone Lake. Trans Am Fish Soc 139: 1536–1550. doi: 10.1577/T09-151.1
72. Klemetsen A, Amundsen P-A, Dempson JB, Jonsson B, Jonsson N, O’Connell MF, et al. (2003) Atlantic salmon, Salmo salar L., brown trout, Salmo trutta L., and Arctic charr, Salvelinus alpinus L.: A review of aspects of their life histories. Ecol Freshwat Fish 12: 1–59. doi: 10.1034/j.1600-0633.2003.00010.x
73. Sánchez-Hernández J, Amundsen P-A (2015) Trophic ecology of brown trout (Salmo trutta L.) in subarctic lakes. Ecol Freshwat Fish 24: 148–161. doi: 10.1111/eff.12139
74. Vadas RL Jr (1990) The importance of omnivory and predator regulation of prey in freshwater fish assemblages of North America. Environ Biol Fish 27: 285–30. doi: 10.1007/BF00002747
75. Thompson R, Hemberg M, Starzomski BM, Shurin J (2007) Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. Ecology 88: 612–617. doi: 10.1890/05-1454 PMID: 17503589
76. Alcorlo P, Baltanás A, Montes C (2001) Food-web structure in two shallow salt lakes in Los Monegros (NE Spain): energetic vs dynamic constraints. Hydrobiologia 466: 307–316. doi: 10.1023/A:1014594408119
77. Havens KE, Bull LA, Warren GL, Crisman TL, Philips EJ, Smith JP (1996) Food web structure in a subtropical lake ecosystem. Oikos 75: 20–32. doi: 10.2307/3546317
78. Sprules WG, Bowerman JE (1988) Omnivory and food chain length in zooplankton food webs. Ecology 69: 418–426. doi: 10.2307/1940440
79. Coll M, Schmidt A, Romanuk T, Lotze HK (2011) Food-Web Structure of Seagrass Communities across Different Spatial Scales and Human Impacts. PLoS ONE 6: e22591. doi: 10.1371/journal.pone.0022591 PMID: 21811637
80. Ciltherow LR, Carrievick JL, Brown LE (2013) Food Web Structure in a Harsh Glacier-Fed River. PLoS ONE 8:e60899. doi: 10.1371/journal.pone.0060899 PMID: 23613751
81. Hellmann C, Wissel B, Winkelmann C (2013) Omnivores as seasonally important predators in a stream food web. Freshw Sci 32: 548–562. doi: 10.1899/12-020.1
82. Pimm SL (1980) Food web design and the effects of species deletion. Oikos 35: 139–149.
83. McCann KS (2012) Food Webs. Monographs in Population Biology. New Jersey: Princeton University Press. 256 pp.
84. Parker SM, Huryn AD (2013) Disturbance and productivity as codeterminants of stream food web complexity in the Arctic. Limnol Oceanogr 58: 2158–2170. doi: 10.4319/lo.2013.58.6.2158
85. Layer K, Hildrew AG, Jenkins GB, Riede JO, Rossiter SJ, Townsend CR, et al. (2011) Long-term dynamics of a well-characterised food web: Four decades of acidification and recovery in the broadstone stream model system. Advan Ecol Res 44: 69–117. doi: 10.1016/S978-0-12-374794-5.00002-X
86. Doi H, Vander Zanden MJ, Hillebrand H (2012) Shorter Food Chain Length in Ancient Lakes: Evidence from a Global Synthesis. PLoS ONE 7(6): e37856. PMID: 22701583
87. Hobbie JE, Peterson BJ, Bettez N, Deegan L, O’Brien WJ, Kling GW, et al. (1999) Impact on global change on the biogeochemistry and ecosystems of an arctic freshwater system. Polar Res 18: 207–214.