Dietary patterns of five freshwater fish species in a large Mediterranean lake

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ABSTRACT
The diet of five freshwater fish species of Lake Trichonis, the largest natural lake of Greece, was studied. Specifically, the studied species were \textit{Atherina boyeri}, \textit{Luciobarbus albanicus}, \textit{Leucos panosi}, \textit{Scardinius acarnanicus} and \textit{Tropidophoxinellus hellenicus}. The diet analysis was based on stomach content analysis of seasonal samples collected during 2019 by experimental Nordic multimesh gill-nets. Additionally, trophic indices were estimated (Shannon-Wiener, Levins’, Schoener, Trophic level) so as to investigate each species’ feeding diversity, trophic niche breadth, trophic level as well as their trophic competition and overlap. Moreover, the annual and the seasonal relative condition factor was estimated. The diet analysis indicated a tendency of the studied species to omnivorous feeding strategy and a seasonal fluctuation in their diet composition. In addition, the estimated trophic indices revealed similar feeding behavior and significant diet overlap between species, suggesting narrow partitioning of the food resources. However, the relative condition factor ranged between 0.973 and 1.041, indicating a state of wellbeing for the fish species and possibly sufficient food availability.

ARTICLE HISTORY
Received 14 October 2021
Accepted 22 January 2022

KEYWORDS
Lake Trichonis; fish species; diet; trophic indices; relative condition factor

Introduction
The knowledge of species diet is important in ecological research as it reveals potential competition for the available food resources and predator-prey interactions which contribute to the understanding of the ecosystem’s structure and the trophic dynamics in the food webs. This has been recognized almost hundred years ago, leading to the development of the scientific field of trophic ecology (Lindeman 1942). Ever since then, several studies have contributed with theoretical background (Hacunda 1981; Carpenter et al. 1985) and a wide variety of methods aiming towards the investigation of the trophic relations (Hyslop 1980; Amundsen and Sánchez-Hernández 2019).
Both advantages and limitations of the stomach analysis method regarding its ease of application, efficiency and accuracy have been extensively analyzed in the literature (i.e. Tirasin and Jørgensen 1999; Ahlbeck et al. 2012; Amundsen and Sánchez-Hernández 2019). The fact that this technique leads to fish losses, the sampling and analysis difficulties (e.g. prey digestion rate), the time required to process the samples, the ontogenetic changes during the individuals’ growth along with the spatial (i.e. region-specific) and temporal (e.g. diurnal activity) changes that can significantly affect the diet of a species (Link and Garrison 2002; Manko 2016), could be considered as limitations. However, the possibilities that the fish diet knowledge provides for the interpretation of the environment, justifies its wide use up today (Amundsen and Sánchez-Hernández 2019).

Except the need for biological understanding, the study of feeding habits can be used to assess changes in abundance and diversity of organisms caused by physical or human related changes, such as climatic or exploitation pressures, producing that way unexpected ‘cascade effects’ (Carpenter et al. 1985; Heath et al. 2013). Since the early 2000s, effective tools (i.e. Ecopath, Ecosim) have been proposed for the construction of food webs in aquatic ecosystems by integrating the plethora of their functional characteristics and thus, attempting to unveil the equilibrium between conservation and sustainable management (Hossain et al. 2010; de Mutsert et al. 2012; Moutopoulou et al. 2018).

During the last years, numerous research initiatives have explored the feeding habits of several greek freshwater fish species (i.e. Leonardos 2008; Kalogianni et al. 2010; Gkenas et al. 2012; Bobori et al. 2013), but recent data show that less than 40% of the species has been studied (Vagenas et al. unpublished data), thus scarce information is available. Moreover, published works that provide information on the species diet and the body condition factor are rather limited in the literature. The aforementioned research gaps stimulated us to explore the combination of feeding habits and the condition factor of five freshwater fish, from Lake Trichonis, the largest natural lake of Greece. The four studied Cyprinidae species *L. albanicus*, *L. panosi*, *S. acarnanicus* and *T. hellenicus* are Greek endemics. In contrast *A. boyeri* is a mainly marine species, landlocked populations of which can be found in some Greek lake ecosystems (Barbieri et al. 2015). A noteworthy fact is that the Cyprinid species and especially *A. boyeri*, attract the scientific interest due to its economic value since it supports a valuable commercial purse-seine fishery in the region (Chrisaﬁ et al. 2007).

In the present study, we assessed seasonal diet patterns and trophic levels for some of the most abundant species in the lake and we estimated the relative condition factor (Kn) which can be derived from the length-weight relationship (Le Cren 1951), a factor utilized as a body health indicator. Throughout the above methodological approach, we attempted to elucidate the underlying feeding interactions of this large multispecies fish aggregation which appear to establish a stable trophic equilibrium.

**Materials & methods**

**Sampling area**

Lake Trichonis is located in the Central-Western Greece (38° 15’N, 21° 30’E) and is the largest national natural lentic ecosystem (Figure 1). The maximum depth of the lake is 58 m, the lake area is around 96.9 km² and the catchment area exceeds 420 km² (Zacharias et al. 2002; Chrisaﬁ et al. 2007). It is described as an oligotrophic, warm monomictic lake with a long period of thermal stratification (Kehayias and Doulka 2014) and belongs to the NATURA 2000 network of protected environmental sites (92/34/EEC).
Fish samplings were seasonally (February, May, August, November) conducted in Lake Trichonis during 2019 within the framework of the ‘ANATHALLOI’ Project, by experimental multi-mesh Nordic gillnets (5–55 mm; height 1.5–6 m; length 27.5–30 m). The gill-nets were set in the late in the afternoon and they were retrieved the very next dawn. All caught specimens were frozen and transfer to the lab where they were identified to species level, measured for their total length (TL, mm) and weight (W, mm).

Overall, the stomach contents of 697 fish specimens were examined. A larger number of specimens per species was also used for estimating the relative condition factor (in total 6493 specimens, see below). For the diet analysis, the gastro-internal tract of subsamples of the species Atherina boyeri (Risso 1810), Luciobarbus albanicus (Steindachner 1870), Leucos panosi (Bogutskaya and Iliadou 2006), Scardinius acarunicus (Economidis 1991), Tropidophoxinellus hellenicus (Stephanidis 1971) was removed and stored in a 4% formaldehyde solution for further examination.

Diet analyses

During the gastro-internal tract examination, each prey type was taxonomically identified with the use of classification keys (Tachet et al. 2000; Patsia 2009) and weighed to the nearest 0.001 g. In species that lack a well-defined stomach (i.e. Cyprinidae), the intestinal bulb or pseudo-gaster was examined in order to determine the feeding habits (Ray and Ringø 2014). The proportion of empty stomachs was calculated as the ratio between the number of empty and the number stomachs in total (vacuity index (VI%); Hureau 1966). The variation of the vacuity index was tested with the use of the non-parametric $\chi^2$ test (based on 999 Monte-Carlo simulations) on the number of the empty stomachs per species. In order to verify whether if the number of stomachs was sufficient, we produced species-specific cumulative prey curves (CPCs) for the variety of the observed prey types.
The CPCs were based on randomly pooled stomachs so as to avoid biased outcomes (Matić-Skoko et al. 2014).

To proceed in a thorough approach of the species diet, all types of prey were recorded according to their numerical abundance (N%), weight (W%) and frequency of occurrence (F%) (Amundsen and Sánchez-Hernández 2019). Numerical abundance was approximately estimated, especially in consumed plant material due to difficulties caused by organisms’ mastication or digestion. Thus, a record was documented when a relatively intact prey type was observed. Subsequently, the standardized Index of Relative Importance (IRI) of each prey was calculated for each prey type $i$ as follows (Manko 2016):

$$IRI_i = (N_i\% + W_i\%)*F_i\%$$

The widely used Index of Relative Importance has been under criticism since it represents a compound index of metrics that does not express percentages of prey types (Liao et al. 2001). In order to overcome this problem, we estimated the proportional form of the index ($IRI_i\%$) according to the following formula:

$$IRI_i\% = 100\*\frac{IRI_i}{\sum_{i=1}^{n} IRI_i}$$

where $IRI_i$ represents the index of relative importance for prey type $i$ and $n$ is the total number of prey types at a given taxonomic level (Manko 2016 and references therein). Moreover, we attempted to reduce the dimensionality of the system with the use of a Principal Component Analysis (PCA) so as to explore the relationship between the values of $IRI_i\%$ and the prey types for each species.

Feeding strategy (i.e. generalized or specialized) and prey importance (i.e. rare or dominant) has been depicted in a Costello graph (Costello 1990), which is used to represent the percentage of frequency of occurrence (F%) and the percentage of the total stomach content mass (W%) of each prey in the diet of the examined species (Karachle and Stergiou 2014). Regarding the feeding indices, the diet diversity of the collected species was initially estimated with the Shannon-Wiener index ($H'$) (Shannon and Weaver 1949; Iglesias-Rios and Mazzoni 2014) according to the following equation:

$$H' = -\sum_{i=1}^{K} P_i \log_e(P_i)$$

where $K$ is the total number of prey categories and $P_i$ is the frequency of occurrence of food item $i$ in the diet of species. For the estimation of the food niche breadth the Levins’ normalized index ($B_n$) has been used, a useful tool that indicates both the number of the consumed resources and the relative frequency of each prey (Levins 1968):

$$B_n = \frac{1}{R} \sum_i p_i^2$$

where $R$ is the range of the available resource types and $p_i$ is the frequency proportion out of all the resources used by the fish population that consumes items of prey type $i$. The $B_n$ index varies from 0 when the species utilizes a unique resource type exclusively (specialists), to 1 when the species uses all resource types (generalist) equally (Feinsinger et al. 1981). Diet overlap between species was estimated with the Schoener’s Index ($S$; Schoener 1970):
\[ S = 1 - \frac{1}{2} \left( \sum_{i=1}^{n} |p_{xi} - p_{yi}| \right) \]

where \( p_{xi} \) and \( p_{yi} \) represent the weight proportions of prey \( i \) found in the stomachs of species \( x \) and \( y \), while \( n \) expresses the total number of prey types in both species. The pair-species values are displayed in a comparison matrix whereas \( S \) index ranges from 0 (\( x \) and \( y \) consume completely different resources) to 1 (\( x \) and \( y \) consume proportionally equally common resources). A significant diet overlap occurs when the \( S \) value is larger than 0.6 (Wallace and Ramsey 1983; Karachle 2017). Finally, the trophic level (\( \tau \)) of each species was estimated using the routine for quantitative (W\%) data in Trophlab (Pauly et al. 2000):

\[ \tau_i = 1 + \sum_{j=1}^{G} (DC_{ij} \cdot \tau_j) \]

where \( \tau_j \) is the trophic level of prey \( j \), \( DC_{ij} \) represents the proportion of \( j \) in the diet of species \( i \) and \( G \) is the total number of prey species (Gascuel et al. 2011). All the aforementioned analyses and produced graphs were performed through the R-v4.0.5 open access statistical language and its subsequent packages (R Core Team 2021).

**Relative condition factor**

The relative condition factor (\( K_n \)) is defined as the ratio \( W/W_e \), where \( W \) is the observed weight of a fish at a given length and \( W_e \) is the predicted weight derived from the length-weight relationships (Le Cren 1951), as estimated in Tsionki et al. (2021). A fish is in good growth condition when \( K_n \geq 1 \), while it is in poor growth condition when \( K_n < 1 \) (Jisr et al. 2018). We estimated the seasonal and annual \( K_n \) for the examined species, except for \( L. albanicus \) for which only the annual \( K_n \) was estimated since seasonal samples were not sufficient. The data of each species approached normal distribution (Kolmogorov-Smirnov normality test; \( p > 0.05 \)) and the statistical differences in \( K_n \) between seasons were tested using a one-way Analysis of Variance (one-way ANOVA). Moreover, the 95% confidence intervals of \( K_n \) were estimated.

**Results**

As already mentioned, 697 fish were examined, though discrete content prey was included in the stomachs of 372 individuals. The total length of these 372 individuals ranged from 6.8 to 47.6 cm for \( L. albanicus \) (sample size; \( N = 73 \)), 6.3–29.1 cm for \( L. panosi \) (\( N = 88 \)), 7.7–43.6 cm for \( S. acarnanicus \) (\( N = 82 \)), 5.2–11.5 cm for \( T. hellenicus \) (\( N = 61 \)) and 5.5–11.6 cm for \( A. boyeri \) (\( N = 68 \)) (Table 1). The mean value of the VI\% index for all species was calculated at 45.6%. The minimum and the maximum VI\% were recorded for \( L. albanicus \) (34.2\%) and \( T. hellenicus \) (54.8\%) respectively, while \( A. boyeri \) (42.8\%) \( S. acarnanicus \) (45.7\%) and \( L. panosi \) (50.8\%) exhibited intermediate proportions. According to the results of the \( \chi^2 \) test, there was not a statistically significant difference between the proportions of the empty stomachs of the species (\( p = 0.253 > 0.05 \)). The CPCs reached a threshold, or close to a stable level (>80–90\% prey included) in cases with accidental or sparse prey types, at about 50 stomachs for \( T. hellenicus \) and \( A. boyeri \) and at 65 for \( L. albanicus \), \( L. panosi \) and \( S. acarnanicus \) (Figure 2). Hence, the sample size can be considered as sufficient enough to describe the diet of the species.
Table 1. Total annual estimation of trophic indices (N: numeric; W: weight; f: Frequency; IRI: index of relative importance) in the five examined species in Lake Trichonis per prey category.

| Species Prey type | Luciobarbus albanicus | Leucos panosi | Scardinius acarnanicus | Tropidophoxinellus hellicus | Atherina boyeri |
|-------------------|-----------------------|---------------|-----------------------|-----------------------------|----------------|
| DS                | N (%)                 | W (%)         | f (%)                 | IRI (%)                     | N (%)          |
| Crustacea Total   | 49.5                  | 15.55         | 32                    | 44.28                       | 51.3           |
| Undefined         | 11.45                 | 1.45          | 1.29                  | 16.4                        | 10.9           |
| Gammaridae        | 22.5                  | 4.1           | 14                    | 35.3                        | 26.6           |
| Calanoida         | -                     | -             | -                     | -                           | -              |
| Malacostraca      | 4.25                  | 3.7           | 7                    | 10.29                       | 4.5            |
| Arachnida Total   | 5                     | 0.1           | 2                    | 0.22                        | 0.9            |
| Insecta Total     | 16.5                  | 45.85         | 33                    | 43.77                       | 11.45          |
| Undefined Insecta | 7                     | 6.23          | 7                    | 16.70                       | 5.86           |
| Diptera Total     | 8.5                   | 19.9          | 13                   | 66.58                       | 2              |
| (a)               | 2.6                   | 7.83          | 4                    | 20.51                       | 1              |
| (l)               | 5.9                   | 12.07         | 9                    | 79.49                       | 1              |
| Ephemeropeta      | 0.9                   | 0.5           | 2                    | 0.50                        | -              |
| Baetidae (a)      | -                     | -             | -                     | -                           | -              |
| (l)               | 0.9                   | 0.5           | 2                    | 0.50                        | -              |
| Trichoptera Total | 4.05                  | 6.1           | 6                    | 37.60                       | 2.05           |
| (a)               | -                     | -             | -                     | -                           | -              |
| (l)               | 4.05                  | 6.1           | 6                    | 37.60                       | 1.37           |
| Hymenoptera (a)   | 0.45                  | 0.1           | 1                    | 0.10                        | -              |
| Heteroptera (a)   | 0.9                   | 3.1           | 1                    | 2.11                        | -              |
| Plecoptera (a)    | -                     | -             | -                     | -                           | -              |
| Coleoptera (a)    | -                     | -             | -                     | -                           | -              |
| Lepidoptera (l)   | 2.24                  | 9.42          | 2                    | 3.99                        | -              |
| (l)               | 22.4                  | 9.42          | 2                    | 3.99                        | -              |
| Neuroptera (l)    | 0.6                   | 0.5           | 1                    | 0.64                        | -              |
| Odonata (l)       | -                     | -             | -                     | -                           | -              |
| Turbellaria Total | 0.45                  | 0.1           | 1                    | 0.01                        | -              |
| Oligochaeta Total | 4.5                   | 1.4           | 6                    | 0.75                        | -              |
| Tubificidae       | 0.9                   | 0.3           | 2                    | 11.32                       | -              |
| Hirudinea Total   | -                     | -             | -                     | -                           | -              |
| Polychaeta Total  | 4.1                   | 2.2           | 6                    | 0.80                        | -              |

(continued)
| Species Prey type | Luciobarbus albanicus | Leucos panosi | Scardinius acarnanicus | Tropidophoxinellus hellenicus | Atherina boyeri |
|------------------|------------------------|---------------|------------------------|-----------------------------|----------------|
| DS: development stage; Tot: Total; (a): adult stage; (b): larvae/pupa stage; (t): tadpoles; N: Samples; T range: Total length range (cm); VI: Vacuity Index; τ: Trophic level; H’: Shannon-Wiener Index; Bn: Levins’ normalized Index; S: Schoener’s Index. | N (%) | W (%) | F (%) | IRI (%) | N (%) | W (%) | F (%) | IRI (%) | N (%) | W (%) | F (%) | IRI (%) | N (%) | W (%) | F (%) | IRI (%) |
| Nematoda Total | 1.4 | 0.1 | 1 | 0.03 | 1 | 2.25 | 1.8 | 0.11 | 1 | 2.7 | 1.5 | 0.07 | 1 | 2.7 | 1.5 | 0.07 |
| Plant Total | 14.5 | 15.3 | 15 | 9.5 | 9.5 | 10.85 | 12 | 4.56 | 17.5 | 37 | 42.4 | 47.8 | 28 | 37.1 | 20.8 | 23.72 |
| Undefined Plant | 10.2 | 4.8 | 5 | 60.58 | 3.4 | 0.35 | 2 | 11.28 | 2.35 | 3.8 | 2.8 | 2.52 | 18 | 1.65 | 4.8 | 30.14 |
| Ceratophyllum spp. | 2 | 7 | 4 | 29.08 | 2.55 | 5.4 | 3.5 | 41.84 | 7.35 | 22.55 | 18.2 | 79.65 | 1.9 | 28.75 | 2.8 | 27.22 |
| Myriophyllum spp. | 1.4 | 2.1 | 3 | 8.48 | 2.55 | 3 | 4.5 | 37.55 | 4.15 | 2.3 | 9.4 | 8.87 | 6.5 | 5.6 | 10.4 | 40.06 |
| Vallisneria spp. | 0.45 | 0.7 | 1 | 0.93 | 1 | 2.1 | 2 | 9.32 | 2.75 | 5.5 | 3.6 | 4.35 | – | – | – | – |
| Potamogeton spp. | 0.45 | 0.7 | 1 | 0.93 | – | – | – | – | 0.9 | 2.85 | 8.4 | 4.61 | 1.8 | 1.1 | 2.8 | 2.58 |
| Mollusca Total | 0.95 | 0.1 | 1 | 0.02 | 6.05 | 10.7 | 2.7 | 0.85 | 1.85 | 1.35 | 0.9 | 0.06 | – | – | – | – |
| Bivalvia | 0.95 | 0.1 | 1 | 100 | 5.55 | 4.35 | 1.8 | 74.30 | – | – | – | – | – | – | – | – |
| Gasteropoda (Potamididae) | – | – | – | – | 0.5 | 6.35 | 0.9 | 25.7 | 1.85 | 1.35 | 0.9 | 100 | – | – | – | – |
| Fish Total | 1.1 | 15.1 | 1 | 0.34 | 3.5 | 23 | 1.8 | 0.89 | 6.9 | 43.85 | 4.5 | 4.72 | – | – | – | – |
| (a) | 1.1 | 15.1 | 1 | 100 | 1.2 | 21.3 | 0.9 | 84.91 | 5.05 | 43.7 | 3.6 | 98.98 | – | – | – | – |
| (b) | – | – | – | – | 2.3 | 1.7 | 0.9 | 15.09 | 1.85 | 0.15 | 0.9 | 1.02 | – | – | – | – |
| Amphibia Total | 2 | 4.2 | 2 | 0.26 | 1 | 0.85 | 0.9 | 0.03 | 2.75 | 2.1 | 2.7 | 0.27 | 2.7 | 2.2 | 2.8 | 0.24 |
| N | 73 | 88 | 82 | 61 | 68 |
| T range | 6.8–47.6 | 6.3–29.1 | 7.7–43.6 | 5.2–11.5 | 5.5–11.6 |
| VI % | 34.2 | 50.8 | 45.7 | 54.8 | 42.8 |
| τ | 3.21±0.47 | 3.4±0.54 | 3.31±0.57 | 2.75±0.35 | 2.8±0.39 |
| H’ Index | 1.35 | 1.61 | 1.62 | 0.66 | 0.72 |
| Bn index | 0.399 | 0.359 | 0.301 | 0.236 | 0.128 |
In the stomachs of *L. albanicus* and *L. panosi*, a major presence of aquatic crustaceans was observed with Gammaridae and Atyidae being an important prey of their diet (IRI = 44.3% and IRI = 71.5%, respectively). Aquatic insects (Diptera, Lepidoptera larvae) were also a dominant prey (IRI = 43.8% and IRI = 21.75%, respectively), while both species shared sparse observations of aquatic worm prey (worms; IRI in total <2%). Regarding plant material, macrophytes (mainly *Ceratophyllum* spp. and *Myriophyllum* spp.) contributed in the diet of both species with a relatively equal proportion (Table 1). A significant observation was that the large individuals of both species consumed sporadically adult and juvenile fish (probably *A. boyeri* based on digested tissue remains) and amphibian tadpoles. The diet of *Scardinius acarnanicus* was prevailed with aquatic macrophytes (IRI = 47.8%) whereas *Ceratophyllum* spp. appeared to be the dominant food type (Table 1). Aquatic crustaceans followed as the second major type of prey (IRI = 42%) with relatively less weight and frequency of occurrence compared to plant material. Adult stage aquatic insects contributed also to the diet of the species (IRI = 4.7%) along with some adult and juvenile fish prey (that was found mainly in the largest examined specimens). The data collected from *T. hellenicus* showed that aquatic crustaceans (IRI = 40%) and insects (IRI = 35.37%) were the majority in the species diet, while plant material made a significant contribution as well (IRI = 23.72%). Additionally, a single observation of a digested tadpole was recorded in one of the largest examined specimens. *Atherina boyeri*, displayed the least omnivorous trophic strategy compared to the rest species since Gammaridae, Atyidae, Malacostraca and other aquatic crustacean were the major prey type (IRI=...
89.8%). Insect larvae (IRI = 7.57%) and macrophytes (IRI = 2.1%) were also found in the species stomach contents, with some sparse observations of worms and mollusks as well (IRI < 2%). The Principal Component Analysis reduced this multispecies predator-prey system in two dimensions (Dim1 - Dim2) which collectively explained the 90.7% of the variation of the IRI% (Figure 3). The ordination biplot shows that *S. acarnanicus* and *L. albanicus* are characterized by their orientation towards plant and insect prey type, while *T. hellenicus* and *A. boyeri* demonstrated a feeding profile which is dominant of microcrustacean prey.

Based on the results of the Costello graph (Figure 4) both *L. albanicus* and *L. panosi* exhibited increased weight densities in microcrustacean and insect prey types. On the contrary, plant material appeared as important food item for species *S. acarnanicus*, while some large individuals of the species consumed fish as well. *Atherina boyeri* and *T. hellenicus* demonstrated a common specialization towards microcrustaceans. However, plant and insect prey appeared to be dominant in the case of *T. hellenicus* (Figure 4). The trophic indices of feeding diversity ($H'$) and breadth ($B_n$) of *S. acarnanicus* ($H' = 1.62; B_n = 0.301$), *L. panosi* ($H' = 1.61; B_n = 0.359$) and *L. albanicus* ($H' = 1.35; B_n = 0.399$) displayed the higher values, while of *A. boyeri* ($H' = 0.72; B_n = 0.128$) and *T. hellenicus* ($H' = 0.66; B_n = 0.236$) the lower (Table 1). The estimated trophic levels of *L. panosi* and

![Figure 3. Histogram of eigenvalues (top-left) and the ordination biplot produced by the Principal Component Analysis (PCA) for the relationship between the proportions of the index of relative importance (IRI%) for each prey items (cross) of the species Luciobarbus albanicus (A; N = 73), Leucos panosi (B; N = 88), Scardinius acarnanicus (C; N = 82), Tropidophxinellus hellenicus (D; N = 61), Atherina boyeri (E; N = 68), from Lake Trichonis.](image-url)
S. acarnanicus was 3.4 (± 0.54) and 3.31 (± 0.57), respectively (Table 1). Luciobarbus albanicus showed a relatively large trophic level value i.e. 3.21 (± 0.47), while the trophic level values estimated for species A. boyeri and T. hellenicus were 2.8 (± 0.39) and 2.75 (± 0.35). Schoener’s index (S) ranged from 0.57 to 0.77 (Table 2). The pair-species

Table 2. Schoener’s Index values based on weight proportion (W%) of each prey type displayed in a combination matrix for the five examined fish species of Lake Trichonis.

| Species                  | Leucos panosi | Scardinius acarnanicus | Tropidophoxinellus hellenicus | Atherina boyeri |
|--------------------------|---------------|------------------------|-------------------------------|----------------|
| – Luciobarbus albanicus  | 0.675         | 0.578                  | 0.638                         | 0.584          |
| Leucos panosi            | 0.574         | 0.659                  | 0.582                         | 0.683          |
| Scardinius acarnanicus   | 0.77          | 0.692                  |                               |                |
| Tropidophoxinellus hellenicus | 0.77   | 0.692                  |                               |                |

Values larger than 0.6 indicate significant diet overlap (Wallace and Ramsey 1983) and are given in bold.

S. acarnanicus was 3.4 (± 0.54) and 3.31 (± 0.57), respectively (Table 1). Luciobarbus albanicus showed a relatively large trophic level value i.e. 3.21 (± 0.47), while the trophic level values estimated for species A. boyeri and T. hellenicus were 2.8 (± 0.39) and 2.75 (± 0.35). Schoener’s index (S) ranged from 0.57 to 0.77 (Table 2). The pair-species

Figure 4. Costello graphs using total percentage of weight (W%) and frequency of occurrence (F%) contributions of the prey items identified in the annual diet of the examined species: Luciobarbus albanicus (A; N = 73), Leucos panosi (B; N = 88), Scardinius acarnanicus (C; N = 82), Tropidophoxinellus hellenicus (D; N = 61), Atherina boyeri (E; N = 68), from Lake Trichonis (N: sample size). Fish drawings derived from Barbieri et al. (2015).
combination that resulted in the lowest S estimated value was that of *L. panosi* and *S. acarnanicus* ($S = 0.57$), while *T. helenicus* and *S. acarnanicus* had the highest ($S = 0.77$).

The diet analysis results per sampling season are provided in Table 3. In spring both *L. albanicus* and *L. panosi* showed a common pattern where both found to consume mainly insects ($W = 34.5\%$; $24.6\%$, respectively), plants ($W = 6\%$; $12.4\%$, respectively) while juvenile fish found to be in high proportions ($W = 39.3\%$; $38.6\%$, respectively). *Scardinius acarnanicus* showed high values in the fish remnants ($W = 72.5\%$). However, the fish remnants found in the three species were a minor observation based on the frequency of occurrence ($F\%$) since they were consumed by a few large individuals. *Tropidophoxinellus helenicus* consumed aquatic insects ($W = 39.9\%$), crustaceans ($W = 22.5\%$) and worms ($W = 22.3\%$) along with some plant tissues ($W = 10.3\%$). For the spring season, the diet of *Atherina boyeri* was dominant from aquatic crustaceans ($W = 61\%$), plants ($W = 22.5\%$) and worms ($W = 16.5\%$). The summer samples differentiate the previous pattern. In particular, crustaceans ($W = 63.5\%$) was the main prey type consumed by *L. panosi* while *L. albanicus* appeared to have a feeding breadth comprised of aquatic insects ($W = 34.4\%$), plant material ($W = 26.15\%$) and crustaceans ($W = 23.1\%$) as well. The species *S. acarnanicus* and *T. helenicus* consumed mainly aquatic crustaceans ($W = 44.1\%$; $26.6\%$) and plants ($W = 30.53\%$; $55.2\%$), while in the stomach contents of *A. boyeri* individuals a major predominance of aquatic worms was observed ($W = 84\%$).

In autumn samples, a significant proportional decrease of crustacean prey and an increase of insects have been recorded in the species *L. albanicus*, *L. panosi* and *S. acarnanicus*. *Tropidophoxinellus helenicus* however, displayed a similar profile to the one recorded in the spring samples, while *A. boyeri* was found to consume mainly microcrustaceans ($W = 59.5\%$) and insects ($W = 40.5\%$). In winter samples, crustaceans ($W = 38.6\%$; $48\%$), insects ($W = 43.9\%$; $39.4\%$) and plants ($W = 17.5\%$; $11\%$) was the main food types in both *L. albanicus* and *L. panosi*. *Scardinius acarnanicus* consumed mainly macrophytes ($W = 66.6\%$), whereas *T. helenicus* aquatic insects ($W = 84\%$). *Atherina boyeri* maintained a similar pattern to the one estimated by the autumn samples, with a dominance of crustacean ($W = 54.5\%$) and insects ($W = 31.5\%$). Regarding the trophic level seasonal variation, *S. acarnanicus* and *T. helenicus* exhibited the largest one while the other species showed a relatively homogenous pattern among seasons (Figure 5).

The range of means of the relative condition factor ($K_n$) estimated for the five species ranged between 0.9732 and 1.0411 (Table 4). For the species *T. helenicus* ($F = 0.200; p = 0.896 \gg 0.05$), *S. acarnanicus* ($F = 0.096, p = 0.962 \gg 0.05$), *L. panosi* ($F = 0.150, p = 0.860 \gg 0.05$), *A. boyeri* ($F = 0.189, p = 0.846 \gg 0.05$) no statistically significant seasonal variation was observed (One-Way ANOVA; F-test < F-critical; $p > 0.05$). The factor of season does not influence the $K_n$ for the species *T. helenicus*, *S. acarnanicus*, *L. panosi* and *A. boyeri*.

**Discussion**

In the present study we provide information that concern the diet of five of the most abundant fish species in the largest natural lake of Greece. Stomach content analysis was performed and also trophic indices were estimated to investigate the feeding diversity, breadth, trophic level and diet overlap between the species. Concurrently, we provide seasonal data on their diet in order to highlight potential fluctuations of feeding shifts throughout the period of a year. The wide range of the caught specimen’s total length (Table 1) was a result of the specific type of the multimesh gillnets that were used. In
Table 3. Seasonal variation of feeding habits for the five examined species per feeding prey, their trophic level estimation by using weight (W%) proportion estimation (SP: spring; SU: summer; AU: autumn; WI: winter; N: Samples; VI: Vacuity Index).

| Species          | Season | Prey items | Luciobarbus albanicus | Leucos panosi | Scardinius acamanicus | Tropidophoxinellus hellenicus | Atherina boyeri |
|------------------|--------|------------|-----------------------|---------------|-----------------------|-----------------------------|---------------|
|                  |        |            | SP        | SU        | AU        | WI        | SP        | SU        | AU        | WI        | SP        | SU        | AU        | WI        | SP        | SU        | AU        | WI        |
| Crustacea        |        |            | 8         | 23.1      | 14.6      | 38.6      | 0.15      | 44.1      | 28.3      | 11.6      | 22.5      | 26.6      | 25.13     | 8          | 61        | 14.6      | 59.5      | 54.5      |
| Arachnida        |        |            | –         | 1.5       | –         | –         | –         | –         | –         | –         | –         | –         | –         | –          | –         | –         | –         | –         |
| Insecta          |        |            | 34.5      | 34.4      | 53.1      | 43.9      | 24.6      | 5         | 22.5      | 39.4      | 0.4       | 2.91      | 14.6      | 21        | 39.9      | 3.8       | 84        | –         | –         |
| Turbelaria       |        |            | –         | 1.7       | –         | –         | 5.5       | –         | –         | –         | –         | –         | –         | –          | –         | –         | –         | –         |
| Oligochaeta      |        |            | 2.7       | 1.4       | 0.8       | –         | –         | –         | –         | 0.15      | –         | –         | –         | –          | –         | –         | –         | –         |
| Hirudinea        |        |            | –         | –         | –         | –         | –         | –         | –         | –         | –         | –         | –         | –          | –         | –         | –         | –         |
| Polychaeta       |        |            | –         | 11.3      | 4        | –         | 11.8      | 5.9       | –         | 1         | –         | –         | –         | 2.8        | –          | –         | –         | –         |
| Nematoda         |        |            | –         | –         | –         | –         | –         | –         | –         | –         | –         | –         | –         | –          | –         | –         | –         | –         |
| Plant            |        |            | 6         | 26.15     | 20       | 17.5      | 12.4      | 7.7       | 5.3       | 11        | 27        | 30.53     | 38        | 66.6       | 10.3      | 52.2      | 68.3      | 2.5       |
| Mollusca         |        |            | –         | 0.45      | 6.4      | –         | 17.7      | 6.5       | 36.1      | 11        | 27        | 30.53     | 38        | 66.6       | 10.3      | 52.2      | 68.3      | 2.5       |
| Fish             |        |            | 39.3      | –         | –         | –         | 38.6      | 6         | –         | –         | 72.5      | 8.65      | 1.2       | –          | –         | –         | –         | –         | –         |
| Amphibia         |        |            | 9.5       | 1.5       | –         | –         | 1.55      | –         | –         | –         | 125       | 2.5       | 0.8       | –          | –         | –         | –         | 5.5       |
| N                |        |            | 15        | 15        | 34        | 9         | 27        | 19        | 20        | 22        | 18        | 21        | 23        | 20        | 16        | 6         | 18        | 21        | 17        |
| VI %             |        |            | 37.5      | 34.7      | 33.3      | 30.7      | 43.7      | 52.5      | 47.3      | 56.8      | 47        | 41.6      | 47.3      | 56.8      | 50        | 60        | 58.1      | 53.3      | 33.3      | 31.2      | 37.5      | 56.8      |
particular, this gillnet type was initially designed to provide a representative picture of the fish community structure of lake ecosystems (Appelberg et al. 1995). The diet of species *L. albanicus* and *L. panosi* was based on aquatic microcrustaceans and insects. Both species exhibited relatively equally high trophic indices (regarding feeding diversity, trophic breadth and trophic level) and significant trophic overlap (Table 2: Schoener’s index >0.6; Wallace and Ramsey 1983). In particular, they exhibited the largest and the most variant utilization of resources a fact that ranked them among the generalists of the studied fish species, thus justifying the higher number of stomachs required to describe of their diet compared to *T. hellenicus* and *A. boyeri* (Figure 2). The more detailed comparison between the species based on the PCA ordination plot and the Costello graph demonstrated that both species consumed prey types (e.g. microcrustacean & aquatic insects) of similar trophic position (Figures 3 and 4). To the best of our knowledge, there is no published information regarding the diet of *L. albanicus* and *L. panosi*, except qualitative records concerning the consumed items of both species which refer the dominance of plant material and zoobenthic prey (Kottelat and Freyhof 2007; Froese and Pauly 2021). The trophic level estimated here for both species was 0.5 units higher than the one registered in FishBase (Froese and Pauly 2021).

Figure 5. Box and whisker plot of the seasonal (spring, summer, autumn, winter) variation of the trophic level based on the diet of species (*Luciobarbus albanicus* (A; N = 73), *Leucos panosi* (B; N = 88), *Scardinius acarmanicus* (C; N = 82), *Tropidophoxinellus hellenicus* (D; N = 61), *Atherina boyeri* (E; N = 68). Fish drawings derived from Barbieri et al. (2015). Each boxplot expresses the variability of the upper and lower quantile and the middle line represents the median of the distribution.
In general, *S. acarnanicus* exhibited a specialized feeding behavior targeted to plant material, compared to the rest of the species (Figure 3). However, some individuals of *S. acarnanicus* consumed high trophic position prey such as small fish, amphibian tadpoles and microcrustaceans. Therefore, the species showed a quite diverse diet characterized by an increased presence of both plant and animal prey, which was affected by the interannual seasonal succession (Figure 5 and Table 3). A common observation between *S. acarnanicus* and *T. hellenicus* was that both species exhibited a diversity of prey types which can be explained by the significant trophic overlapping (S > 0.6) induced by the availability of food resources (Table 2). Concerning those findings, the trophic level of the species was found relatively higher (s = 3.31) compared to the one that is registered in FishBase (s = 2.00; Froese and Pauly 2021). The piscivorous ability of the species was first observed by Tsounis and Kehayias (2019) who later found that this behavior was more intense in the presence of artificial fishing lights (Tsounis and Kehayias 2021). These results are in total contrast to those of Iliadou (1991) who classified the species as exclusively herbivorous.

*Tropidophoxinellus hellenicus* did not display the same wide feeding breadth as *S. acarnanicus*, since it was more focused on prey items such as insects and microcrustaceans. The estimated indices for the species resulted in a quite limited and non-variant feeding breadth and a relatively low (s = 2.75) trophic level. Our results agree with those of Crivelli (2006) who also confirmed the consumption of plant material and zoobenthos. The trophic level estimation for the species remained almost equal to the one provided in FishBase (τ = 2.7; Froese and Pauly 2021). Besides however the aforementioned differences, *S. acarnanicus* and *T. hellenicus* demonstrated a large and significant feeding overlap (S = 0.77) suggesting interspecific competition for the available resources.

Aquatic microcrustacean was the most important prey type in the diet of *A. boyeri* while the presence of aquatic insects and plant material was occasionally observed. The estimated trophic level for the species did not differ among seasons. According to the estimated trophic indices, the species exhibited a specialized feeding behavior and a relatively significant trophic overlap (S = 0.683) with *S. acarnanicus* (Tables 1 and 2). Our results are partially in agreement with previous works conducted in Lake Trichonis for the

### Table 4. Relative condition factor (Kn) estimated for the five examined species caught in Lake Trichonis, 2019 (N: sample size; SD: standard deviation; CI: confidence interval).

| N    | Species                        | Kn   | SD   | 95 % CI of Kn |
|------|--------------------------------|------|------|---------------|
| 470  | *Scardinius acarnanicus*        | 1.009| 0.123| 0.9979        |
| 117  | Winter                         | 1.008| 0.120| 0.9864        |
| 66   | Spring                         | 1.007| 0.136| 0.9732        |
| 70   | Summer                         | 1.005| 0.102| 0.9808        |
| 217  | Autumn                         | 1.005| 0.100| 0.9915        |
| 317  | *Tropidophoxinellus hellenicus*| 1.009| 0.135| 1.0055        |
| 81   | Winter                         | 1.006| 0.114| 1.0022        |
| 78   | Spring                         | 1.009| 0.134| 1.0011        |
| 80   | Summer                         | 1.009| 0.139| 1.0005        |
| 78   | Autumn                         | 1.008| 0.126| 0.9992        |
| 1359 | *Leucos panosi*                | 1.007| 0.103| 1.0014        |
| 137  | Winter                         | 1.003| 0.096| 0.9873        |
| 431  | Spring                         | 0.993| 0.109| 0.9827        |
| 344  | Summer                         | 1.002| 0.077| 0.9940        |
| 447  | Autumn                         | 1.005| 0.094| 0.9960        |
| 974  | *Atherina boyeri*              | 1.008| 0.128| 1.0005        |
| 369  | Winter                         | 1.003| 0.088| 0.9948        |
| 122  | Spring                         | 1.006| 0.122| 0.9844        |
| 338  | Summer                         | 1.011| 0.147| 0.9952        |
| 145  | Autumn                         | 1.009| 0.136| 0.9866        |

In general, *S. acarnanicus* exhibited a specialized feeding behavior targeted to plant material, compared to the rest of the species (Figure 3). However, some individuals of *S. acarnanicus* consumed high trophic position prey such as small fish, amphibian tadpoles and microcrustaceans. Therefore, the species showed a quite diverse diet characterized by an increased presence of both plant and animal prey, which was affected by the interannual seasonal succession (Figure 5 and Table 3). A common observation between *S. acarnanicus* and *T. hellenicus* was that both species exhibited a diversity of prey types which can be explained by the significant trophic overlapping (>0.6) induced by the availability of food resources (Table 2). Concerning those findings, the trophic level of the species was found relatively higher (τ = 3.31) compared to the one that is registered in FishBase (τ = 2.00; Froese and Pauly 2021). The piscivorous ability of the species was first observed by Tsounis and Kehayias (2019) who later found that this behavior was more intense in the presence of artificial fishing lights (Tsounis and Kehayias 2021). These results are in total contrast to those of Iliadou (1991) who classified the species as exclusively herbivorous.
species (Chrisafi et al. 2007; Doulka et al. 2012). The fact that no copepods and cladocerans were recorded in the species diet, can be attributed to the advanced digestion that took place before diet analysis which probably prevented the identification of small sized preys. The estimated trophic level for the species ($\tau = 2.8$) was lower than the one provided in FishBase ($\tau = 3.2$). This is a result of the sporadic presence of plant material that was observed in the examined specimens of the present study.

The main hypothesis linked to condition factor indices is that heavier individuals at a certain body length are in a better condition compared to lighter ones (Froese 2006; Miller et al. 2015; Gubiani et al. 2020). However, the relative condition factor can only indicatively be used as an index of species wellbeing as beyond food availability is also influenced by season (Ayoade and Ikulala 2007; Mazumder et al. 2016; Tribuzy-Neto et al. 2017) and many other environmental factors. In the present study, no significant seasonal variation in the $K_n$ of the species was observed and the $K_n$ was higher than 1 indicating sufficient food resources for the lake’s fish populations.

In conclusion, *L. albanicus* along with *L. panosi* and *S. acarnanicus* exhibited the highest prey diversity while *T. hellenicus* and *A. boyeri* showed a more specialized feeding behavior. The trophic level estimation for the studied Cyprinidae species resulted in higher values compared to former assessments (Froese and Pauly 2021), while for *A. boyeri* to lower. The studied fish species exhibited predation towards crustaceans, insects and plant material as the most abundant food items during stomach content analysis, revealing a tendency to omnivorous feeding strategy. A diet overlap was revealed among the studied species which may result in inter-species competition for the available resources. Based on the hypothesis that the species have altered their feeding behavior compared to previous works, similar to the case of *S. acarnanicus*, it is possible that an increase in the abundance of the studied fish species which proceed in feeding shifts towards mid-level consumers (e.g. crustaceans, insect larvae), may lead to successively top-down cascade ecosystemic effects (Heath et al. 2013). Nevertheless, Li et al. 2015 have shown that an increase in the omnivore level of fish species has increased alternative dynamic states and reduced the strength of trophic cascade effects, respectively. Our data indicate that despite the inter-specific feeding competition, there are no crucial alternations in the feeding strategy of the species except some seasonal fluctuations during the course of a year. Hence, additional spatiotemporal data is required in order to clarify the cause (e.g. natural or anthropogenic), the magnitude (e.g. high or low) and the potential outcomes of similar phenomena.

Despite all possible limitations of the stomach content analysis, this method provides important information on ecological and biological aspects of fish behavior, condition, habitat use, inter- and intra-species interactions and therefore on the food web of aquatic ecosystems. Such information is essential in ichthyological research, fisheries management, fish protection and in general all ecological studies. Considering the above, the results of the present study can contribute significantly to the knowledge of the ecosystem structure of the studied lake and the development of management plans. Relevant studies should also be encouraged considering the limited available information for the majority of Greek freshwater fish species.

**Acknowledgements**

Funding for this research was provided by Greece and the European Regional Development Fund under the Operational Program ‘Competitiveness, Entrepreneurship and Innovation, NSRF 2014–2020’ (research project ANATHALLOI).
Declaration of interest

The authors declare that there is no conflict of interest regarding the publication of this article.

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Data availability statement

The data that support the findings of this study are available on request from the corresponding author, G.V. The data are not publicly available due to privacy/ethical restrictions.

References

Ahlbeck I, Hansson S, Hjerne O. 2012. Evaluating fish diet analysis methods by individual-based modeling. Can J Fish Aquat Sci. 69(7):1184–1201.
Amundsen P, Sánchez-Hernández J. 2019. Feeding studies take guts – critical review and recommendations of methods for stomach contents analysis in fish. J Fish Biol. 95:1364–1373.
Appelberg M, Berger HM, Hesthagen T, Kleiven E, Kurkilähti M, Raitaniemi J, Rask M. 1995. Development and intercalibration of methods in Nordic freshwater fish monitoring. Water Air Soil Pollut. 85(2):401–406.
Ayoade AA, Ikulala AOO. 2007. Length weight relationship, condition factor and stomach contents of Hemichromis bimaculatus, Sarotherodon melanotheron and Chromidotilapia guentheri (Perciformes: Cichlidae) in Eleiyele Lake, Southwestern Nigeria. Rev Biol Trop. 55(3–4):969–977.
Bargiotti R, Zogaris S, Kalogianni E, Stoumboudi MT, Chatzinikolaou Y, Giakoumi S, Kapakos Y, Kommatas D, Koutsikos N, Tachos V, et al. 2015. Freshwater fishes and lampreys of Greece: an annotated checklist. Monographs on Marine Sciences No. 8. Athens (Greece): Hellenic Centre for Marine Research; p. 130.
Bobori D, Salvarina I, Michaloudi E. 2013. Fish dietary patterns in the eutrophic Lake Volvi (East Mediterranean). J Biol Res Thessaloniki. 19:139–149.
Carpenter SR, Kitchell JF, Hodgson JR. 1985. Cascading Trophic Interactions and Lake Productivity. BioScience. 35(10):634–639.
Chrisafis E, Kaspiris P, Katselis G. 2007. Feeding habits of sand smelt (Atherina boyeri, Risso 1810) in Trichonis Lake (Western Greece). J Appl Ichthyol. 23(3):209–214.
Costello M. 1990. Predator feeding strategy and prey importance: a new graphical analysis. J Fish Biol. 36(2):261–263.
Crivelli AJ. 2006. Scardinius acarnanicus. The IUCN Red List of Threatened Species 2006: e.T61214A12449678. https://dx.doi.org/10.2305/IUCN.UK.2006.RLTS.T61214A12449678.en.
de Mutsert K, Cowan JH, Jr, Walters CJ. 2012. Using ecopath with ecosim to explore nekton community response to freshwater diversion into a Louisiana estuary. Marine Coastal Fisheries. 4(1):104–116.
Gascuel D, Guénette S, Pauly D. 2011. The trophic-level-based ecosystem modelling approach: theoretical overview and practical uses. ICES J Mar Sci. 68(7):1403–1416.
Gkenas C, Oikonomou A, Economou A, Kiosse F, Leonaros I. 2012. Life history pattern and feeding habits of the invasive mosquitofish, Gambusia holbrooki, in Lake Pamvotis (NW Greece). J Biol Res. 17:121–136.
Gubiani EA, Ribeiro VR, Fé UMG, de S. 2020. Relative condition factor: Le Cren’s legacy for fisheries science. Acta Limnol Bras. 32(3).
Hacunda J-S. 1981. Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine. Fishery Bull. 79(4):775–788.
Heath MR, Speirs DC, Steele JH. 2013. Understanding patterns and processes in models of trophic cascades. Ecol Lett. 17(1):101–114.
Hossain MM, Matuishi T, Arhonditsis G. 2010. Elucidation of ecosystem attributes of an oligotrophic lake in Hokkaido, Japan, using Ecopath with Ecosim (EwE). Ecol Modell. 221(13-14):1717–1730.
Hureau J-C. 1966. Biologie comparee des quelques poissons antartiques (Nototheniidae). Bull Inst Oceanogr Monaco. 68:1–429.
Hyslop EJ. 1980. Stomach contents analysis – a review of methods and their application. J Fish Biol. 17(4):411–429.
Iglesias-Ríos R, Mazzoni R. 2014. Measuring diversity: looking for processes that generate diversity. Nat Conserv. 12(2):156–161.
Iliadou K. 1991. (Pisces: Cyprinidae) from lakes Lysimachia and Trichonis, Greece. J Fish Biol. 38(5):669–680.
Jisr N, Younes G, Sukhn C, El-Dakdouki MH. 2018. Length-weight relationships and relative condition factor of fishes inhabiting the marine area of the Eastern Mediterranean city, Tripoli-Lebanon. Egypt J Aquat Res. 44(4):299–305.
Kalogianni E, Giakoumi S, Andriopoulou A, Chatzinikolaou Y. 2010. Feeding ecology of the critically endangered Valencia letourneuxii (Valenciidae). Aquat Ecol. 44(1):289–299.
Karachle P, Stergiou K. 2014. Diet and feeding habits of Spicara maena and S. smaris (Pisces, Osteichthyes, Centracanthidae) in the North Aegean Sea. Acta Adriatica. 55:75–84.
Karachle PK. 2017. Diet composition and overlap for 43 fishes in the North Aegean Sea. Acta Adriat. 58(1):125–136.
Kehayias G, Doulka E. 2014. Trophic state evaluation of a large Mediterranean lake utilizing abiotic and biotic elements. JEP. 05(01):17–28.
Kottelat M, Freyhof J. 2007. Handbook of European freshwater fishes. Cornol (Switzerland): Kottelat; Berlin (Germany): Freyhof.
Le Cren ED. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (Perca fluviatilis). J Anim Ecol. 20(2):201.
Leonardos I. 2008. The feeding ecology of Aphanius fasciatus (Valenciennes, 1821) in the lagoonal system of Messolongi (western Greece). Sci Mar. 72(2):393–401.
Levins R. 1968. Evolution in changing environments: some theoretical explorations (No. 2). Princeton (NJ): Princeton University Press.
Li J, Huang P, Zhao Z, Zhang R. 2015. Ambiguous influences of omnivorous fish on trophic cascade and alternative states: implications for biomanipulation from an ecological model. Aquat Ecosyst Health Manage. 18(1):105–113.
Liao H, Pierce CL, Larscheid JG. 2001. Empirical assessment of indices of prey importance in the diets of predacious fish. Trans Am Fish Soc. 130(4):583–591.
Lindeman R. 1942. The trophic-dynamic aspect of ecology. Ecology. 23(4):399–417.
Link JS, Garrison LP. 2002. Trophic ecology of Atlantic cod Gadus morhua on the northeast US continental shelf. Mar Ecol Prog Ser. 227:109–123.
Mankó P. 2016. Stomach content analysis in freshwater fish feeding ecology. Slovakia: Vydavatelstvo Presovské University.
Matič-Skoko S, Tutman P, Bojanić Varezić D, Skaramuca D, Dikić D, Lisić D, Skaramuca B. 2014. Food preferences of the Mediterranean moray eel, Muraena Helena (Pisces: Muraenidae), in the southern Adriatic Sea. Mar Biol Res. 10(8):807–815.
Mazumder SK, Das SK, Bakar Y, Ghaffar MA. 2016. Effects of temperature and diet on length-weight relationship and condition factor of the juvenile Malabar blood snapper (Lutjanus malabaricus [Bloch & Schneider, 1801]). J Zhejiang Univ Sci B. 17(8):580–590.
Miller SJ, VanGenechten DT, Cichra CE. 2015. Length–weight relationships and an evaluation of fish-size and seasonal effects on relative condition ($K_w$) of fishes from the Wekiva River, Florida. Florida Sci. 78(1):1–19. http://www.jstor.org/stable/24321839.
Moutopoulos DK, Stoumboudi MT, Ramfos A, Tsagarakis K, Gritzalis KC, Petriki O, Patsia A, Barbieri R, Machias A, Stergiou KI, et al. 2018. Food web modelling on the structure and functioning of a Mediterranean lentic system. Hydrobiologia. 822(1):259–283.
Patsia AT. 2009. Photographic key characters of the Hellenic Evaluation System taxa of benthic macroinvertebrates. Case studies: Strymonas and Nestos rivers. Aristotle University of Thessaloniki; [accessed 2021 Apr]. http://ikee.lib.auth.gr/record/123047.
Pauly D, Froese R, Sa-A P, Palomares M-L, Christensen V, Rius J. 2000. Trophlab manual. Manila (Philippines): ICLARM.

R Core Team. 2021. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing; [accessed 2021 Oct]. https://www.R-project.org/.

Ray AK, Ringø E. 2014. The gastrointestinal tract of fish. In: Merrifield D, Ringø E, editors. Aquaculture nutrition. USA: John Wiley & Sons, Ltd; p. 1–13.

Schoener TW. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology. 51(3): 408–418.

Shannon C, Weaver W. 1949. The mathematical theory of communication. Urbana (IL): University of Illinois Pres; p. 14.

Tachet H, Richoux P, Bournaud M, Amd Usseglio-Polatera P. 2000. Invertebres d’Eau Douce. Systematique, biologie, ecologie. Paris (France): CNRS Editions; p. 587.

Tirasin M, Jørgensen T. 1999. An evaluation of the precision of diet description. Mar Ecol Prog Ser. 182: 243–252.

Tribuzy-Neto IA, Conceição KG, Siqueira-Souza FK, Hurd LE, Freitas CEC. 2017. Condition factor variations over time and trophic position among four species of Characidae from Amazonian floodplain lakes: effects of an anomalous drought. Brazilian J Biol. 78(2):337–344.

Tsionki I, Petriki O, Leonardos ID, Karachle PK, Stoumboudi MT. 2021. Length-weight relationships of 6 fish species caught in a Mediterranean lake (Trichonis-NW Greece). J Appl Ichthyol. 37(4):631–634.

Tsounis L, Kehayias G. 2019. Can an herbivorous fish become predator? The case of Scardinius acarnanicus (Economidis, 1991) in Lake Trichonis (Greece). Front Mar Sci. Conference Abstract: XVI European Congress of Ichthyology. doi:10.3389/conf.fmars.2019.07.00014.

Tsounis L, Kehayias G. 2021. Alteration of the feeding behavior of an omnivorous fish, Scardinius acarnanicus (Actinopterygiia: Cypriniformes: Cyprinidae), in the presence of fishing lights. AIeP. 51(2): 131–138.

Wallace RK, Ramsey JS. 1983. Reliability in measuring diet overlap. Can J Fish Aquat Sci. 40(3):347–351.

Zacharias I, Bertachas I, Skoulkidis N, Koussouris T. 2002. Greek lakes: limnological overview. Lakes Reservoirs. 7(1):55–62.