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Foraging habits of invasive three-spined sticklebacks (*Gasterosteus aculeatus*) – impacts on fisheries yield in Upper Lake Constance

S. Roch[a,*], L. von Ammon[a], J. Geist[b], A. Brinker[a,c]

[a] *Fisheries Research Station Baden-Württemberg, Argenweg 50/1, 88085 Langenargen, Germany*
[b] *Aquatic Systems Biology Unit, Technical University of Munich, Muehlenweg 22, 85354 Freising, Germany*
[c] *University of Konstanz, Mainaustraße 252, 78464 Konstanz, Germany*

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ABSTRACT

A massive increase in the pelagic population of non-endemic three-spined sticklebacks, *Gasterosteus aculeatus* L. in Lake Constance has coincided with drastic declines in fishery yields. This study assesses the possible direct and indirect impact of the mass occurrence on native fish species in the lake. Laboratory foraging experiments showed that larvae of roach *Rutilus rutilus* L., perch *Perca fluviatilis* L. and whitefish *Coregonus lavaretus* L. are accessible to sticklebacks as food. However, distinct species effects were apparent, with whitefish showing no effective predator avoidance strategy and therefore experiencing drastically increased mortality risk compared to the other predator adapted prey species. Furthermore, in absence of larval prey, sticklebacks were shown to feed predominantly on *Daphnia* in the field, indicating a strong interspecific food competition with whitefish.

The results suggest that sticklebacks, acting as both an invasive species and a predator in the pelagic zone where prior no predator or neozoon existed, create a unique challenge to the unadapted autochthonous fish, and thus threaten the ecological resilience of the lake. Impacts on recruitment, e.g. through larval predation and interspecific competition for zooplankton could explain recent drastic declines in fishing yields.

1. Introduction

With a surface area of approximately 535 km^2 and a mean water depth of 100 m, Lake Constance is one of the largest lakes in Europe (Petri, 2006). Situated north of the Alps, its natural character is that of a typical oligotrophic pre-alpine lake (Müller, 1997) but its waters have undergone pronounced changes in trophic state during the last century. After a strong increase of nutrient loading in the first half of the 20th century with peaking total phosphorous concentrations of up to 87 mg L^{-1} in the late 1970s (IGKB, 2014), the current total phosphorous levels between 7 and 8 mg L^{-1} are close to pre-eutrophication values (IGKB, 2016). These changes have also affected commercial and recreational fisheries since trophic state is the most crucial factor in determining Lake Constance productivity (Stich and Brinker, 2010). Until 2014, annual catches corresponded closely to primary production performance and catch composition was broadly consistent with historic records (Baer et al., 2016). More recently, however, yields for whitefish (*Coregonus* sp.) in the Upper Lake have shown drastic declines, from around 300 mt (metric tons) in 2013 to less than 150 mt in 2015 (Fig. 1; IBKF, 2016). This finding cannot exclusively be explained by the observed changes in trophic state, which would predict a return to pre-eutrophication yields i.e. total catches around 300 mt (Baer et al., 2016). Furthermore, whitefish caught in the pelagic zone of Lake Constance (age classes: 1–4) revealed an abrupt weight loss of 17%–51% (arithmetic mean: 33%) between the time periods 2001–2012 and 2013–2015 (Rösch et al., 2017). Again, such an abrupt change cannot be explained by the more subtle occurring changes in trophic state. A recently observed invasion of three-spined sticklebacks *Gasterosteus aculeatus* L. (hereafter referred to sticklebacks) and the resulting interspecific interaction with the local fish fauna, particularly whitefish, may provide an alternative explanation, yet this hypothesis remains to be tested.

In 2014, a large-scale survey was instigated by the collaborative initiative “Projet Lac” (Projet Lac, 2016) in which the abundance and biomass of fish in Upper Lake Constance was quantified. The study revealed that 96% of fish specimens in the pelagic zone were sticklebacks, now contributing 28% to the total fish biomass (Alexander et al., 2016). The same study also revealed that individuals of stickleback in the lake reach exceptionally large body sizes of up to 10 cm total length. This is unusual, given that the normal range for adult freshwater specimens is between 3 and 8 cm (Baker, 1994; Bell, 1984), and individuals longer than 8 cm are rare in freshwater systems elsewhere (Gambling

* Corresponding author.
E-mail address: samuel.roch@lazbw.bwl.de (S. Roch).

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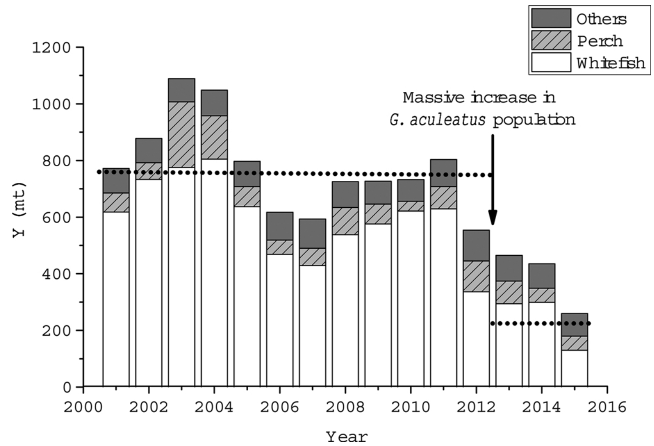

Fig. 1. Annual capture fisheries yields in Lake Constance between 2001 and 2015. Dotted lines represent mean yields before (2001–2012) and after (2013–2015) the massive increase in the pelagic three-spined stickleback (*Gasterosteus aculeatus)* population.

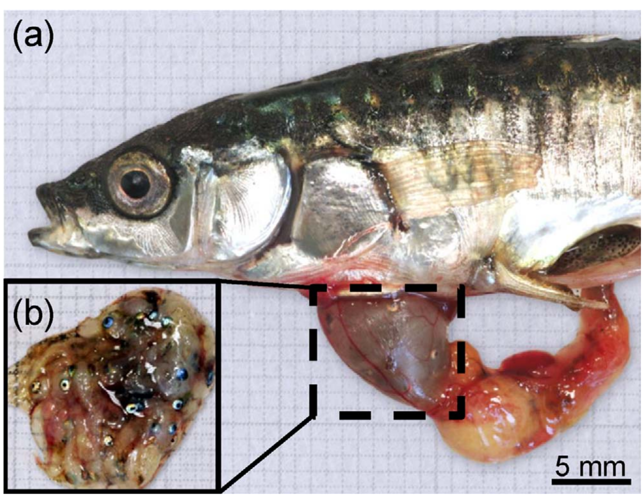

Fig. 2. Three-spined stickleback (*Gasterosteus aculeatus*) caught in spring 2016 following stocking with pre-hatched whitefish (*Coregonus lavaretus*) larvae derived from wild offspring in Upper Lake Constance. **(a)** Dissected specimen with full stomach. **(b)** Stomach content, comprising mainly small whitefish larvae.

and Reimchen, 2012; Moodie and Reimchen, 1976; Reimchen, 1992). Lake Constance had already experienced a mass occurrence of sticklebacks in the mid-1960s (Muckle, 1972; Nümann, 1972). However, trophic conditions at that time differed considerably and the population increase was probably limited to the littoral zone of the lake (Muckle, 1972). Another recent survey, which was carried out in close vicinity of a routine stocking campaign of hatchery-reared whitefish *Coregonus lavaretus* L. larvae in spring 2016, revealed that 60% of the stomachs of sticklebacks (n = 40) contained large numbers of whitefish larvae (Fig. 2).

The recent findings of the coincidence of an increase of sticklebacks and the simultaneous decline in fisheries yields raised speculations about sticklebacks being a potential predator and/or a food competitor for other fish species, potentially changing food web structure in the lake. Especially whitefish, which was previously the principle plankton feeder in the pelagic zone of Upper Lake Constance, could be severely affected by an expanding pelagic stickleback population. A similar situation has been described in the Baltic Sea where a recent and comparable increase in the native stickleback population has altered the coastal food web, with a pronounced effect on the fish community (Bergström et al., 2015; Byström et al., 2015). The situation may be exacerbated in Upper Lake Constance, as studies suggest that stickleback predation pressure on fish larvae increases when regular food resources are scarce (Gotceitas and Brown, 1993; Kean-Howie et al., 1988).

The present study addresses the following possible direct and indirect impacts of sticklebacks on native fish species in Lake Constance: (i) larval predation potential of sticklebacks on different wild offspring larvae from Lake Constance, and (ii) potential interspecific food competition to pelagic fish species. These investigations aim to help understand the effects of sticklebacks on the pelagic food web of Upper Lake Constance and shed light on the ongoing decline of local fish yields.

2. Material and methods

2.1. Study site

Lake Constance is a deep, warm-monomictic lake, located north of the Alps (47° 30′ N; 09° 30′ E) with shorelines in southern Germany, Austria and Switzerland. There are two main basins, usually referred to as the "Upper Lake" and "Lower Lake". The Upper Lake has a maximum depth of 254 m and a surface area of 473 km^2 (Petri, 2006). The lake harbours a total of 29 fish species (excluding subspecies), with whitefish and perch *P. fluviatilis* L. being historically the two most important ones in economic terms (Eckmann and Rösch, 1998). For this study, individuals of sticklebacks were sampled in Upper Lake Constance at locations close to the small town of Langenargen, on the northern shore (Fig. S1). All fishing was conducted in early summer and the results are summarized in Table S1.

2.2. History of sticklebacks in Lake Constance

How and when sticklebacks were introduced into Lake Constance has been the subject of scientific debate in the last years. What is certain is that sticklebacks are not endemic to the Lake Constance basin. Their presence is attributed to human activity and probably a result of a deliberate or unintentional introduction (Ahnelt and Amann, 1994; Marques et al., 2016; Muckle, 1972). An alternative suggestion put forward by Roesti et al. (2015) based on genetic data, is that sticklebacks colonized the lake several thousand years ago via the upper Danube drainage. However this contradicts several historic sources with detailed descriptions of the fish community in Lake Constance since the 16th century (Table S2). None of them reported sticklebacks in the upper Danube region before the end of the 19th century (Ahnelt, 1986; Heller, 1871; Rauther, 1926; von Siebold, 1863). Another scenario involves the colonization via the adjacent Rhine system into the lake. As the Rhine Falls form an insuperable barrier downstream of Lake Constance, natural colonization from downstream direction is highly unlikely (Gouskov et al., 2016). Furthermore, genetic analyses indicate that Lake Constance sticklebacks are not closely related to those found in the downstream Rhine (Lucek et al., 2010; Moser et al., 2012). However, there is one record mentioning an occurrence of sticklebacks in the Rhine system upstream of the lake (Heller, 1871). It is therefore proposed that this population dispersed into Lake Constance and its tributaries around 140 years ago (Berner et al., 2010; Lucek et al., 2010). In contrast, several historic sources between 1880 and 1955, which investigated the fish community in Lake Constance in detail, did not mention sticklebacks (Table S1). There is only one source which notes their presence in the lake without giving any further details (K. K. Statistische Central-Commission, 1874). Therefore, it seems unlikely that sticklebacks were prevalent in the entire lake at that time, especially considering that even a number of rare and hidden species like the gudgeon *Gobio gobio* L. were properly and repeatedly described (Hartmann, 1795; Klunzinger, 1892; Scheffelt and Schweizer, 1926). Muckle (1972) tried to reconstruct the dispersal of an increasing population in the Lower Lake since the early 1950s by gathering confirmed sightings data from fishers and fishing authorities. The first confirmed record could only be dated to the year 1951 (Muckle, 1972).