Alteration of the feeding behavior of an omnivorous fish, *Scardinius acarnanicus* (Actinopterygii: Cypriniformes: Cyprinidae), in the presence of fishing lights

Lambros TSOUNIS¹, George KEHAYIAS²

¹ Department of Environmental Engineering, University of Patras, Agrinio, Greece
² Department of Food Science and Technology, University of Patras, Agrinio, Greece

http://zoobank.org/67569BF9-6FE8-444D-AD15-6721233B0836

Corresponding author: Lambros Tsounis (ltsounis@upatras.gr)

Academic editor: A. Tokaç

Received 18 November 2020

Accepted 18 January 2021

Published 8 June 2021

Citation: Tsounis L, Kehayias G (2021) Alteration of the feeding behavior of an omnivorous fish, *Scardinius acarnanicus* (Actinopterygii: Cypriniformes: Cyprinidae), in the presence of fishing lights. Acta Ichthyologica et Piscatoria 51(2): 131–138. https://doi.org/10.3897/aiep.51.63299

Abstract

Fishing with light is an old and common practice yielding a substantial catch volume globally. Despite the popularity of the method and the efforts to improve it, there is a lack of field studies on the effects of light on the feeding preferences of the attracted fishes. A previous report suggested that purse seine fishing lights can differentiate the feeding preferences of the approaching fishes, such as *Atherina boyeri* Risso, 1810 in Lake Trichonis (Greece). The presently reported study aims to verify these findings by investigating the diet of the endemic *Scardinius acarnanicus* Economidou, 1991. The feeding behavior of *S. acarnanicus* was studied from 2016 to 2019 through gut content analysis, in specimens from Lake Trichonis that came from purse seining with light and specimens caught without light. The same investigation was carried out comparatively in specimens taken by gillnets from two nearby lakes (lakes Ozéros and Amvrakia), where *S. acarnanicus* is present, but no fishing with light is exercised. The stomach content analysis conducted on 699 *S. acarnanicus* specimens revealed the intense effect of light on its diet resulting in the alteration of its feeding habits towards fish predation and especially *Atherina boyeri*. On the contrary, the specimens taken with the use of gillnets, from the three lakes, showed a typical omnivorous feeding behavior. The findings of the presently reported study support the assumption that the elevated concentration of fish close to fishing lights alters the feeding behavior of certain species making them predators. Considering that fishing with light is practiced worldwide, this could be of great ecological significance to the ichthyofauna not only of inland waters but also of marine areas, affecting perhaps several commercial species.

Keywords

*Atherina boyeri*, feeding, fishing lights, purse seine, *Scardinius acarnanicus*

Introduction

Artificial light sources have been used to aid fishing for thousands of years, ever since humans first observed that many fish species exhibit a positive phototactic response to light sources. Historical records show that the earliest applications of light-assisted fishing include the use of large beach bonfires to attract fish; these simple techniques have slowly been developed and refined so that large numbers of fish can now be caught with impressive efficiency. Kerosene and electric lamps were introduced in the 20th century and, more recently, light-emitting diode (LED) lamps have entered the field as the light-source of choice due to their strong luminosity, high ener-
gy efficiency, long lifespan, chromatic performance, and reduced environmental impact compared to non-LED lamps (Nguyen and Winger 2019).

Zooplankton exhibits a positive phototactic response to light, and its behavior attracts fish larvae and zooplanktivorous fishes, as well as larger fish species and top predators, initiating a trophic chain reaction (Maeda 1951; Ben-Yami 1976). Although light-assisted fishing has enabled large catches of fish around the world, and significant efforts have been made to improve fishing gear and techniques, there is poor understanding of how the presence of artificial light influences fish feeding behavior and diet preferences.

A common marine and freshwater fishing technique around the world is to combine the use of purse seine fishing gear with artificial light (Ben-Yami 1976; Acros and Oro 2002). In this technique, rafts of lamps are anchored and turned on to attract large schools of different fish species. Once the desired concentration of the target species is achieved, the main fishing boat, assisted by a small skiff, encircles the school by releasing the seine net. The base of the seine net is then closed to form a ‘bag’ that traps the fish so that the net can then be hauled into the main fishing boat and the fish collected (Tsagarakis et al. 2012).

Light-assisted purse seine fishing is a common technique in Lake Trichonis, the largest natural lake in Greece, where the landlocked and zooplanktivorous species *Atherina boyeri* Risso, 1810 is targeted by fishermen. Previous behavioral studies conducted in Lake Trichonis by Kehayias et al. (2018a, 2018b) found that the presence of artificial light alters the dietary preferences of species such as *A. boyeri* (see Doulka et al. 2013). Specifically, artificial light causes *A. boyeri* to prey heavily on *Economidichthys trichonis* Economidis et Miller, 1999 larvae, an endangered fish that is endemic to Lake Trichonis. During those field expeditions, it was determined that artificial light attracts not only *A. boyeri*, but also *Scardinius acarnanicus*, which encircle the *A. boyeri* schools. *Scardinius acarnanicus* Economidis, 1991, Trichonis rudd or ‘Tseroukla’ in Greek, is an endemic fish species of the freshwater ecosystems of western Greece. In the only previous study of its feeding behavior, which was performed nearly 40 years ago in Lake Trichonis and the nearby Lake Lysimachia, *S. acarnanicus* was found to be herbivorous, with a diet of only aquatic vegetation and phytoplankton (Iliadou 1991). More recently, however, Tsounis (2016) reported that, in Lake Trichonis and nearby lakes, *S. acarnanicus* feeds not only on aquatic vegetation and phytoplankton but also on small invertebrates and insects, as well as fishes, suggesting it to be omnivorous. Thus, the observation that dense schools of *S. acarnanicus* swarm around *A. boyeri* during light-assisted purse seine fishing suggests that, in the presence of artificial light, *S. acarnanicus* is a predator of *A. boyeri*.

The presently reported study, which continues recent investigations by Kehayias et al. (2018a, 2018b), further supports the hypothesis that the presence of artificial light influences fish feeding preferences, with a tendency to make fish more predatory. This study investigates the feeding behavior of *S. acarnanicus* using gut content analysis. *Scardinius acarnanicus* specimens from Lake Trichonis were obtained both from purse seining with light, and without light with the use of gillnets. In addition, a similar investigation was carried out comparatively in specimens from two nearby lakes (Lakes Ozeros and Amvrakia), where *S. acarnanicus* is present, but no fishing with light is exercised. The issues addressed are a) Whether the presence of light can alter the diet of *S. acarnanicus* and in which degree concerning season and size; b) Are these results valid given the parallel feeding investigation in other lake ecosystems of the area? c) Which could be the possible local as well as global ecological consequences of the light-driven alteration of the fish diet towards predatory?

### Materials and methods

#### Study area

The study was conducted at three natural lakes of western Greece: Lake Trichonis, Lake Ozeros, and Lake Amvrakia (Fig. 1). Lake Trichonis is Greece’s largest natural lake, covering an area of 98.6 km² and having a catchment area of 421 km². It is a warm monomictic lake with oligotrophic to mesotrophic characteristics and a maximum depth of 57 m (Doukla and Kehayias 2008; Kehayias and Doukla 2014). Lake Ozeros is a karstic lake covering an area of 10.1 km² and having a catchment area of 59 km². It is a typical shallow Mediterranean lake with a maximum depth of 5.6 m. The trophic state of the lake can be characterized as mesotrophic (Chalkia and Kehayias 2013). Finally, Lake Amvrakia is the second largest lake in the area, covering an area of 14.5 km² and having a catchment area of 177 km², with a maximum depth of about 50 m. Lake Amvrakia can be characterized as mesotrophic (Chalkia et al. 2012).

![Figure 1. Geographic location of the three lakes, Trichonis, Ozeros, and Amvrakia](image-url)
Field operations

A total of 699 *S. acarnanicus* specimens were collected and analyzed from 2016 to 2019. All specimens, which were selected at random from fish catches at the three study lakes, were preserved by immersing them immediately in 10% formalin solution; this minimized post-capture digestion of gut content.

In the period June 2016 to July 2019, 151 specimens were collected from Lake Trichonis using Nordic multi-mesh gillnets (length: 30 m, height: 1.5 m, mesh sizes: 43 mm, 19.5 mm, 6.25 mm, 10 mm, 55 mm, 8 mm, 12.5 mm, 24 mm, 15.5 mm, 5 mm, 35 mm, and 29 mm), while 138 specimens were collected using purse seine nets (length: 150 m, height: 20 m, mesh size: 6 mm). Purse seine fishing was performed monthly (in May, July, August, October, and November 2017) on moonless nights, assisted by rafts of green LED lamps. The purse seine lamp rafts, which were anchored at roughly 200 m intervals, were switched on just before dusk and remained on for 6–8 h, depending on the time of year. The LED lamps, which were powered by 12 V/60 A lead-acid batteries to give a luminosity of 2400 lm, were positioned above the surface of the water. In contrast, no light was used in the case of the gillnets, which were set late at night and were picked up early in the morning. A total of 196 and 214 specimens were collected from Lake Ozeros and Lake Amvrakia, respectively; all these specimens were collected using Nordic multi-mesh gillnets, due to the lack of purse seine fishing in those lakes. Specimens were collected from Lake Ozeros in the period May 2016 to August 2018, and from Lake Amvrakia from April 2016 to July 2019.

Laboratory measurements

Once transferred to the laboratory, whole specimen lengths [cm] and weights [g] were recorded before then weighing and analyzing gut content of the entire intestine using a stereomicroscope. For specimens that were collected using light-assisted purse seine fishing, it was necessary to eliminate food that had been ingested after the specimens were confined within the purse seine nets; this was done by disregarding food that was (i) still in the specimens’ mouths, or (ii) had been ingested but had not yet reached the stomach. Food content was grouped into the following food categories: (i) plant material, (ii) fish remains, (iii) mollusks, and (iv) insects. The ‘plant material’ category included all macrophytic vegetation and phytoplankton; it was frequently difficult to identify macrophytic vegetation in the gut content due to maceration by the pharyngeal teeth. The ‘fish remains’ category included all identifiable fish species as well as unidentifiable fish bones, fins, and other fish parts. The ‘mollusks’ category included bivalves and gastropods, and the ‘insects’ category included all terrestrial insects. The percentage contribution by weight of each food category was roughly estimated and then recalculated into real weights based on the weight of the total gut content. The vacuity index (VI) was calculated as the number of specimens with empty stomachs divided by the total number of specimens, multiplied by 100 (Molinero and Flos 1992). Due to frequent difficulties in numerically estimating whole food items, the relative frequency of occurrence (F%) for each of the four food categories, was selected as the best way to present the results, focusing on the presence of fish remains (Hyslop 1980; Silveira et al. 2020). To investigate seasonal trends in the diet of *S. acarnanicus*, F-values were pooled, irrespective of sampling year, and divided by season. Seasons were defined as follows: (i) summer covered June, July, and August; (ii) autumn covered September, October, and November; (iii) winter covered December, January, and February; and (iv) spring covered March, April, and May. Statistical significance between the two fishing methods was tested using the Chi-square test.

To determine the feeding strategy, the modified Costello graphical method was used. According to this method, the prey-specific abundance (Pi), which is defined as the percentage of a prey item over the total of prey items in only those predators in which the actual prey occurs, is plotted against the frequency of occurrence (Fi) on a two-dimensional graph. Information about prey importance and feeding strategy of the predator is provided by the distribution of points along the diagonals and the axes of the diagram (Amundsen et al. 1996).

Results

The dietary analysis of *S. acarnanicus* specimens collected from the three study lakes revealed five macrophyte species (*Vallisneria spiralis*, *Najas marina*, *Phragmites australis*, *Ceratophyllum demersum*, and *Myriophyllum spicatum*), one bivalve mollusk species (*Dreissena bugensis*), two gastropod mollusk species (*Theodoxus varius*, *Valvata piscinalis*) and one fish species (*Atherina boyeri*). The vacuity index (VI) was calculated for each lake: Lake Trichonis had a VI of 18.5% for gillnet specimens and 11.3% for light-assisted purse seine specimens, while Lake Ozeros and Lake Amvrakia had VI’s of 20.4% and 24.8%, respectively.

Specimens collected from gillnet fishing in Lake Trichonis were observed to have a diet of macrophytes and phytoplankton, which were categorized as plant material (F = 82.1%), fish remains (F = 22.7%), terrestrial insects (F = 2.4%), and mollusks (F = 0.8%). The overall F values for the fish remains found were remarkably higher in the samples taken by purse seining with the use of light (F = 73.1%), instead of those taken without light using gillnets (Chi-square test, P < 0.05). The samples taken using gillnets had slightly higher F values for prey types such as the terrestrial insects and bivalves, in contrast to the samples taken with the use of light, where the F value for the insects was 1.6%, while no mollusks were present in the diet (Fig. 2). The diet of specimens collected from light-assisted purse seine fishing included a large,
but seasonally diverse, amount of *A. boyeri*, with *F* values ranging from 52.4% in November to 70% in August (Fig. 3). In contrast, the diet of specimens collected from gillnet fishing did not include *A. boyeri*; this can probably be explained by the longer time-lag between collection and preservation for these specimens, resulting in some of their gut content having been digested before preservation.

The dietary analysis of the *S. acarnanicus* specimens from Lake Ozeros revealed a lower *F* value for the fish remains (*F* = 19.2%) in comparison to Lake Trichonis, while the respective value for Lake Amvrakia was the lowest among the 3 lakes (*F* = 8.1%). The overall *F* value for the plant material for Lake Ozeros was 93.5%, for the terrestrial insects 25.6% and for the bivalve mollusks 0.6%, while for Lake Amvrakia the overall *F* value for the plant material was 74.8%, for the terrestrial insects 5.6% and 1.2% for the bivalve and gastropod mollusks.

In Lake Trichonis, the highest *F* value for the fish remains in the samples taken with the use of light was recorded in summer (81.8%) and the lowest in autumn (66.6%), while no samples were taken in winter (Fig. 4). In contrast, in the samples taken with the use of gillnets, the *F* values

---

**Figure 2.** The overall frequency of occurrence of the main food types found in the gut contents of the *Scardinius acarnanicus* specimens collected in Lake Trichonis (separately for the samples taken with or without light), Lake Ozeros and Lake Amvrakia. The numbers of the *Scardinius acarnanicus* individuals with the specific type of food are given.

**Figure 3.** The frequency of occurrence of unidentified fish remains and *Atherina boyeri* found in the gut contents of the *Scardinius acarnanicus* specimens taken from Lake Trichonis using light between May and November 2017.

**Figure 4.** The frequency of occurrence of the main food types found in the gut contents of the *Scardinius acarnanicus* specimens collected during the four seasons from A: Lake Trichonis (with light), B: Lake Trichonis (without light), C: Lake Ozeros and D: Lake Amvrakia. The numbers of the *Scardinius acarnanicus* individuals with fish remains in their gut content are given.
In contrast, Macrophytes and phytoplankton had a general contribution to the diet, while insect remains contributed significantly in autumn and winter. Finally, in Lake Amvrakia, the highest F value for the fish remains occurred during summer (26.0%), while no fishes had been preyed upon during autumn and winter. In the same lake, the highest F value for the fish remains occurred during summer (20.0%), with no fish remains in the diet during autumn.

Considering the dietary differences in respect to the total length of S. acarnanicus (Fig. 5), it is observed that in the samples taken with light from Lake Trichonis, the F values of fish remains fluctuated between 44.4% and 100% with no obvious trend among size classes. Indeed, even the smaller specimens (<16 cm) were found to prey upon other fishes and especially A. boyeri. In contrast, no fish predation was recorded from the specimens being less than 16 cm in the other two lakes, as well as in the samples taken with gillnets from Lake Trichonis.

For the entire sampling period, S. acarnanicus demonstrated an opportunistic feeding strategy (Fig. 6). In the samples taken with the use of gillnets from the three lakes, the species showed a greater consumption of macrophytic vegetation and phytoplankton in their diet. Some individuals include occasionally other food types in their diet, such as terrestrial insects, bivalves and gastropod mollusks, and fish. On the contrary, in the samples taken by purse seining with light, S. acarnanicus present greater consumption upon A. boyeri. Macrophytes and phytoplankton had a general contribution to the diet, while there was specialized predation upon A. boyeri. The combination of A. boyeri and unidentified fish remains have as a result the high specialization of S. acarnanicus in the consumption of fishes (TotFish).

**Figure 5.** The frequency of occurrence of the main food types found in the gut contents of the different size classes of the Scardinius acarnanicus specimens taken from A: Lake Trichonis (with light), B: Lake Trichonis (without light), C: Lake Ozeros, and D: Lake Amvrakia. The numbers of Scardinius acarnanicus individuals with fish remains in their gut content are given.

**Figure 6.** Graphical analysis of Scardinius acarnanicus feeding strategy using the modified Costello method in A: Lake Trichonis (with light), B: Lake Trichonis (without light), C: Lake Ozeros, and D: Lake Amvrakia.

**Discussion**

Similar to what happens on land, the presence of artificial light in the water creates a strong focus of attraction for aquatic organisms that exhibit positive phototaxis. Although there is substantial literature on how aquatic organisms respond to artificial light, little is known about why they respond as they do (Nguyen and Winger 2019). In the most recent review article concerning the fish behavior in response to artificial light (Nguyen and Winger 2019), there was a thorough quotation of the negative ecological impacts of light ‘pollution’. It seems that artificial light affects the behavior of various species including turtles and seabirds, however, underwater lights like
those used in fishery, impact fish foraging and schooling behavior, spatial distribution, predation risk, migration, and reproduction (Nightingale et al. 2006). Although some studies investigate how the feeding behavior of natural predators changes in the presence of artificial light (Becker et al. 2013), as predators achieve greater feeding success (Downing and Litvak 2001, Migaud et al. 2009, Sierra-Flores et al. 2016), few studies investigate how the presence of artificial light influences the feeding behavior of fish species other than the natural predators.

Among the objectives of this study was to confirm the suggestion that fishing lights can differentiate the feeding behavior of the approaching fishes towards predatory, even of those species that are not natural fish predators (Kehayias et al. 2018a, 2018b). According to the presently reported findings, S. acarnanicus collected using light-assisted purse seine fishing in Lake Trichonis fed on other fish species, especially the commercially important A. boyeri. These S. acarnanicus fed on A. boyeri primarily in the summer, which is when the A. boyeri population peaks (Leonardos 2001). Interestingly, even young S. acarnanicus fed on A. boyeri. In contrast, S. acarnanicus that were collected using simple gillnet fishing were omnivorous, with a mainly plant-based diet that included only small numbers of terrestrial insects, mollusks, and fish remains. Very similar feeding patterns were found for S. acarnanicus in the two nearby lakes, where only gillnet fishing is practiced.

Although Lake Ozeros has a dense A. boyeri population, due to their natural introduction to the lake from the Acheloos River, A. boyeri are not targeted by local fishermen, who use gillnets that target larger species. The gut content analysis revealed that S. acarnanicus that were caught by gillnet fishing in both Lake Ozeros and Lake Trichonis had similar feeding patterns of preying upon fish. The high F-values of lakes Ozeros and Trichonis, in contrast to those of Lake Amvrakia, which is not inhabited by A. boyeri, suggest that S. acarnanicus likely benefits from the dense A. boyeri population in those lakes, resulting in its preying upon this species, although this hypothesis needs further examination.

Findings from this study indicate that the presence of night-time artificial light in Lake Trichonis promotes predatory instincts of S. acarnanicus, so that they take advantage of the rich A. boyeri food source. These findings are supported by those of Kehayias et al. (2018a, 2018b), who found that the normally zooplanktivorous A. boyeri showed elevated predation of the endangered endemic Economidichthys trichonis larvae in areas close to artificial fishing lights. More specifically, Kehayias et al. (2018b) found that, on average, and at certain times of the year, larger A. boyeri specimens had a nightly consumption of up to 14.5 E. trichonis larvae. This consumption placed an overall nightly predation pressure of 260 000 E. trichonis larvae when A. boyeri schooled around the lamp rafts of a single purse seine fishing boat (Kehayias et al. 2018b).

The presence of artificial night-time light sources in Lake Trichonis initiates a trophic food chain reaction. During the initial hours of illumination, numerous zooplankton and larval fish species start to gather around the lamp rafts (Kehayias et al. 2016, Kehayias personal observations). Gradually, zooplanktivorous species, in this case, A. boyeri, create large schools around the lamp rafts, and they start to prey heavily upon zooplankton and E. trichonis larvae. Larger species, such as S. acarnanicus, then start to gather around the lamp rafts and, in turn, they start to prey upon A. boyeri and other fish species. Our findings are supported by those of other studies from across the world that observe similar changes to fish feeding behavior in the presence of artificial night-time light (Ben-Yami 1976; Prinslow et al. 1980; Tabor et al. 2001; Nightingale et al. 2006; Bolton et al. 2017).

The presently reported study of S. acarnanicus diet in three lakes of western Greece showed that S. acarnanicus is an omnivorous species that can, in specific circumstances, become a fish predator. This is, to the best of our knowledge, the first report of fish predation by a member of the genus Scardinius in European inland waters. It is already known that the most widespread species, Scardinius erythrophthalmus, can be piscivorous in other geographical regions, where it is allochthonous (Kapuscinski et al. 2012; Guinan et al. 2015; Collier and Grainger 2015). Scardinius acarnanicus has many similar morphological and ecological characteristics to those of S. erythrophthalmus; indeed, only recently was a clear distinction made between the two species in Greece by Prof. Economidis in 1991 (Iliadou et al. 1996).

The only previous study of S. acarnanicus diet was conducted from 1977 to 1979, in the lake system of Tri-chonis–Lysimachia Lake (Iliadou 1991), and there have been no previous equivalent studies in either Lake Ozeros or Lake Amvrakia. The present results, concerning the composition of the plant material in the diet, are in general accordance with the reports of Iliadou (1991). However, they are in direct contrast to her reports according to which the species was strictly herbivorous, feeding exclusively on reeds, other aquatic vegetation, and phytoplankton. Considering similarities in the methodology used for gut content analysis both in previous studies and the presently reported study, and the large number of specimens collected from Lake Trichonis (289 and 360 specimens in the presently reported and previous studies, respectively), it is challenging to explain the apparent dietary shift of S. acarnanicus from herbivorous to omnivorous, and more specifically towards fish predation. This species showed a preference of feeding upon A. boyeri. Neither the existence, nor the dominance of A. boyeri is new for this ecosystem and, thus, it cannot be incriminated as the prime cause of a possible change of S. acarnanicus diet during the last 40 years. Instead, we suggest that changes to fishing practices might explain why the S. acarnanicus diet has changed. Until the early 1980s, A. boyeri were mostly caught using bottom trawling methods, while trammel nets and set gillnets were used to fish for other larger species; these methods were used to collect
Acknowledgments

We are grateful to Kostas Xirokostas for his help with collecting fish specimens using gillnets and Giorgos Zarkadas and his crew, for their help with collecting fish specimens using purse seines in Lake Trichonis. We are also grateful to Spyros Paleogiorgos and Stelios Charalambous for their help with collecting fish specimens in lakes Ozeros and Amvrakia, respectively.

References

Acros JM, Oro D (2002) Significance of nocturnal purse seine fisheries for seabirds: A case study off the Ebro delta (NW Mediterranean). Marine Biology 141(2): 277–286. https://doi.org/10.1007/s00227-002-0828-3
Amundsen PA, Gabler HM, Staldvik FJ (1996) A new approach to graphical analysis of feeding strategy from stomach contents data—Modification of the Costello (1990) method. Journal of Fish Biology 48: 607–614. https://doi.org/10.1111/j.1095-8649.1996.tb01455.x
Becker A, Whitfield AK, Cowley PD, Jamrengn J, Naeeg TF (2013) Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behavior of estuary-associated fishes. Journal of Applied Ecology 50(1): 43–50. 10.1111/1365-2664.12024
Ben-Yami M (1976) Fishing with light. FAO fishing manuals. Fish News Books Ltd, Farnham, Surrey, UK.
Bolton D, Mayer-Pinto M, Clark GF, Daftorn KA, Brassil WA, Becker A, Johnston EL (2017) Coastal urban lighting has ecological consequences for multiple trophic levels under the sea. Science of the Total Environment 576: 1–9. https://doi.org/10.1016/j.scitenv.2016.10.037
Chalkia E, Kehayas G (2013) Zooplankton community dynamics and environmental factors in Lake Ozeros (Greece). Mediterranean Marine Science 14(3): 32–41. https://doi.org/10.12681/mms.534
Chalkia E, Zacharias I, Thomatou AA, Kehayas G (2012) Zooplankton dynamics in a gympsum karst lake and interrelation with the abiotic environment. Biologia 67(1): 151–163. https://doi.org/10.2478/s11756-011-0147-6
Collier KJ, Grainger NPJ (2015) New Zealand invasive fish management handbook. Lake Ecosystem Restoration New Zealand (The University of Waikato, Hamilton) and Department of Conservation.
Doula E, Kehayas G (2008) Spatial and temporal distribution of zooplankton in Lake Trichonis (Greece). Journal of Natural History 42(5–8): 575–595. https://doi.org/10.1080/00222930701835555
Doula E, Kehayas G, Chalkia E, Leonards I (2013) Feeding strategies of Atherina boyeri (Risso 1810) in a freshwater ecosystem. Journal of Applied Ichthyology 29(1): 200–207. https://doi.org/10.1111/j.1365-2664.2012
Downing G, Litvak MK (2001) The effect of light intensity and spectrum on the incidence of first feeding by larval haddock. Journal of Fish Biology 59(6): 1566–1578. https://doi.org/10.1046/j.1095-8649.2001.tb00221.x
Guinan Jr ME, Kapuscinski KL, Teese MA (2015) Seasonal diet shifts and trophic position of an invasive cyprinid, the Rudd Scardinius erythrophthalmus (Linnaeus, 1758), in the upper Niagara River. Aquatic Invasions 10(2): 217–225. https://doi.org/10.3391/ai.2015.10.2.10
Hyslop EJ (1980) Stomach content analysis—A review of methods and their application. Journal of Fish Biology 17(4): 411–429. https://doi.org/10.1111/j.1095-8649.1980.tb02775.x

Iliadou K (1991) Feeding of Scardinius acarnanicus Stephanidis, 1939 (Pisces: Cyprinidae) from Lakes Lysimachia and Trichonis, Greece. Journal of Fish Biology 38(5): 669–680. https://doi.org/10.1111/j.1095-8649.1991.tb03156.x

Iliadou K, Sourdis J, Economidis PS, Wheeler A (1996) Morphological differentiation among species of the genus Scardinius (Pisces: Cyprinidae) in Greece. Journal of Natural History 30(3): 459–473. https://doi.org/10.1080/0022293600770241

Kapucinski KL, Farrell JM, Willinson MA (2012) Feeding patterns and population structure of an invasive cyprinid, the rudd Scardinius erythrophthalmus (Cypriniformes, Cyprinidae), in Buffalo Harbor (Lake Erie) and the upper Niagara River. Hydrobiologia 693(1): 169–181. https://doi.org/10.1007/s10750-012-1106-0

Kehayias G, Doulka E (2014) Trophic state evaluation of a large Mediterranean lake utilizing abiotic and biotic elements. Journal of Environmental Protection 05(01): 17–28. https://doi.org/10.4236/jep.2014.51003

Kehayias G, Bouliopoulos D, Chiotis N, Koutra P (2016) A photovoltaic-battery-LED lamp raft design for Lakes Lysimachia and Trichonis, Greece. Thesis. University of Patras, Greece. [In Greek] http://nemertes.lis.upatras.gr/jspui/handle/10889/10132

Kehayias G, Tzavali A, Iliadou K (1991) Feeding of Atherina boyeri (Actinopterygii: Atherinidae) in a Greek Lake. Acta Ichthyologica et Piscatoria 21(4): 51–60. https://doi.org/10.3750/AIEP/02329

Kehayias G, Tzavali A, Gini M, Michopoulou E, Tsounis L (2018a) Fish predation in the proximity of purse seine fishing lights: The case of Atherina boyeri (Actinopterygii: Atheriniformes: Atherinidae) in a Greek Lake. Acta Ichthyologica et Piscatoria 48(1): 51–60. https://doi.org/10.3750/AIEP/02329

Kehayias G, Tzavali A, Gini M, Michopoulou E, Tsounis L (2018b) Fishery lights result in elevated predation of the endangered fish Economidchthys trichonis by Atherina boyeri in Lake Trichonis (Greece). Ecology and Safety 12: 116–127.

Leonardos ID (2001) Ecology and exploitation pattern of a landlocked population of Sand Smelt, Atherina boyeri (Risso, 1810), in Trichonis Lake (western Greece). Journal of Applied Ichthyology 17(6): 262–266. https://doi.org/10.1046/j.1439-0426.2001.00296.x

Maeda H (1951) Analytical studies on marine lamp-communities. Publications of the Seto Marine Biological Laboratory 1(4): 195–213. https://doi.org/10.5134/174444

Migaud H, Davie A, Carboni S, Murray J, Lysaa PA (2009) Effects of light on Atlantic cod (Gadus morhua) larvae performances: Focus on spectrum. In: Hendry CI, Van Strappen G, Wille M, Sorgeloos P (Eds) LARVI’09—Fish and Shellfish Larviculture Symposium: Special Publication, No. 38. European Aquaculture Society, Ghent, Belgium, 265–269.

Moliner A, Flos R (1992) Influence of season on the feeding habits of the common sole Solea solea. Marine Biology 113(3): 499–507. https://doi.org/10.1007/BF00349177

Nguyen KQ, Winger PD (2019) Artificial light in commercial industrialized fishing applications: A review. Reviews in Fisheries Science and Aquaculture 27(1): 106–126. https://doi.org/10.1080/23308249.2018.1496065

Nightingale B, Longcore T, Simenstad GA (2006) Artificial night lighting and fishes. Pp. 257–276. In: Rich C, Longcore T (Eds) Ecological consequences of artificial night lighting. Island Press, Washington DC, USA.

Prinslow TE, Whitmus CJ, Dawson JJ, Bax NJ, Snyder BP, Salo EO (1980) Effects of wharf lighting on outmigrating salmon, 1979. Fisheries Research Institute, University of Washington, Seattle, WA, USA.

Sierra-Flores R, Davie A, Grant B, Carboni S, Attack T, Migaud H (2016) Effects of light spectrum and tank background colour on Atlantic cod (Gadus morhua) and turbot (Scophthalmus maximus) larvae performances. Aquaculture 450: 6–13. https://doi.org/10.1016/j.aquaculture.2015.06.041

Silveira EL, Semmar N, Cartes JE, Tuset VM, Lombarte A, Ballester EL, Vaz-dos-Santos AM (2020) Methods for trophic ecology assessment in fishes: A critical review of stomach analyses. Reviews in Fisheries Science & Aquaculture 28(1): 71–106. https://doi.org/10.1016/j.rfsa.2019.1678013

Tabor R, Brown G, Hird A, Hager S (2001) The effect of light intensity on predation of sockeye salmon fry by cottids in the Cedar River. U.S. Fish and Wildlife Service, Western Washington Office, Fisheries and Watershed Assessment Division, Lacey, WA, USA.

Tsagarakis K, Vassilopoulou V, Kallianiotis A, Machias A (2012) Discards of the purse seine fishery targeting small pelagic fish in the eastern Mediterranean Sea. Scientia Marina 76(3): 561–572. https://doi.org/10.3989/scimar.03452.02B

Tsounis I (2016) [Dietary habits of Scardinius acarnanicus in lakes of western Greece: Ecological and management implications.] MSc Thesis. University of Patras, Greece. [In Greek] http://nemertes.lis.upatras.gr/jspui/handle/10889/10132

Wong BMB, Candolin U (2015) Behavioural responses to changing environments. Behavioural Ecology 26(3): 665–673. https://doi.org/10.1093/beheco/aru183