universität wien

MASTERARBEIT

Titel der Masterarbeit

Seasonal course of larval drift of selected native and invasive benthic fish species along two different shore types in the main channel of a large river (Danube, Austria)

Verfasser

David Ramler, BSc MSc

angestrebter akademischer Grad

Master of Science (MSc)

Wien, 2014

Studienkennzahl lt. Studienblatt:	A 066 879
Studienrichtung lt. Studienblatt:	Masterstudium Naturschutz und Biodiversitätsmanagement
Betreuer:	ao. Univ.-Prof. Dr. Hubert Keckeis

Table of Contents

Abstract

The drift of early development stages is an important event in the lifecycle of many riverine fishes. It is an essential element of dispersal and ensures that larvae reach suitable nursery habitats that provide food and shelter. Due to large-scale river engineering measures and resulting changes in the hydrological and hydraulic conditions, however, it is assumed that the number and availability of spawning grounds and nurseries have declined. This study compares the drift of selected families (Percidae and Gobiidae) along an artificial (rip-rap plus groynes) and a rehabilitated (gravel bar) shore in the Austrian Danube. The representatives of percids are native and, in part, endemic or endangered. Three out of four gobiid species, in contrast, are characterized by their high invasive potential.

As the drift is highly species specific, analyses were carried out on the lowest applicable taxonomic level. Accordingly, all specimens were identified to genus level. Due to a lack of complete and practical larval keys, and the strong similarity of the young stages of some species, no unambiguous identification at species level was possible. Nevertheless, eight out of ten potentially occurring species of percids and gobiids were confirmed. Information on genus and species identification is given in the supplement.

On both shores, the drift density of gobies (four species) was generally significantly higher compared to percids (eight species). Percid drift density was substantially higher on the rehabilitated shore. Within the Percidae, the genera *Sander* and *Zingel* showed the highest abundances. Among the Gobiidae, the invasive (formerly) *Neogobius* species (*N. melanostomus, Ponticola kessleri*, and possibly *Babka gymnotrachelus*) clearly dominated (>99%) over the native tubenose goby (*Proterorhinus semilunaris*). Substantial differences were found for the seasonal and nocturnal course of drift. Percid drift is restricted to a few weeks during spring, whereas the gobiids show continuous spawning and were still drifting at late June. The analysis of young fish size indicates a rather rapid shift to a benthic lifestyle for the genera *Gymnocephalus* and *Zingel*, as well as for the gobiids in general. *Perca* and *Sander* exhibit a longer drifting phase, lasting until juvenile stages. If the occurrence of young stages in the drift is proportional to their overall abundance in the river, the re-structuring of artificial shorelines can be considered to benefit early life stages of native species and possibly mitigates the impact of invaders.

Keywords

Drift, rip-rap, gravel bar, Percidae, Gobiidae, regulated rivers

Zusammenfassung

Die Drift früher Entwicklungsstadien ist ein wichtiger Bestandteil im Lebenszyklus vieler Flussfischarten. Sie dient der Verbreitung und stellt sicher, dass die Larven an geeignete Aufwuchshabitate gelangen, die Schutz und Nahrung bieten. Durch die gewässermorphologischen und hydraulischen Veränderungen der intensiven Regulierung der meisten Flüsse hat die Verfügbarkeit von Laich- und Larvalhabitaten für Fische stark abgenommen. Erst in den letzten Jahrzehnten wurde begonnen, zuvor verbaute Ufer wieder in einen naturnahen Zustand zu versetzen. Diese Studie vergleicht die Drift ausgewählter Familien (Percidae und Gobiidae) entlang einem verbauten Blockwurfufer mit Buhnen und einem restrukturierten Ufer (Schotterbank) im Hauptstrom der freifließenden österreichischen Donau östlich von Wien. Die Barsche (Percidae) sind heimisch und zum Teil durch endemische und gefährdete Arten in der Donau vertreten, während drei der vier vorkommenden Meergrundelarten (Gobiidae) vor allem durch ihr hohes Invasionspotential gekennzeichnet sind.

Das Ziel der Arbeit bestand darin, die Analysen auf dem niedrigsten anwendbaren taxonomischen Niveau durchzuführen, um neue Informationen über die Drift der zum Teil seltenen und gefährdeten, sowie der invasiven Arten zu erhalten. Hierzu wurden alle Exemplare zuerst auf Gattung bestimmt. Aufgrund der großen Ähnlichkeit der frühen Entwicklungsstadien der behandelten Arten und des Fehlens von vollständigen und praktikablen Larven-Bestimmungsschlüsseln, war in vielen Fällen eine eindeutige Artbestimmung nicht möglich. Dennoch gelang der Nachweis von acht der zehn potentiell vorkommenden Barsch- und Grundelarten. Eine im Rahmen dieser Arbeit entwickelte Bestimmungshilfe zur Gattungs- und Artbestimmung ist im Anhang angeführt.

Die Driftdichte der Grundeln war an beiden Ufern generell signifikant höher als jene der Barsche, jedoch war der proportionale Anteil an Barschen am naturnahen Ufer wesentlich höher. Innerhalb der Perciden zeigten die Gattungen *Sander* und *Zingel* die höchsten Abundanzen. Bei den Gobiiden dominierten die invasiven (ehemals) *Neogobius*-Arten (*N. melanostomus, Ponticola kessleri* und möglicherweise *Babka gymnotrachelus*) mit über 99% klar über der heimischen Halbmondgrundel (*Proterorhinus semilunaris*; ehemals als Marmorierte Grundel bezeichnet). Deutliche Unterschiede weist der saisonale und nächtliche Verlauf der Drift auf. Barsche drifteten nur während weniger Wochen im Frühling, wohingegen die Grundeln mehrmals im Jahr laichten und durchgehend bis zum Ende der Untersuchungszeit in ähnlichen Driftdichten und in einem engen Größenbereich in der Drift vorkamen. Die Größenanalyse der Jungfische lässt Rückschlüsse auf die Reproduktion und Biologie der Arten zu. Für die Gattungen *Gymnocephalus* und *Zingel*, sowie für die Gobiiden allgemein, lässt sich auf einen rascheren Wechsel zu einer benthischen Lebensweise schließen. *Perca* und *Sander* sind auch als Juvenile noch in höheren Abundanzen zu finden. Zusammenfassend ist davon auszugehen, dass eine naturnahe Ufermorphologie heimische Arten begünstigt, und dieser Trend ebenso deutlich bei rückgebauten Ufern zu beobachten ist und zusätzlich die Etablierung von invasiven Arten abzuschwächen scheint.

Schlüsselworte

Drift, Blockwurf, Schotterbank, Percidae, Gobiidae, Flussregulierung

Introduction

The downstream drift of early stages is a common and important life-history event in many fish species. It is important for dispersal, as well as for reaching suitable nursery habitats (Pavlov *et al.*, 1978; Brown and Armstrong, 1985; Pavlov, 1994; Fuiman and Werner, 2002). Larval drift is thought to be a combination of both passive and active elements, governed by abiotic physical conditions, behaviour, and developmental processes. Passive components include environmental as well as hydrological and hydraulic factors such as river discharge (Harvey, 1987; Johnston *et al.*, 1995), currents and turbulences (Wolter and Sukhodolov, 2008; Schludermann *et al.*, 2012; Lechner *et al.*, 2013), or temperature (Pavlov *et al.*, 2000). Active elements are linked to behavioural aspects such as phototaxis (Reichard *et al.*, 2002a; Nunn *et al.*, 2010), rheotaxis (Pavlov, 1994), or habitat choice (Robinson *et al.*, 1998; Freeman *et al.*, 2001; Humphries and King, 2004). Given the many factors that influence larval drift, shoreline characteristics and habitat structure are clearly crucial for the survival of early life stages of fish. The assumption is, that a high connectivity between spawning grounds and nursery habitats, and also between single nurseries, reduces mortality rates of early stages (Brown and Armstrong, 1985; Harvey, 1987; Keckeis *et al.*, 1997). Larval habitats should offer a high retention capacity, which mitigates the risk of washouts and promotes the establishment and persistence of larval communities in rivers (Schiemer *et al.*, 2001).

Large-scale river engineering measures have drastically changed the hydrology and shore morphology in many rivers (Dynesius and Nilsson, 1994). These include measures for power generation (dams, hydropower plants), flood prevention, and navigation (bank reinforcements, rip-rap, groynes). As a result, only very few free-flowing sections and natural shores remain in the Danube and many other river systems (Dynesius and Nilsson, 1994; Schiemer *et al.*, 2004). Early stages of fish are particularly vulnerable to river regulations because suitable spawning grounds and nursery habitats decline in number and area (Schiemer *et al.*, 1991; Quigley and Harper, 2004). Until now, most research was focussed on the impact of flow regulations (e.g. by dams for electricity generation or water irrigation) on recruitment of fish larvae in regulated rivers (Scheidegger and Bain, 1995; Humphries and Lake, 2000; Humphries *et al.*, 2002; Pavlov *et al.*, 2008). Information on how artificial shore-lines affect drift and dispersal of early fish stages is crucial (Schiemer *et al.*, 1991) but scarce (Humphries *et al.*, 2006; Lechner *et al.*, 2013). Among the most common shore types in the Danube are near-natural gravel bars and artificial rip-raps, each with very distinct

characteristics. Natural sand or gravel banks are considered to be more suitable for larvae due to their generally shallower-sloped banks and higher retention capacities (Schiemer *et al.*, 1991; Schiemer *et al.*, 2001). Constantly re-shaped shorelines increase the flowage line and habitat diversity, which are able to meet the requirements of different development stages and species (Schiemer *et al.*, 1991). Artificial shorelines are of uncertain ecological relevance. They may increase overall habitat diversity along with (adult) fish abundances (Erős *et al.*, 2008; White *et al.*, 2010), but are generally considered as very poor spawning and nursery habitats (Schiemer *et al.*, 1991; Quigley and Harper, 2004). Groynes, in contrast, have been suggested to be important habitats for young fishes, but only under certain conditions (Bischoff and Wolter, 2001).

This study was designed to assess shore-dependent differences regarding several aspects of the drift of early fish stages. The hypothesis is that the taxonomic composition, seasonality, nocturnal patterns, and size structure of caught fish will differ amongst different shore types, providing hints on the suitability of these shores for young fishes. This was tested by examining two selected benthic fish families of high ecological importance, the Percidae (perches) and Gobiidae (gobies). The percids (eight species in Austria) include several endemic and endangered species of great conservation concern (Wolfram and Mikschi, 2007). The gobiids (four species in Austria), in contrast, are notorious for their invasiveness (Charlebois *et al.*, 1997; Wiesner, 2005). Only one gobiid species, the tubenose goby, is considered to be native, and endangered (Ahnelt, 1988; Wolfram and Mikschi, 2007).

Percids in Eurasian river systems generally drift in relatively low abundances compared to the cyprinids, which are repeatedly the dominant fish family in the drift (Reichard *et al.*, 2002b; Zitek *et al.*, 2004b; Sonny *et al.*, 2006). As a result, percid species are often excluded from detailed analysis, which then focus on more common taxa. Percids, however, may be among the most abundant taxa in North American rivers (Johnston *et al.*, 1995; D'Amour *et al.*, 2001). Percids are known to start to drift relatively early in the year (spring), sometimes being the first fishes to appear in the drift (Brown and Armstrong, 1985; Johnston *et al.*, 1995; Zitek *et al.*, 2004a). The perch (*Perca fluviatilis*) is known to drift as pre-larva (i.e. free embryo), larva and juvenile (Pavlov, 1994), although some European researchers have supposed a drift avoidance for this species (Reichard *et al.*, 2002b; Zitek *et al.*, 2004b). Information on seasonal patterns in other European percids is sparse, especially for the less common and less commercially important *Gymnocephalus* and *Zingel* species.

The drift in gobiids is considered to be a stable and opportunistic dispersal strategy (Zitek *et al.*, 2004b). In combination with continuous spawning, shown by most species, it helps explain the invasion success of Ponto-Caspian gobies across Europe and North America (Charlebois *et al.*, 1997; Kornis *et al.*, 2012; Janáč *et al.*, 2013). In invaded rivers, especially those with paved shores, gobiids may also be the dominant family in the drift, despite the relatively low number of species (Zitek *et al.*, 2004b; Lechner *et al.*, 2010). Drifting, however, seems to be restricted to a certain ontogenetic stage or size (Janáč *et al.*, 2013). Downstream migrations are usually nocturnal, with highest drift rates approximately two to three hours after dusk (Janáč *et al.*, 2013). Some goby species may also drift at daytime under certain conditions (Iguchi and Mizuno, 1991). In any case, knowledge about the drift and dispersal patterns of gobies is vital to understand and counter invasion events.

This study compares the larval drift during May and June 2011, along an artificial rip-rap and a semi-natural gravel bar in the Austrian Danube. Both differ but are characteristic shore types of today's large rivers. Considering the different characteristics of natural and artificial shores mentioned above, the following hypotheses are put forward:

(1) The gravel bar is inhabited by a larger total number of fish larvae, resulting in higher drift densities.
(2) Disturbed, or artificial, shores often act as starting points for opportunistic invaders; therefore the abundance of non-native species (i.e. gobiids) is higher at the rip-rap.
(3) Natural shores benefit the autochthonous local fish communities, resulting in higher abundances of native fish species (i.e. percids) at the rehabilitated shore.

Additionally, this study focuses on:
(4) The seasonal and nocturnal courses of drift, which are described and compared.
(5) The analysis of the size of caught larvae and juveniles, which provides further information on drift duration, pointing to divergent importance of drift for different taxa.
(6) By analysing the size structure throughout the sampling period, conclusions can be drawn on the number and duration of spawning events.

Material & Methods

Study area

This study was conducted on two shores of the main channel of the Austrian Danube between river kilometers 1890.0 to 1893.8, within the "Danube Alluvial Zone National Park" (Fig. 1). This section exhibits two different, but characteristic shore types of large rivers. The right side is heavily modified and was straightened and paved by basaltic blocks (rip-rap), which form artificial embankments. Groynes, perpendicular to the axis of the main channel, have been installed for navigation purposes. These measures stabilize the banks against erosion and improve the navigability at low water (Fig. 2B). The areas between the groynes (i.e. groyne fields) have distinct hydro-morphological features and were suggested to be important habitats for young fish in the Elbe River (Bischoff and Wolter, 2001). The left shore was once similar to the right shore, but has been re-structured by removing the rip-rap and by installing new types of modified groynes during the years 2007 to 2009 during an ecologically orientated river engineering project (Schiemer *et al.*, 1999; Reckendorfer *et al.*, 2005). These rehabilitation measures re-established a bankside flow and improved the longitudinal and lateral connectivity of near-shore habitats. Self-dynamic processes formed gravel bars, which are constantly re-shaped by the river (Fig. 2A).

Previous studies in the same sampling area have characterized the shorelines in detail (Lechner *et al.*, 2013). The gravel bar exhibits evenly distributed shallow areas along the whole sampling range. Lateral velocities were very low (<0.1 m s^{-1}), as was turbulence. The shallow areas in the rip-rap, however, are scattered and only very close to the shore. The flow patterns within the groyne fields varied, but all showed a steep velocity gradient between the fields and the main channel. Turbulence was higher compared to the gravel bar, but remained relatively constant with increasing distance from the shore. Water depth was generally greater at the artificial shore side.

Sampling design

Acquisition of larvae

Sampling took place on 18 days between the 9 May and 20 June, with increasing intervals from one to seven days between two sampling dates. At four sampling stations at

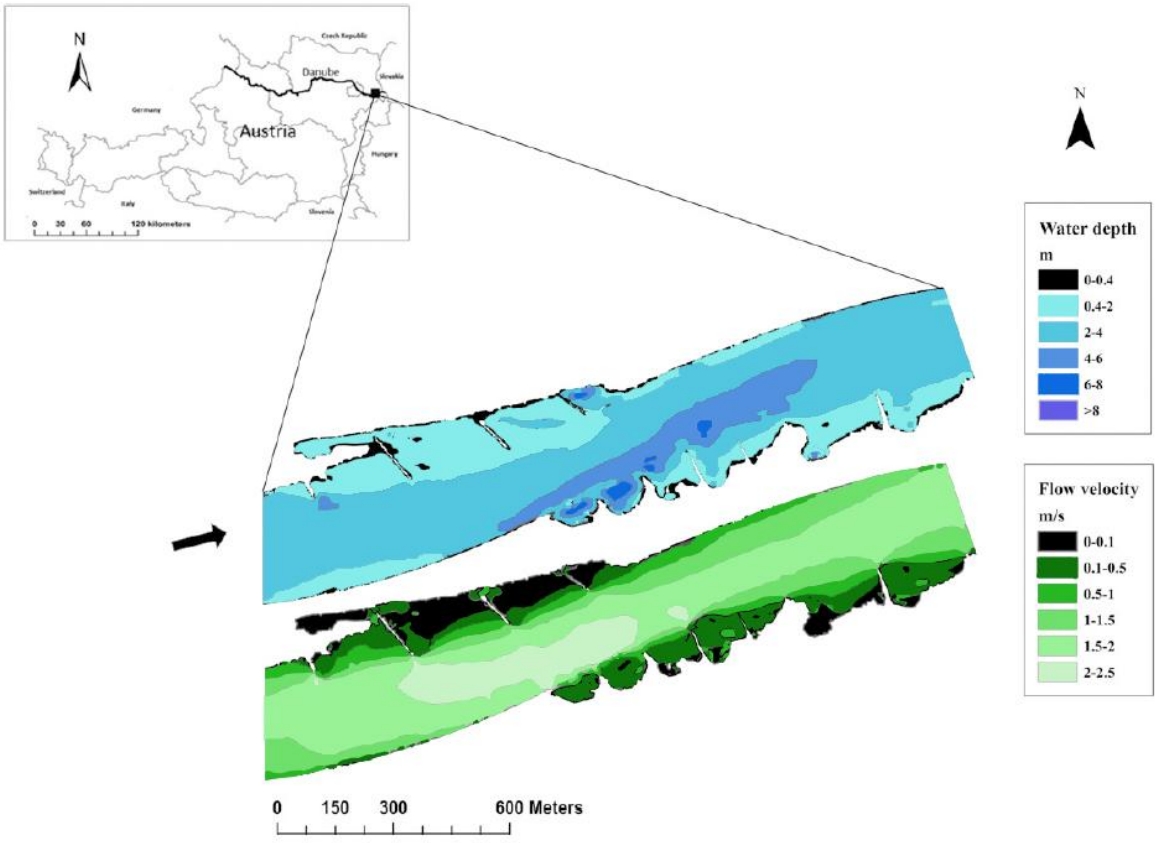

Fig. 1: Map of study area with water depths (blue) and flow velocities (green). The arrow indicates the direction of flow. Modified after Lechner *et al.* (2013).

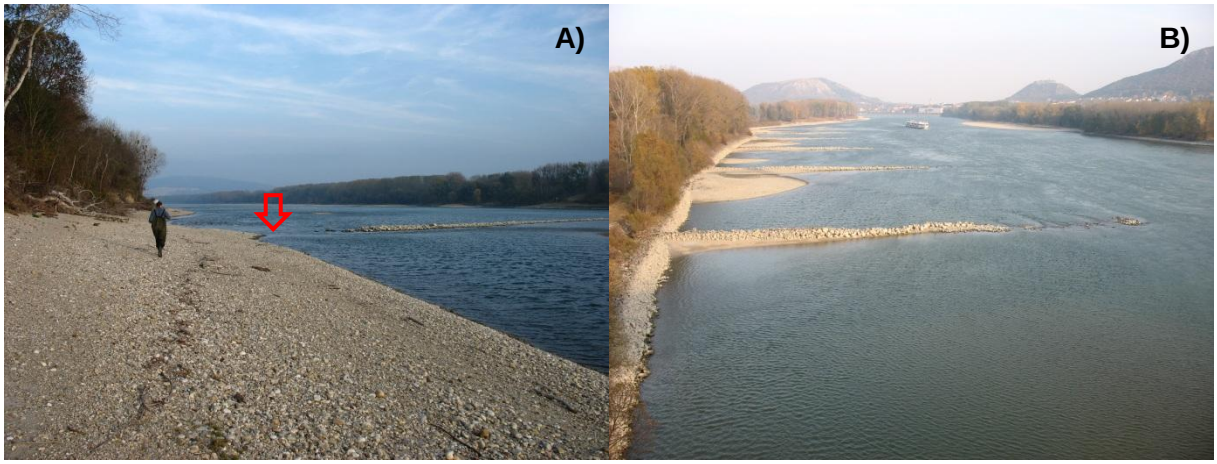

Fig. 2: Shoreline characteristics. (A) restored shore, exhibiting gravel bar and groynes cut at their roots to enable bankside flow (red arrow). (B) artificial shore, exhibiting rip-rap and groynes, with adjacent groyne fields. Photographs courtesy of H. Keckeis.

each shore, samples were taken at three different distances from the bank (inshore IN, midshore MID, and offshore OFF). Due to different shore morphologies and water levels, the distances between the poles (and from the most inshore pole to the shoreline) varied between approximately 0.5 and 2 meters. Synchronous sampling took place in one-hour

intervals, up to five times a day (from 7 pm to midnight), yielding a maximum of 60 samples per day and shore.

Conically shaped drift nets (0.5 m diameter, 1.5 m long, 500 μm mesh), equipped with detachable collecting boxes, were used to catch fish larvae. Nets were suspended on metal poles, which had been driven into the ground, allowing the nets to follow the current (see also Humphries and King, 2004). All net triplets (IN, MID, OFF) were simultaneously exposed and left in the flow for 30 minutes. A flowmeter (2030R, General Oceanics®, Miami) was attached at the lower third of the entrance of each net to measure the volume of filtered water. All captured fish larvae were killed with an overdose of MS-222 (Tricaine methanesulfonate, Sigma-Aldrich®, St Louis) and preserved in 96% ethanol.

Sample processing and identification of larvae

In the laboratory, all samples were processed, separating fishes from organic and inorganic material entrapped in the drift nets. The specimens were then separated into taxonomic families and the larvae of the Gobiidae and Percidae where further identified to genus and, when possible, down to species level. Identification of genera and species was accomplished using papers on early development (Mansueti, 1964; Kovac, 1992; 1993a; b; 1994; 2000; Leslie *et al.*, 2002; Leslie and Timmins, 2004; Specziar *et al.*, 2009), as well as general larval identification keys (Koblickaya, 1981; Urho, 1996b). Reliable and complete sources on the identification of larval stages were not available for all species, and the figures in the available literature are often ambiguous and poorly comparable. As a consequence, species identification was not possible for most larval stages.

This study focuses on percids and gobiids because of their high conservation value and ecological concern. While the percids consist of many threatened or even endangered species in Austria (Wolfram and Mikschi, 2007), some of the gobiids are notorious for their invasiveness (Wiesner, 2005; Harka and Bíró, 2007; Wiesner *et al.*, 2010; Kornis *et al.*, 2012). The species within the Percidae are: Danube ruffe *Gymnocephalus baloni* HOLCIK & HENSEL 1974, ruffe *G. cernua* (L. 1758), schraetzer *G. schraetser* (L. 1758), European perch *Perca fluviatilis* (L. 1758), pikeperch *Sander lucioperca* (L. 1758), Volga pikeperch *S. volgensis* (GMELIN, 1788), Danube streber *Zingel streber* (SIEBOLD, 1863), zingel *Z. zingel* (L. 1766). Within the Gobiidae the relevant species are: Western tubenose goby *Proterorhinus semilunaris* (PALLAS, 1814), racer goby *Babka gymnotrachelus* (KESSLER, 1857), round goby *Neogobius melanostomus* (PALLAS, 1814), bighead goby *Ponticola kessleri* (GÜNTHER, 1861).

The general nomenclature used here is after Kottelat and Freyhof (2007), except gobiid nomenclature, which follows Neilson and Stepien (2009).

The total length (TL) of all fish was measured as a proxy for development stage. Sliding callipers (±0.5 mm) were used for the length measurements. If the number of larvae in a sample exceeded 35 individuals, then subsamples of 30 larvae were taken and the identification and length measurement results were extrapolated for the whole sample.

Data analysis

Before analysis, all samples were standardized by calculating drift densities (DD; number of individuals per 100 m^3 of filtered water). Non-parametric tests were used for the statistical analysis because Kolmogorov-Smirnov tests revealed non-normal distributions (all $p<0.001$). Mann-Whitney-*U* tests were used to detect shore-dependent differences of the genera. Kruskal-Wallis tests were used to detect differences related to shore distance. Kendall's τ-b coefficient was used to analyse correlations between size and season and time of day, respectively. Correlations are based on raw data. Drift density data were transformed because of the high frequency of zero catches and the high variation, by a logarithmic transformation $b=\log(x+d)-c$, where x is the original DD, d a decimal constant, and c an order of magnitude constant (following McCune *et al.*, 2002). Statistical analyses were conducted using PASW Statistics 18.0 (SPSS Inc.®, Chicago). Diagrams were generated and linear regressions fitted using SigmaPlot 12.0 (Systat Software®, San Jose). All statistical significances were Bonferroni corrected by multiplying the obtained significances by the number of tests.

Results

General

A total of 924 drift samples were examined, containing 29,163 individual larvae from five families. The Cyprinidae (*n*=21,037; 74.3% of total catch) accounted for the highest abundances, followed by the Gobiidae (*n*=6,322; 20.1%) and the Percidae (*n*=1,748; 5.5%). The families Cottidae and Gasterosteidae comprised only 21 and 5 individuals, respectively (Fig. 3A). Regarding shore type, more individuals were found on the left shore, mainly due to a significantly larger proportion of cyprinids (Table 1).

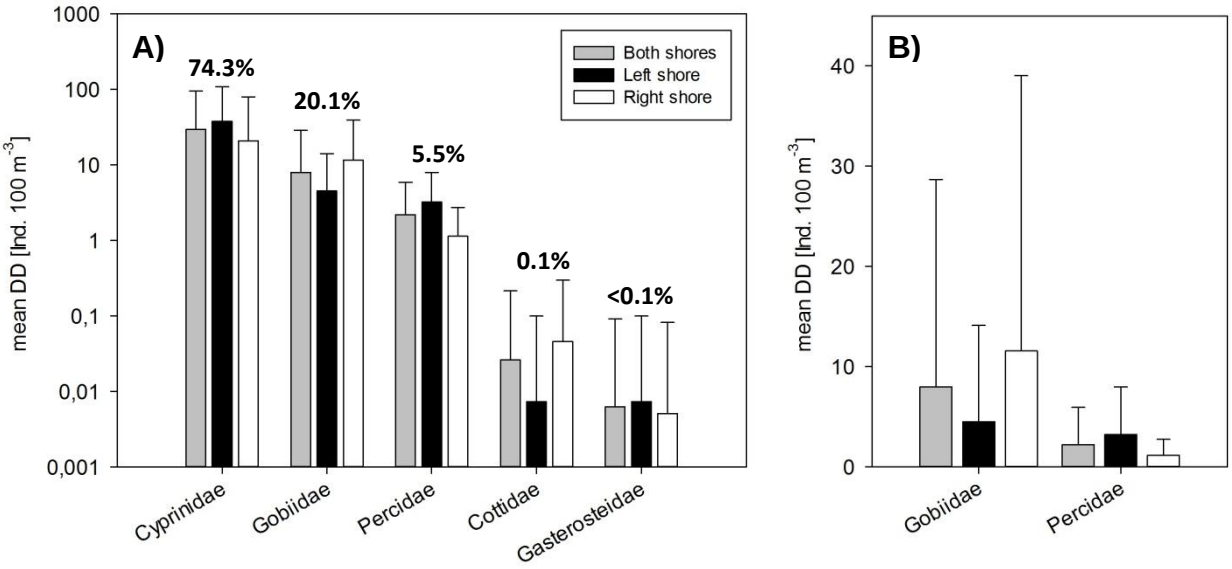

Fig. 3: Mean drift densities of all occurring families (A) and for Gobiidae and Percidae only (B). Percentages relate to both shores combined. Note that the y-axis of the family diagram is scaled logarithmically. Error bars are standard deviation. Untransformed data.

Genera and Species Identification

Percids are represented in Austria by eight species in four genera. All genera were distinguishable from each other. The perch (*Perca fluviatilis*) is the only member of the genus *Perca* and can therefore be addressed on species level. Juvenile pikeperch (*Sander lucioperca*) and Volga pikeperch (*S. volgensis*) can be separated by their head shape and the presence or absence of canine teeth. An unambiguous species identification of *Sander* larvae failed. The same applies to the genus *Zingel*. The zingel (*Zingel zingel*) can be distinguished from the Danube streber (*Zingel streber*) by the number of fin rays, when they have reached approximately 15 mm TL, which corresponds to larval stage L6 *sensu* Penaz (2001). The

larvae of *Gymnocephalus* species are very similar and were not distinguishable, except for single findings of ruffe (*G. cernua*) and schraetzer (*G. schraetser*), which showed distinct pigmentation or morphological features. Larvae of the Danube ruffe (*G. baloni*) could not be confirmed. Therefore, seven of the eight percid species occurring in Austria were found.

The gobiids of Austria are represented by four monotypic genera (Neilson and Stepien, 2009). Definitive identification was possible for the native Western tubenose goby (*Proterorhinus semilunaris*), enabling a clear discrimination from the three other invasive species. In contrast, no distinction between the three invasive species round goby (*Neogobius melanostomus*), bighead goby (*Ponticola kessleri*), and racer goby (*Babka gymnotrachelus*) was possible. Exceptions are larger individuals of *P. kessleri* and *N. melanostomus* (>10 mm TL), which already exhibit adult-like shape and pigmentation. However, individuals of this size were rarely observed. As an unambiguous species identification of early life stages was not possible, the three invasive species were grouped under their former genus name as "*Neogobius*" in the analyses.

See Supplement I for further comments on identification.

Table 1: Sampling dates, start and end time of sampling, number of 1 h intervals (rounds), and total sample size of all families (*n*) with sums.

Shore	Date	Start	End	Rounds	*n*
left	09.05.2011	20:30	22:30	3	274
	10.05.2011	19:00	23:00	5	329
	13.05.2011	19:00	23:00	5	2,179
	16.05.2011	19:00	23:00	5	3,016
	19.05.2011	19:30	23:30	5	1,435
	24.05.2011	19:30	23:30	5	4,748
	31.05.2011	20:00	0:00	5	2,118
	08.06.2011	20:30	23:30	4	1,183
	17.06.2011	20:30	23:30	4	959
					Σ 16,241
right	11.05.2011	19:30	23:30	5	437
	12.05.2011	19:00	23:00	5	577
	15.05.2011	19:00	23:00	5	797
	17.05.2011	19:00	23:00	5	627
	20.05.2011	19:30	23:30	5	2,702
	26.05.2011	19:30	23:30	5	3,068
	01.06.2011	20:30	23:30	4	3,431
	15.06.2011	20:30	23:30	4	751
	20.06.2011	20:30	23:30	4	532
					Σ 12,922

Spatial distribution

The drift density of gobiids was higher than of percids on both shores, though with substantial differences regarding bank side. Gobiids clearly dominated the right shore: the mean DD was more than twice as high as on the left shore. In contrast, percid drift density was almost threefold higher on the left versus right side (Fig. 3B). Accordingly, the proportion of percids in the samples was much higher on the left shore. While the drift density of gobiids on the right side (rip-rap) was more than ten times higher than that of percids, this ratio was only 1:1.4 at the left shore (gravel bar; Table 2).

Regarding percids, most caught larvae belonged to the genus *Zingel*, followed by *Sander* species (probably predominantly *S. lucioperca*, which would account for the most common percid species). Specimens of *Gymnocephalus* and *Perca* were found at much lower DD. All genera showed significantly higher drift densities on the left shore (all $p>0.01$). The exception is *Gymnocephalus*, although not statistically significant ($p=0.582$; Fig. 4).

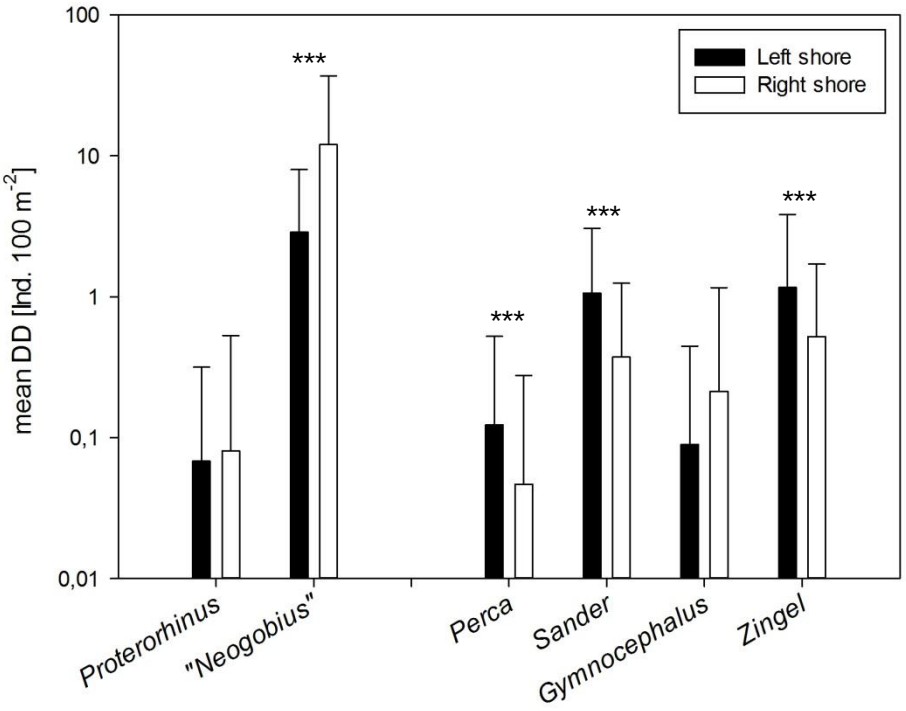

Fig. 4: Mean drift densities of all gobiid (left columns) and percid (right columns) genera. Note that the y-axis is scaled logarithmically. Error bars are standard deviation. Asterisks indicate significant differences between shores: * $p<0.05$, ** $p<0.01$, *** $p<0.001$. Untransformed data.

Concerning gobiids, the genus "*Neogobius*" was overwhelmingly dominant. The native species *Proterorhinus semilunaris* accounted for only approximately 1% of all gobiid larvae. The proportion of *Proterorhinus* amongst the gobiids, however, was higher on the left

shore (ca. 2.5%) than on the right shore (ca. 0.5%), although without statistical significance (p=0.072). "*Neogobius*" larvae showed significantly higher DD on the right shore (p<0.01), with twice as high mean DD (Fig. 4).

Temporal distribution

Seasonal patterns

The seasonal course of drift was specific for each genus, and was characterized by differences in abundance (i.e. maximum DD) as well as by the different timing and number of peaks (uni-, bi-, or multimodal; Fig. 5).

Percids were present in the samples from the first sampling day on, indicating an earlier start of drifting season. Drift densities increased, peaking in mid-May, and then declined to nearly zero in late June. The seasonal course in percid genera was bimodal for *Perca* (mid-May, early June) and *Sander* (mid-May, late May), but unimodal for *Gymnocephalus* and *Zingel* (both mid-May). Beyond the abundance differences, the general seasonal course was relatively similar for both shores.

Gobiid drift started in the second week of May and reached a first maximum in late May, followed by constantly high DD throughout the remaining sampling period. The seasonal course showed no clear pattern and lacked distinctive peaks. While *Proterorhinus* showed a relatively similar course on both shores, the patterns for *Neogobius* were different: the first peak occurred approximately two weeks earlier on the right shore.

Nocturnal patterns

The timing of sunset varied from 8:17 pm to 8:56 pm. Percids were already drifting before sunset, although at low abundances. After dusk, the drifting density rose moderately and increased until the end of the sampling time along the left bank. At the right shore, drift density also increased after sunset but remained relatively constant thereafter. This general pattern was found in all percid genera (Fig. 6).

Gobiids were almost absent in the drift before sunset. After dusk, their density strongly increased on both shores. On the right shore, however, drift densities of *Proterorhinus* and *Neogobius* dropped again after approximately 10 pm. The left shore, in contrast, showed a more or less constant increase until the end of sampling (Fig. 6).

Size

All percids rapidly increased in mean size (TL) throughout the sampling period (Fig. 7), with significant correlations (*Perca* right shore p=0.023, all other genera p<0.001) for all percid genera and shores. The only non-significant correlations were found for *Gymnocephalus*, though only at one shore (p=0.122; right shore). Correlation coefficients of larval size and date were generally high, ranging from 0.45 to 0.74 (Table 4). Percidae were characterized by a higher proportion of larger larvae and juveniles in the drift compared to gobiids (Fig. 8). For instance, more than 50% of all pikeperches drifted at sizes >20 mm TL. *Sander* also showed the highest mean and maximum lengths. Smallest average and maximum lengths were found in *Gymnocephalus* (Table 3). In all percids, except *Perca*, the slope of the linear regression between date and size indicates higher growth rates on the left shore (Fig. 7).

Regarding sampling period, no or only a marginal increase in size was found for *Proterorhinus* and "*Neogobius"*, respectively (Fig. 7). 95% of all gobies drifted at sizes <10 mm TL (Fig. 8A). No differences between shores were found. The slopes of the linear regression lines were not significantly different from zero for *Proterorhinus* (95% confidence intervals ranging from -0.031 to +0.032). This indicates no ontogenetic effects on larval drifting and a more or less continuous production of offspring throughout the investigation period. Body size, however, was significantly correlated with date for "*Neogobius*", though the correlation coefficients are relatively small, ranging from 0.17 to 0.33 (Table 4).

Table 2: Individual number (n), percentage of total catch (%), average drift density (mean DD), and standard deviation (SD) of different families for each shore and the total catch (both shores combined).

	Left shore				Right shore				Both shores comb.			
Family	*n*	%	mean DD	SD	*n*	%	mean DD	SD	*n*	%	mean DD	SD
Cyprinidae	13,095	80.6	37.87	70.29	7,942	61.5	20.75	58.73	21,037	72.1	29.47	65.41
Gobiidae	1,832	11.3	4.51	9.59	4,514	34.9	11.55	27.47	6,346	21.8	7.96	20.71
Percidae	1,309	8.1	3.22	4.73	445	3.4	1.14	1.60	1,754	6.0	2.20	3.71
Cottidae	3	< 0.1	0.01	0.09	18	0.1	0.05	0.25	21	0.1	0.03	0.19

Significant, albeit small correlations of size and time of day were found only for "*Neogobius*" (p<0.001; both shores) and *Sander* (p<0.001; left shore). Correlation coefficients ranged between 0.08 and 0.20. All other correlations were statistically not significant (Table 5).

Table 2: Median, mean, standard deviation, minimum, and maximum size (total length in mm), and number of caught larvae (*n*) of percid and gobiid genera. Note that the total number of individuals of each family is lower than in Table 2, because size measurement was not possible for all caught larvae.

Genus	Median	Mean	SD	Min	Max	*n*
Proterorhinus	7	6.6	±1.0	5	12	67
"Neogobius"	9	8.6	±1.2	6	22	6,255
Perca	11	14.8	±7.6	6.5	37	91
Sander	21	22.2	±6.7	8	57	773
Gymnocephalus	6	7.0	±2.8	4	20	116
Zingel	9	10.4	±3.6	6	35	768

Table 3: Correlation of size and date. Kendall's τ-b correlation coefficients and statistical significances (Bonferroni corrected) of correlations between larval body size and date of capture. Asterisks indicate significance: * p<0.05, ** p<0.01, *** p<0.001.

	left shore			right shore		
Genus	Kendall's τ		Sign.	Kendall's τ		Sign.
Proterorhinus	0.011		≤ 1	-0.118		≤ 1
"Neogobius"	0.174	***	< 0.001	0.329	***	< 0.001
Perca	0.739	***	< 0.001	0.519	*	0.023
Sander	0.638	***	< 0.001	0.558	***	< 0.001
Gymnocephalus	0.452	***	< 0.001	0.249		0.122
Zingel	0.477	***	< 0.001	0.309	***	< 0.001

Table 4: Correlation of size and time of day. Kendall's τ-b correlation coefficients and statistical significances (Bonferroni corrected) of correlations between larval body size and time of day. Asterisks indicate significance: * p<0.05, ** p<0.01, *** p<0.001.

	left shore			right shore		
Genus	Kendall's τ		Sign.	Kendall's τ		Sign.
Proterorhinus	0.05		≤ 1	-0.416		0.48
"Neogobius"	0.08	***	< 0.001	0.11	***	< 0.001
Perca	0.098		≤ 1	0.098		≤ 1
Sander	0.198	***	< 0.001	0.163		0.10
Gymnocephalus	-0.06		≤ 1	0.197		≤ 1
Zingel	0.022		≤ 1	0.096		0.98

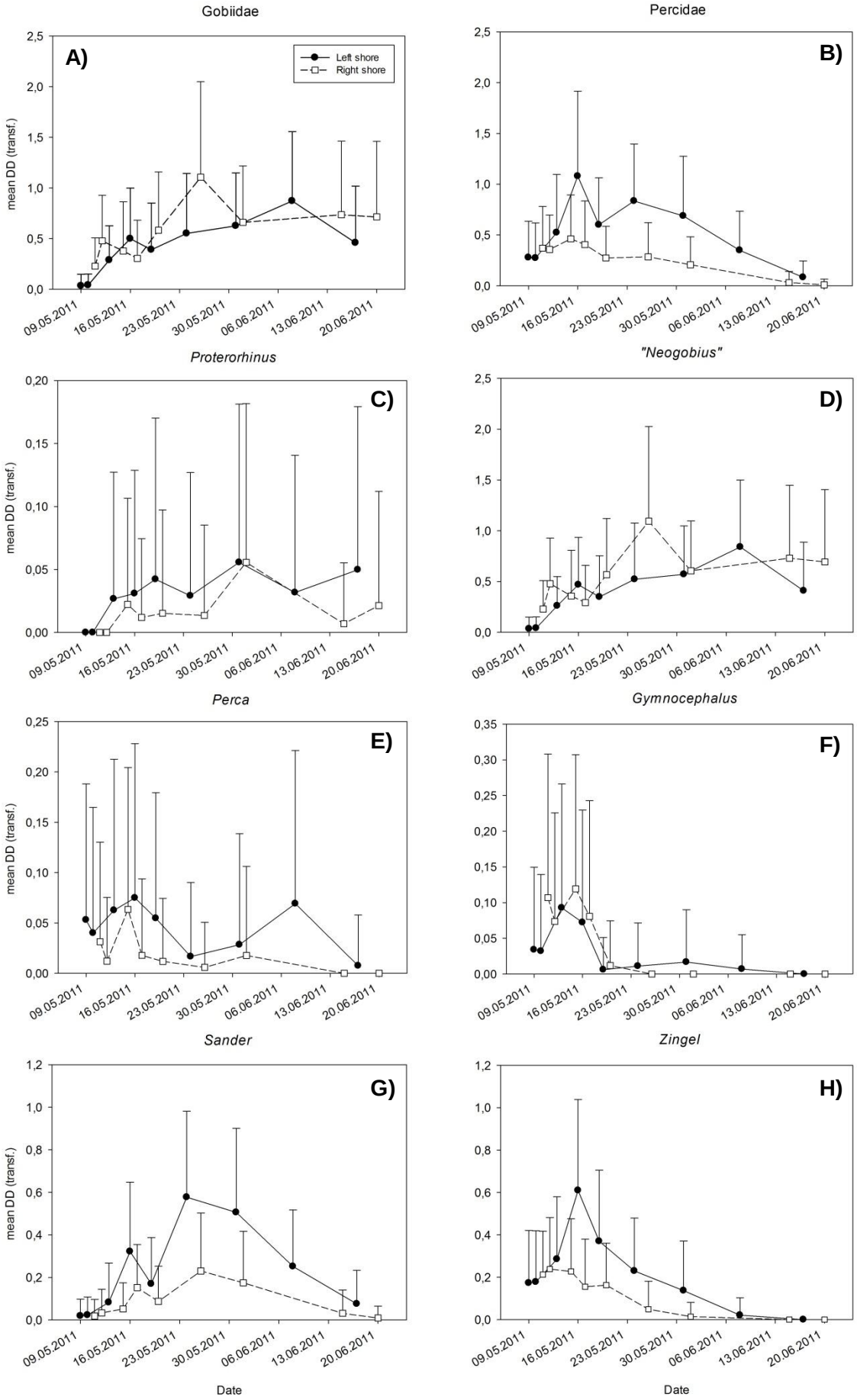

Fig. 5: Seasonal course of mean transformed drift densities of Gobiidae (A) and Percidae (B), gobiid genera (C-D), and percid genera (E-H). Note that y-axes are differently scaled. Error bars indicate standard deviation.

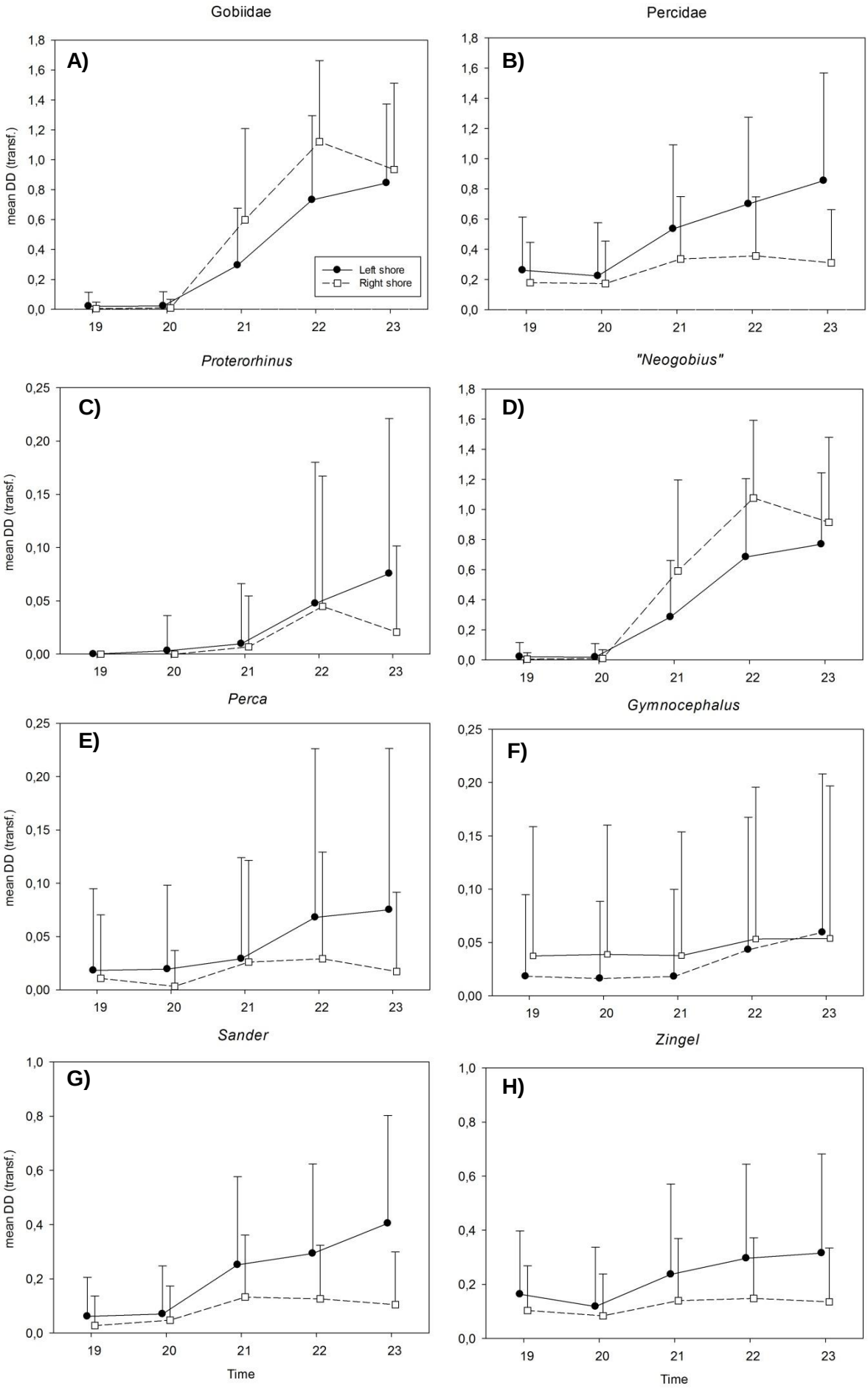

Fig. 6: Nocturnal course of mean transformed drift densities of Gobiidae (A) and Percidae (B), gobiid genera (C-D), and percid genera (E-H). Note that y-axes are differently scaled. Error bars indicate standard deviation.

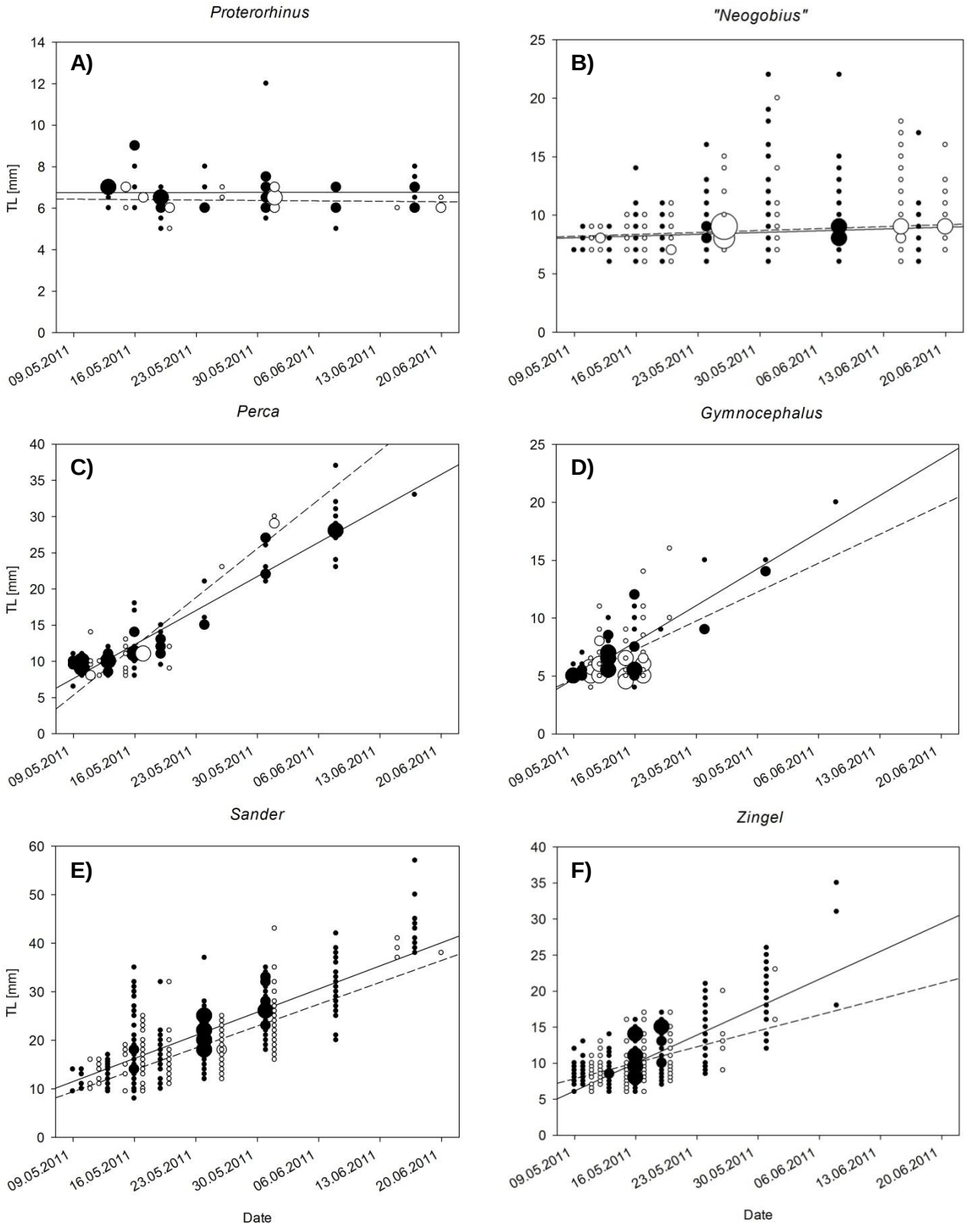

Fig. 7: Size changes throughout sampling period for gobiid (A-B) and percid (C-F) genera. Bubble size indicates the number of individuals at a given size and date. Linear regression lines are shown for illustrational purpose only. Bubble size legend valid for a) *Proterorhinus*, *Perca*, *Gymnocephalus*; b) *Sander*, *Zingel*; c) *"Neogobius"*. Note that y-axes are differently scaled.

Discussion

General

The hydrological parameters differ substantially along the two shorelines, likely resulting in different conditions for fish larvae. In a previous study in the same sampling area, Lechner *et al.* (2013) calculated a more than fourfold higher value of suitable larval habitats for the rheophilic nase carp, *Chondrostoma nasus* (L., 1758), along the gravel banks compared to the rip-rap. Gravel bars are more suitable for the larvae of most riverine (rheophilic) species.

This study confirmed drift in 10 of 12 species of gobiids and percids in Austria, including the endangered Western tubenose goby, Volga pikeperch and Danube streber (Wolfram and Mikschi, 2007). This provides evidence that these species are still able to successfully spawn in this section of the Danube. Drifting individuals of *Zingel streber*, though in very low numbers, have also been found by Zitek *et al.* (2004b) in the Marchfeld-kanal, an artificial side branch of the Danube. Larvae or juveniles of *Sander volgensis* have not yet been found in comparable drift studies (e.g. Reichard *et al.*, 2002b; Zitek *et al.*, 2004b). Somewhat surprisingly is the dominance of *Zingel* species in the samples, because both zingel and Danube streber are generally rarely caught as adults (Schabuss and Reckendorfer, 2002; Erős *et al.*, 2008; Keckeis, 2013; Loisl *et al.*, 2013). The same applies for individuals of the genus *Sander*, at least in the Austrian Danube (Schabuss and Reckendorfer, 2002; Keckeis, 2013; Loisl *et al.*, 2013). In a study in the Hungarian Danube, however, *Sander lucioperca* was the second-most common percid (Erős *et al.*, 2008). The high abundances of early stages of *Sander* and *Zingel* species, but low abundances of adult fishes point to high mortality rates of young fish of these genera. In contrast, *Perca fluviatilis* showed rather low drifting densities, but is generally the most abundant adult percid in the Danube and its backwaters (Schabuss and Reckendorfer, 2002; Erős *et al.*, 2008; Loisl *et al.*, 2013). This supports the suggestion of some authors that this species, at least partly, avoids drift (Reichard *et al.*, 2002b; Zitek *et al.*, 2004b). In the gobiids, the equally high abundances in the drift (Loisl *et al.*, 2013) corroborates the view of an obligatory and stable drifting phase.

In comparable studies in the Danube and its tributaries, drift was dominated by gobies, followed by cyprinids and percids (Zitek *et al.*, 2004b; Lechner *et al.*, 2010). The proportion of gobiids in the present study is notably lower, with Cyprinidae being the

dominant family. Nevertheless, the fact that young stages of only four gobiid species make up for the second most abundant family in the drift (cf. Cyprinidae: 39 spp. in Austria) highlights their invasive potential. Since 1990, these gobies, originating from Ponto-Caspian regions, have spread across the European continent, the Baltic Sea and the Great Lakes of North America (Ricciardi and MacIsaac, 2000; Harka and Bíró, 2007; Kornis *et al.*, 2012). Deliberate introductions by aquarists and unintentional transport with commercial ships (ballast-water, eggs sticking to outer hull), in combination with natural dispersal, are a likely explanation for the rapid spread of gobies (Polacik *et al.*, 2008; Wiesner *et al.*, 2010). Multiple introduction events, high tolerance levels, and fast local adaptations facilitate their invasiveness (Harka and Bíró, 2007; Kornis *et al.*, 2012). Deleterious effects on native fish species after an invasion by gobies are well known, especially regarding *N. melanostomus* (reviewed in Kornis *et al.*, 2012). As an example, the introduction of round gobies has led to a drastic decline in abundances and even local extinctions of the benthic fishes mottled sculpin *Cottus bairdii* GIRARD, 1850 and Johnny darter *Etheosoma nigrum* RAFINESQUE, 1820 in Lake Michigan, USA (Janssen and Jude, 2001; Lauer *et al.*, 2004). It remains unclear, but conceivable, that the rarity of the European bullhead *Cottus gobio* (L., 1758) - the only member of the Cottidae in Austria - in this study is also caused by competition with gobiid species. Unfortunately, historical data or time series are lacking. Bullheads are known to spawn relatively early in the year (Mills and Mann, 1983; Kottelat and Freyhof, 2007); this, in combination with a probably very short drifting phase, may explain the low abundances in the samples. Furthermore, a general avoidance of drift entry was suggested (Lechner *et al.*, 2010).

Spatial distribution

The occurrence of larvae (and juveniles) clearly shows that (1) suitable spawning grounds exist, (2) conditions were suitable for the eggs to develop, and (3) adequate larval habitats are present, in which the larvae were able to feed and grow (see also Humphries and Lake, 2000). Gobiids showed higher drift densities on both shores, but the proportion of percids was much higher on the left shore. Therefore, the left, restored shore is apparently more suitable for early stages of percids. The number of unambiguously identified individuals (larger larvae and juveniles) of the endangered Volga pikeperch and Danube streber was also higher on the left shore, which further emphasizes the importance of

natural shores and a continuation of restoration measures. Note, however, that these ratios must be interpreted with caution because both species were found in very low abundance. Other authors came to similar results regarding juvenile and adult fishes (Loisl *et al.*, 2013). Artificial shorelines may share the same species pool with natural shores, but the relative abundances of eurytopic and habitat specialist (e.g. rheophilic) species are often different. Habitat specialists, which account for most species of high conservation concern (Schiemer *et al.*, 2004), are generally more dominant on natural shores in the Danube (Schiemer *et al.*, 1991; Schiemer and Waidbacher, 1992; Erős *et al.*, 2008; Keckeis, 2013).

Most gobies, particularly the highly invasive species *N. melanostomus* and *P. kessleri*, prefer rocky habitats such as rip-raps. They can, however, also thrive on gravel, sand, and mud, even at equally high densities in some locations (Ray and Corkum, 2001; Polacik *et al.*, 2008; Taraborelli *et al.*, 2009; Young *et al.*, 2010). Thus, the substantially lower abundance of "*Neogobius*" on the restored left shore may indicate a lower habitat suitability for the larvae, or reflect a lower suitability as a spawning ground for adults. Another perspective is that an intact and abundant native fish community may mitigate the impact of invasive species in terms of an 'invasion resistance' (Baltz and Moyle, 1993; Stachowicz *et al.*, 1999; Lyons and Schwartz, 2001; but see Moyle and Marchetti, 2006), although whether this is also true on a larval level remains to be determined.

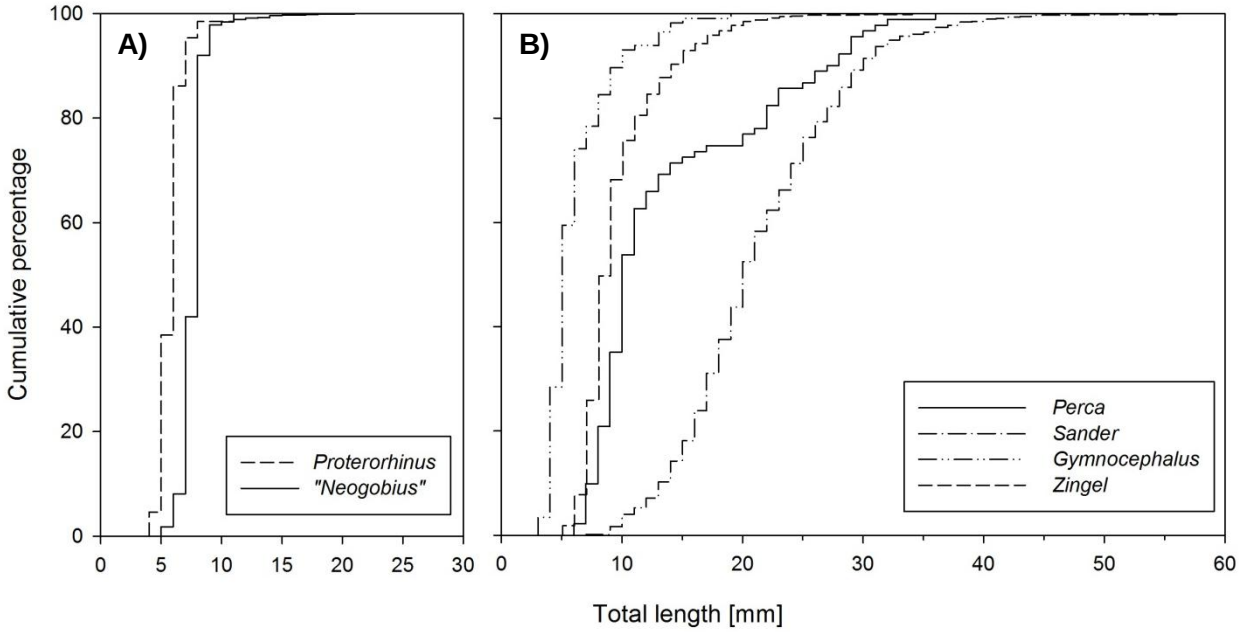

Fig. 8: Size frequency distribution diagram of gobiid (A) and percid (B) genera.

Note also, that the total DD of all fish families was highest on the left side, mainly due to the abundant cyprinid larvae. This supports the proposed hypothesis that the gravel bar is

inhabited by a larger total number of fish larvae. Since it is unknown which species/genera are amongst the Cyprinidae in this study, no general conclusions about the suitability of the shore types for native and invasive species can be made. However, the distribution and abundance of percids and gobiids alone strongly support the proposed hypotheses that native species perform better on the restored shore, while invaders thrive on the rip-rap.

Temporal distribution and size

Seasonal patterns

Seasonal drift patterns are family- and genus-specific. The timing of first occurrence and peak abundances in the drift is highly dependent on spawning time (Brown and Armstrong, 1985; Pavlov, 1994). A multimodal course of drift density may therefore indicate multiple spawning events. Timing of spawning in the Danube and its tributaries is in turn primarily influenced by water temperature, day length, and flow (Ahnelt and Keckeis, 1994; Reichard *et al.*, 2002b; Zitek *et al.*, 2004a; Rakowitz *et al.*, 2008). This holds also true for the development of the embryos and larvae, as well as for developmental events such as hatching, filling of the swim bladder, or beginning of exogenous feeding (Kamler *et al.*, 1998; Keckeis *et al.*, 2001).

The seasonal pattern of percid drift was similar on both shores. This suggests that general drift patterns are not strongly affected by shore type and prevailing hydrological conditions. *Gymnocephalus* and *Zingel* showed single peaks, followed by a steep decrease in drift density thereafter, pointing to a relatively narrow time window of spawning and drifting. Little is known about the larval biology of *Gymnocephalus* and *Zingel*. *Gymnocephalus* species are supposed to have completely benthic larvae (*G. schraetser*), or only a brief pelagic phase (*G. cernua*) followed by a switch to a benthic lifestyle (Kottelat and Freyhof, 2007). In percids, ontogenetic switches may be accompanied by a migration to, and settlement in, near-shore habitats. Once the young fish are settled, drifting and thus the first long-range dispersal is probably mostly over (Coles, 1981; Miehls and Dettmers, 2011). Note, however, that dispersal may not be the ultimate trigger for habitat shifts: changes in predation risk or food sources as the young fish grow are more likely causes (Urho, 1996a; Persson and Crowder, 1998; Byström *et al.*, 2003; Miehls and Dettmers, 2011). Nevertheless, a habitat switch to benthic, near-shore areas is ought to coincide with the end of the drifting phase. In *Gymnocephalus*, a very brief pelagic phase can be inferred from the frequency

distribution diagram because most larvae drift at small sizes <10 mm TL (Fig. 8). The genus *Zingel* shows a very similar course, although at generally larger sizes than *Gymnocephalus*. Information on the early life history of the native *Zingel* species is scarce. Kottelat and Freyhof (2007) report a switch from pelagic to benthic habitats at approximately 25 mm TL for the closely related apron *Z. asper* (L., 1758). The present study was unable to confirm this rather long pelagic (and likely drifting) phase. As 90% of *Zingel* larvae drift at sizes <15 mm TL, *Z. zingel* and *Z. streber* apparently switch to a benthic lifestyle substantially earlier than their congener.

Broader time ranges with bimodal courses were exhibited by *Perca* and *Sander*, with larger proportions of drifting juveniles compared to the other two percid genera. This is in concordance with the literature, which reports a relatively long pelagic phase, followed by a switch to benthic habitats at approximately 20 to 30 mm TL for *Perca* (Spanovskaya and Grygorash, 1977; Coles, 1981; Miehls and Dettmers, 2011) and *Sander* (Specziár, 2005).

Minimum sizes of all percids increased during the sampling period. Therefore, no newly hatched larvae emerge in the drift beyond a certain time. This indicates a rather short spawning season for all percids. As the sampling period did not cover the start of the drifting season of all percid genera, further conclusions about spawning time and duration cannot be drawn. However, the prolonged spawning season of some percids (perch: February to July; schraetser: April to June; Kottelat and Freyhof, 2007), could not be confirmed. It is possible, though unlikely, that later spawning events not covered in the sampling period occurred. The drift densities of all percid genera cease in late June. Spawning and larval development, as well as dispersal, seem to be mostly restricted to the spring months. This is followed by settlement of later ontogenetic stages in near-shore habitats, or drift avoidance due to improved swimming abilities.

The seasonal course of gobiid drift is multimodal and does not follow any clearly recognizable pattern. Moreover their drift densities remain relatively constant during the sampling period. Spawning and drifting probably continue throughout the summer, as continuous spawning is well known in gobies. According to the literature, spawning takes place every three to four weeks, from approximately April to September (Charlebois *et al.*, 1997; Kottelat and Freyhof, 2007). The results of the present study also point to continuous spawning because the mean sizes of *Proterorhinus* and "*Neogobius*" remained constant throughout the season and recently hatched individuals were found even at the last sampling days. Similar results were also found for the Czech Danube (Janáč *et al.*, 2013). This

points to an advantage of gobiids over most native fishes and is one explanation for their invasiveness. Interestingly, although *Proterorhinus* and the "*Neogobius*" species share many similarities, the invasive gobies have larger mean body sizes (Table 3), probably creating competitive advantages. This may be one of the reasons for the decline of the native tubenose goby in the Danube (Mikschi *et al.*, 1996; Wolfram and Mikschi, 2007) and the resulting low abundances in the drift.

More than 95% of all gobies drift at sizes <10 mm TL. This most likely reflects a rather early and rapid shift to a benthic lifestyle, with corresponding drift avoidance, above a certain size. Therefore, dispersal in gobiids is limited to the very early life stages, followed by settlement in, and exploitation of, benthic habitats.

While there seem to be no major shore-dependent difference in drift patterns for *Proterorhinus*, the "*Neogobius*" species exhibit an earlier drifting peak on the right shore. The reason, however, remains unclear. A shore-related cause (such as an increased likelihood of being washed out by waves) seems improbable because this peak is not evident in any other genus or in larvae of other similarly-sized species.

Nocturnal patterns

The nocturnal course of drift shows distinct patterns in the Percidae and Gobiidae. Illumination is a key factor in fish larvae drift. Usually, drift density is negatively correlated with illumination level (Reichard *et al.*, 2002a). Accordingly, most larvae drift between dusk and dawn (Pavlov, 1994; Reichard *et al.*, 2002a; Zitek *et al.*, 2004a). This was also confirmed by the present study, though with family dependent differences. As percids already drift before sunset, illumination level is apparently not the only trigger for drift entry and has a lesser influence than in gobiids. Other proposed reasons for higher nocturnal activity, reflected in higher drift entries at night, are an avoidance of (visual) predators (Corbett and Powles, 1986; Harvey, 1991), or inversely the following of food sources, like invertebrates (Armstrong and Brown, 1983).

Within families, the night-time drift patterns of the genera were relatively similar for Percidae and Gobiidae, respectively. This overall pattern could potentially change in the second half of the night, which was not sampled here. However, previous studies suggested that the loss of information is acceptable, i.e. if only the first few hours of darkness are sampled (Persat and Olivier, 1995; Zitek *et al.*, 2004a). In contrast, Janáč *et al.* (2013), who monitored drift patterns from sunset to sunrise, found differences in the nocturnal course of

round and tubenose gobies. While the abundance of the former rapidly decreased after a peak 2.5 h after dusk, numbers of the latter varied until dawn. These distinctions would not have been found with early night sampling.

The loss of visual orientation in darkness was proposed as a main cause for the high drift densities of early fish stages at night (Pavlov *et al.*, 1978; Pavlov, 1994). Drifting would in this case be a passive process. If this hypothesis is true, larger individuals should be less susceptible to drift, due to better vision (Fernald, 1990), resulting in a later drift entry. No such significant correlations were found for *Proterorhinus* and all percids (except *Sander*, right shore). Thus, larger individuals are not less (or more) prone to drift than smaller ones regarding time or illumination level. Significant correlations were found for "*Neogobius*" and *Sander* (left shore; Table 5). Nonetheless, the correlation coefficients, and therefore the fractions of explained variance, were relatively low. Therefore, time of day apparently has no major influence on the size distribution of these species in the drift. Combined, this information indicates that the drift in Percidae and Gobiidae is, at least in part, an active behavioural decision rather than a mere passive act. Similar conclusions have been drawn for cyprinid fishes (Reichard *et al.*, 2002a; but see Zitek *et al.*, 2004a).

Conclusion

Seasonal and nocturnal drift patterns differed distinctly between Percidae and Gobiidae. Percids stop drifting, and therefore dispersing, much earlier in the year than gobiids, which were still abundant at the end of the sampling period in June. In gobies, this reflects multiple spawning events (continuous spawning). The size of drifting larvae gradually increased with season in percids, but remained constant for the gobiids. Drifting is therefore restricted to a fairly narrow time or size-window in gobies. While gobiids are almost absent in the drift before sunset, percids were already drifting at the start of sampling (early May), though at low abundances.

Although both shores shared the same species (genera) pool, abundances and drift densities differed substantially. Percids were more abundant along the semi-natural shore, whereas gobiids clearly dominated the rip-rap. Re-structuring of formerly artificial shorelines is therefore also beneficial for the larvae of native fishes, especially for species of high conservation concern. Removal of rip-rap and other artificial embankments are an appropriate measure to promote the availability of sufficient spawning and nursery areas for

native riverine fishes (see also Keckeis *et al.*, 2014). This will help support a diverse native fish community and, according to the results of this study, mitigate the impact of invading species.

Acknowledgements

First of all, I want to thank Hubert Keckeis for his excellent supervison, as well as Harald Ahnelt, who had an open ear for all my questions. Michael Stachowitsch kindly improved the English. I want to thank my colleagues Aaron, Bernhard, Reinhard, Franz, and Max for giving advice and for fruitful discussion, but also for being the reason why I will have fond (if sometimes blurred) memories of Master's thesis time. Also deserving mention are all the helpers who took and processed the samples.

I would also like to extend thanks to the Land Niederösterreich (Lower Austria) for supporting my thesis with a Top-Stipendium für Abschlussarbeiten (grant for final theses), as well as the FWF (Project MODI P22631-B17 "Modelling dispersal patterns of fish larvae in a large river") for funding the wider project of which my thesis is a part.

Last but not least, a big thank you to my girlfriend, my family, and my friends, who always supported my studies wherever they could.

Danksagung

Zuerst möchte ich mich bei Hubert Keckeis für die sehr gute Betreuung bedanken, sowie bei Harald Ahnelt, der genauso immer ein offenes Ohr für mich hatte. Michael Stachowitsch hat dankenswerterweise das Manuskript Korrekturgelesen. Bedanken will ich mich auch bei meinen Kollegen Aaron, Bernhard, Reinhard, Franz und Max, die mir nicht nur mit Rat und Diskussion bei der Masterarbeit zur Seite standen, sondern generell dafür gesorgt haben, dass ich gerne an die Zeit zurückdenken werde (wenn auch manchmal lückenhaft). Nicht unerwähnt sollen auch all jene Helfer bleiben, die an der Probennahme und -aufbereitung beteiligt waren.

Dank möchte ich auch dem Land Niederösterreich aussprechen, dass mich mit einem Top-Stipendium für Abschlussarbeiten unterstützt hat, sowie dem FWF (Projekt MODI P22631-B17 „Modelling dispersal patterns of fish larvae in a large river"), der das meiner Masterarbeit übergeordnete Projekt finanziert hat.

Zu guter Letzt geht mein Dank an meine Freundin, meine Familie und meine Freunde, die mich während des Studiums immer unterstützt haben wo sie konnten.

Literature

Ahnelt, H. (1988). Zum Vorkommen der Marmorierten Grundel (*Proterorhinus marmoratus* (Pallas), Pisces: Gobiidae) in Österreich. *Annalen des Naturhistorischen Museums Wien* **90**, 31-42.

Ahnelt, H. & Keckeis, H. (1994). Breeding tubercles and spawning behaviour in *Chondrostoma nasus* (Teleostei: Cyprinidea): a correlation. *Ichthyological Exploraton of Freshwaters* **5**, 321-330.

Arlet, J. (1945). Note sur la fécondation artificielle et le développement des alevins de perche. *Bulletin Français de Pisciculture*, 32-37.

Armstrong, M. L. & Brown, A. V. (1983). Diel drift and feeding of channel catfish alevins in the Illinois River, Arkansas. *Transactions of the American Fisheries Society* **112**, 302-307.

Baltz, D. M. & Moyle, P. B. (1993). Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications* **3**, 246-255.

Bischoff, A. & Wolter, C. (2001). Groyne-heads as potential summer habitats for juvenile rheophilic fishes in the Lower Oder, Germany. *Limnologica* **31**, 17-26.

Brown, A. V. & Armstrong, M. L. (1985). Propensity to drift downstream among various species of fish. *Journal of Freshwater Ecology* **3**, 3-17.

Byström, P., Persson, L., Wahlström, E. & Westman, E. (2003). Size- and density-dependent habitat use in predators: consequences for habitat shifts in young fish. *Journal of Animal Ecology* **72**, 156-168.

Charlebois, P. M., Marsden, J. E., Goettel, R. G., Wolfe, R. K., Jude, D. J. & Rudnika, S. (1997). The round goby, *Neogobius melanostomus* (Pallas): a review of European and North American literature. *Illinois-Indiana Sea Grant Program and the Illinois Natural History Survey Special Publication* **20**, 1-76.

Coles, T. F. (1981). The distribution of perch, *Perca fluviatilis* L. throughout their 1st year of life in Llyn-Tegid, North-Wales. *Journal of Fish Biology* **18**, 15-30.

Corbett, B. & Powles, P. (1986). Spawning and larva drift of sympatric walleyes and white suckers in an Ontario stream. *Transactions of the American Fisheries Society* **115**, 41-46.

D'Amour, J., Thibodeau, S. & Fortin, R. (2001). Comparison of lake sturgeon (*Acipenser fulvescens*), *Stizostedion* spp., *Catostomus* spp., *Moxostoma* spp., quillback (*Carpiodes cyprinus*), and mooneye (*Hiodon tergisus*) larval drift in Des Prairies River, Quebec. *Canadian journal of zoology* **79**, 1472-1489.

Dynesius, M. & Nilsson, C. (1994). Fragmentation and flow regulation of river systems in the northern third of the world. *Science* **266**, 753-762.

Erős, T., Tóth, B., Sevcsik, A. & Schmera, D. (2008). Comparison of Fish Assemblage Diversity in Natural and Artificial Rip-Rap Habitats in the Littoral Zone of a Large River (River Danube, Hungary). *International Review of Hydrobiology* **93**, 88-105.

Fernald, R. D. (1990). Teleost vision: seeing while growing. *Journal of Experimental Zoology* **256**, 167-180.

Freeman, M. C., Bowen, Z. H., Bovee, K. D. & Irwin, E. R. (2001). Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. *Ecological Applications* **11**, 179-190.

French, J. R. & Edsall, T. A. (1992). Morphology of ruffe (*Gymnocephalus cernuus*) protolarvae from the St. Louis River, Lake Superior. *Journal of Freshwater Ecology* **7**, 59-68.

Fuiman, L. & Werner, R., eds. (2002). *Fishery Science: The Unique Contributions of Early Life Stages*. Cornwall, UK: Blackwell Science.

Harka, A. & Bíró, P. (2007). New patterns in Danubian distribution of Ponto-Caspian gobies – a result of global climatic change and/or canalization. *Electronic Journal of Ichthyology* **1**, 1-14.

Harvey, B. C. (1987). Susceptibility of young-of-the-year fishes to downstream displacement by flooding. *Transactions of the American Fisheries Society* **116**, 851-855.

Harvey, B. C. (1991). Interaction of abiotic and biotic factors influences larval fish survival in an Oklahoma stream. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 1476-1480.

Humphries, P., Cook, R. A., Richardson, A. J. & Serafini, L. G. (2006). Creating a disturbance: manipulating slackwaters in a lowland river. *River Research and Applications* **22**, 525-542.

Humphries, P. & King, A. (2004). Drifting fish larvae in Murray-Darling Basin rivers: composition, spatial and temporal patterns and distance drifted. In *Downstream movement of fish in the Murray-Darling Basin. Statement, recommendations and supporting papers.* (Lintermans, M. & Phillips, B., eds.), pp. 51-58. Canberra: Murray-Darling Basin Commission.

Humphries, P. & Lake, P. (2000). Fish larvae and the management of regulated rivers. *Regulated Rivers: Research & Management* **16**, 421-432.

Humphries, P., Serafini, L. G. & King, A. J. (2002). River regulation and fish larvae: variation through space and time. *Freshwater Biology* **47**, 1307-1331.

Iguchi, K. i. & Mizuno, N. (1991). Mechanisms of embryonic drift in the amphidromous goby, *Rhinogobius brunneus*. *Environmental Biology of Fishes* **31**, 295-300.

Janáč, M., Šlapanský, L., Valová, Z. & Jurajda, P. (2013). Downstream drift of round goby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus semilunaris*) in their non-native area. *Ecology of Freshwater Fish* **22**, 430-438.

Janssen, J. & Jude, D. J. (2001). Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, Southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. *Journal of Great Lakes Research* **27**, 319-328.

Johnston, T. A., Gaboury, M. N., Janusz, R. A. & Janusz, L. R. (1995). Larval fish drift in the Valley River, Manitoba: influence of abiotic and biotic factors, and relationships with future year-class strengths. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 2423-2431.

Kamler, E., Keckeis, H. & Bauer-Nemeschkal, E. (1998). Temperature-induced changes of survival, development and yolk partitioning in *Chondrostoma nasus*. *Journal of Fish Biology* **53**, 658-682.

Keckeis, H. (2013). Short-term effects of inshore restoration measures on early stages, benthic species, and the sublittoral fish assemblage in a large river (Danube, Austria). *Hydrobiologia*, 1-16.

Keckeis, H., Kamler, E., Bauer-Nemeschkal, E. & Schneeweiss, K. (2001). Survival, development and food energy partitioning of nase larvae and early juveniles at different temperatures. *Journal of Fish Biology* **59**, 45-61.

Keckeis, H., Lumesberger-Loisl, F., Reiter, K. & Schulze, C. H. (2014). Restrukturierungsmaßnahmen in großen Flüssen: Auswirkungen des Uferrückbaues und der Buhnenoptimierung im Hauptstrom der freifließenden Donau in Witzelsdorf (NÖ) auf die Artengemeinschaft von Indikatororganismen (Vegetation, Vogel- und Fischfauna). *Österreichs Fischerei* **67**, 57-66.

Keckeis, H., Winkler, G., Flore, L., Reckendorfer, W. & Schiemer, F. (1997). Spatial and seasonal characteristics of 0+ fish nursery habitats of nase, *Chondrostoma nasus* in the River Danube, Austria. *Folia Zoologica* **46**, 133-150.

Koblickaya, A. (1981). *Identification keys for young freshwater fishes in Russian)*. Moscow: Consumer and Food Industry Press.

Kornis, M. S., Mercado-Silva, N. & Vander Zanden, M. J. (2012). Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of Fish Biology* **80**, 235-285.

Kottelat, M. & Freyhof, J. (2007). *Handbook of European freshwater fishes*. Berlin, Germany: Kottelat, Cornol and Freyhof.

Kovac, V. (1992). Early development of the yellow pope, *Gymnocephalus schraetser*. *Folia Zoologica* **41**, 365-377.

Kovac, V. (1993a). Early development of ruff, *Gymnocephalus cernuus*. *Folia Zoologica* **42**, 269-280.

Kovac, V. (1993b). Early development of the Balons ruff, *Gymnocephalus baloni* Holcik and Hensel, 1974. *Folia Zoologica* **42**, 349-360.

Kovac, V. (1994). Early ontogeny of 3 *Gymnocephalus* species (Pisces, Percidae) - Reflections on the evolution of the genus. *Environmental Biology of Fishes* **40**, 241-253.

Kovac, V. (2000). Early development of *Zingel streber*. *Journal of Fish Biology* **57**, 1381-1403.

Lauer, T. E., Allen, P. J. & McComish, T. S. (2004). Changes in mottled sculpin and johnny darter trawl catches after the appearance of round gobies in the Indiana waters of Lake Michigan. *Transactions of the American Fisheries Society* **133**, 185-189.

Lechner, A., Keckeis, H., Schludermann, E., Loisl, F., Humphries, P., Glas, M., Tritthart, M. & Habersack, H. (2013). Shoreline configurations affect dispersal patterns of fish larvae in a large river. *ICES Journal of Marine Science*.

Lechner, A., Schludermann, E. & Keckeis, H. (2010). Jungfischdrift in der österreichischen Donau: Taxonomische Zusammensetzung, Entwicklungsstadien und Driftdichte. *Österreichs Fischerei* **63**, 96-100.

Leslie, J. K. & Timmins, C. A. (2004). Description of age-0 round goby, *Neogobius melanostomus* Pallas (Gobiidae), and ecotone utilisation in St. Clair Lowland Waters, Ontario. *Canadian Field-Naturalist* **118**, 318-325.

Leslie, J. K., Timmins, C. A. & Bonnell, R. G. (2002). Postembryonic development of the tubenose goby *Proterorhinus marmoratus* Pallas (Gobiidae) in the St. Clair River/Lake system, Ontario. *Archive for Hydrobiology Supplement* **154**, 341-352.

Loisl, F., Singer, G. & Keckeis, H. (2013). Method-integrated fish assemblage structure at two spatial scales along a free-flowing stretch of the Austrian Danube. *Hydrobiologia*, 1-18.

Lyons, K. G. & Schwartz, M. W. (2001). Rare species loss alters ecosystem function–invasion resistance. *Ecology letters* **4**, 358-365.

Mansueti, A. J. (1964). Early development of the Yellow Perch, *Perca flavescens*. *Chesapeake Science* **5**, 46-66.

McCune, B., Grace, J. B. & Urban, D. L. (2002). *Analysis of ecological communities*. Gleneden Beach, Oregon: MjM Software Design

Miehls, S. M. & Dettmers, J. M. (2011). Factors influencing habitat shifts of age-0 yellow perch in southwestern Lake Michigan. *Transactions of the American Fisheries Society* **140**, 1317-1329.

Mikschi, E., Wolfram, G. & Wais, A. (1996). Long-term changes in the fish community of Neusiedler See (Burgenland, Austria). In *Conservation of Endangered Freshwater Fish in Europe* (Kirchhofer, A. & Hefti, D., eds.), pp. 111-120. Basel: Birkhäuser Verlag.

Mills, C. A. & Mann, R. H. K. (1983). The bullhead *Cottus gobio*, a versatile and successful fish. *Freshwater Biological Association Annual Report* **51**, 76-88.

Moyle, P. B. & Marchetti, M. P. (2006). Predicting invasion success: freshwater fishes in California as a model. *Bioscience* **56**, 515-524.

Neilson, M. E. & Stepien, C. A. (2009). Escape from the Ponto-Caspian: Evolution and biogeography of an endemic goby species flock (Benthophilinae: Gobiidae: Teleostei). *Molecular Phylogenetics and Evolution* **52**, 84-102.

Nunn, A. D., Copp, G. H., Vilizzi, L. & Carter, M. G. (2010). Seasonal and diel patterns in the migrations of fishes between a river and a floodplain tributary. *Ecology of Freshwater Fish* **19**, 153-162.

Pavlov, D., Pakhorukov, A., Kuragina, G., Nezdoliy, V., Nekrasova, N., Brodskiy, D. & Ersler, A. (1978). Some features of the downstream migrations of juvenile fish in the Volga and Kuban rivers. *Journal of Ichthyology* **19**, 363-374.

Pavlov, D., Sadkovskii, R., Kostin, V. & Lupandin, A. (2000). Experimental study of young fish distribution and behaviour under combined influence of baro-, photo- and thermo-gradients. *Journal of Fish Biology* **57**, 69-81.

Pavlov, D. S. (1994). The Downstream Migration of Young Fishes in Rivers - Mechanisms and Distribution. *Folia Zoologica* **43**, 193-208.

Pavlov, D. S., Mikheev, V. N., Lupandin, A. I. & Skorobogatov, M. A. (2008). Ecological and behavioural influences on juvenile fish migrations in regulated rivers: a review of experimental and field studies. *Hydrobiologia* **609**, 125-138.

Penaz, M. (2001). A general framework of fish ontogeny: a review of the ongoing debate. *Folia Zoologica* **50**, 241-256.

Persat, H. & Olivier, J. (1995). The first displacements in the early stages of *Chondrostoma nasus* under experimental conditions. *Folia Zoologica* **44**, 43-50.

Persson, L. & Crowder, L. B. (1998). Fish-habitat interactions mediated via ontogenetic niche shifts. *Ecological Studies* **128**, 3-23.

Polacik, M., Janác, M., Trichkova, T., Vassilev, M., Keckeis, H. & Jurajda, P. (2008). The distribution and abundance of the *Neogobius* fishes in their native range (Bulgaria) with notes on the non-native range in the Danube River. *Archiv für Hydrobiologie. Supplementband: Large rivers* **18**, 192-208.

Quigley, J. & Harper, D. (2004). Streambank protection with rip-rap: an evaluation of the effects on fish and fish habitat. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* **2701**, XIV + 76 p.

Rakowitz, G., Berger, B., Kubecka, J. & Keckeis, H. (2008). Functional role of environmental stimuli for the spawning migration in Danube nase *Chondrostoma nasus* (L.). *Ecology of Freshwater Fish* **17**, 502-514.

Ray, W. J. & Corkum, L. D. (2001). Habitat and site affinity of the round goby. *Journal of Great Lakes Research* **27**, 329-334.

Reckendorfer, W., Schmalfuss, R., Baumgartner, C., Habersack, H., Hohensinner, S., Jungwirth, M. & Schiemer, F. (2005). The Integrated River Engineering Project for the free-flowing Danube in the Austrian Alluvial Zone National Park: contradictory goals and mutual solutions. *Archive for Hydrobiology Supplement* **15**, 613-630.

Reichard, M., Jurajda, P. & Ondračková, M. (2002a). The effect of light intensity on the drift of young-of-the-year cyprinid fishes. *Journal of Fish Biology* **61**, 1063-1066.

Reichard, M., Jurajda, P. & Ondračkovaá, M. (2002b). Interannual variability in seasonal dynamics and species composition of drifting young-of-the-year fishes in two European lowland rivers. *Journal of Fish Biology* **60**, 87-101.

Ricciardi, A. & MacIsaac, H. J. (2000). Recent mass invasion of the North American Great Lakes by Ponto–Caspian species. *Trends in Ecology & Evolution* **15**, 62-65.

Robinson, A. T., Clarkson, R. W. & Forrest, R. E. (1998). Dispersal of larval fishes in a regulated river tributary. *Transactions of the American Fisheries Society* **127**, 772-786.

Schabuss, M. & Reckendorfer, W. (2002). *Die Hydrologie als Schlüsselparameter für die Verteilung der Adult-und Jungfischfauna im Altarmsystem der Unteren Lobau*. Wien: Eigenverlag der Universität Wien, Institut für Ökologie und Naturschutz.

Scheidegger, K. J. & Bain, M. B. (1995). Larval fish distribution and microhabitat use in free-flowing and regulated rivers. *Copeia*, 125-135.

Schiemer, F., Baumgartner, C. & Tockner, K. (1999). Restoration of floodplain rivers: The 'Danube restoration project'. *Regulated Rivers: Research & Management* **15**, 231-244.

Schiemer, F., Guti, G., Keckeis, H. & Staras, M. (2004). *Ecological status and problems of the Danube River and its fish Fauna: a review.* Bangkok, Thailand: FAO Regional Office for Asia and the Pacific.

Schiemer, F., Keckeis, H., Reckendorfer, W. & Winkler, G. (2001). The" inshore retention concept" and its significance for large rivers. *Archiv für Hydrobiologie, Supplement* **135**, 509-516.

Schiemer, F., Spindler, T., Wintersberger, H., Schneider, A. & Chovanec, A. (1991). Fish fry associations: important indicators for the ecological status of large rivers. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **24**.

Schiemer, F. & Waidbacher, H. (1992). Strategies for conservation of a Danubian fish fauna. *River conservation and management* **26**, 363-382.

Schludermann, E., Tritthart, M., Humphries, P., Keckeis, H. & Bradford, M. J. (2012). Dispersal and retention of larval fish in a potential nursery habitat of a large temperate river: an experimental study. *Canadian Journal of Fisheries and Aquatic Sciences* **69**, 1302-1315.

Schlumberger, O. & Proteau, J. P. (1996). Reproduction of pike-perch (*Stizostedion lucioperca*) in captivity. *Journal of Applied Ichthyology* **12**, 149-152.

Sonny, D., Jorry, S., Wattiez, X. & Philippart, J. (2006). Inter-annual and diel patterns of the drift of cyprinid fishes in a small tributary of the Meuse River, Belgium. *Folia Zoologica* **55**, 75.

Spanovskaya, V. D. & Grygorash, V. A. (1977). Development and Food of Age-O Eurasian Perch (*Perca fluviatilis*) in Reservoirs near Moscow, USSR. *Journal of the Fisheries Research Board of Canada* **34**, 1551-1558.

Specziár, A. (2005). First year ontogenetic diet patterns in two coexisting *Sander* species, *S. lucioperca* and *S. volgensis* in Lake Balaton. *Hydrobiologia* **549**, 115-130.

Specziar, A., Bercsenyi, M. & Muller, T. (2009). Morphological characteristics of hybrid pikeperch (*Sander lucioperca* Female X *Sander volgensis* Male) (Osteichthyes, Percidae). *Acta Zoologica* **55**, 39-54.

Stachowicz, J. J., Whitlatch, R. B. & Osman, R. W. (1999). Species diversity and invasion resistance in a marine ecosystem. *Science* **286**, 1577-1579.

Taraborelli, A. C., Fox, M. G., Schaner, T. & Johnson, T. B. (2009). Density and habitat use by the round goby (*Apollonia melanostoma*) in the Bay of Quinte, Lake Ontario. *Journal of Great Lakes Research* **35**, 266-271.

Urho, L. (1996a). Habitat shifts of perch larvae as survival strategy. *Annales Zoologici Fennici* **33**, 329-340.

Urho, L. (1996b). Identification of perch (*Perca fluviatilis*), pikeperch (*Stizostedion lucioperca*) and ruffe (*Gymnocephalus cernuus*) larvae. *Annales Zoologici Fennici* **33**, 659-667.

Vlavonou, R. S., Masson, G. & Moreteau, J. C. (1999). Growth of *Perca fluviatilis* larvae fed with *Artemia* spp. nauplii and the effects of initial starvation. *Journal of Applied Ichthyology* **15**, 29-33.

White, K., Gerken, J., Paukert, C. & Makinster, A. (2010). Fish community structure in natural and engineered habitats in the Kansas River. *River Research and Applications* **26**, 797-805.

Wiesner, C. (2005). New records of non-indigenous gobies (*Neogobius* spp.) in the Austrian Danube. *Journal of Applied Ichthyology* **21**, 324-327.

Wiesner, C., Wolter, C., Rabitsch, W. & Nehring, S. (2010). Gebietsfremde Fische in Deutschland und Österreich und mögliche Auswirkungen des Klimawandels. *BfN-Skripten* **279**, 1-196.

Wolfram, G. & Mikschi, E. (2007). Rote Liste der Fische (Pisces) Österreichs. In *Rote Listen gefährdeter Tiere Österreichs. Checklisten, Gefährdungsanalysen, Handlungsbedarf* (Zulka, K. P., ed.), pp. 61-198: Grüne Reihe des Bundesministeriums für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft.

Wolter, C. & Sukhodolov, A. (2008). Random displacement versus habitat choice of fish larvae in rivers. *River Research and Applications* **24**, 661-672.

Young, J. A., Marentette, J. R., Gross, C., McDonald, J. I., Verma, A., Marsh-Rollo, S. E., Macdonald, P. D., Earn, D. J. & Balshine, S. (2010). Demography and substrate affinity of the round goby (*Neogobius melanostomus*) in Hamilton Harbour. *Journal of Great Lakes Research* **36**, 115-122.

Zitek, A., Schmutz, S. & Ploner, A. (2004a). Fish drift in a Danube sidearm-system: II. Seasonal and diurnal patterns. *Journal of Fish Biology* **65**, 1339-1357.

Zitek, A., Schmutz, S., Unfer, G. & Ploner, A. (2004b). Fish drift in a Danube sidearm-system: I. Site-, inter- and intraspecific patterns. *Journal of Fish Biology* **65**, 1319-1338.

Supplement I - Comments on identification

Family identification

Cyprinidae: single dorsal fin
anus in posterior half of body
no teeth visible

Percidae: two dorsal fins (separate or connected)
anus in anterior half of body
wedge-shaped head
jaws toothed (from L3)

Gobiidae: two dorsal fins (connected)
club-shaped body
ventral fins fused to suction discs

Cottidae: big, sail-like pectoral fins
head flattened dorso-ventrally
ventral fins not fused

Gasterosteidae: three to nine spines in front of first dorsal fin
juveniles with lateral bony plates, no scales

Percidae

Larvae can be separated by the number of myomeres on the trunk (head to anus) and tail (anus to caudal fin). If the yolk sac is not already consumed, the myomeres between the yolk sac and anus can be counted (Table S1; Urho, 1996b; personal observation).

Table S1: Distinctions of percid genera based on myomere counts

Genus	yolk sac – anus	trunk	tail
Perca	4-6	17-19	23-26
Sander	7-9	18-21	27-31
Gymnocephalus	2-3	13-16	22-24
Zingel	<3	14-15	28-33

Genera also differ regarding size-at-hatching (Tab. S2). This is particularly valuable in distinguishing between *Gymnocephalus* and *Zingel*, as they differ only in the number of tail

myomeres, which are difficult to count in yolk sac larvae (i.e. larvae <6 mm probably do not belong to the genus *Zingel*).

Table S2: Average size-at-hatching and minimum/maximum values (range) for percid genera

Genus	avg. size	range (mm)	References
Perca	5.5	5 - 6	(Arlet, 1945); Urho (1996b); (Vlavonou *et al.*, 1999)
Sander	4.5	4 - 5.5	(Koblickaya, 1981; Schlumberger and Proteau, 1996)
Gymnocephalus	3.5	2.5 - 4	(French and Edsall, 1992; Kovac, 1992; 1993a; b)
Zingel	6	6	(Kovac, 2000)

Larger larvae (> 10 mm TL) can also be separated by the length of the upper jaw (maxilla) in relation to the eye (Table S3; Urho, 1996b; personal observation).

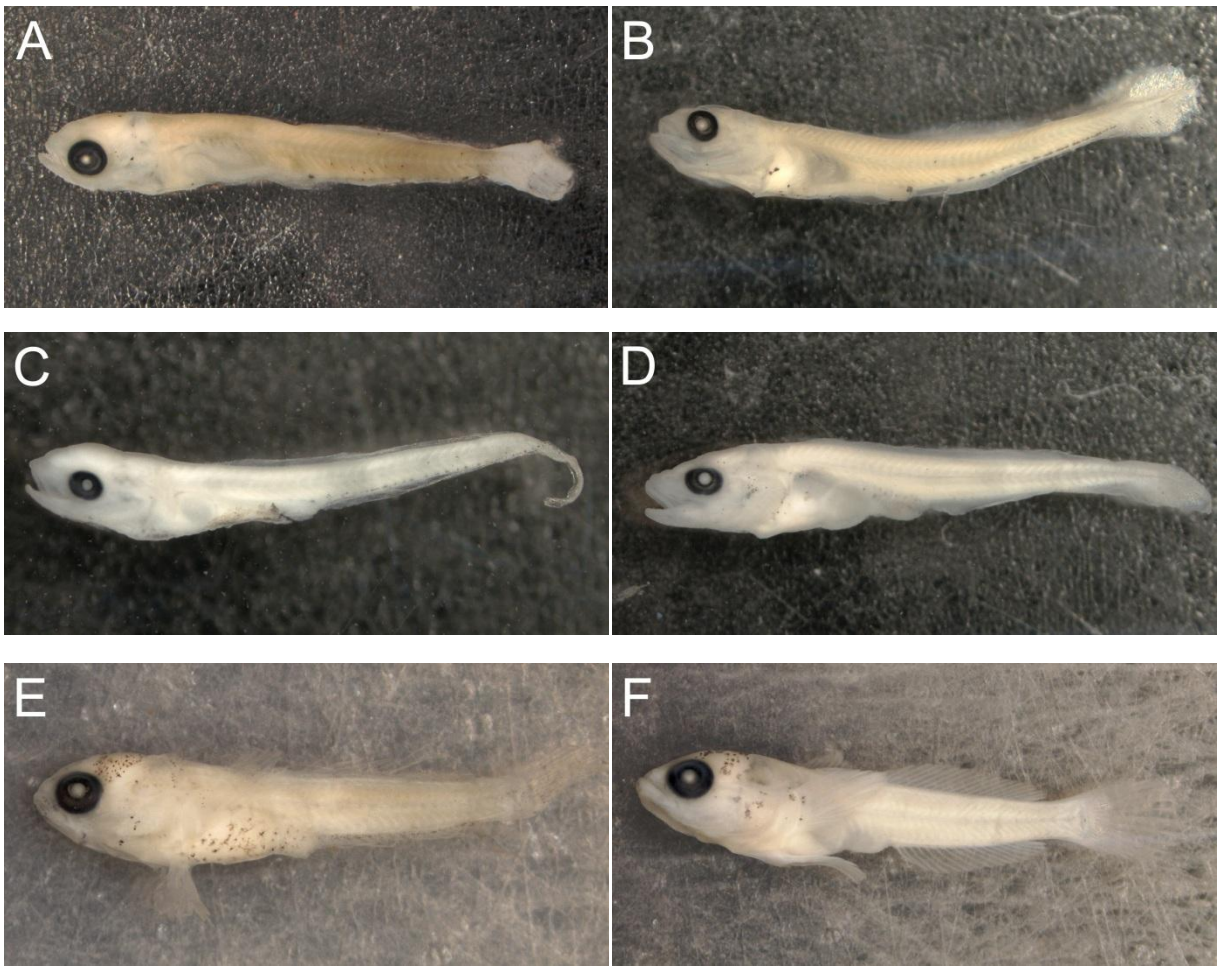

Fig. S1: Habitus of larvae and young fishes of the genera of percids (A-D) and gobiids (E-F) in drift samples from the Austrian Danube. (A) *Perca*, TL: 9,0 mm. (B) *Sander*, TL: 9,5 m. (C) *Gymnocephalus*, TL: 6,5 mm. (D) *Zingel*, TL: 10 mm. (E) *Proterorhinus*, TL: 7,0 mm. (F) *Neogobius*, TL: 8,0 mm.

Table S3: Category of threat (after Wolfram and Mikschi, 2007), length of upper jaw (maxilla) in relation to the distance from snout to eye center, and number of fin rays for percid and gobiid genera.

Family	Genus	Species	Category of threat	Maxilla vs. eye center	Number of fin rays		
					Dorsalis 1	Dorsalis 2	Analis
Percidae	*Perca*	*fluviatilis*	LC	equal	14-20	13-16	9-12
	Sander	*lucioperca*	NT	longer	12-14	21-24	12-14
		volgensis	EN	equal	12-13	21-26	11-13
	Gymnocephalus	*baloni*	VU	shorter	14-15	11-12	7-8
		cernua	LC	shorter	11-14	11-16	7-8
		schraetser	VU	shorter	17-19	11-14	8-9
	Zingel	*streber*	EN	shorter	7-10	10-14	13-15
		zingel	VU	shorter	12-15	18-22	13-15
Gobiidae	*Proterorhinus*	*semilunaris*	EN	shorter	6	16-18	13-16
	Neogobius	*melanostomus*	invasive	shorter	6	15-18	13-14
		kessleri	invasive	equal	6	18-19	13-16
		gymnotrachelus	invasive	shorter	6-7	16-19	13-16

The perch (*Perca fluviatilis*; Fig. S1A) is the only representative of the genus *Perca* in Austria. It can be confused with pikeperches, but is besides the characteristics mentioned above identifiable by the following attributes: relatively small, edgy head; lower jaw rising steeply; slender body; possibly linear pigmentation between (!) the myomeres on tail (Fig. S2A). In addition, perches have fewer fin rays in the dorsal and anal fin than pikeperches (Table S3).

Sander species (Fig. S1B) can be unambiguously identified at about 15 mm TL. Characteristics for the pikeperch (*S. lucioperca*) are: canine teeth present; upper jaws (maxilla) reach beyond eye center; snout pointed; eyes relatively small (Fig. S2D). For the Volga pikeperch (*S. volgensis*): no canine teeth; upper jaw does not reach beyond eye center; snout less pointed; eyes relatively large (Fig. S2E). See also Specziar et al. (2009)

Species of the genus *Gymnocephalus* (Fig. S1C) are hardly distinguishable because they show very similar meristic features (number of fin rays, myomeres) as well as body shapes. Identification on species level is only possible in exceptional cases. The ruffe (*G. cernua*) may be distinguished from other *Gymnocephalus* species by a possible protruding lower jaw (Fig. S2B). The schraetzer (*G. schraetser*) shows a characteristic stripe-like pigmentation on the anterior trunk (Fig. S2C), which, however, may be not visible on larvae or weakly pigmented individuals. See also Kovac (1994).

Zingel (*Z. zingel*) and Danube streber (*Z. streber*) can be distinguished by the number of rays in the dorsal fin, when the development of fin rays is completed at approximately 15 mm TL (Table S3; Fig. S2F,G). The thickness of the caudal peduncle is less clearly different than in adult fish and therefore not suitable for identification.

Gobiidae

The genus *Proterorhinus* (containing the Western tubenose goby as the only species; Fig. S1E) can be distinguished from other gobies by its characteristic pigmentation. The head (occipital region) exhibits a ring-like pigmentation, which looks crescent-shaped when viewed from lateral. Furthermore, the tubenose goby is the only gobiid which shows a completely pigmented yolk sac or a pigmented ventral abdominal area in more developed larvae (Fig. S3A). The name-giving nasal tubes can be found on larger individuals (> 10 mm TL). These can be tightly fitted to the head and therefore difficult to see. Note that round gobies may also exhibit small nasal tubes, but never as long as in tubenose gobies.

The pigmentation of the "*Neogobius*" species (Fig. S1F) is irregular on the head and linear, ribbon-like, or pointed on the rest of the body. Small individuals are hardly identifiable because the important distinguishing features develop only later. Identification also relies on relative measurements, which are also less pronounced in smaller individuals. The pigmentation of gobies is generally very heterogeneous and can also vary within a species. Pigmentation patterns are thus not suited as a distinguishing characteristic, at least in 0+ fishes.

The round goby (*N. melanostomus*) can be easily identified by the typical black spot on the posterior edge of the first dorsal fin (Fig. S3B). However, small individuals and weakly pigmented ones may lack a clear spot. Other gobiids can also show a pigmented dorsal fin, but usually featuring a paler and more stripe-like pigmentation. Further characteristics of the round goby are: steep-sloping forehead; thin lips; mouth gap not reaching center of eye (Fig. S3D).

Larger individuals of the bighead goby (*Ponticola kessleri*) show a large, broad head, with a shallow-sloping forehead. The lips are thick and the mouth gap reaches to or beyond the center of the eye (Fig. S3C). The first dorsal fin is pigmented, usually exhibiting a double, linear pigmentation.

The racer goby (*Babka gymnotrachelus*) is the fourth goby occurring in Austria. It is the rarest species and could not be identified in the samples of the present study. Its appearance is similar to that of the round goby, or intermediate between round and bighead goby. The main distinguishing features of the adult fishes, such as the scale-less operculum and the diagonal stripes on the body (Kottelat and Freyhof, 2007), are not applicable for young individuals (no scales on whole body, underdeveloped pigmentation).

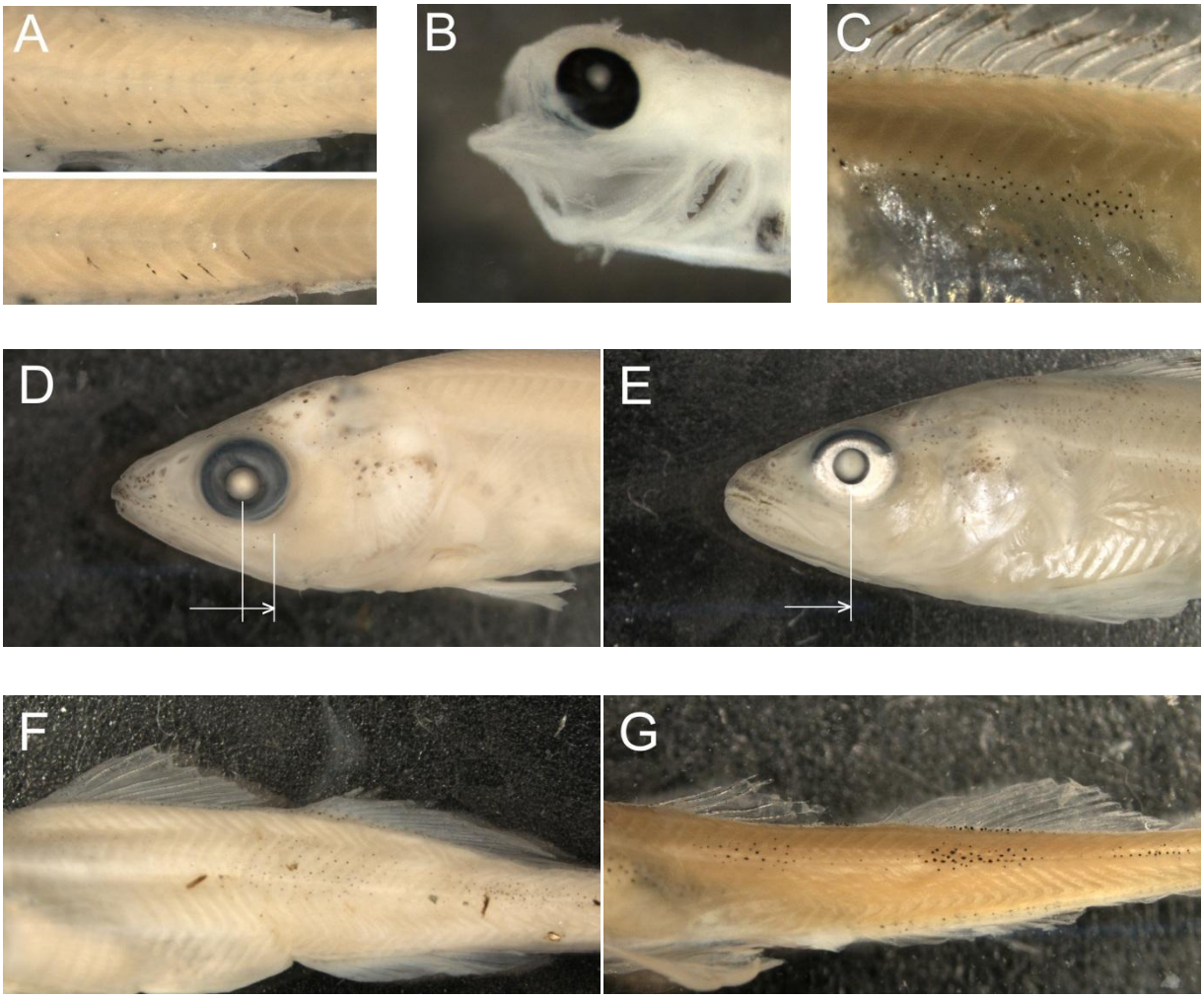

Fig. S2: Distinguishing features for species of larval and juvenile percids. (A) *Perca fluviatilis*: characteristically point-like or linear pigmentation between (!) the myomeres of the trunk. (B) *Gymnocephalus cernua*: the lower jaw of larvae may project over the anterior end of the upper jaw. (C) *Gymnocephalus schraetser*: characteristic ribbon-like pigmentation on trunk. (D) *Sander lucioperca*: the posterior end of the maxilla extends beyond the center of the eye; snout pointed. (E) *Sander volgensis*: the posterior end of the maxilla does not extend beyond the center of the eye; snout blunt. (F) *Zingel zingel*: longer dorsal fins with higher number of fin rays. (G) *Zingel streber*: shorter dorsal fins with fewer fin rays.

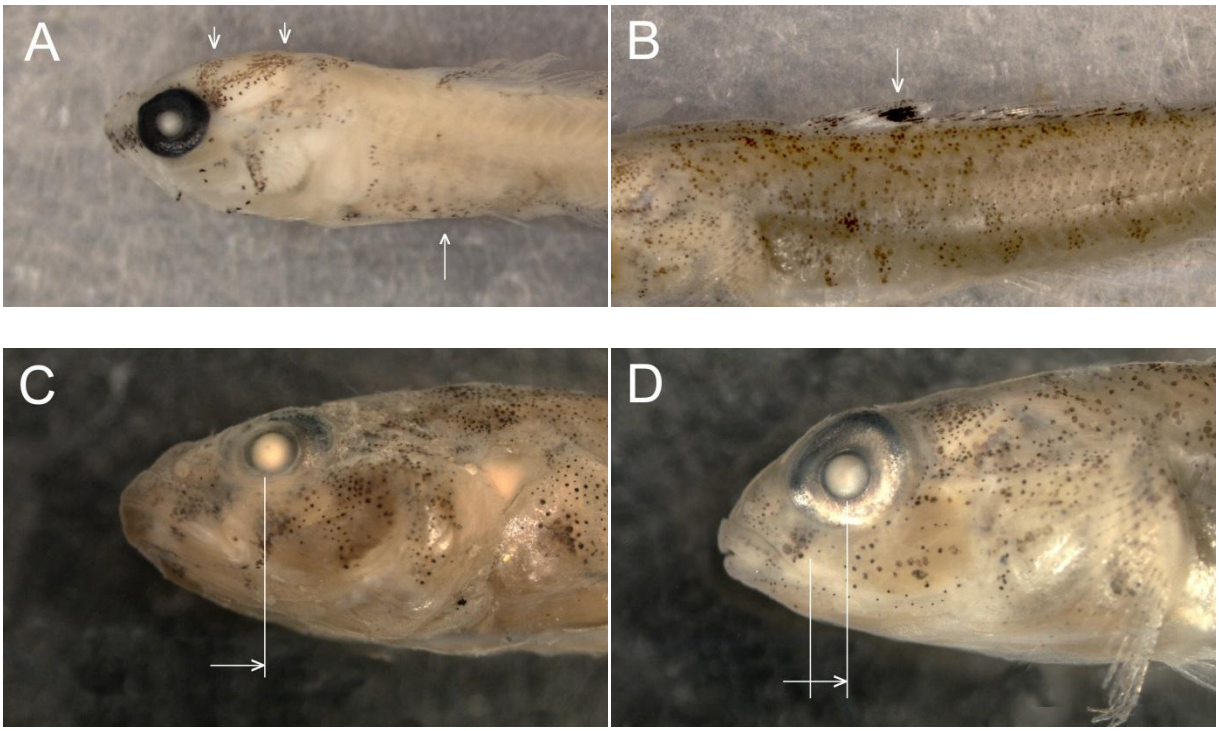

Fig. S3: Distinguishing features for species of 0+ gobiids. (A) *Proterorhinus semilunaris*: characteristic crescent-like pigmentation on head (short arrows); yolk sac, or ventral abdominal region, respectively, pigmented (long arrow). (B) *Neogobius melanostomus*: distinct black spot on posterior region of first dorsal fin. (C) *Ponticola kessleri*: mouth gap extends to or beyond the center of the eye; thick lips; broad, flat head. (D) *Neogobius melanostomus*: mouth gap does reach center of eye; thinner lips, head less broad, steep slope of forehead.

Supplement II - Curriculum vitae

David Ramler, BSc MSc

EDUCATION

WS 2011 – SS 2013	Master's study of zoology at the University of Vienna, Austria; completed with honours. Master's thesis: "*The effect of temperature on the body shape in threespine stickleback juveniles*". Supervisor: Univ.-Doz. Dr. Harald AHNELT
WS 2010 – WS 2013	Master's study of nature conservation and biodiversity management at the University of Vienna, Austria. Master's thesis: "*Seasonal course of larval drift of selected native and invasive benthic fish species along two different shore types in the main channel of a large river (Danube, Austria)*". Supervisor: ao. Univ.-Prof. Dr. Hubert KECKEIS
WS 2007 – SS 2010	Bachelor's study of biology (major: zoology) at the University of Vienna, Austria
2006 – 2007	compulsory community service
2001 – 2006	HTBL u. VA St. Pölten (IT department)
1997 – 2001	Öko-Hauptschule Ober-Grafendorf
1993 – 1997	Volksschule Weinburg

JOURNAL ARTICLES

RAMLER D., MITTEROECKER P., SHAMA L.N.S., WEGNER M. & AHNELT H. 2014: Non-linear effects of temperature on body form and developmental canalization in the threespine stickleback. *Journal of Evolutionary Biology* **27**: 497-507.

CONGRESS CONTRIBUTIONS

RAMLER D., MITTEROECKER P., SHAMA L.N.S. & AHNELT H. 2013: The effect of temperature on the body shape in threespine stickleback juveniles.

Poster presentation at the workshop „Evolutionary potential of marine populations" at the Wadden Sea Station List/Sylt of the Alfred Wegener Institute for Polar and Marine Research.

WORK EXPERIENCE

February 2012	intern at the “die umweltberatung” Österreich
September 2008	intern as zookeeper at the Zoo Vienna

SKILLS AND QUALIFICATIONS

Languages

German	(first language)
English	(proficient in speech and writing)

Computer literacy

MS Office, statistics (R, Mathematica), GIS (arcGIS10), graphics (Photoshop), basic programming skills (C++, Basic)

Additional qualifications

Exercise instructor for bouldering and sports climbing

Driving license (classes A & B)