New insights into the ecology of perch *Perca fluviatilis* L. and burbot *Lota lota* (L.) with special focus on their pelagic life-history

Dissertation

Zur Erlangung des akademischen Grades
des Doktors der Naturwissenschaften (Dr. rer. nat.)
an der Universität Konstanz
Mathematisch-Naturwissenschaftliche Sektion
Fachbereich Biologie

Vorgelegt von

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Konstanz, August 2008

Tag der mündlichen Prüfung: 05.12.2008

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Konstanzer Online-Publikations-System (KOPS)
URL: http://www.ub.uni-konstanz.de/kops/volltexte/2009/7267/
URN: http://nbn-resolving.de/urn:nbn:de:bsz:352-opus-72670

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1. General introduction

The fish community of Lake Constance has been well studied (Appenzeller, 1998a & b, Ptak & Appenzeller, 1998, Eckmann, 1995, Appenzeller, 1995, Eckmann & Rösch, 1998, Appenzeller, 1998), and a considerable amount of research has been directed towards the biology of harvestable adult whitefish *Coregonus lavaretus* L. (Appenzeller, 1995, Appenzeller, 1998a & b, Becker, 1992, Eckmann *et al.*, 2002, Thomas & Eckmann, 2007, Eckmann & Rösch, 1998) and perch *Perca fluviatilis* L. (Eckmann *et al.*, 2006, Hartmann, 1977). The distributions of the two abundant young-of-the-year (YOY) fish species in the pelagic zone of Lake Constance perch and burbot *Lota lota* (L.) have been studied with less intensity (Wang & Appenzeller, 1998, Miler & Fischer, 2004), and some gaps on the precise spatial and temporal distribution as well as the interaction between both species existed.

The pelagic zone of Lake Constance provides a similar habitat experienced by many marine fish larvae with strong vertical gradients in light and temperature, high wave intensities, and lack of physical structure. Because these pelagic conditions prevail during the early life-history stages of perch and burbot, they may have substantial impacts on the year-class strength of both species. Hence, the comprehension of the distribution and behaviour of perch and burbot during their early life-history in the pelagic zone may eventually lead to a more precise understanding of their fluctuating abundances (Eckmann *et al.*, 2006) and future perspectives in a lake undergoing considerable environmental changes.

Lake Constance – a lake in transition

Lake Constance is the second largest prealpine lake in Europe and as such has undergone drastic changes during the last decades. Since the 1950s the loading of total phosphorous had increased from less than 10 µg l^{-1} to more than 80 µg l^{-1} in the mid-1980s (Mürle *et al.*, 2004). To overcome the eutrophication of Lake Constance, nutrient loadings were reduced since the 1970s by lake-wide installations of sewage plants and the introduction of phosphorous-free detergents. Consequently, the content of total phosphorous has decreased to about 10 µg L^{-1} since the mid-1980s. The reduction of nutrient loading has been demonstrated to affect lake whitefish growth (Thomas & Eckmann, 2007), and may have caused a decline of ruffe

(Schleuter & Eckmann, 2007) and zooplankton biomass during spring and summer (Bürgi *et al.*, 2006).

Global climate change is one of the most challenging environmental issues since the last quarter of the 20th century (Friedlingstein, 2008). The influence of altering climate conditions has been traced in Lake Constance (Seebens *et al.*, 2007, Straile *et al.*, 2007, Straile *et al.*, 2003), but the implications for its fish communities are uncertain (Hartmann, 1995, Trippel *et al.*, 1991, Eckmann *et al.*, 2006). Straile *et al.* (2007) found an influence of the North Atlantic Oscillation (NAO) on the early life history stages of whitefish. Warmer temperatures in the winter prior to spawning caused shorter development times and larval growth rates, but may increase the probability of mismatch between the zooplankton abundance and larval food demands of whitefish. Eckmann *et al.* (2006) suggest, that warmer summers will cause a higher survival of YOY perch, but decreasing food supply may not yield higher growth rates for this age-class. Instead, rates of cannibalism of older perch on YOY may increase.

The introduction of invasive species is often feared to have adverse effects on the native community. One example is the introduction of ruffe, which entered the Lake Constance in the 1980s (Schleuter, 2007, Schleuter & Eckmann, 2005, Schleuter & Eckmann, 2007). The population of ruffe increased dramatically and it was suspected, that it will cause severe declines in the growth and abundance of perch. However, after an initial peak the population of ruffe now seems to have stabilised at low levels. Due to the re-oligotrophication of Lake Constance the competition between ruffe and perch seems to be of minor importance for perch populations (Schleuter, 2007). The previous example demonstrates the difficulties in predicting the consequences of species introduction and it remains to be assessed how the recent introduction of various invertebrates such as the omnivorous amphipod *Dikerogammarus villosus* (Sowinsky, 1894) and the freshwater shrimp *Limnomysis benedeni* (Czerniavsky, 1882) will alter the food web dynamics of Lake Constance.

Boat traffic is an ever increasing anthropogenic impact on the lake's hydrodynamic regime. Besides the intense passenger cruise traffic during summer, new ferry routes such as the catamaran between Konstanz and Friedrichshafen have been established. Additionally, more than 30,000 private motor boats are registered for Lake Constance (Mürle *et al.*, 2004), resulting in high frequencies of wave events in many littoral zones of the lake (Hofmann *et al.*, 2008). The impacts of ship-induced waves on the littoral fish community of large lakes are poorly understood and are currently investigated by my fellow- PhD student Stefan Stoll. The experiment presented in Chapter 2 emerged as cooperation between Stefan and my projects embedded in the CRC 454 “The littoral zone of Lake Constance” and are thus included in this thesis.

The life-cycle of perch and burbot

The spawning of perch in prealpine lakes occurs usually in May (Zeh *et al.*, 1989, Wang & Eckmann, 1994), when gravid males and females have migrated from their overwintering habitats at 40 – 60 m depth (Eckmann & Imbrock, 1996) towards the littoral zone to spawn. The larvae hatch after an incubation period of 2 – 3 weeks and get transported into the pelagic zone within 4 – 5 days (Urho, 1996). Consequently, perch larvae can be found in the pelagic zone of Lake Constance from the middle of May and usually remain there until July, when they migrate towards the littoral zone (Treasurer, 1988, Wang & Eckmann, 1994a). During their pelagic stage perch feed exclusively on zooplankton (Wang & Appenzeller, 1998). Their diet consists of rotifers and copepod nauplii during the first week of hatch, shifting towards copepods and daphnia as they grow (Wang, 1994a, Guma'a, 1978). After migrating to the littoral zone perch spend the rest of the summer in the shallow littoral zone foraging on zooplankton and zoobenthos (Schleuter & Eckmann, 2007) until severe autumn storms chill the water and cause a decline in macrophyte habitat. In October and November juvenile perch migrate towards to their profundal overwintering habitats at depths of 30 m and more for overwintering (Wang & Eckmann, 1994a).

Adult burbot usually spawn between late February and early April in a single spawning event (Hartmann, 1977, Hirning, 2006). The eggs are laid at the lake bottom in the profundal zone at 40 – 120 m depth (Hirning, 2006). The incubation period at 4 °C takes approximately 43 days (Taylor & MacPhail, 2000). The newly hatched larvae feed between 6 to 9 days on their yolk reserves, until the mouth opening has developed (Fischer, 1999). During this time the larvae ascend towards the surface to fill their swim bladder (McPhail & Paragamian, 2000). Burbot larvae inhabit the pelagic zone of Lake Constance from late April/early May,

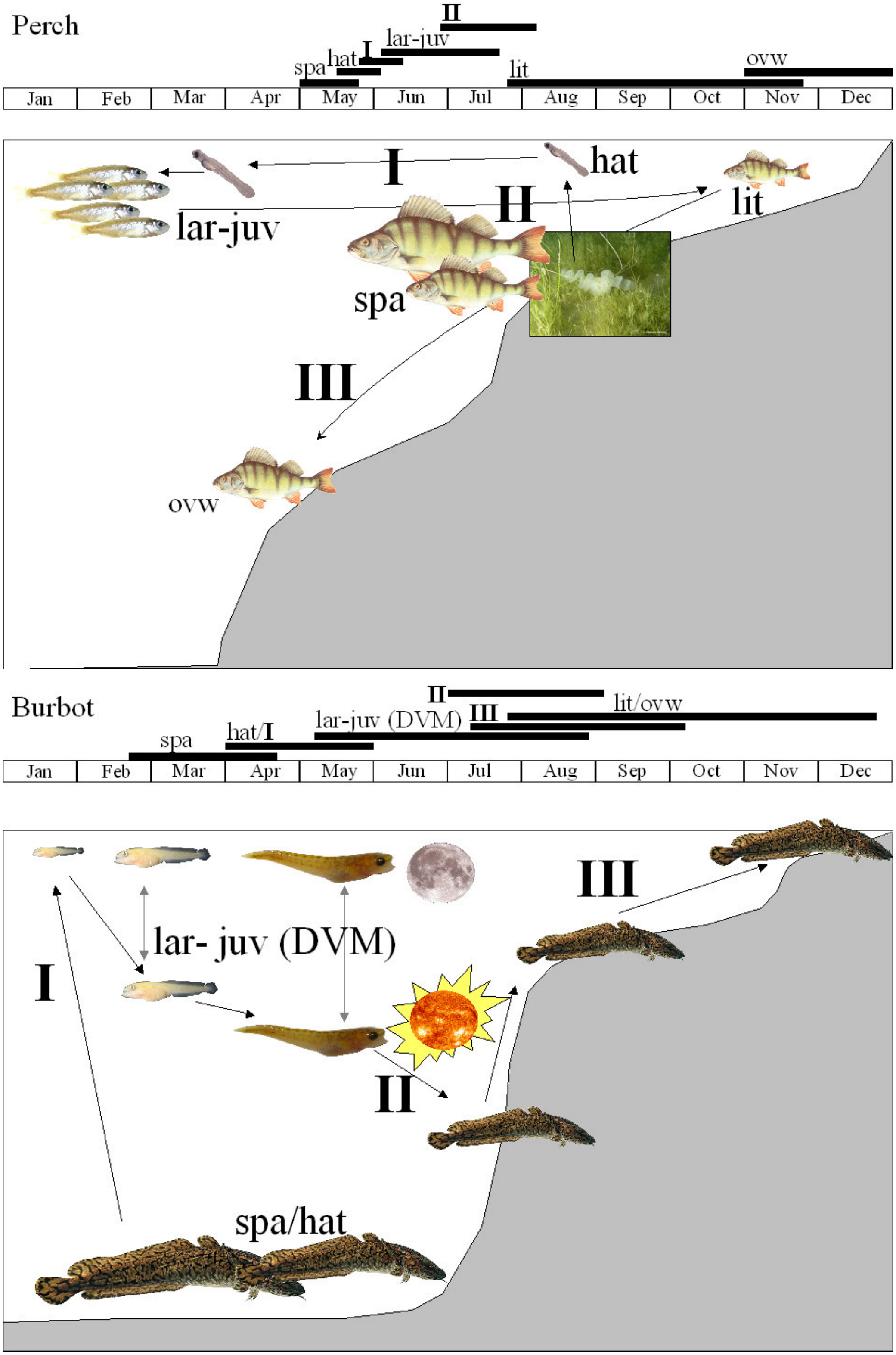

Fig.1.1: The life-cycle of perch (**upper**) and burbot (**lower**) in first year of life. Spa = location and period (black bars) of spawning, hat = location and period of hatch, lar-juv = location and period of larval and juvenile stages in the pelagic zone, lit = juveniles in the littoral zone, ovw = location and period of overwintering, I = habitat shift to the pelagic zone, II = habitat shift to the littoral (perch) or profundal zone (burbot), III = habitat shift to the profundal (perch) or littoral zone (burbot). Photograph of perch spawn by Manuel Hirning. Sun and moon indicate time of diel vertical migrations (DVM) of burbot. After data from various authors (Hirning, 2006, Hofmann & Fischer, 2001, Fischer, 1999, Wang & Eckmann, 1994a).

where they can be found until the end of August (see following Chapters 3 + 4). Larval burbot commence feeding on rotifers, followed by copepod nauplii, cyclopoid copepods and larger cladocerans (Ghan & Sprules, 1993, Hartmann, 1983, Hartmann, 1986). Juvenile burbot are assumed to settle to the lake profundal zone between the end of June until the end of August and presumably migrate along the slope of the lake bottom towards the littoral zone (Fischer, 1999). They remain in the littoral zone from autumn until spring and migrate towards the profundal zone in the second year of life (Hofmann & Fischer, 2001).

Hydroacoustics as tool in fish ecology

The vertical and horizontal distribution of perch and burbot has been investigated by Miler & Fischer (2004) and Wang and Appenzeller (1998). However, both studies inferred the information on the distribution of YOY perch and burbot exclusively from net catches.

Alternatively, the application of hydroacoustics allows the real-time observation of fish distributions over large vertical and horizontal scales (Simmonds & MacLennan, 2005). Echosounding is a non-invasive method and thus does not harm the investigated organisms. It further allows to accumulate large amounts of information within a short time frame and with limited effort. The advances in hardware and software technology have proceeded considerably within the last two decades, and split beam echosounding has become the method of choice for many investigations on freshwater fishes (Hrabik *et al.*, 2006, Imbrock *et al.*, 1996, Prchalova *et al.*, 2003, Scheuerell & Schindler, 2003, Cech *et al.*, 2005, Cech & Kubecka, 2002, Cech *et al.*, 2007, Prchalova *et al.*, 2006). Split-beam echosounding has become well established, as it allows to separate different groups of fish by the measurement of target strengths. Fortunately, this effective method could also be used in several of the here presented investigations yielding deeper insights into fine-scale distribution of YOY perch and burbot.

Research area

Upper Lake Constance (ULC) is situated at the borders of Germany, Switzerland and Austria. ULC is a warm monomictic prealpine lake with a maximum water depth of 254 m and an average water depth of 101 m. Its surface area is 473 km² and it has a perimeter of 186 km (Mürle *et al.*, 2004). Due to its steep shoreline more than 90 % of the lake can be classified as pelagic zone (Lorke *et al.*, 2007, Mürle *et al.*, 2004). The main tributaries are the River Rhine, the River Bregenzer Aach and the River Argen. ULC can be separated into the north-western Überlinger See and the main basin of Lake Constance.

During summer, the lake stratifies and a thermocline is established at 10 - 15 m depth. At this time of the year water temperatures in the hypolimnion usually range between 4 and 6 °C, whereas the epilimnion can heat up to 25 °C. The Secchi-depth in the pelagic zone of the lake varies between 3 m in summer and 12 m in winter (Probst, personal observation).

Of the zooplankton community in the lake 75 % consist of copepods and cladocerans (Straile, 1998), among these typical species of the summer community are *Eudiaptomus gracilis* (G.O. Sars, 1862), *Cyclops vicinus* (Uljanin 1875), *Daphnia galeata* (Sars, 1863) and *Daphnia hyalina* (Leydig 1860), *Bosmina longirostris* (O.F. Müller, 1785) as well as the carnivorous cladocerans *Leptodora kindtii* (Focke, 1844) and *Bythotrephes longimanus* (Leydig, 1860) (Mürle *et al.*, 2004, Stich, 1989).

Except for the study on the spawning depth preference of perch, all investigations and surveys, from which the following results were obtained, were conducted in the western part of Lake Constance's main basin where the lake has a depth exceeding 100 m (Figure 4.1).

Objectives

Though the ecology of YOY perch and burbot in Lake Constance has been subject to previous research (Wang, 1994a & b, Wang & Appenzeller, 1998, Miler & Fischer, 2004, Fischer, 1999, Appenzeller, 1995), the following chapters demonstrate that some gaps of knowledge on the ecology of early life-history stages of both species remained. The compilation of this thesis endeavours to serve two purposes: **I)** to gather further insights into the biology of perch and burbot in a large lake and **II)** to provide a basis for comparison to earlier data e.g. by

Wang & Appenzeller (1998), who conducted their investigations during a phase of elevated phosphorus levels.

The spawning preference of female perch with regards to hydrodynamic influences is explored in Chapter 2. It is common knowledge that perch prefer hard substrates to deposit their spawn and that their spawning season commences in early May when water temperatures rise above 10 °C. However, the influence of anthropogenic waves on the spawning site selection of perch has not been investigated before.

Chapter 3 describes an application of a new method of echosounding invented by Professor Dr. Reiner Eckmann. The vertical upward beaming from a submersed tow-body allowed observing the surface-related fish community resulting in a description of the shoaling behaviour of YOY perch, which could not have been observed by conventional downward beaming.

The diel vertical migration behaviour (DVM) of burbot and its adaptative value are treated in Chapters 4 and 5. The DVM of burbot larvae in Lake Constance has been described 10 years ago by Wang and Appenzeller (1998). Miler and Fischer (2004) found, that larval burbot were distributed well below the thermocline during the day, but as they did not catch larvae below 50 m depth, the knowledge on precise depth distribution of burbot and its relation to environmental parameters remained sparse. In Chapter 4 it is demonstrated, how the DVM behaviour of burbot is related to light. The preferred light levels of burbot seem to be related to body size, suggesting predator evasion as the original mechanism of DVM. However, as discussed in Chapter 5, the DVM may serve as a multiple adaptation favouring simultaneously evasion of predation by YOY perch, the feeding on migrating zooplankton prey and the enhancement of bioenergetic budget.

Finally, Chapter 6 aims to asses the potential for inter- and intraspecific competition of YOY perch and burbot by quantifying the diet overlap between both species and between conspecific individuals. The assessment of diet overlap allows to estimate the magnitude of potential exploitative competition between both species and to explain motivation for the observed habitat segregation of perch and burbot.

2. Spawning site selection of Eurasian perch *Perca fluviatilis* L. in relation to temperature and wave exposure

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Ecology of Freshwater Fish (in press)

Introduction

The littoral zones of lakes are important spawning locations for many freshwater fish species. The substrata upon which eggs are deposited may vary considerably in composition and structure, with features including macrophytes, cobbles and stones, submersed woody debris and anthropogenic structures (Gerstmeier & Romig 2003; Winfield 2004). Eggs spawned in the littoral zone benefit from a number of advantages, because eggs experience warmer water temperatures compared to pelagic or profundal habitats (Huff *et al.* 2004), can attach better to substrate with low periphyton cover (Gafny *et al.* 1992) and larvae/juvenile fish find refuge from predators (Fischer & Eckmann 1997; Stoll *et al.* 2008). Consequently, spawning in lake littorals is a common strategy among many fish species. In central Europe, littoral spawners include many cyprinid species such as bleak *Alburnus alburnus* (L.), roach *Rutilus rutilus* (L.) and bream *Abramis brama* (L.) and as well as pike *Esox lucius* L. and Eurasian perch *Perca fluviatilis* L. (Gerstmeier & Romig 2003).

Eurasian perch spawn during April and May, when water temperatures rise above 10°C (Gillet & Dubois 2007; Treasurer 1988; Wang & Eckmann 1994). The eggs are embedded into a gelatinous, ribbon-like structure, which is deposited by the female in a single spawning event. Spawning females typically favour substrata in which eggs can be deposited amongst complex structures such as woody debris or macrophytes (Gillet & Dubois 2007), but newly spawned egg ribbons can also be found on substrata comprising only sandy or muddy sediment (Probst, personal observation).

In addition to substratum structure, other factors known to influence spawning site selection in perch include temperature, UV-radiation and hydrodynamic stress. Temperature influences the onset of spawning, which is strongly related to surface temperatures between 10 °C and 14 °C (Gillet & Dubois 2007; Gillet *et al.* 1995). The temperature controlled onset of spawning provides an adaptation to the optimal egg survival, hatching success and swim-up of perch larvae (Wang 1994). Hydrodynamic stress caused by wave-generated currents can damage eggs directly and may also dislodge attached eggs and remove them to a less favourable location. Both scenarios may result in severe rates of mortality (Rupp 1965). Local wind regimes during the spawning season may also govern the thermal regime within spawning habitats and have been shown to influence larval survival in North American yellow perch *Perca flavescens* (Mitchill, 1814) (Aalto & Newsome 1993). UV-radiation can inflict high mortalities on eggs of yellow perch, which have been found to favour shallower spawning sites in lakes in which high dissolved organic carbon concentrations result in greater turbidity (Huff et al. 2004; Williamson *et al.* 1997).

The present study investigates the influence of hydrodynamic forces on spawning site selection in Eurasian perch. The depth distribution of perch egg ribbons was compared between two experimental sites in which substratum type was artificially standardised, but wave exposure differed. We hypothesized that egg ribbons would be found at greater depths at the site with frequent and high-amplitude wave events than at the sheltered site. Furthermore, if spawning depth was affected by hydrodynamic forces, we expected egg ribbon size to be an additional factor in depth distribution, because large egg ribbons should be more prone to wave dislodgment and damage than smaller ribbons.

Materials & methods

Study sites

Upper Lake Constance, situated on the borders of Germany, Switzerland and Austria, is the second largest prealpine lake in Europe. It is a deep oligotrophic, warm-monomictic lake with a maximum depth of 254 m and a surface area of 473 km² (Stoll et al. 2008). In summer and spring the lake is popular with tourists and subject to heavy boat traffic in the form of ferries, passenger boats and other pleasure craft (Hofmann *et al.* 2008).

The experiments were conducted at two sites in the eastern part of Überlinger See, a fjord-like bay in the western basin of Upper Lake Constance. The two sites, in the following named Mainau (MAI) and Littoral Garden (LIT) experience different wave exposure, but have similar topography with a shallow 50 - 70 m wide littoral fringe extending to about 2 m depth, from where the lake bottom slopes downward at an angle of approximately 40°. MAI is located on the sheltered northern shore of the island of Mainau, while LIT lies on the lake shore between Konstanz-Egg and Konstanz-Staad and is subject to frequent ship waves generated by car ferries and passenger cruise ships (Hofmann *et al.* 2008).

Depth preference

To test the preferred spawning depth of perch in the absence of substratum limitation, artificial substrates were brought into the lake at the depth range where perch spawning had been observed in previous years. At each experimental site, a total of 18 spruce trunks (with twigs) were installed on 24.04.2007. The trunks were trimmed to a height of approx. 1.2 m and a width of approximately 0.8 m and introduced in sets of three at each of six depths; 0.5 m, 1 m, 2 m, 5 m, 10 m and 15 m. Each trunk was weighted with a 3 kg paving slab and pinned to the lake bottom with a 40 cm long iron hook. The three trunks at each depth were spaced approximately 3 m apart, thus ensuring that each trunk was far enough from its neighbours to be considered an independent replicate, but still easy for divers to locate on subsequent occasions.

SCUBA divers visited the sites weekly between 02.05.2007 and 16.05.2007 to record the abundance and size distribution of perch egg ribbons, thus providing data from three weeks (week 1 = 24.04.2007 - 02.05.2007, week 2 = 02.05.2007 – 10.05.2007, week 3 = 10.05.2007 – 16.05.2007). The divers counted the number of egg ribbons on each spruce trunk and measured the width at the middle of each ribbon. Once counted, all egg ribbons were removed from the spruce trunks to ensure that no ribbon was counted more than once on consecutive sampling dates.

Temperature & wave exposure

Water temperatures were recorded at three depths at each site using logging devices (ONSET, Bourne MA, USA) attached to spruce trunks at 0.5 m, 5 m and 15 m. The temperature was logged with a precision of 0.1 °C every 15 minutes over the entire duration of the experiment. In order to establish the relative degree of wave exposure at each site, surface wave fields were measured using a pressure sensor between 02.05.2007 and 10.05.2007, a period covering peak perch spawning when no strong wind events occurred. Thus the wave velocities recorded at both sites reflected only the impact of ship-induced waves, which may be considered representative of other weeks of perch spawning because the commercial boat traffic in Lake Constance follows a very regular schedule during the summer season. The pressure sensor has a full-scale range of 7 m, an accuracy of 0.1 mbar, and was deployed at a water depth of 2 m. Pressure measurements were made at 16 Hz. Wave parameters were calculated for burst intervals of 1,024 (~1.1 min) samples using the procedure described in Hofmann *et al.* (2008).

Maximum near-bottom current velocity u_{max} (m s^{-1}) is a parameter that characterizes the influence of surface waves on shearing forces close to the bottom, where perch eggs are deposited (Brown *et al.* 2005; Kundu & Cohen 2008). U_{max} was calculated for each burst interval and water depth (0.5, 1, 2, 5, 10, and 15 m) by using the appropriate dispersion relation. Based on site specific u_{max} time series, overall daily means and means of the upper 10 % of u_{max} with their standard deviation were calculated for all water depths.

Statistical analysis

The influence of spawning week, experiment site and depth on the abundance of egg ribbons was tested with a full-factorial three-way ANOVA. The abundance data of egg ribbons per spruce tree was sqrt (x + 0.5) transformed to achieve variance homogeneity.

A general linear model (GLM) was applied to analyse the influence of spawning week, experimental site and depth on the observed width of egg ribbons. In the GLM, depth was considered as a continuous factor, because egg ribbons were not found at all depths, thus ANOVA was not applicable due to imbalanced cell design.

Differences in average diel water temperatures between MAI and LIT at 0.5 m, 5 m and 15 m depth were tested with a GLM to examine potential influences of experiment site, depth (categorical factors) and date (continuous factor).

The differences in daily mean u_{max} were tested with a full-factorial two-way ANOVA, in which experiment site and depth were used as predictive factors. The data was log-transformed to achieve homogeneity of variances. Furthermore, because less than 4 % of perch egg ribbons were found at 15 m depth and no egg ribbons were found at 0.5 m depth, these depth layers were considered as negligible and were also excluded from the analysis. Values for u_{max} were so variable at 0.5 m depth, that the homogeneity of variances could not be achieved when this data was included.

Results

Substrate & depth preference

The spawning season of perch commenced by the end of April 2007, with the first egg ribbon in the lake littoral zone reported on 24.04.2007. A total of 296 egg ribbons were counted and measured on the spruce trunks between 02.05.2007 and 16.05.2007. Peak spawning occurred in week 2 of the experiment (Fig.2.1). In week 3, spawning activity was reduced and only 20 egg ribbons were recorded in the last census.

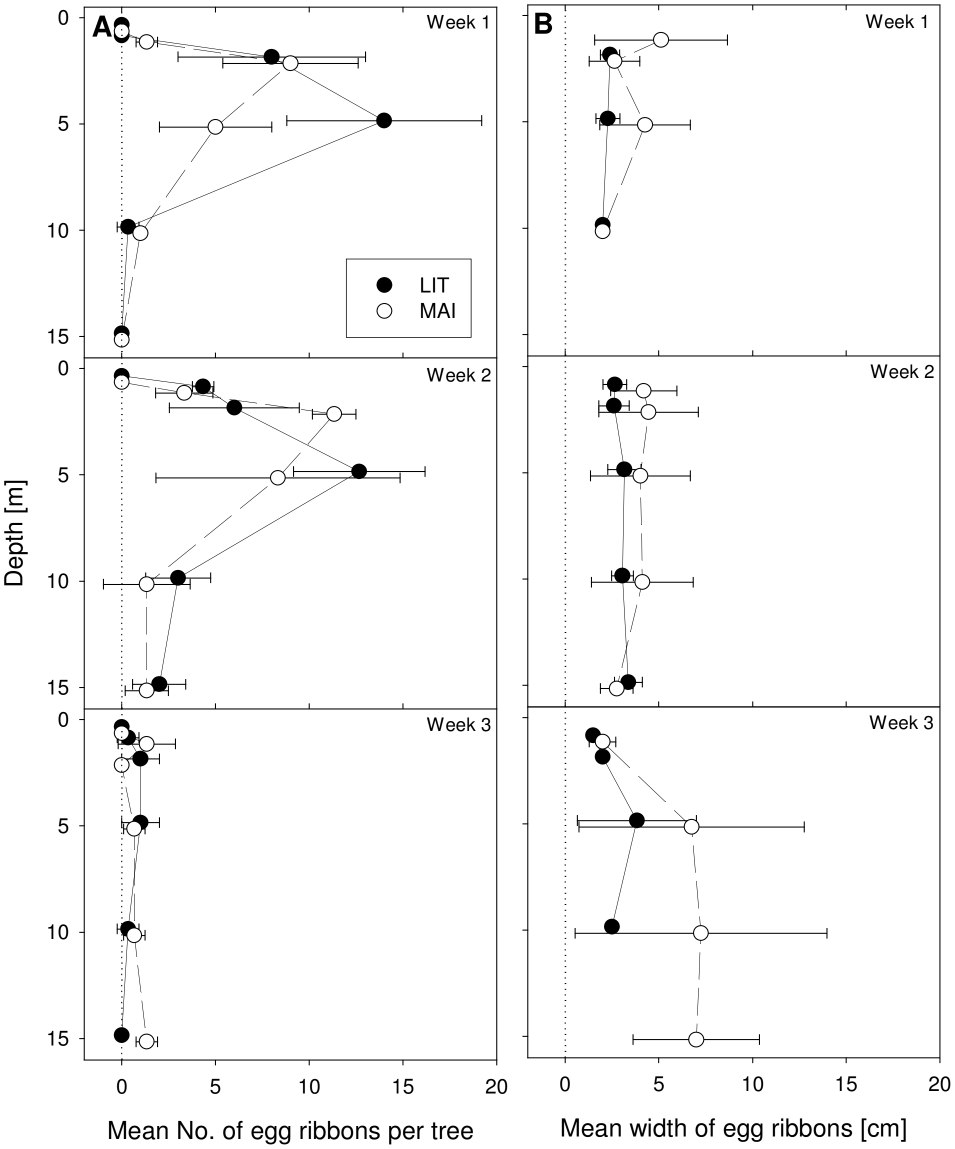

Figure 2.1: Differences in egg ribbon abundance and width at the sites of MAI and LIT in three weeks of perch spawning. **A)** The mean abundance of egg ribbons (± S.D.) in relation to depth. **B)** The mean width of egg ribbons (± S.D.).

The full factorial three-way ANOVA indicated that the total egg ribbon abundance did not differ between the sites MAI and LIT (Table 2.1). However egg ribbon abundance was affected by the week of spawning and depth and there were significant interactions between experiment site*depth and week*depth. The interaction between site*depth resulted from the fact that peak ribbon abundance occurred at 2 m depth at MAI and at 5 m depth at LIT (Fig.1). The interaction between week*depth resulted from changes in the depth distribution of egg ribbons from week to week. No egg ribbons were found above 1 m at either site and only 11 egg ribbons (= 4 %) were found deeper than 10 m (Fig.2.1).

Table 2.1: Results of full factorial three-way ANOVA and GLM for the abundance per spruce trunk (total N = 108) and width of egg ribbons (total N = 296). Week indicates the week of spawning, site refers to two experiment locations of MAI and LIT and depth refers to the six water depths (0.5 m, 1 m, 2 m, 5 m, 10 m and 15 m). The third degree-interaction Week*Site*Depth was excluded from the GLM analysis on egg ribbon width, because it was not significant. Df = degrees of freedom, F = value of F-statistic, P = level of significance, which was considered as significant and printed in bold italic when P < 0.05.

Variable	*Factor*	*Df*	*F*	*P*
Abundance	*Week*	2	42.926	**< 0.001**
	Site	1	0.058	0.811
	Depth	5	43.616	**< 0.001**
	*Week * Site*	2	0.557	0.575
	*Week * Depth*	10	10.044	**< 0.001**
	*Site * Depth*	5	3.530	**0.007**
	*Week * Site * Depth*	10	2.224	**0.026**
Width	*Week*	2	3.979	**0.020**
	Site	1	12.043	**< 0.001**
	Depth	1	6.097	**0.014**
	*Week * Site*	2	0.297	0.743
	*Week * Depth*	2	7.382	**< 0.001**
	*Site * Depth*	1	1.432	0.232

The width of observed egg ribbons differed significantly from week to week, between sites and also with depth (Table 2.1). Wider egg ribbons were found later in the spawning season and in deeper water. The egg ribbons found at MAI were generally wider than those from LIT (mean egg ribbon width MAI: 4.266 cm ± 0.232 cm S.E:, LIT, 2.655 cm ± 0.204 cm S.E.). The results suggest that larger females tend to spawn later and that they favour deeper water and more sheltered habitats than smaller conspecifics. The interaction between week and depth indicates that in week 1 the largest egg ribbons were found at 1 m depth, whereas by week 3 the largest egg ribbons were found at 10 m depth (Fig.2.1)

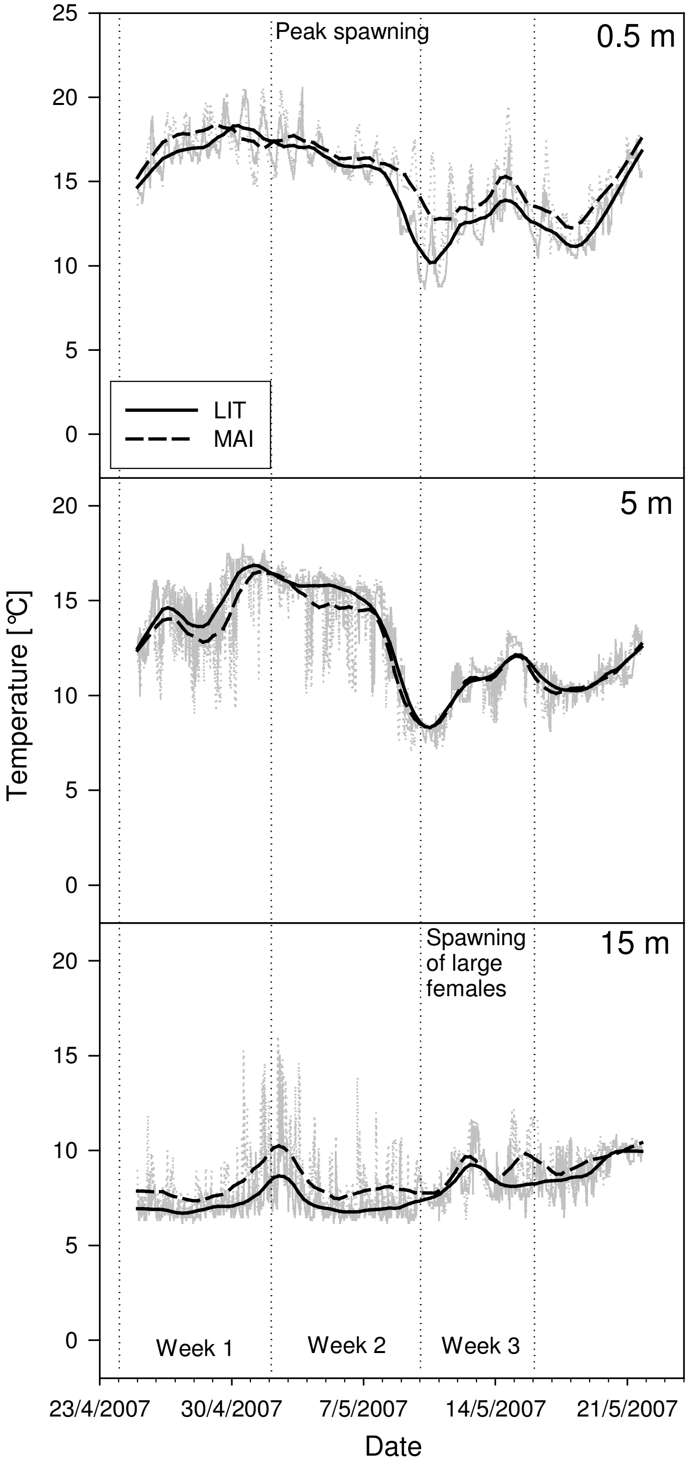

Figure 2.2: Water temperatures at 0.5 m, 5 m and 15 m depth at the experimental sites LIT (straight lines) and MAI (dashed lines) between 25.04.2007 and 24.05.2007. Black lines are spline lines of the running 10 % average mean, grey lines are plots from raw data measured in 15 min intervals. Dotted lines indicate the period of peak spawning and the period of large female spawning.

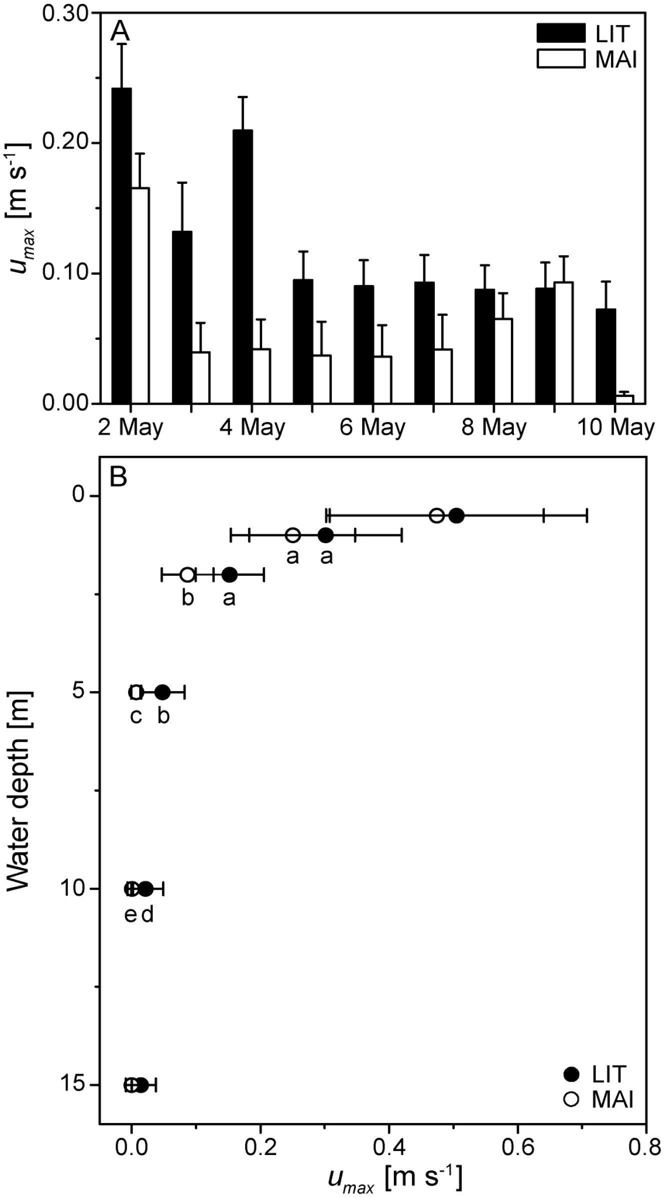

Figure 2.3: Wave exposure of the two experimental sites LIT and MAI during the peak spawning season (week 2) of perch. **A)** Daily means of the upper 10% of occurring wave-generated maximum near-bottom current velocities u_{max} (± S.D.) at 2 m depth. **B)** Overall means of the upper 10% of occurring wave-generated u_{max} (± S.D.) at the sampling depths 0.5, 1, 2, 5, 10, and 15 m. The letters indicate homogenous groups calculated by Student-Newman-Keuls-test for daily mean u_{max}.

Temperatures & hydrodynamic stress

Water temperatures did not differ significantly between MAI and LIT (GLM, Df = 1, F = 2.245, P = 0.136), but were significantly affected by date and by depth (GLM, Date: Df = 1, F = 32.421, p < 0.001, depth: Df = 2, F = 202.591, P < 0.001, Fig.2.2). There was a drop in water temperatures during the week of peak spawning (between 02.05.2007 and 10.05.2007), which was detectable at 0.5 m and 5 m depth. At 15 m, the water temperatures rose to 10 °C at MAI by the end of April without appearing to stimulate perch spawning, then dropped again to 8 °C until the last week of spawning.

Daily mean u_{max} during the week of peak spawning were generally lower at MAI than at LIT (two-way ANOVA, Df = 1, F = 113, 477, P < 0.001; Fig. 2.3A). Daily mean u_{max} also varied between depths (two-way ANOVA, Df = 3, F = 168.129, P < 0.001), but were similar at the main spawning depths of both sites (0.0115 m s^{-1} at 2 m depth at MAI; 0.0079 m s^{-1} at 5 m depth at LIT, Student-Newman-Keuls-Test, Df = 64, P > 0.05). Depth and site related differences in u_{max} were also apparent when considering the mean of the upper most 10 % of u_{max} (Fig.2.3A & B).

Discussion

The present results demonstrate the influence of hydrodynamic stress on the distribution of egg ribbons of perch. The environmental influences at the site of egg incubation may have severe impacts on the survival off perch eggs (Sandström *et al.* 1997) and thus it can be assumed, that female perch select favourable sites for spawning.

Among factors influencing the spawning behaviour and site selectivity of perch, temperature is the best studied. However, since mean water temperatures did not significantly differ between the two sites in this study, the differing depths of peak egg ribbon abundance in week 2 cannot be interpreted as a compensative behaviour of perch for different water temperatures. Instead, the possibility that the observed differences in egg ribbon abundances result from differential survival rates should not be discounted. Egg ribbons laid at 2 m depth at LIT may have been dislodged by the boat waves, leading to an underestimated number of observed egg ribbons in the subsequent census. However, the similarity in total numbers of spawned egg ribbons at MAI and LIT suggest that the observed differences in spawning depth rather reflect a selection behaviour of perch than differential survival during egg incubation.

The delayed spawning of large female perch and the apparent preference of large females for deeper areas of the littoral zone recorded in this study are in accordance with previous observations in Lake Geneva (Gillet & Dubois 2007). In the present study, large females spawned deeper and more frequently during week 3, when the water temperatures at 15 m depth increased steadily. However, if water temperature was the main determinant of spawning site selection, why would larger females not come to the shallower areas preferred by their smaller conspecifics? Larger females may find advantages at deeper spawning habitats that are not related to temperature and hence delay their spawning until adequate temperatures are reached at their preferred depth. Likely environmental influences may be the avoidance of UV-radiation and reduced wave exposure.

UV-radiation has been shown to cause severe damage to eggs of yellow perch *P. flavescens* and has an influence on spawning depth in lakes with varying water clarity (Huff et al. 2004; Williamson et al. 1997). However, because it is unlikely that the eggs of large female Eurasian perch should be more susceptible to UV-radiation than the eggs of smaller conspecifics, UV avoidance cannot explain the different depth preferences exhibited by perch of different sizes. Furthermore, water turbidity was usually higher at LIT than at MAI (Probst, personal observation). If UV-radiation was a factor in spawning depth selection of perch, the main spawning depth should have been deeper at MAI than at LIT, because turbidity reduces the penetration depth of UV (Huff et al. 2004). However, the opposite pattern was observed making UV-radiation an unlikely factor in the depth distribution of perch egg ribbons in our study.

While temperature and UV-radiation do not explain the differences observed in spawning depth and the relative abundances of large egg ribbons (> 5 cm) between the two experiment sites, the influence of hydrodynamics may account for several aspects of the present results. The main spawning zone was deeper at the more wave-exposed site LIT than at the sheltered site MAI. The impact of surface waves in terms of u_{max} decreases with depth and thus perch may be compensating for the greater hydrodynamic stress at LIT by depositing the eggs on deeper substrata. This seems plausible and may also explain the different depth preferences or large females favouring deep spawning sites, because their egg ribbons are more affected by wave-generated currents than small ribbons. This would further explain the greater number of large egg ribbons at the sheltered site MAI, which large females may prefer due to lower wave exposure.

Hydrodynamic stress may impact egg ribbons of perch directly by disrupting the egg ribbon via shear forces, or indirectly by smothering the egg ribbons with resuspended particles, causing mortality by oxygen deprivation. Disrupted egg ribbons may become detached from their substratum and be washed ashore (Clady & Hutchinson, 1975) or drop to the lake bottom and die (Smith *et al.*, 2001). The attachment of eggs to the substratum of calm, sheltered waters seems to be crucial in the reproductive success of perch, which may select spawning sites not only based on temperature and substratum structure, but also with respect to wave exposure.

Acknowledgements

The work for this project was conducted as part of the collaborate research centre CRC 454 “The Littoral zone of Lake Constance”. Jochen Seidel donated as many spruces as our car could carry across the rolling hills of Baden-Württemberg. We further thank Alfred Sulger (tenant of fishery permission at both study sites), Jörg Bambusch (City administration of Konstanz, Department of Urban Development and Environment) and Heinrich Straub (Mainau GmbH) for the permission to set up our experiment. The research dive group from the University of Konstanz deployed and recovered the spruce trunks and counted the perch egg ribbons. Four reviewers provided valuable comments on an earlier version of this manuscript and Amy-Jane Beer improved language and style.

3. Hydroacoustic observations of surface shoaling behaviour of young-of-the-year perch *Perca fluviatilis* L. with a towed upward-facing transducer

Wolfgang Nikolaus Probst, Gregor Thomas & Reiner Eckmann

Fisheries Research (in press)

Introduction

Echosounding is one of the most feasible methods for *in situ* observation and documentation of fish distribution (Simmonds and MacLennan, 2005). Unfortunately, each echosounding application has its drawbacks: In vertical downward echosounding a blind zone of several meters below the surface has to be tolerated, as the transducer is mounted in a certain depth and cannot reliably measure objects within its near-field. Therefore objects within the first 2 – 3 meters below the surface cannot be detected (Cech *et al.*, 2005). Horizontal echosounding cannot determine the precise depth of an object, as the sound beam emitted by the transducer is bent by the vertical gradient in water temperature and reflected or scattered in an unpredictable manner at the thermocline and the surface. The only method for the detection of near-surface objects with precise depth information is thus vertical upward beaming, where the near-field of the transducer is not at the same depth as the investigated objects.

In larval and juvenile fish, behavioural adaptations have evolved to reduce the risk of mortality and optimize growth. Among these, shoaling is a common phenomenon among fish species experiencing high predation likelihood (Krause & Ruxton, 2002, Pavlov & Kasumyan, 2000). Shoaling decreases the risk for an individual to become a victim of a predator. The formation and synchronous swimming behaviour of schools distract the predator and reduce their capture efficiency. Shoaling is often species-, size- and even kin-assortive (Behrmann-Godel *et al.*, 2006, Hoare *et al.*, 2000, Krause, 1994). Besides reducing predation risk for the individual, shoaling can increase the foraging efficiency of planktivorous fish, when food resources are distributed in horizontal patches (Krause & Ruxton, 2002).

Perch larvae *Perca fluviatilis* (Linnaeus, 1758) hatch in the littoral zone in May and are transported into the open water within a few days after hatch (Urho, 1996). Wang & Appenzeller (1998) found perch in the open water of Lake Constance until the end of July, where they inhabited the epilimnion during day and night. During their pelagic stage they first feed on rotifers and small copepods and switch to large copepods and *Daphnia* with increasing gape size (Wang 1994). While the abundance and distribution of pelagic perch has been investigated by Wang & Appenzeller (1998), the observation of their fine-scale depth distribution during day and night has not been attempted.

In the pelagic zone of Lake Constance, perch shoals are found directly below the surface during daytime and thus within the blind zone (mounting depth of transducer plus near-field) of a downward-beaming echosounder. In this study the shoaling behaviour of juvenile perch was observed by a towed upward beaming transducer as a method for the observation of near-surface objects.

Materials & methods

Research area

All data were sampled from the main basin of Upper Lake Constance, a warm monomictic pre-alpine lake with an average water depth of 101 m and a surface area of 456 km² (Mürle *et al.*, 2004). During the summer, the lake stratifies and a thermocline is established between 10 to 15 m depth. The echosounding surveys were conducted in the western part of Upper Lake Constance (02.06.2007 and 24.06.2007, Fig.3.1, Area A) and in the south-eastern part of the main basin (07.07.2007, Area B). During the surveys the boat cruised on transects parallel to the main axis of the lake (NW - SE) within the research area (Fig.3.1).

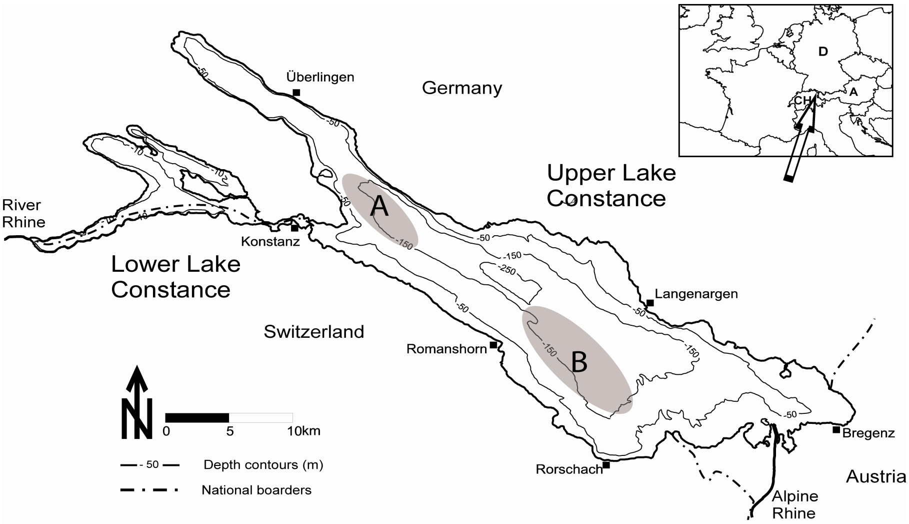

Fig. 3.1: Location of Lake Constance at the borders of Switzerland, Austria and Germany (small map, open arrow). The shaded areas indicate the areas of net catches and upward-beaming hydroacoustic surveys. Area A: net catches on the 30.05.2007, 29.06.2007 and hydroacoustic surveys on the 02.06.2007 and 24.06.2007. Area B: hydroacoustic survey on the 07.07.2007.

Net catches

From the middle of May until the beginning of August 2007 net catches were conducted in Area A (Fig.1). Pelagic fish larvae/juveniles were caught with two conical ichthyoplankton nets at 0, 5 and 10 m depth to confirm the presence of YOY perch. Unfortunately, catches were not performed quantitatively and thus abundance data from net catches were lacking. Instead, the minimum number of caught perch is indicated in Table 3.1.

Table 3.1: No. of young-of-the-year (YOY) perch and burbot caught in the pelagic zone of Lake Constance. TL refers to the mean total length of all perch and burbot caught on the according day. Day refers to 6:00 – 21:00, dusk to 21:00 – 23:00, night to 23:00 – 4:30 and dawn to 4:30 – 6:00. Note that on the 30.05.2007 and 29.06.2007 the no. caught are not quantitative and hence do not indicate relative abundances of YOY perch and burbot! On the 29.06.2007 neither perch nor burbot were caught during daytime, because perch displayed strong gear avoidance and burbot migrated to the hypolimnion.

Species	Date	Time	Catch Depth (m)	No. caught	Mean TL (± S.D.) (cm)
Perch	30.05.2007	Day	0	52	1.26 (± 0.21)
		Dusk	0	42	
		Night	0	40	
		Dawn	0	30	
	29.06.2007	Day	0, 3	no catch	2.14 (± 0.63)
		Dusk	0	24	
		Night	0	27	
		Dawn	0	24	
	22.07.2007	Dusk	5	3	4.63 (± 0.21)
Burbot	30.05.2007	Day	28	12	0.87 (± 0.17)
		Dusk	20	29	
		Night	5	8	
		Dawn	0, 28	17	
	29.06.2007	Day	25	no catch	1.36 (± 0.21)
		Dusk	20, 0	14	
		Night	0	12	
		Dawn	0, 28	9	
	22.07.2007	Dusk	5	4	1.98 (± 0.38)

The ichthyoplankton nets had a length of three meters, a circular opening of 1.4 m diameter and mesh sizes of 1200/800 µm and 1600/1200 µm in the front and rear, respectively. The net with 1200/800 µm mesh size was used on the 30.05.2007, while the net with 1600/1200 µm mesh size was used on the 29.06.2008 and 22.07.2008. Depending on tow depth and weather conditions, the nets were trawled with a speed of 0.7 - 1.5 m s^{-1} for 5 to 15 minutes. The speed was adjusted to maintain a constant depth, but was held as fast as possible. Caught fish were anesthetized and killed in trichloromethyl-propanol (2g l^{-1}) directly after catch and subsequently put on ice. Within 6 hrs, all fish were stored into a freezer at –18 °C until they were further processed. In the lab, the total length (TL) of frozen fish was measured to the nearest 0.1 mm under a dissecting microscope.

Hydroacoustic surveys and data processing

Surveys were conducted with a SIMRAD EK60 split-beam echo sounder equipped with an E120-7C transducer with 120 kHz operating frequency and a nominal circular beam width of 7°. The EK60 was operated with a power output of 100 W, a pulse length of 0.256 ms and 8.71 kHz bandwidth. The ping interval ranged from 0.2 to 0.5 seconds per ping and was adjusted to avoid false bottom echoes. Data were stored on the hard drive of a laptop computer, which was also used to control the echosounder settings (PANASONIC Toughbook CF-27). A GPS system was attached to the computer and position data of the boat (WGS84) were logged. The system was calibrated in May 2007 with a 23 mm diameter copper sphere of -40.4 dB target strength (at 1490 m s^{-1} sound speed) according to the manufacturer’s manual.

The transducer was mounted into a hydrodynamic metal tow-body, which was towed behind the boat by a 100 m connection cable (Fig.3.2). The shape of the tow-body caused a hydrodynamic drag, pulling the tow-body to the starboard side and downwards. At a tow speed of 1.4 m s^{-1} the tow-body usually reached a depth of 18 – 21 m. The deviation angles of the transducer’s vertical beam axis from the horizontal (α) and vertical plain (β) were measured with a pitch and roll sensor (sensor type: LIS3L02DQ, ST Microelectronics, Germany) during a pre-trial with an additional data cable (connecting the pitch and roll sensor and a laptop computer) attached to the tow-cable by straps. After the pre-trial the transducer was adjusted accordingly within the tow-body to achieve a beam axis perpendicular to the lake surface.

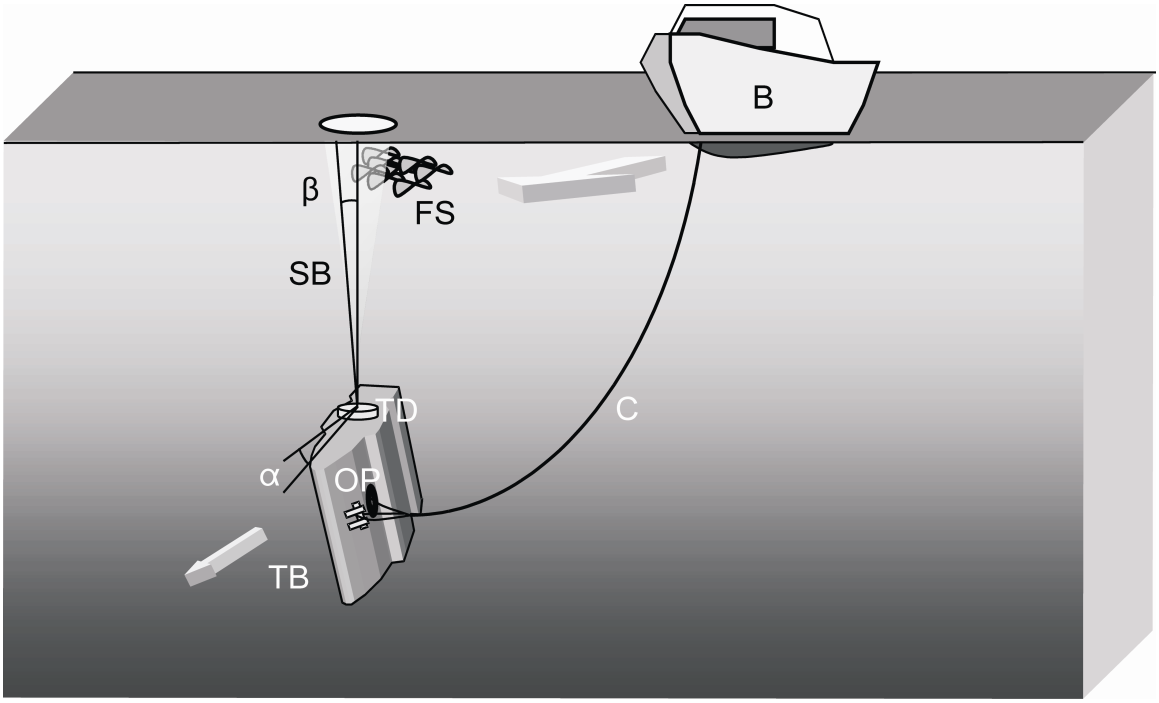

Fig. 3.2: Orientation of the tow-body for vertical upward beaming. B = boat, , C = tow- & data cable, FS = fish shoal, SB = sound beam (shaded area), TB = tow-body, TD = transducer, OP = opening for cable. α and β are the pitch and roll angles of the transducer. Arrows indicate the direction of boat and the drag momentum on the tow-body.

Hydroacoustic data were analysed with SONAR5_Pro 5.9.6 (Balk & Lindem, 2006). The settings for single echo detection (SED) were a returned pulse width between 0.8 and 1.6 of the transmitted pulse length (0.256 ms) and a maximum one-way gain compensation of 3 dB. Noise thresholds were set at –75 dB in the 40 log R (SED) and –100 dB in the 20 log R (amplitude) echograms for the 02.06.2007 and the 24.06.2007. On the 07.07.2007 SED noise threshold was set to –70 dB to further reduce the influence of noise on abundance estimation. The surface was automatically detected with the bottom detection algorithm of SONAR5_Pro and adjusted manually, when the automatic detection did not provide an adequate fit.

The mean depth of perch was calculated as the volume density-weighted depth of 1 m thick sub-layers from the surface to 10 m depth. Shoal width and shoal height were measured within the echogram window of SONAR5_Pro and corrected according to Simmonds & MacLennan (2005).

Results

The catches in the pelagic epilimnion of Lake Constance consisted exclusively of YOY perch and burbot *Lota lota* (Linnaeus, 1758) (Table 3.1). Only very few perch juveniles (N = 3) were caught on the 22.07.2007, and hence the majority of YOY perch had left the pelagic zone before this date. The length-frequency (LF) distributions indicated that during the observation period burbot were usually smaller than perch (Fig.3.3) and that the difference in the LF-distributions of perch and burbot increased from the 30.05.2007 to the 29.06.2007.

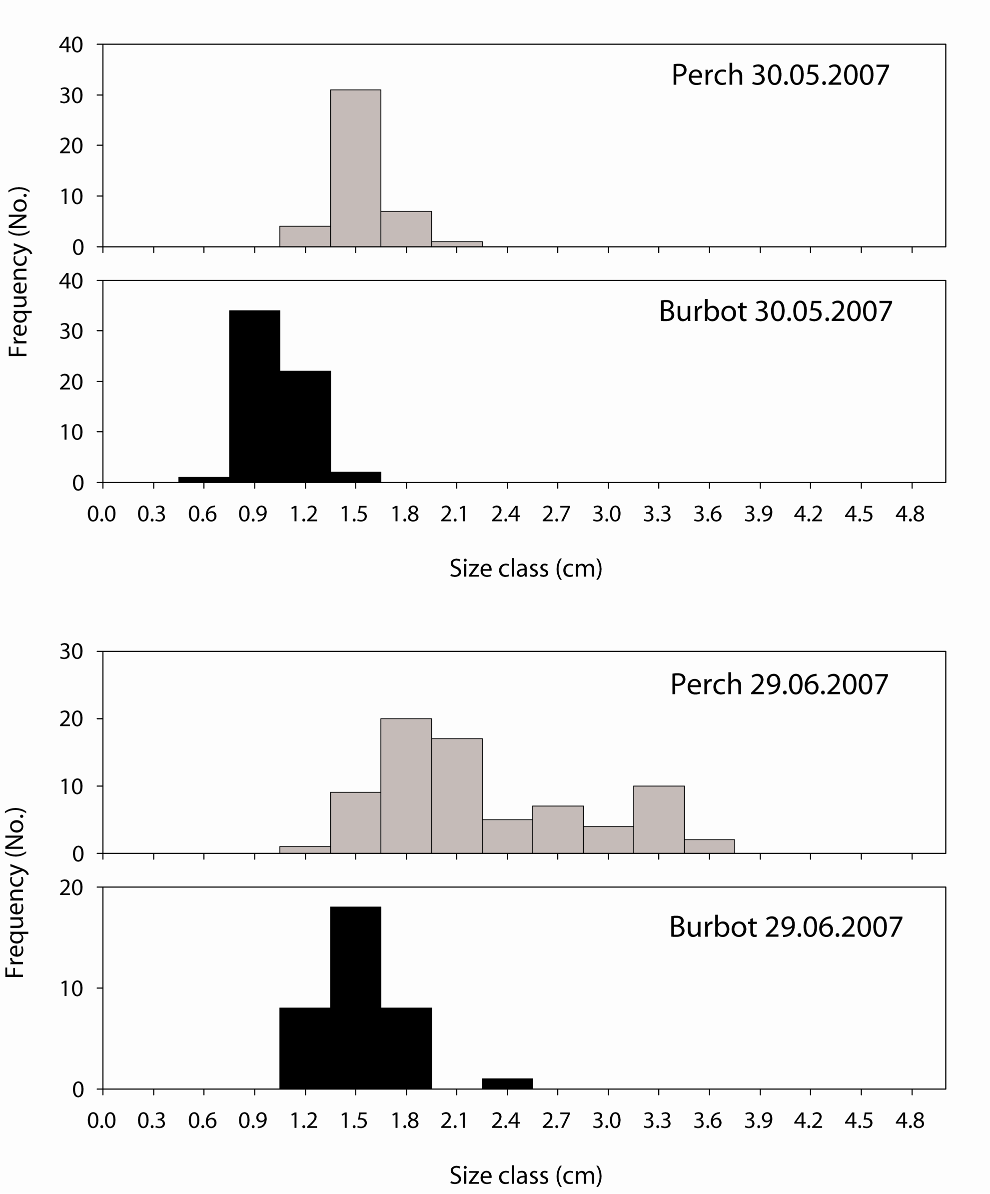

Fig. 3: Total - length frequency distribution of YOY perch and burbot on the 30.05.2007 and the 29.06.2007. X-axis labels indicate the upper limit of 3 mm size classes.

Contrary to the LF-distributions, the target-strength (TS) distributions of perch and burbot remained similar until the 24.06.2007 (Fig.3.4). In spite of their smaller total length (TL) burbot seemed to have larger TS than perch on the 02.06.2007. Three weeks later on the 24.06.2007, the TS-distributions of perch and burbot were similar while the TL of burbot was smaller than the TL of perch (see Fig.3.3 on the 29.06.2008). On the 07.07.2007 the larger TL of perch in relation to burbot was also evident in the TS-distribution.

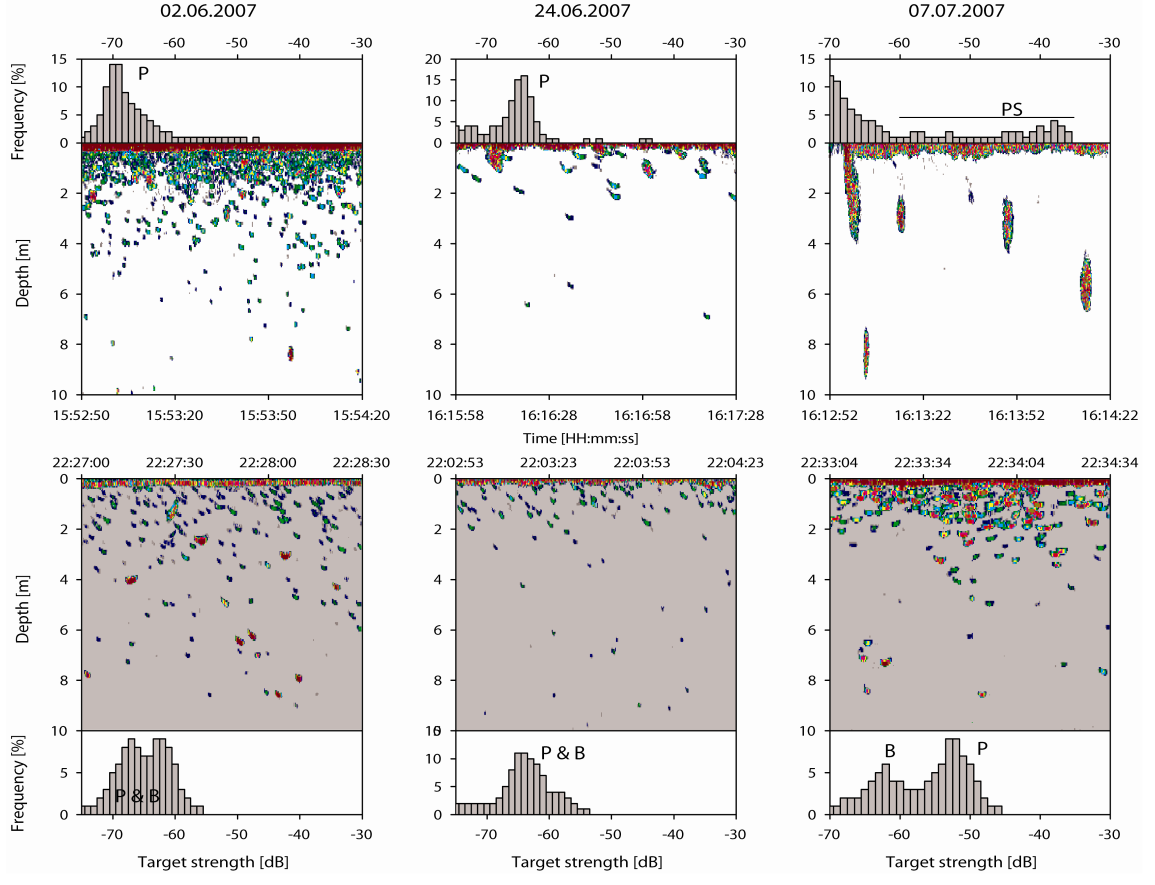

Fig. 3.4: Shoaling behaviour of juvenile perch and target strength (TS) on 02.06.2007 (left), 24.06.2007 (middle) and 07.07.2007 (right) at day (top) and night (bottom). Displayed are amplitude echograms (20logR) recorded by vertical upward echosounding during 90 seconds. P = TS-peak attributable to YOY perch, B = TS-peak attributable to YOY burbot, PS = TS-peak attributable to perch in shoals.

Upward echosounding revealed the shoaling of perch during daytime from the end of June (24.06.2007). No shoals could be detected on the 02.06.2007 (Fig.3.4). The onset of shoaling coincided with the metamorphosis from larvae to juveniles. Shoal size increased from 4.9 m mean width and 2.35 m mean height in late June to 6.6 m mean width and 0.69 mean height in early July (Table 3.2). During the day perch shoals were distributed between 0 and 10 m depth (Fig.3.5). At night, perch dispersed below the surface. After nightfall 66 % of the echo energy was observed in the first meter below the surface. Break-up of shoals occurred shortly after sunset (around 22:00 on the 07.07.2007, Fig.3.6).

Table 3.2: Daytime depth range and average shoal dimensions (± S.D.) of YOY perch in summer 2007 determined by vertical upward echosounding. Shoal dimensions were corrected to account for the pulse length and beam width (Simmonds & MacLennan, 2005). A total of 36 and 54 shoals were measured on the 24.06.2007 and the 07.07.2007, respectively. Distance refers to the length of the analysed transect and no. pings is the number of pings contained within the transect.

Date	Distance (m)	No. Pings	Min. Depth (m)	Mean Depth (m)	Max. Depth (m)	Mean width (m)	Mean height (m)
02.06.2007	3262	8050	*n.s.	1.28	*n.s.	n.s.*	n.s.*
24.06.2007	2946	7994	0.00	3.16	9.33	4.9 (±1.77)	0.69 (± 0.50)
07.07.2007	3193	7999	0.00	3.55	10.93	6.6 (±3.50)	2.35 (±1.33)

*n.s. = no shoaling on the 02.06.2007.

Discussion

The upward-beaming echosounder is a useful application to observe the behaviour of near-surface fish. Accordingly, the here presented system would also allow to estimate the abundance of YOY perch, which would be underestimated by a conventional downward-beaming hydroacoustic system. At day many shoals and at night 66 % of the echo energy was right below the surface and would have been within the blind-zone of a downward-beaming transducer. Further, the tow-body may have the advantage of reducing adverse effects of shooing by the boat (Guillard et al. 2006). Hence abundance estimates of juvenile fish showing a distinct vessel avoidance reaction should be more reliable with a towed echosounder system. Unfortunately, the presented data do not allow a quantitative comparison of perch abundance estimates by downward- and upward-beaming and this objective has to be addressed in future research endeavours.

The upward-beaming system proved to be applicable in calm conditions (wind speed less than 2.8 m s^{-1}) when the lake surface was smooth. However, wind-induced waves as well as waves from commercial ferry boats resulted in a blurry surface line from which the fish could not be separated. Upward echosounding will therefore be most applicable in inland waters or sheltered marine areas with little wave disturbance at the surface.

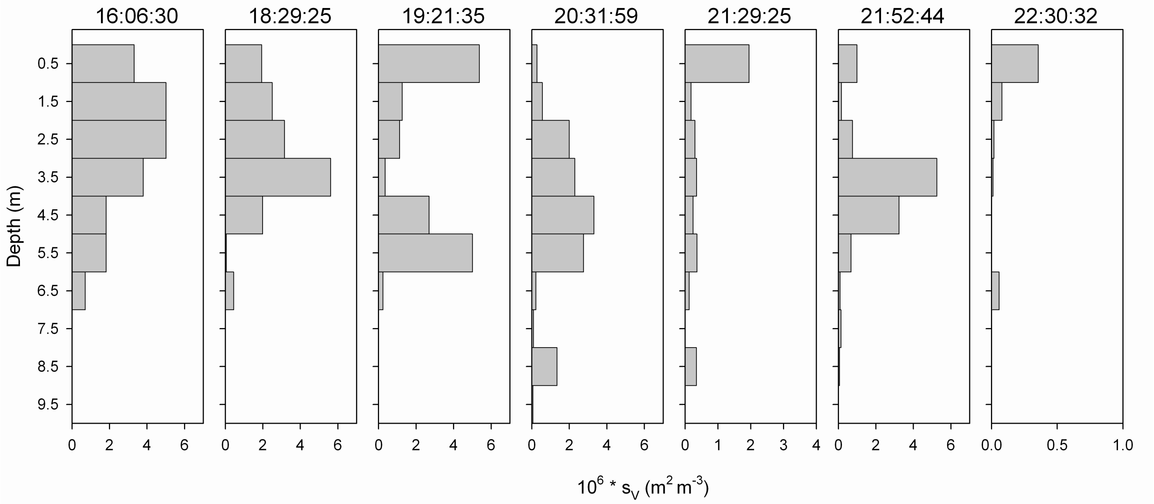

Fig. 3.5: Depth distribution of acoustic biomass (s_V) on the 07.07.2008. S_V was calculated at the indicated times (hh:mm:ss) for 1 m thick sub-layers from echogram sections containing 1000 pings, covering a period of at least 6 minutes and a distance of at least 395 m (depending on boat velocity).

Because the tow-body was towed by a 100 m long cable, it exerted considerable drag in the water. This resulted in a reduced manoeuvrability of the towing vessel. When turning the boat, wide curves of at least 250 m radius had to be made. The wide turning radius may limit the application of the presented system in small and narrow water bodies such as rivers or fjords. However, due to its limited size (0.57 m height x 0.85 m length x 0.38 cm depth) and weight (approximately 30 kg) the tow-body can be deployed and retrieved by two persons. Thus in smaller lakes and narrow fjords the tow-body can be retrieved before turning the towing vessel.

Until the 24.06.2007 the TS-distributions were larger for burbot than for perch, whereas the LF-distributions indicated that perch usually had a larger TL than burbot. Hence YOY burbot seem to have better acoustic scattering properties than perch, which may be related to their swim bladder size. Because YOY burbot perform deep diel vertical migrations of 60 m amplitude (Miler & Fischer, 2004, Probst & Eckmann, 2008), their swim bladder may be fully inflated when coming to the surface after dusk.

During their larval ontogeny burbot perform diel vertical migrations with increasing amplitudes (Probst & Eckmann, submitted). Hence burbot were not present in the epilimnion during the day and the daytime echograms in Fig.4 consisted mainly of perch.

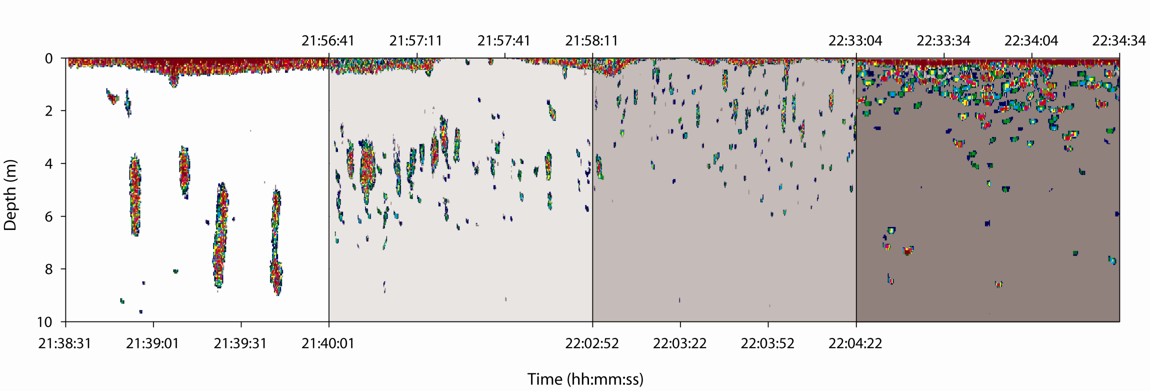

Fig. 3.6: Break-up of perch shoals on the 07.07.2007 between 21:38 and 22:34. The background colors in the amplitude echograms represent the declining light intensities during nightfall.

The single echo detections within perch shoals during the day were larger than the single echo detections of dispersed perch at night suggesting an artefact due to acoustic scattering within the shoals (Simmonds & MacLennan, 2005). Fig.4 clearly indicates that the large TS measured within the shoals at day do not derive from larger fish. After the break-up of shoals at dusk no targets larger than –44 dB were present, which would be the expected TS size of adult lake whitefish *Coregonus lavaretus* (Linnaeus, 1758) (Eckmann, 1995). The mean TS of perch increased from –66 dB on the 02.06.2007 to –52 dB on the 07.07.2007, which corresponds to 0.9 cm and 3.5 cm total length, respectively (Frouzova & Kubecka, 2004). These mean TS are in accordance with the observed TL of YOY perch (Table 1) and confirm their presence in the echograms of Fig.4.

Shoaling behaviour of perch is most likely related to predator avoidance. Increased body size and metamorphosis may render perch more vulnerable to visual predators (Urho, 1996), aggravating the need for shoaling. Consequently, shoal size increased during the summer as indicated in Table 2. Predation on YOY perch by older age classes was observed in the middle of July 2006, when 1+ perch caught in the pelagic zone of Lake Constance had up to six YOY perch in their stomach.

Perch stayed in the epilimnion of Lake Constance during the entire day, which has also been documented by Wang & Appenzeller (Wang & Appenzeller, 1998). A minor vertical displacement towards the surface was performed by perch, moving upward underneath the surface at night (Fig.5 & 6). However, a distinct diel vertical migration below the thermocline as described by Cech *et al.* (2005) could not be observed. Instead, perch shoals were distributed randomly within the epilimnion, probably driven by the exploitation of patchily distributed zooplankton.

Pelagic shoaling of juvenile perch has been described in Lake Annecy, where large shoals could be detected from the beginning of June and remained in the pelagic zone until winter (Guillard *et al.*, 2006). By contrast, YOY perch leave the pelagic zone of Lake Constance and migrate to the shallow littoral zone by late June or early July (Wang & Eckmann, 1994). The ontogenetic habitat shift of juvenile perch is commonly assumed to be induced by declining zooplankton abundance in summer (Wu & Culver, 1992), but its timing and extent may be influenced by lake size, lake trophic status and competition with other planktivorous fish (Persson & Greenberg, 1990).

General conclusions

The upward-beaming echosounding system presented in this study is a useful method to observe the distribution of near-surface fish. However, to obtain a good surface signal, which allows the separation of fish and surface signals, calm weather conditions and a smooth water surface are required.

Perch start to form shoals as they grow to approx. 2 cm total length. This size corresponds to the transition between the larval and juvenile stage and thus shoaling can be assumed to occur as a reaction to increased predation risk resulting from larger size and increased pigmentation.

Acknowledgements

This work was funded by the Deutsche Forschungsgemeinschaft (DFG) through the Collaborate Research Center CRC 454 “The littoral zone of Lake Constance”. The plan for the tow-body was provided by Dr. Eckhard Bethke and Hans-Eberhard Götze from the Johann Heinrich von Thünen-Institut / Institute of Sea Fisheries, Hamburg. The tow-body was constructed by the workshop of the University of Konstanz. Joachim Böhler, Julia Mohs, John Hesselschwerdt and many others helped in the field.

4. The influence of light on the diel vertical migration of young-of-the-year burbot *Lota lota* (L.) in Lake Constance

Wolfgang Nikolaus Probst & Reiner Eckmann

Journal of Fish Biology (in press)

Introduction

Diel vertical migration (DVM) is a common behaviour of aquatic organisms and can be found among taxa of phytoplankton (Sommer & Gliwicz, 1986), zooplankton (Stich, 1989), planktivorous fish (Cech *et al.*, 2005) and sharks (Sims *et al.*, 2006). Levy (1987) defined DVM as a "synchronized movement by aquatic organisms in the vertical plane which has a periodicity of 24 hours". The common pattern of DVM comprises the ascent at dusk and the descent at dawn, but this pattern can reverse (Sims *et al.*, 2005, Levy, 1990).

The amplitude of larval and juvenile fish DVM can range from a few meters (Hensler & Jude, 2007, Cech *et al.*, 2005) to more than 50 m (Auth *et al.*, 2007, Voss *et al.*, 2007, Scheuerell & Schindler, 2003, Harden Jones, 1968). Among freshwater fishes, the deep DVM of larval and juvenile sockeye salmon *Oncorhynchus nerka* (Walbaum, 1792) is one of the best known examples and has been studied extensively (Brett, 1971, Levy, 1987, Narver, 1970).

The changes of light intensity during dusk and dawn generally initiate the ascent and descent of migrating organisms, hence light is considered as the proximate factor for DVM (Lampert & Sommer, 1999). The influence of light on the DVM behaviour of fish has been described by many authors (Appenzeller & Leggett, 1995, Cech *et al.*, 2005, Eckmann & Imbrock, 1996) and is usually as such, that the migrating fish start the ascent during dusk and the descent during dawn. In this way, fish avoid bright light levels at any time of the day, evading potential predation by visual predators. The depth, where migrating fish are found, is usually considered to optimise the trade-off between the evasion of predators and the ability to forage on zooplankton. This depth, which changes as the sun rises and sets, is termed the "antipredation window" (Clark & Levy, 1988, Scheuerell & Schindler, 2003).

In large lakes of the northern hemisphere, burbot larvae hatch between March and May in the profundal zone and within a few days emerge to the surface to fill their swim bladder (McPhail & Paragamian, 2000). After swim bladder inflation larval burbot inhabit the pelagic zone, feeding on plankton (Ryder & Pesendorfer, 1992). In Lake Constance, pelagic burbot larvae have been observed to perform DVM by Miler & Fischer (2004) and Wang & Appenzeller (1998). However, the exact DVM behaviour, the duration of the pelagic stage, the location of settlement and the pathway to the littoral zone of YOY burbot in Lake Constance remained uncertain, as in both studies only data from net catches were used. After spending between approximately two months in the pelagic zone of the lake, burbot are assumed to settle to the profundal zone (Miler & Fischer, 2004). From the profundal zone they probably migrate along the slope of the lake bottom towards the littoral zone where they arrive as juveniles (Fischer, 1999). The earliest burbot juveniles come to the littoral zone in late June (Fischer, 1999), but the majority of YOY burbot arrives in August or September (Fischer & Eckmann, 1997).

While the DVM of YOY burbot has been known since 1994 (Wang & Appenzeller, 1998), the understanding of its causes is still lacking. Several zooplankton species in Lake Constance perform distinct DVM during summer (Stich, 1989). Miler & Fischer (2004) therefore suggested that YOY burbot follow their zooplankton prey. Alternatively, Miler & Fischer (2004) assumed, that the DVM of burbot might mark a period of transition between the pelagic and benthic life-style. However, the precise relationship between the vertical distribution of burbot and environmental variables remained unknown.

In the present study the relationship between light and the DVM behaviour of YOY burbot is investigated. A prerequisite for this objective is the knowledge of the temporal and spatial fine-scale distribution of burbot, which was investigated by split-beam echosounding. The observed depth of burbot was related to light intensities above the surface and at depth to explore how and to which extent light can explain the vertical distribution of YOY burbot during their pelagic stage in Lake Constance.

Materials & methods

Light intensity

Light intensities above the water surface (I_0) were measured by a stationary light sensor on the roof of the Limnological Institute. The sensor recorded light intensities every 30 seconds. Arithmetic mean light intensities for 10 min time intervals were calculated, which corresponded to the time interval of the analysed hydroacoustic transects. Light intensities at the mean depth of burbot were calculated after Uhlmann & Horn (2001):

$$I_Z\ [\mathrm{W\ m^{-2}}] = I_0 * e^{-k*Z} \qquad \text{(Eq. 4.1)}$$

where Z is the mean depth [m] of burbot, I_Z is the light intensity at depth Z, I_0 is the light intensity above the surface and k is the extinction coefficient. K was determined from *in situ*-measurements of light intensity in the water column with a waterproof luxmeter (LTM, Berlin) during each survey. The values for I_Z were corrected for sun inclination related changes in surface albedo by calculating the sun inclination SI [°] at Konstanz at the given date and time. A regression between water albedo and sun inclination obtained from Blüthgen & Weischel (1980) was used to calculate a factor by which I_Z was multiplied to obtain albedo corrected light values at depth (I_{Zcorr}):

$$I_{Zcorr} = \left[1 - \frac{(77.481 * e^{-0.0752*SI})}{100}\right] * I_Z \qquad \text{(Eq.4. 2)}$$

where term in the brackets describes the relative amount of light, which is transmitted through the water surface.

Hydroacoustic surveys and data processing

Hydroacoustic surveys were conducted weekly or in two week intervals from the beginning of May until beginning of September in 2006 and end of August in 2007 (Table 4.1). The surveys were conducted in the western part of ULC following standard transect routes at day, dusk and night (Fig.4.1) and cruising randomly on the lake in the meantime. For the analysis of mean burbot depth only hydroacoustic data from lake areas with more than 100 m depth were used.

Surveys were usually performed from noon/afternoon until nightfall. On four occasions (04.05.2006, 01.06.2006, 31.05.2007 and 21.06.2007) the hydroacoustic surveys were extended until the next morning to observe the descent of YOY burbot.

For the hydroacoustic recordings SIMRAD EY500 (2006) and SIMRAD EK60 (2007) echo sounders equipped with an E120-7C split-beam transducer (120 kHz, nominal circular beam width of 7°, SIMRAD, Kongsberg, Norway) were used. The EY500 was operated with a power output of 63 W, medium pulse length (0.3 ms) and 12 kHz bandwidth. The EK60 was operated with a power output of 100W, a pulse length of 0.256 ms and 8.71 kHz bandwidth.

Ping intervals during the surveys ranged from 0.2 to 1.3 seconds per ping and were adjusted to avoid false bottom echoes. Data were stored on a laptop computer, which was also used to control the echosounder settings. The system was calibrated in April 2006 and May 2007 with a 22 mm diameter copper sphere of -40.4 dB reference target strength (at 1490 m s^{-1} sound speed) according to the manufacturer's manual.

Table 4.1: Dates and locations of determined mean burbot depth in 2006 and 2007. Locations are abbreviated according to Fig.4.1 as SA = survey area, TA = transect A and TB = transect B. Times of day were defined as dawn between 4.30 - 6.30, day between 6.30 - 20.00, dusk between 20.00 – 22.00 and night between 22.00 - 4.30.

Date	*Day of year*	*Location*	*Total No. of observations*	*No. of samples at…*			
				Dawn	*Day*	*Dusk*	*Night*
04.05.2006	123	SA	3	1	2		
22.05.2006	141	TB	1		1		
01.06.2006	151	SA,TB	5	1	2		2
19.06.2006	169	SA,TB	4		2		2
26.06.2006	176	SA, TB	6		3	1	2
04.07.2006	184	SA, TB	6		5		1
10.07.2006	190	SA, TB	9		6	1	2
24.07.2006	204	SA, TB	8		4	2	2
31.07.2006	211	SA, TB	5		1	2	2
07.08.2006	218	SA, TB	5		3	1	1
21.08.2006	232	SA, TB	10		8	1	1
05.09.2006	247	SA	4		2		2
03.05.2007	122	SA	1		1		
12.05.2007	131	SA	2		2		
14.05.2007	133	SA	2		2		
16.05.2007	135	SA	1		1		
21.05.2007	140	SA,TA	5		2	1	2
31.05.2007	150	SA,TA	7	1	3	1	2
12.06.2007	167	SA,TA	5		2	1	2
22.06.2007	172	SA	2		2		
29.06.2007	179	SA,TA	12	2	5	1	4
11.07.2007	191	SA	1		1		
22.07.2007	202	SA,TA	6		3	1	2
18.08.2007	229	SA,TA	3		2		1
27.08.2007	238	SA	1		1		
Σ			114	5	66	13	30

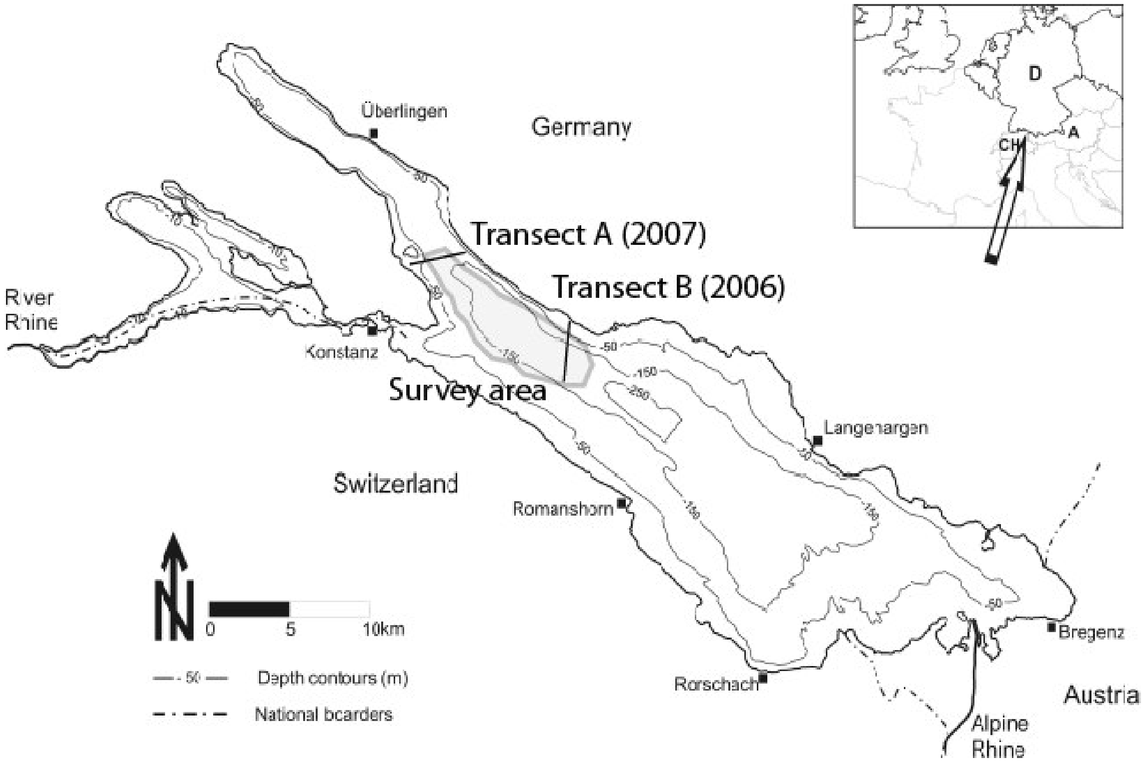

Figure 4.1: Location of Lake Constance (open arrow, small map) and survey areas for hydroacoustic observations of vertical burbot distribution in 2006 and 2007. The transects were regularly surveyed by hydroacoustics at day, dusk and night. Transect A was monitored in 2007 and Transect B in 2006. Additional recordings at various times of the day were performed in both years randomly within the survey area (hatched polygon). For dates and times of surveys refer to Table 1. Net catches were obtained in vicinity of the transects within the survey area.

Hydroacoustic data were analysed with SONAR5_Pro 5.9.5 and 5.9.6 (Balk & Lindem, 2006). The settings for single echo detection (SED) were a returned pulse length between 0.8 and 1.6 of the transmitted pulse and a maximum one-way gain compensation of 3 dB. For data conversion, the base thresholds were set at –100 dB in the 40 log R (SED) and 20 log R (amplitude) echograms.

To determine the mean depth and volume density of YOY burbot at a given time and day, a pelagic transect (lake depth > 100 m) containing at least 500 pings (corresponding to approx. 5 minutes) was analysed. Within this transect, echoes were erased, when they were attributable to shoals of lake whitefish *Coregonus lavaretus* L. or perch *Perca fluviatilis* L. or were induced by hydrodynamic disturbances (boat waves, wind waves). Echoes were attributed to burbot, when they were classified as distinct single echo detections below a depth of 10 m during day and were within a target strength (TS)-range between –80 to –58 dB. Any other fish species would not occur below 10 m depth (e.g. YOY perch, see Table 4.2) or would have considerably larger TS. For burbot echoes, the range of minimum and maximum target strengths at a given date was determined, which was then used for the calculation of

SED volume density (VD, No. SED m^{-3}) by counting the number of SED per volume within this TS-range. TS outside the determined TS-range were excluded from the volume density calculation. To obtain the number of SED per volume the analysed transect was divided into 1m-thick layers from 3 to 103 m depth and the number of SED was divided by the SED beam volume (volume of an ideal conical beam equivalent to the sampled beam volume, beam volume is calculated by SONAR5_Pro) in the according layer. The depth range from 3 to 103 m was chosen to account for the near field of the transducer and to cover the depth range of migrating burbot until the end of the summer.

Mean (Z) and standard deviation (SD_Z) of burbot depth were calculated as the weighted mean and standard deviation of class-grouped data:

$$Z[m] = \frac{\sum_{1}^{i}(z_i * VD_i)}{\sum VD_i} \qquad \text{(Eq. 4.3)}$$

and

$$SD_Z\,[m] = \sqrt{\frac{1}{(\sum VD_i)-1} * \sum_{1}^{i}\left[VD_i * (z_i - Z)^2\right]} \qquad \text{(Eq. 4.4)}$$

with z_i as the depth of the layer i, VD_i as the volume density within layer i. The total density of burbot was calculated as the sum of burbot densities from each 1m-depth layer.

Net catches

To confirm the presence of YOY burbot and to obtain their size distribution, burbot larvae and juveniles were caught approximately every second to third week between May and September in 2006 and 2007. In May and June burbot larvae were caught at day, dusk, night and dawn. From the end of June burbot were too deep to be caught during the day and were only caught at dusk and night.

Larvae and juveniles were caught with three meter long ichthyoplankton nets with a circular opening of 1.4 m diameter and mesh sizes of 1200/800 µm and 1600/1200 µm in the front and the rear, respectively. The same boat that was used for the hydroacoustic surveys was also used for towing the nets, which were attached to a 160 m long tow line. The nets were fitted with a flow meter to calculate the sampled volume of water in 2006.

Unfortunately, this was not done in 2007 and thus abundance estimates from net catches are lacking for this year. To adjust the trawl depth, appropriate weights were attached. For towing depths > 10 m, a hydrodynamic V-fin with 15 kg weight (HYDROBIOS Kiel) was used. Information on net depth was obtained from an ultrasonic depth transponder attached to the bridle of the nets.

In 2006, stratified samples were conducted at the surface, 5, 10 and 20 m depth. In 2007 the tow depth was adjusted according to the depth distribution of burbot echoes displayed by the echosounder. Depending on tow depth and weather conditions, the nets were trawled with a speed of 0.7 m s^{-1} - 1.5 m s^{-1}. The speed was adjusted to maintain a consistent depth, but was held as fast as possible.

Caught fish were anaesthetized and killed in trichloromethyl-propanol (2g/L) directly after catch and subsequently preserved in 4 % formalin or put on ice. Within 6 hours, all fish that had been put on ice were stored into a freezer at –18 °C until they were further processed. In the lab, the total length (TL) of frozen fish was measured to the nearest 0.1 mm under a dissecting microscope.

Statistics

Mean depth of burbot calculated from echograms from 25 survey days and at various times of the day in 2006 and 2007 (see. Table 4.1, N = 114) were combined with data on light for the according times and days, which was used to model the influence of surface light intensity and day of the year (Doy) on mean burbot depth using a non-linear regression with a user-defined equation:

$$Z_{MD} = (Doy + m) * a * \log(I_0) + z_N \qquad \text{(Eq. 4.5)}$$

where Z is the mean depth of burbot, Doy the day of the year (counted continuously from the 1 January as Doy 1) and I_0 the light intensity at the surface. Doy was used as a proxy for burbot total length (TL), which was significantly correlated (Mean TL = 0.0917 * $e^{0.0147*Doy}$, N = 13, $r^2 = 0.92$, $P < 0.001$). Values for I_0 were log-transformed to obtain linearity. M, a, and z_N are the coefficients estimated by the non-linear regression module of STATISTICA 6. Z_N is an estimate of the depth of burbot (at night), the term m accounts for the increasing influence of the day of the year and ‘(Doy + m)*a’ describes the slope of the light-depth relationship.

A second non-linear regression was used to model the influence of daytime and day of the year on the light intensity at the mean depth of burbot (I_{Zcorr}):

$$I_{Zcorr} = [a * e^{b*Doy}] * e^{\left[-0.5*\left(\frac{time-n}{m}\right)^2\right]} \qquad \text{(Eq. 4.6)}$$

with time as the daytime and a, b, n, and m as coefficients estimated by the non-linear regression module of STATISTICA 6. A and b are the coefficients of the exponential relationship between light intensity at depth and day of the year (due to exponential light extinction in the water column, see Equation 4.1), m and n are the coefficients of a Gaussian bell-shaped curve, which is suitable to describes the light intensity in relation to daytime (see Fig.4.4).

Both non-linear-regressions were fitted with Levenberg-Marquard-Least-Squares algorithm with a maximum numbers of 1000 iterations and convergence criteria of 10^{-6}. The initial values, from which the iterations were started, were set to 0.1 for all coefficients in the first (a, m and z_N) and to 1.0, 0.1, 0.1 and 0.1 in the second non-linear regression for a, b, m and n, respectively.

Results

Burbot distribution

During the two years of our investigation, only one lake whitefish and two cyprinid larvae were caught. The rest of the catch consisted of YOY perch and burbot. The first burbot larvae were caught by the middle of May and pelagic juveniles could be caught until August (Table 4.2). From the middle of August, juvenile burbot were difficult to catch but could still be observed by echosounding and identified by their target strengths (TS). The observed TS of burbot ranged from –80 to –70 dB in May to –69 to –58 dB in August. SED of YOY burbot could be observed in the echograms from the 04.05.2006 and 03.05.2007 until 05.09.2006 and until 27.08.2007 in 2006 and 2007, respectively.

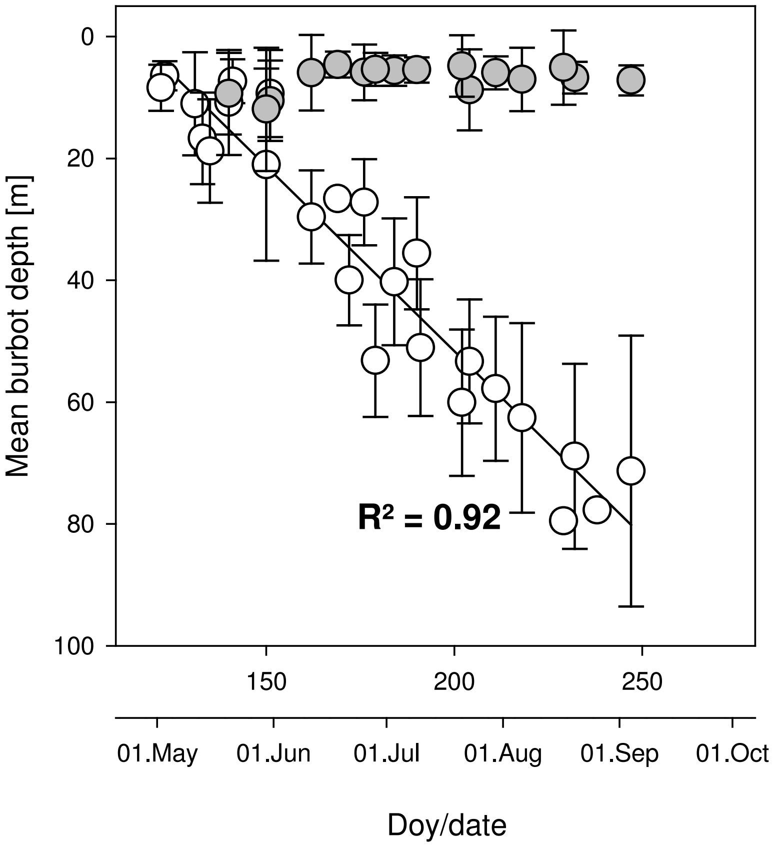

Figure 4.2: The maximum (at day, white circles) and minimum (at night, gray circles) mean depth of young-of-the-year (YOY) burbot at a given survey date between May and September. Mean depth of burbot was calculated after Equation 4.3. Error bars represent the standard deviation of the mean depth as calculated after Equation 4.4. Combined data from hydroacoustic surveys performed in 2006 and 2007 are shown.

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During May, burbot depths at day and night were similar (Fig.4.2). From June onwards, burbot performed pronounced DVM, staying in the epilimnion (between 5 and 10 m depth) at night and at the meta- or hypolimnion during the day. Burbot ascended to the epilimnion at dusk and descended to the hypolimnion at dawn (Fig.4.3). By August burbot DVM reached amplitudes of 70 m (Fig.4.2). Mean depths of burbot at day increased from May to August and were strongly correlated to the day of the year (Fig.4.2). Nighttime depths of burbot decreased during May and early June and remained constantly above 10 m depth after the middle of June.

The relationship between light and burbot DVM

Within the 114 burbot observations from 25 surveys performed in 2006 and 2007, the light intensity above the surface ranged from 0.0 W m^{-2} (several occasions at night) to 922.8 W m^{-2} on 22.07.2007 at 13.42. A maximum light intensity of 116.0 W m^{-2} experienced by larval burbot was calculated on the 03.05.2007 at 10.36 at a mean depth of 8.4 m.

The ascent and descent of burbot was related to the light intensity at the surface, because the highest changes in depth occurred at sunrise and after sunset (Fig.4.4). Furthermore, the mean burbot depth was significantly related to surface light intensities, which increasingly affected the mean depth of burbot as the summer progressed (Fig.4.5A).

The model after Equation 4.5 provided a good fit to the observed data ($R^2 = 0.91$), with all estimated coefficients contributing significantly to the model (Table 4.3). The model also provided an adequate value for the minimum depth of burbot of 4.5 m (± 2.4 m C.I.), which was similar to the depth at night observed by hydroacoustic and net catches (see Fig.4.2 and Table 4.2). The regression model confirmed the increasing influence of I_0 on the DVM of YOY burbot during the progression of the summer.

The second non-linear regression model (Equation 4.6) indicated that burbot live in illuminated water layers until approx. to day of the year 180 (which is the 30 June), but afterwards do not inhabit water layers with light intensities higher than 0.1 W m^{-2} (Fig. 4.5B, Table 4.4). In other words, the amplitude of the burbot DVM became so high by the end of June, that YOY burbot experience low light intensities < 0.1 W m^{-2} during the entire day.

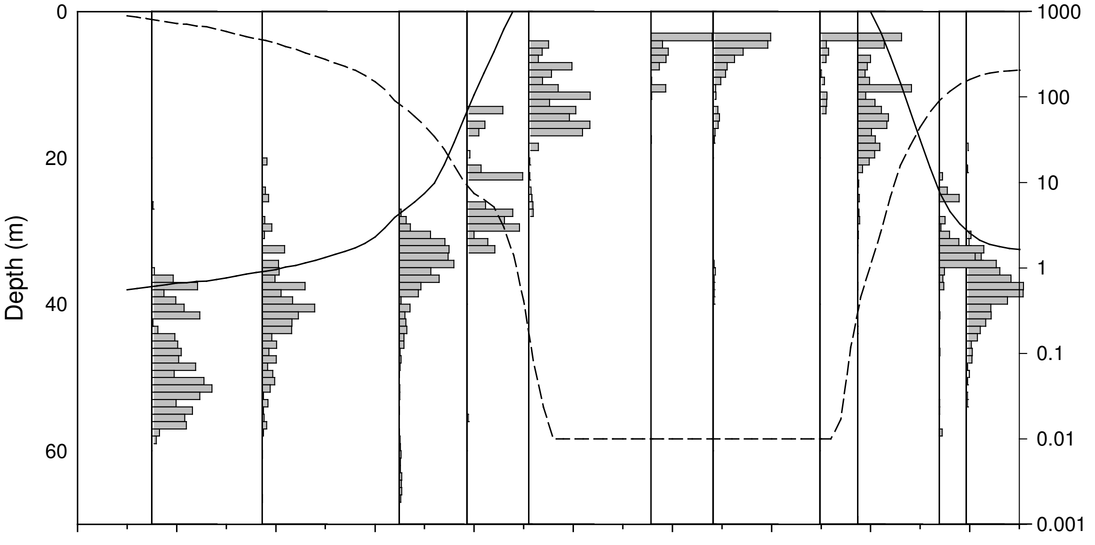

Figure 4.3: Diel vertical migration of burbot on the 29.06.2007. The grey bars indicate the relative abundance at depth of young-of-the-year burbot at the various times of the day, for which the reference is the y-axis of the bar charts. The straight line indicates the depth of the 0.01 W m^{-2} isolume, the dashed line describes light levels above the surface (I_0).

Table 4.2: Catches of YOY burbot in 2006 and 2007. No. caught refers to the number of caught burbot within each haul, % of catch refers to relative number of burbot in the catch. The rest of the catch consisted of YOY perch. Data from 2007 was not sampled quantitatively, so density measures and proportions of catch could not be calculated. Mean TL was calculated from all caught individuals from one of the 12 sampling campaigns.

Date	*Day of year*	*Time of day*	*Depth [m]*	*No. caught*	*Catch density [Ind. 1000 m^{-3}]*	*% of catch*	*TL (± S.D.) [cm]*
23.05.2006	142	Day	0	0	0	0	0.60 (± 0.10)
			5	2	2.3	1	
			10	30	49.8	91	
			20	7	8.7	100	
07.06.2006	157	Night	0	3	4.03	2	0.97 (± 0.12)
20.06.2006	170	Dusk	5	4	13.9	10	1.10 (± 0.16)
			10	1	2.1	10	
11.07.2006	191	Dusk	8	15	6.6	100	1.36 (± 0.23)
08.08.2006	219	Dusk	20	7	1.9	100	2.21 (± 0.27)
14.05.2007	133	Day	15	10			0.71 (± 0.07)
21.05.2007	140	Day	13	3			0.76 (± 0.09)
		Dusk	17	9			
		Night	13	12			
30./31.05.2007	149/ 150	Dusk	0	9			0.96 (± 0.14)
			20	20			
		Night	5	8			
		Dawn	0	9			
			27	8			
		Day	27	12			
12.06.2007	162	Dusk	2	17			1.00 (± 0.16)
		Night	4	21			
22.06.2007	172	Day	35	13			1.20 (± 0.23)
29./30.06.2007	179/ 180	Dusk	0	14			1.31 (± 0.18)
		Night	0	12			
		Dawn	0	5			
			28	4			
22.07.2007	202	Dusk	5	4			1.98 (± 0.38)

Table 4.3: Results from the non-linear regression modelling the influences of day of the year (Doy) and surface light intensity (I_0) on the mean depth of burbot (Z_{MD}). M, a and z_N are the coefficients of the model equation estimated by a Levenberg-Marquardt-Least-Squares algorithm. R^2 is the amount of variance explained by the regression-model, F is the F-value from the model-validating ANOVA, which compares the variance explained by the model against the variance within the residuals, C.I. delimits the 95% confidence interval for the coefficient estimate, t is the value from the t-statistic to confirm significant contribution of the coefficient to the regression model. No. It. refers to the number of iterations, until the convergence criteria of 10^{-6} were met. P-values represent the significance values from the F- and t-statistics and are printed bold when < 0.5.

Model-Equation	*R^2*	*F*	*P*	No. It.
$Z_{MD} = (Doy + m) * a * \log(I_0) + z_N$	0.908	1021.067	**< 0.001**	6

Coefficient	*Estimate*	*C.I.*	*t*	*P*
m	-120.648	± 7.698	-31.054	**< 0.001**
a	0.214	± 0.018	23.385	**< 0.001**
z	4.501	± 2.239	3.982	**< 0.001**

In May and until mid-June, I_{Zcorr} was highest during daylight hours, but from the end of June (Day of the year 176) there was evidence for crepuscular light windows before dusk and during dawn, at which burbot experience the highest light levels within the diel cycle (Fig.4.6). Thus the occurrence of crepuscular light windows in the diel light cycle coincided with the avoidance of bright light levels at day. The I_{Zcorr} at these crepuscular light windows decreased by more than two orders of magnitude during the summer (from 0.016 W m^{-2} on doy 176 to 0.0001 W m^{-2} on doy 232).

The mean light intensity at depth (I_{Zcorr}) at a given day of the year was negatively correlated with the total length of burbot at the same day of the year (N = 12 catch dates, see Table 4.2, $r^2 = 0.93$, $p < 0.001$, Fig.4.7). Thus, the larger burbot grew, the lower the light intensities they experienced.

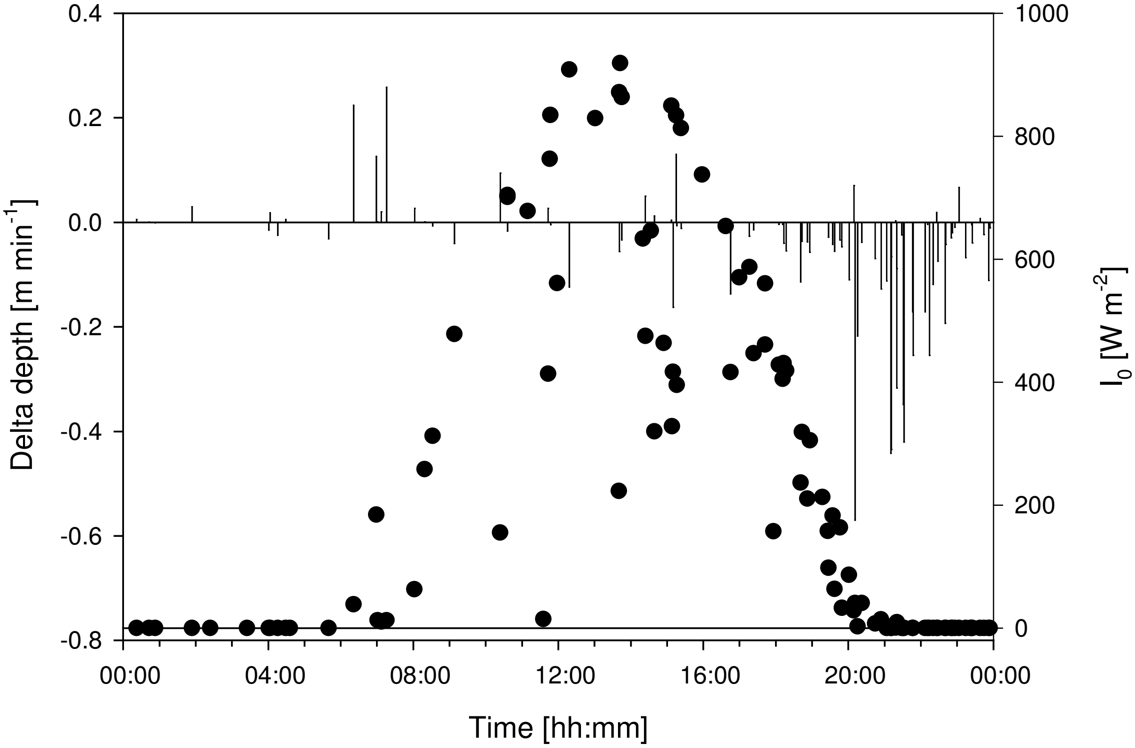

Figure 4.4: The relationship between light intensity above the surface (I_0, black circles) and the change in depth (Delta depth, black bars) of YOY burbot. Data are from 114 times at 25 survey dates, but recordings from dawn were performed on four occasions, resulting in a lower number of samples at dawn.

Discussion

The DVM of Lake Constance burbot is another example for the importance of hydroacoustic methods to observe the fine-scale distribution of fish. YOY burbot were present in the pelagic zone from the beginning of May until the end of August, which is much longer than previously assumed (Miler & Fischer, 2004; Wang & Appenzeller, 1998).

Miler & Fischer (2004) were the first to discover the daytime distribution of YOY burbot below the thermocline in Lake Constance. However, the precise temporal and spatial distribution patterns remained unknown and consequently, the great amplitude of burbot DVM exceeding 70 m was not detected.

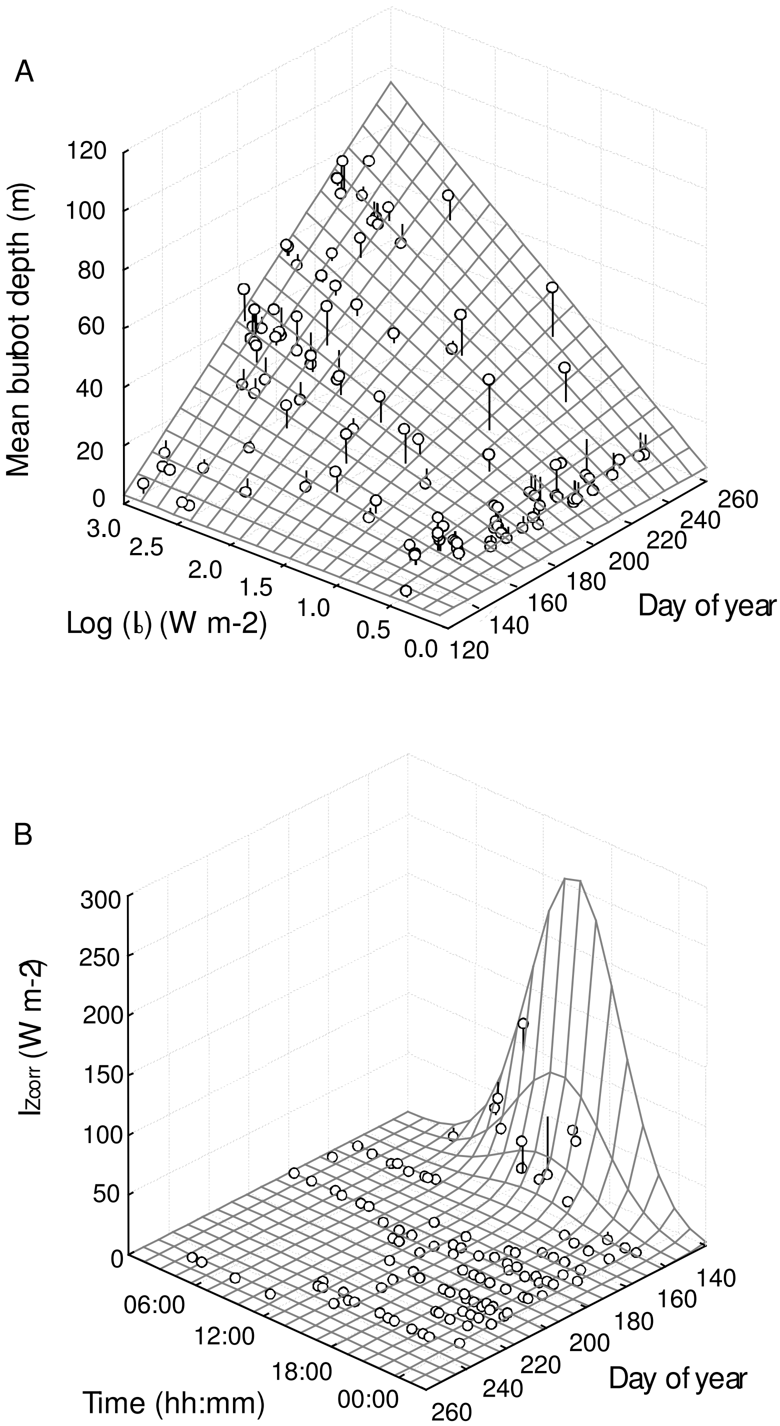

Figure 4.5: The relationship between burbot DVM and light intensity at the surface (I_0), day of the year and daytime estimated by non-linear regressions. **A)** The influence of day of the year and I_0 on the mean depth of burbot. **B)** The influence of daytime and day of the year on the light intensity at depth (I_{Zcorr}) experienced by burbot. Open circles indicate data points, black lines are the reference line to the three-dimensional model fit (grey grid).

Table 4.4: Results from the non-linear regression modelling the influences of daytime (time) and day of the year (Doy) on the experienced light intensity at depth (I_{Zcorr}). For explanations of abbreviations please refer to Table 4.3 and the M&M section.

Model-Equation	R^2	*F*	*P*	No. It.
$I_{Zcorr} = [a * e^{b*Doy}] * e^{\left[-0.5*\left(\frac{time-n}{m}\right)^2\right]}$	0.92	333.321	**< 0.001**	101

Coefficient	*Estimate*	*C.I.*	*t*	*P*
a	$1.336 * 10^9$	$\pm 2.740*10^9$	0.967	0.336
b	-0.129	± 0.273	-16.171	**< 0.001**
n	0.615	± 0.025	49.664	**< 0.001**
m	0.163	± 0.019	17.329	**< 0.001**

A similar DVM behaviour as described in the present study has been observed in Atlantic cod *Gadus morhua* L. and haddock *Melanogrammus aeglefinus* L., for which the daytime depth was also constantly increasing during the season (Lough & Potter, 1993). However, Lough and Potter (1993) interpreted this DVM behaviour as pre-settlement behaviour, because later in spring, both species did not migrate towards the surface at night. DVM behaviour of Lake Constance burbot as a transition between the pelagic larval and demersal juvenile stage has also been discussed by Miler & Fischer (2004). However, the YOY burbot in Lake Constance migrated to the surface throughout their entire pelagic stage and only on rare occasions small echoes were observed in the vicinity of the lake bottom. Further, Fischer (1999) observed that settling of burbot juveniles in laboratory tanks occurs rather abruptly within a few days. The switch between pelagic and demersal life-style can therefore be assumed to occur rather suddenly, and the steady daily increment in DVM amplitude must be related to other causes.

The DVM of burbot seems to be regulated by the light intensity above the surface, because burbot commenced their ascent after sunset and descended to their daytime depth with sunrise. Light intensity regulates the DVM behaviour of many organism (Cech *et al.*, 2005, Lampert & Sommer, 1999, Appenzeller & Leggett, 1995), because DVM is commonly regarded as an antipredation behaviour (Hrabik *et al.*, 2006, Scheuerell & Schindler, 2003, Stich, 1989, Stratton & Kesler, 2007, Hays, 2003) and the risk of predation is directly related to ambient light levels (Clark & Levy, 1988). Though the amplitude and timing of DVM may be flexible within organisms adapting to different environmental conditions (Levy, 1990, Sims *et al.*, 2005), DVM behaviour itself has recently been suggested to be a genetically inherent trait (Mehner *et al.*, 2007). Because no evidence for the acute predation of YOY burbot was found (neither in stomach of perch nor whitefish, the two most abundant species in the pelagic zone of Lake Constance; Probst & Thomas, personal observations), the DVM behaviour of YOY burbot may represent a genetic fixation from "a ghost of the predation past" (Gliwicz & Jachner, 1992).

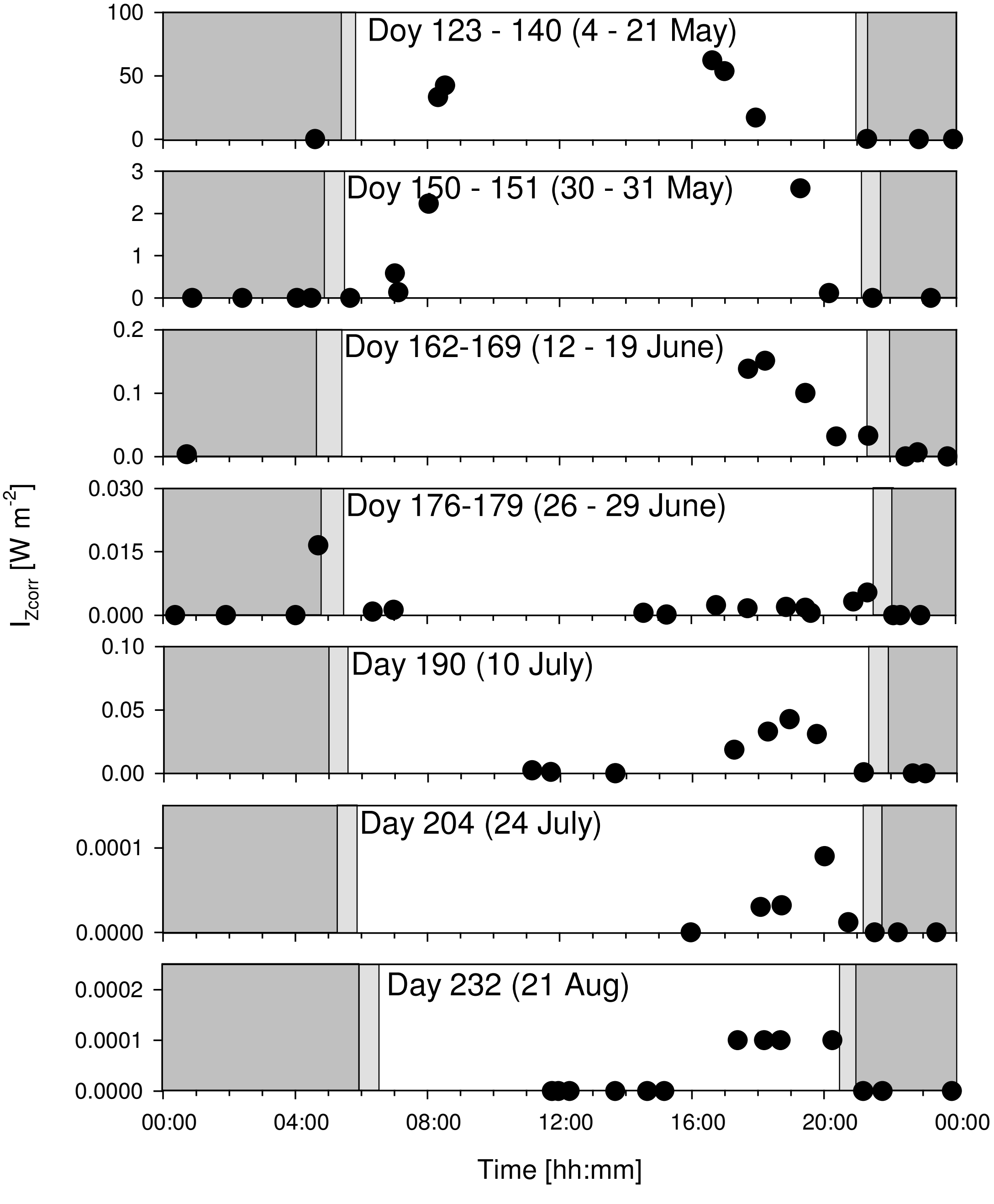

Figure 4.6: Evidence for crepuscular light windows at dusk and dawn from day of the year 176. Before, light intensities (I_{Zcorr}) at the mean depth of burbot were following the diel light cycle, as shown in Figure 4.5B. Note the different scale on the y-axis! Dark grey areas indicate night and light grey areas indicate crepuscular hours.

Furthermore, the DVM of burbot is very strictly related to the day of the year, which also correlated strongly with the size of YOY burbot. It seems therefore plausible, that the increasing amplitude of burbot DVM is a result of the increasing body size and pigmentation, which in turn may increase their perceived predation risk. Accordingly, burbot do not commence their DVM before the beginning of June. At this time of the year, burbot are still in the larval stage without significant skin pigmentation and an average total length of less than 1.0 cm (Wang & Appenzeller, 1998, Plate 1). Larval burbot remain in well illuminated water layers, where they experience high light intensities, which are directly related to light intensities above the surface. Contrary, as burbot metamorphose into juveniles by the middle/end of June, their skin becomes pigmented and develops a golden-brown colour. The proceeding metamorphosis from the larval into the juvenile stage, which also coincides with an increasing body size, may therefore induce DVM and determine its amplitude.

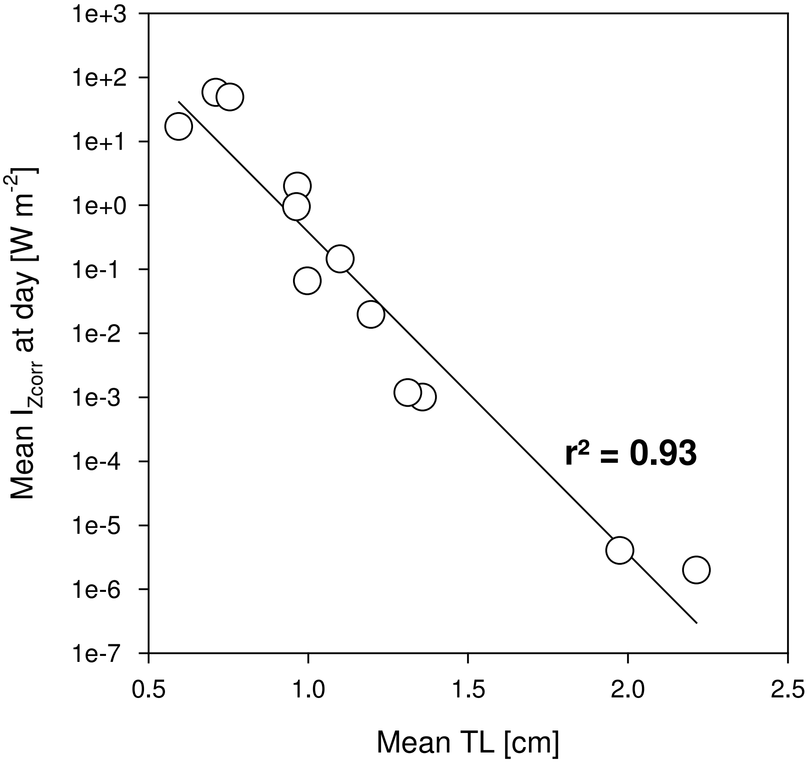

Figure 4.7: Relationship between the total length (TL) from net catches in 2006 and 2007 and the ambient light intensity at mean depth of burbot (I_{Zcorr}). I_{Zcorr} was averaged for all daytime values within a day and TL was averaged for all burbot caught on the same day of the year (see Table 4.1). Note the logarithmic scale on the y-axis!!

When YOY burbot commence their DVM, they increasingly inhabit dark water layers with low light intensities, at which successful feeding may be impaired. Fig.4.6 suggest, that from the End of June onwards, burbot adjust their DVM to experience crepuscular light windows, at which they can optimise the risk between (potential) predation and feeding (Scheuerell & Schindler, 2003, Appenzeller & Leggett, 1995, Clark & Levy, 1988). Furthermore, Hartmann (1983) observed higher stomach contents of Lake Constance YOY burbot at dusk, supporting the assumption of crepuscular feeding. Whether the light intensities, which burbot experience during the day (ranging in the magnitudes of 10^{-4} and 10^{-5} W m^{-2} in mid-August), are sufficient for feeding is uncertain, as due to their great depth, burbot could not be caught during daytime and thus their stomach contents could not be analysed. However, the visual irradiance threshold for zooplanktivorous feeding of juvenile salmonids lies between 10^{-3} and 10^{-4} W m^{-2} (Henderson & Northcote, 1985), which is about one or two magnitudes higher than the light experienced by burbot (at day in August). Hence, the low light levels experienced by deep migrating burbot during the day suggest, that feeding may be limited at this time of the day.

Conclusions

The influence of light on the DVM of YOY burbot in Lake Constance is obvious and in accordance with other studies on vertically migrating fish. Because the DVM amplitude is strictly dependent on the day of the year and relates to the size and morphology of burbot, the DVM behaviour of burbot may result from a genetically fixed avoidance of maximum light intensities, which alters during their ontogeny.

Acknowledgements

Thanks to Timo Basen, Markus Pehr, Lars F. Martinussen, Caitlin A. Lyman, Arnd Weber, Karl Fütterer, Alfred Sulger, Corinna Geiss, Julia Unger, Svein R. Hetland, Alexander Moßbruckner, Stefan Stoll and Joachim Böhler for field assistance. Robert Hofmeister helped with the formula on standard deviation of class grouped data. Two anonymous reviewers provided valuable comments to earlier versions of this manuscript.

5. Diel vertical migration of young-of-the-year burbot *Lota lota* (L.) as multiple adaptation to predation, foraging and bioenergetics

Wolfgang Nikolaus Probst & Reiner Eckmann

Introduction

Diel vertical migration (DVM) is a common behaviour of aquatic organisms and can be found among taxa of phytoplankton (Sommer & Gliwicz, 1986), zooplankton (Stich, 1989), planktivorous fish (Cech *et al.*, 2005) and sharks (Sims *et al.*, 2006). Levy (1987) defined DVM as a “synchronized movement by aquatic organisms in the vertical plane which has a periodicity of 24 hours”. The common pattern of DVM comprises the ascent at dusk and the descent at dawn, but this pattern can reverse (Sims *et al.*, 2005, Levy, 1990). While light is the proximate trigger for DVM (Cech *et al.*, 2005, Eckmann & Imbrock, 1996, Appenzeller & Leggett, 1995, Lampert & Sommer, 1999), the ultimate adaptations of DVM are more complex and usually assumed in the evasion of predators (Hrabik *et al.*, 2006), the improvement of foraging opportunities (Voss *et al.*, 2007, Sims *et al.*, 2005), or the enhancement of the bioenergetic budget (Brett, 1971).

The presence of predators in a certain depth layer may force organisms to move to deeper water layers to reduce their mortality (Hrabik *et al.*, 2006). Even if the actual predation risk is low, DVM behaviour may be the result of a genetic fixation to account for fluctuating predator abundances in the evolutionary past (Mehner *et al.*, 2007, Gliwicz & Jachner, 1992). This fixation may manifest in a preferred range of light levels, to which the fish adjust constantly. The depth, where this light level exists, is commonly termed the “antipredation window”, in which the fish can optimise the trade-off between seeing its prey and not being seen by its predators (Scheuerell & Schindler, 2003).

Contrary to predator evasion, DVM may also be performed to improve foraging opportunities, when predators follow their migrating prey. In this case, the DVM pattern of the predator is very tightly coupled to the DVM behaviour of its prey and may reverse, when additional predators induce a shift in the prey’s DVM cycle (Sims *et al.*, 2005).

Ecophysiological processes such as consumption, food conversion efficiency and growth the of fish are dependent on the environmental temperature (Schmidt-Nielsen, 1997). Gains in the bioenergetic budget may result from increased food consumption at depth of high prey abundance (Narver, 1970), reduced metabolic costs (Brett, 1971) and increased food conversion efficiency at lower temperatures (Hofmann & Fischer, 2003). Bioenergetic driven DVM has been described for the benthic shark *Scyliorhinus canicula* L., which reduced its daily energy costs by about 4% by resting and digesting in cooler water during daytime, while hunting in warmer waters during the night (Sims *et al.*, 2006). For bear lake sculpin *Cottus extensus* Bailey & Bond, 1963 , the limiting growth factor was gut evacuation rate, which was enhanced by migrating to warmer waters at night (Neverman & Wurtsbaugh, 1994). Bear lake sculpin therefore processed more food and grew three times faster at a mimicked DVM temperature cycle than at a constant temperature of 5 °C.

In large lakes of the northern hemisphere, burbot *Lota lota* (L.) hatch between March and May in the profundal zone and within a few days emerge to the surface to fill their swim bladder (McPhail & Paragamian, 2000, Ghan & Sprules, 1993, Ryder & Pesendorfer, 1992). After swim bladder inflation, larval burbot inhabit the pelagic zone feeding on plankton. In Lake Constance, pelagic burbot larvae have been observed to perform DVM (Miler & Fischer, 2004, Wang & Appenzeller, 1998), with increasing amplitude during the summer (Probst and Eckmann, previous chapter). The latter is assumed to be related to a size-related predation susceptibility, which forces YOY burbot to seek deeper water layers as they grow. In the investigations of Probst & Eckmann (Chapter 4) the last migrating YOY burbot were observed in late August and their DVM had amplitudes of 70 m or more (Fig.4.1). Otolith microstructure analysis of Lake Constance burbot indicated that burbot larvae settle to the lake bottom after spending 67 days (± 12.9 days S.D.) in the pelagic zone (Fischer, 1999). From the profundal zone they are assumed to migrate along the slope of the lake bottom towards the littoral zone. The earliest burbot juveniles come to the littoral zone in late June (Fischer, 1999), but the majority of YOY burbot arrives in August or September (Fischer & Eckmann, 1997).

Several zooplankton species in Lake Constance perform distinct DVM during summer, e.g. *Daphnia hyalina* (Leydig, 1860) and various groups of copepods (Stich, 1989). Miler & Fischer (2004) therefore suggested that YOY burbot follow their zooplankton prey when the abundance of near surface zooplankton becomes sparse.

In the present study the seasonal progression of the vertical zooplankton, predator and temperature distribution were correlated with burbot depth to test, which of these factors is related to burbot DVM. Three hypotheses for the ultimate cause of burbot DVM are discussed in respect to the presented results: I) Burbot perform DVM to evade predation, II) burbot forage on migrating zooplankton and adapt to the DVM cycle of their prey and III) burbot gain bioenergetic advantages through DVM.

Materials & methods

Hydroacoustic surveys, data processing, net catches and stomach samples

Hydroacoustic surveys, data processing and net catches were conducted as described in Chapter 4.

Fish were dissected under a stereo microscope to obtain stomach contents, which were enumerated to the lowest taxonomical level possible. Biomass estimates of stomach contents were calculated with the same formulae used for zooplankton samples (see below).

Predator distribution

Mean depth and volume density of potential predators was assessed in the same transects used for the YOY burbot analysis. Mean depth and density of predators were determined with the same procedure used for YOY burbot, except the TS range for SED was set between –52 dB and –12 dB. The lower threshold of –52 dB corresponds to physostome fish such as lake whitefish *Coregonus lavaretus* L. > 10 cm TL (Foote, 1987) as well as to juvenile perch *Perca fluviatilis* L. in July (Probst, personal observation). Because lake whitefish and YOY perch are the most abundant fish species in the pelagic zone of Lake Constance, both species were considered to be the most probable predators of YOY burbot.

Zooplankton samples

Zooplankton was sampled at 17 occasions at daytime and 13 occasions at night time in 2006 and 2007 during the hydroacoustic surveys. The zooplankton was sampled with an Apstein closing net with 17 cm opening diameter and 250 µm mesh size. The samples comprised five 10 m layers from the surface to 50 m depth and two 20 m layers from 50 to 90 m depth. For the latter two strata, zooplankton abundance was standardized to a 10 m water column by dividing the counted abundance by two. Taxa were identified and enumerated to the lowest taxonomical level possible (for classification of taxa please refer to Chapter 6). Biomass (as µg wet mass) was estimated using equations from the literature (Eckmann *et al.*, 2002, Mehner *et al.*, 1995, Becker, 1992).

Median depths of zooplankton taxa were assigned to the depth layer, in which the cumulative sum of zooplankton abundances first exceeded 50 % of the total abundance. For this purpose, each sampled layer, in which the zooplankton was assumed to be homogenously distributed, was divided into 0.5 m thick sub-layers. For each 0.5 m sub-layer the relative density of zooplankton biomass was calculated. E.g. a sample from 0 – 10 m depth with 20 % of total zooplankton biomass (from 0 – 90 m depth) resulted in 1 % zooplankton biomass per 0.5 m sub-layer between 0 - 10 m depth. The calculated zooplankton biomass was then cumulatively added from the surface to the depth layer, where 50 % of total zooplankton biomass was reached.

Temperature profiles

Temperature profiles were measured simultaneously to the hydroacoustic surveys with a temperature-depth probe down to a depth of 40 m. Additional temperature profiles were sampled weekly from the research vessel "Robert Lauterborn" with a CTD probe at Lake Überlingen from the surface to 120 m depth.

Statistical analysis

The mean depth of burbot at a given day and time was correlated to the mean depth of predators, zooplankton and ambient temperature using a general linear model (GLM), in which the aforementioned parameters were entered as continuous factors. Because the data from the surveys were conducted in 2006 and 2007, the year was entered into the GLM as categorical factor. Data on ambient water temperature at mean depth of burbot was log-transformed to achieve linearity. Data on mean burbot depth was tested for variance homogeneity with the Cochran- and Bartlett-tests.

To investigate, whether burbot DVM was related to feeding and thus to the DVM of zooplankton, it was necessary to determine the time of the day, at which peak feeding occurred. A preliminary analysis of stomach content data suggested that burbot fed mainly around dusk. To validate this assumption, a non-linear regression on the influence of time of day (TOD) and burbot total length (TL) was fitted to the stomach content (SC) data after the following equation:

$$SC = (a * TL + b) * e^{-0.5*\left(\frac{TOD-n}{m}\right)^2} \quad \text{(Eq.5.1)}$$

with a, b, n and m as regression parameters estimated by Statistica 6. The time of day was transformed to relative value, where 00.00 represented 0 and 23.59 represented 1. Because stomach content was fitted to a Gaussian bell-shaped curve before and around midnight, all relative time data was + 0.5 transformed, to shift the peak of the bell-shaped curve into the midday. The non-linear-regression was fitted with Levenberg-Marquard-Least-Squares algorithm with a maximum

of 1000 iterations and convergence criteria of 10^{-6}. The initial values, from which the iterations were started, were set to 0.1 for all coefficients.

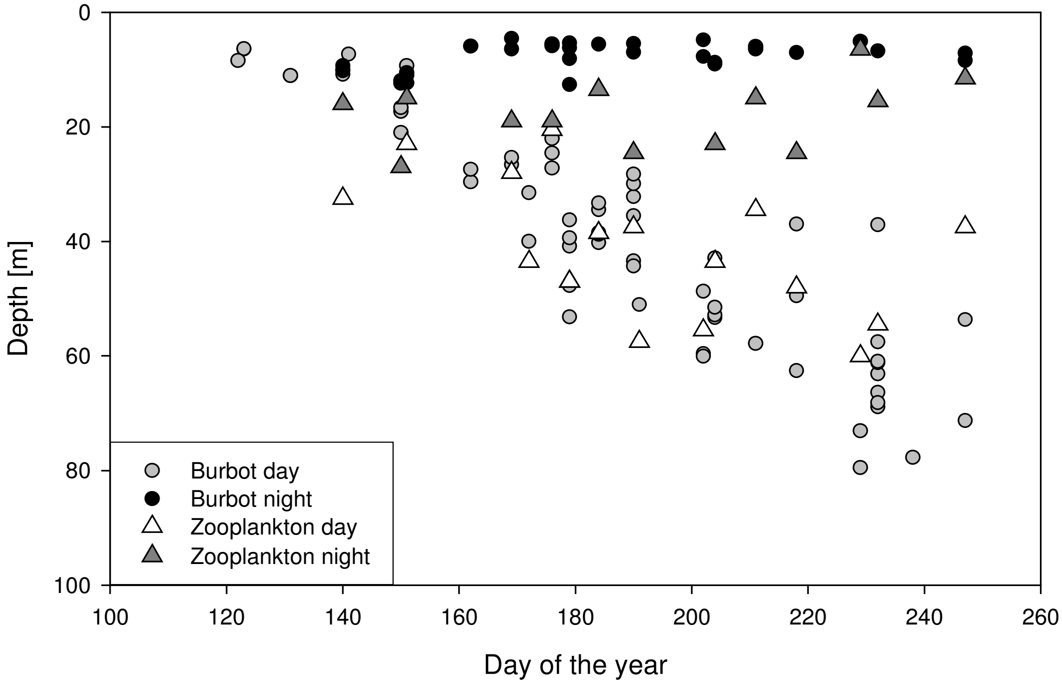

Figure 5.1: Depth of young-of-the-year burbot and their prey during the summers of 2006 and 2007 at day (white) and night (black). Shown are mean depths of burbot (circles) and the median depth of their preferred prey taxa (triangles). For detailed description please refer to the materials & methods section. Note, that the mean depth of burbot was determined by hydroacoustics several times per day, thus several points of mean burbot depth may occur at a given day of the year.

Results

Burbot DVM

Burbot commenced their DVM by the beginning of June, which coincided with the stratification of the water column. The daytime depth of burbot increased constantly during the summer, but the mean depth of burbot was not different between 2006 and 2007 (Fig.5.1, Table 5.1). At night, burbot stayed around 5 m depth during the entire summer.

Table 5.1: Results from general linear model (GLM) analysis on the correlation between mean predator depth, median zooplankton (ZP) depth, ambient water temperature and mean burbot depth in 2006 and 2007. Total N = 26 (at four out of 30 zooplankton sampling dates the predator density was 0), multiple $R^2 = 0.893$, Df = degrees of freedom, F = value of F-statistic, P = significance level, which is printed in bold when < 0.05.

Factor	*Df*	*F*	*P*
Mean predator depth [m]	1	2.064	0.166
ZP median depth [m]	1	13.055	**0.002**
Log (ambient temp.) [°C]	1	16.400	**< 0.001**
Year	1	< 0.001	0.993

Stomach contents

Burbot fed almost exclusively on one prey taxon at a given date, which were small cyclopoid copepods < 0.8 mm in May/June, large cyclopoid copepods > 0.8 mm in the first half of July and large *Daphnia sp.* and large cyclopoid copepods from the second half of July until August. According to the non-linear regression (Table 5.2, N = 204, $R^2 = 0.437$, F = 87.746, P < 0.001), the stomachs were fullest around 23.20 (± 95.04 min C.I.), supporting the assumption of a unimodal peak feeding activity at dusk (Fig.5.2).

Predator distribution

The analysis of stomach contents from YOY perch (Probst, unpublished data) and adult lake whitefish (G. Thomas, personal communication) did not provide any evidence for the predation of YOY burbot. Further, the spatial overlap between potential predators (TS larger than –52 dB) and YOY burbot was not significant (Table 5.1, Fig.5.3A) and burbot continued to perform DVM even after juvenile perch had migrated from the pelagic to the littoral zone. All these results combined do not provide any evidence for acute predation of YOY burbot in the pelagic zone of Lake Constance.

Zooplankton

The prey of burbot performed DVM between 10 – 20 m depth at night to about 60 m depth at day (Fig.5.1). The median zooplankton depth and mean burbot depth correlated significantly

(Table 5.1, Fig.5.3B), indicating a high spatial overlap of predating burbot and their prey. Interestingly, the DVM amplitude of zooplankton prey increased similar to burbot during the summer, but zooplankton tended to stay shallower than YOY burbot by the end of the summer.

Table 5.2: Results from the non-linear regression modelling the influences of total length (TL) and time of day (TOD) on the biomass stomach content (SC) of burbot. A, b, n and m are the coefficients of the model equation estimated by a Levenberg-Marquardt-Least-Squares algorithm. R² is the amount of variance explained by the regression-model, F is the F-value from the model-validating ANOVA, which compares the variance explained by the model against the variance within the residuals, C.I. delimits the 95 % confidence interval for the coefficient estimate, t is the value from the t-statistic to confirm significant contribution of the coefficient to the regression model. P-values represent the significance values from the F- and t-statistics and are printed bold when < 0.05. N is the coefficient, which marks the peak of the Gaussian bell-curve on the time-axis and is translated into a daytime as follows: 0.472 + 0.5 (transformation to midday) = 0.972 * 24 = 23.33 hour of the day, which corresponds to 23.20.

Model-Equation	*R²*	*F*	*P*	*No. It.*
$SC = (a*TL+b)*e^{-0.5*\left(\frac{TOD-n}{m}\right)^2}$	0.437	87.746	**< 0.001**	22

Coefficient	*Estimate*	*C.I.*	*t*	*P*
a	2.358	± 0.485	9.583	**< 0.001**
b	-1.184	± 0.582	-4.001	**< 0.001**
n	0.472	± 0.066	14.195	**< 0.001**
m	-0.223	± 0.082	5.409	**< 0.001**

Ambient temperature

The ambient temperature was correlated to mean depth of burbot (Table 5.1, Fig.5.3C), so that burbot experienced cooler temperatures between 4.5 °C to 6 °C during the day and warmer temperatures between 8 °C and 24 °C in the epilimnion at night.

Discussion

The present study cannot attribute a single ultimate adaptation to the DVM of YOY burbot in Lake Constance. Neither predator evasion, zooplankton DVM nor bioenergetics can exclusively explain the DVM behaviour of burbot. Instead, the DVM of burbot could provide a multiple adaptations to all of the three aforementioned ultimate causes commonly assumed to select for DVM behaviour.

In most organisms, DVM is commonly regarded as an antipredation behaviour (Hays, 2003, Clark & Levy, 1988, Scheuerell & Schindler, 2003). Accordingly, the DVM of YOY burbot may have originated as an antipredation defence, inherent to larval and juvenile gadoids, as DVM behaviour has also been observed in marine pelagic haddock *Melanogrammus aeglefinus* (L.) and Atlantic cod *Gadus morhua* L. (Lough & Potter, 1993). Probst & Eckmann (Chapter 4) found a strong relationship between light, burbot DVM amplitude and burbot size in Lake Constance, which lead to the suggestion, that the DVM of pelagic YOY burbot reflects an adaptation to a perceived predation risk. During their pelagic stage in Lake Constance, YOY perch are numerically dominant and grow to more than twice the size of YOY burbot (Wang & Appenzeller, 1998). Also, juvenile perch can prey on fish (Heermann *et al.*, 2007), rendering YOY perch a very probable predator of burbot from late June onwards. However, the evidence of acute predation of YOY burbot was nil, which either implies a lack of predation pressure or DVM to be a very efficient method to avoid predation e.g. by YOY perch.

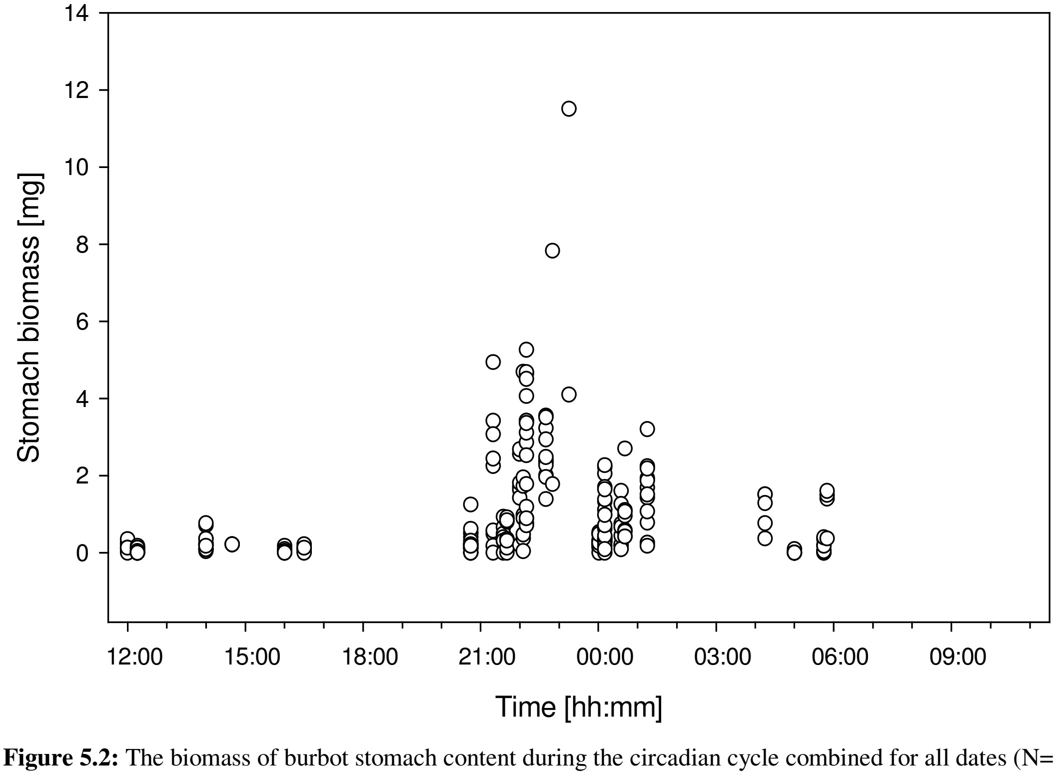

Figure 5.2: The biomass of burbot stomach content during the circadian cycle combined for all dates (N=204) collected in 2006 and 2007.

The DVM of burbot and their zooplankton prey was closely correlated, as both groups had a high spatial overlap during their diel cycle. However, it is not certain, whether burbot actively followed their prey or if both are influenced by the same environmental factors such as light and/or temperature. The simultaneous increase of DVM amplitude of predator (burbot) and prey (copepods and daphnids) suggests that burbot DVM is an adaptation allowing to forage during the day. However, the low stomach contents during the day contradict this hypothesis, as burbot did not seem to feed intensively at this time. Instead, burbot fed most intensely around dusk, when they were migrating with their prey towards the surface. Probst & Eckmann (Chapter 4) found evidence for crepuscular windows, at which burbot experience the brightest light intensities within their diel cycle. Especially at dusk, burbot seem to utilize this light window for feeding, probably because during their upward migration they see their prey against the bright lake surface, which enhances the contrast between prey and background (Cech & Kubecka, 2002, Thetmeyer & Kils, 1995). Crepuscular feeding has also been observed during the DVM of juvenile sockeye salmon *Oncorhynchus nerka* (Walbaum, 1792) (Scheuerell & Schindler, 2003, Clark & Levy, 1988) and may be related to an overlap of predators and zooplankton prey at favourable light conditions during crepuscular hours.

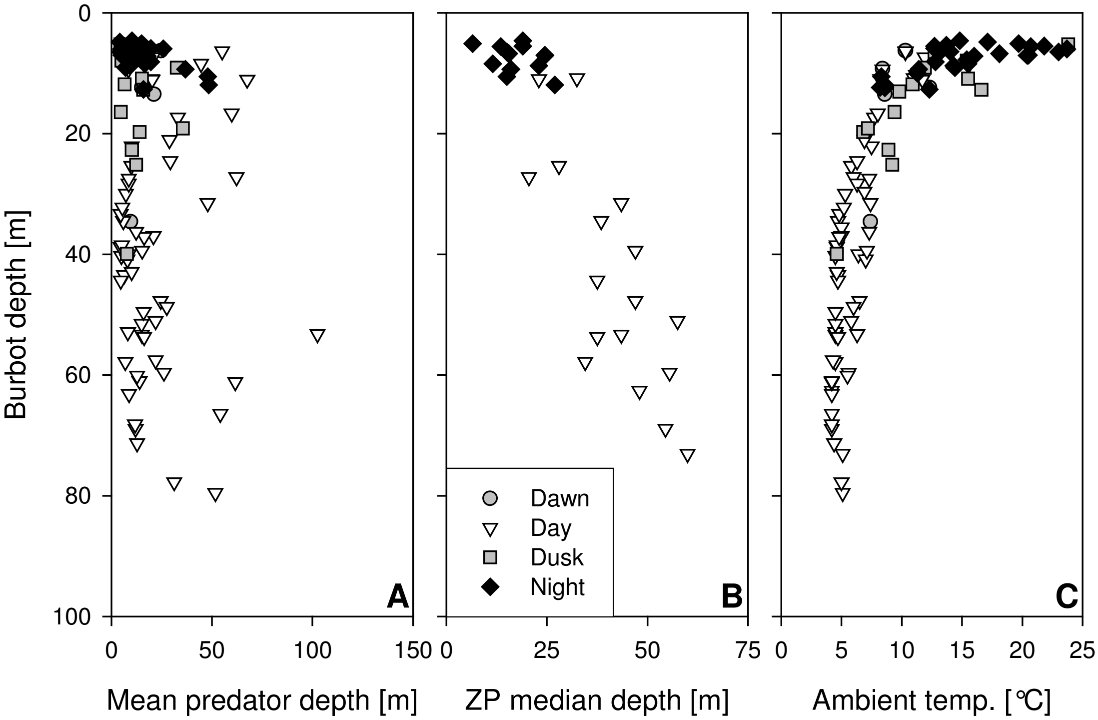

Figure 5.3: Relationships between mean burbot depth at dusk (grey squares), night (black diamonds), dawn (grey circles) and day (white triangles) and **A)** the mean depth of potential predators, **B)** the median depth of zooplankton prey and **C)** ambient temperature.

Burbot larvae seem to prefer water temperatures around 20 °C (Harzevili *et al.*, 2004, Ferguson, 1958), and therefore the diurnal migration to the hypolimnion can be expected to impose a severe constraint on burbot growth. However, the temperature gradient in a stratified lake may help migrating burbot to maintain a positive energy budget when feeding on migrating prey. Remaining at the surface during day would lead to high respiration costs and low food intake, when the preferred prey taxa descend into the hypolimnion. Instead, the pursuit of prey would increase the probability of ingestion and reduce metabolic costs (Brett, 1971).

DVM of burbot may provide a benefit in terms of growth optimisation at night, as growth rates of YOY burbot increase with temperature (Kjellman & Eloranta, 2002) and optimal growth rates of larval and juvenile burbot are found around 16 °C (Harzevili *et al.*, 2004, Hofmann & Fischer, 2003). Burbot may optimise their growth during the night, a period of low susceptibility to predators, as has been observed for larval New Zealand bullies *Gobiomorphus cotidianus* MacDowall 1975 (Rowe & Chisnall, 1996). This may also explain the occurrence of distinct growth rings found in burbot otoliths during their pelagic stage (Fischer, 1999).

Conclusions

The DVM of YOY burbot in Lake Constance may provide multiple ultimate adaptations, as it allows the simultaneous escape from potential predators and increased encounter probability with zooplankton prey during the day and at dusk, while optimising growth in warmer epilimnetic water at night during a period of low predator susceptibility. Contrary, abandoning DVM would result in increased predation risk by YOY perch, low encounter rates of prey and high respiration costs at epilimnetic water temperatures during the day. Hence, the DVM of YOY burbot may be the optimal adaptation to the conditions in a temperature-stratified pelagic environment with migrating prey and surface-associated predators.

Acknowledgements

Thanks to Timo Basen, Markus Pehr, Lars F. Martinussen, Caitlin A. Lyman, Arnd Weber, Karl Fütterer, Alfred Sulger, Corinna Geiss, Julia Unger, Svein R. Hetland, Alexander Moßbruckner, Stefan Stoll and Joachim Böhler for field assistance. Pia Mahler counted zooplankton samples. Data on water temperature for August and September 2006 were provided by the IFS Langenargen, additional temperature data was provided by Beatrix Rosenberg.

6. Diet-overlap as a measure for the potential of intra- and interspecific competition between young-of-the-year perch and burbot during early life-history stages

Wolfgang Nikolaus Probst & Reiner Eckmann

Introduction

Competition arises when 'one organism has negative effects upon another by consuming or controlling access to a resource, that is limited in availability' (Keddy, 2001). Competitive co-existence may impair the growth, reproduction and survival of the inferior competitor, unless the latter is able to exploit new resources and consequently evade the competition with its superior competitor (Lampert & Sommer, 1999, Begon *et al.*, 1996). This principle applies to competition among species as well as to intraspecific competition.

During their earliest life-history stages young-of-the-year (YOY) perch *Perca fluviatilis* L. and burbot *Lota lota* (L.) co-exist in the pelagic zone of Lake Constance (Wang, 1994b, Wang & Appenzeller, 1998). Whereas perch larvae get transported from the littoral towards the pelagic zone within a few days after hatch (Wang & Eckmann, 1994a), burbot larvae migrate from the lake profundal zone towards surface waters (Fischer, 1999). Both species can be found in the pelagic zone between May and July. From the beginning of June burbot start to perform diel vertical migrations, which increase constantly during the summer and achieve considerable amplitudes of more than 50 m by July (Miler & Fischer, 2004). Contrary, YOY perch always remain in epilimnetic waters and are rarely found below 10 m depth (Wang & Appenzeller, 1998). The feeding periodicity of both species indicates that perch feed during the day and crepuscular hours (Wang, 1994a), whereas burbot seem to feed mainly around dusk (Chapter 5, Fig.5.2). Thus, the spatial overlap between YOY perch and burbot during feeding hours, which is a prerequisite for interference competition, is confined to daylight hours in May and early June. However, while being spatially segregated both species may exploit the same zooplankton resources. Several crustacean zooplankton taxa of Lake Constance are also know to perform diel vertical migrations (Stich, 1989). In this case, burbot might feed on ascending zooplankton prey during early dusk, whereas perch may feed on the prey population at late dusk and early dawn (exploitative competition).

The re-oligotrophication of Lake Constance has caused a decline in crustacean zooplankton abundance since the middle of the 1990s (Bürgi *et al.*, 2006). As consequence the food resources for larval and juvenile fish are assumed to have become limited (Eckmann *et al.*, 2006, Schleuter & Eckmann, 2007). Under these conditions, the potential for competition between perch and burbot may have increased. While similar zooplankton prey taxa preferences of perch and burbot have been described (Wang & Appenzeller, 1998, Hartmann, 1983, Hartmann, 1986), no attempt has been made to investigate the potential for exploitive competition between YOY perch and burbot during their pelagic stage.

During the ontogeny of perch and burbot it is reasonable to expect, that the magnitude of exploitative competition, expressed as diet overlap, is decreasing. Both species will overcome the gape size limitation for large zooplankton taxa and thus become able to diversify their diet. A more diverse spectrum of ingestible prey increases the potential for individual specialization, which may reduce intra- as well as interspecific competition (Bolnick *et al.*, 2003, Svanbäck & Eklov, 2003). However, because of their faster growth (Wang & Appenzeller, 1998), perch overcome gape size limitation for each taxon earlier than burbot. As a consequence, the diet overlap between both species should decrease not linearly but in a zigzag manner (see below). The diet overlap should increase when burbot become able to feed on the same resource as perch and decrease when perch overcome gape size limitation for taxa, which burbot cannot yet ingest.

The aim of this study is therefore the assessment of diet overlap as an indicator for potential competition between perch and burbot during their larval and early juvenile life-history stages. The trajectory of diet overlap between both species is compared to a hypothetical trajectory, which results from changes in gape size limitation for various zooplankton prey. Furthermore, the multivariate methods applied in this study also allow the analysis of intraspecific diet overlap within both species, which especially for YOY perch may indicate a major source of competition, as perch abundance outweighs the abundance of burbot by two orders magnitude (Wang & Appenzeller, 1998).

Materials & methods

Catches

Larval and juvenile perch and burbot were caught as described in Chapter 4.

Total length (TL) of larvae and juveniles (only frozen individuals) were recorded in the laboratory. Fish were dissected under a stereo microscope, and stomach contents were counted and classified into the following taxa: *Daphnia sp.* < 1.6 mm carapace length (CP) , *D. sp.* > 1.6 mm CP, *Daphnia galeata* (Sars, 1863) < 1.6 mm CP, *D. galeata* > 1.6 CP, cyclopoid copepods < 0.8 mm CP and cyclopoid copepods > 0.8 mm CP, calanoid copepods < 0.8 mm CP and calanoid copepods > 0.8 mm CP, *Leptodora kindtii* (Focke, 1844), *Bythotrephes longimanus* (Leydig 1860), *Bosmina longirostris* (O.F. Müller, 1785), and copepods nauplia. The numerical abundance of prey taxa was converted into biomass by using mean lengths and wet weights from the literature (Mehner *et al.*, 1995, Eckmann *et al.*, 2002, Becker, 1992)

Gape size calculation

At the time of first catches in the middle of May, burbot and perch had similar TL (~ 0.6 to 0.7 cm), but at the end of the summer in August, perch had grown to more than twice the size of YOY burbot (Fig.6.1).

The gape size (GS) of perch and burbot were calculated after the following equations:

$$GS_{Perch}\ [mm] = 0.2152 + 0.0781 * TL\ [mm] \quad \text{(Guma'a, 1978)} \qquad \text{(Eq.6.1)}$$

$$GS_{Burbot}\ [mm] = -36 + 0.15 * TL\ [mm] \quad \text{(Ghan \& Sprules, 1993)} \qquad \text{(Eq.6.2)}$$

From the regression between the day of the year (doy) and TL ($TL = a * e^{doy*b}$) the doy was calculated at which perch and burbot overcame the gape sizes of 0.8 mm and 1.6 mm (Fig.6.1).

Because the stomach content and the predicted doys of gape limitation showed a good agreement, the periods of various diet overlap scenarios were assigned as follows: Before day of the year (doy) 138 both perch and burbot were gape size limited for all taxa except small cyclopoid and calanoid copepods < 0.8 mm and copepod nauplii (Table 6.1). Between doy 138 and doy 147 perch could ingest larger copepods (>0.8 mm), but burbot were still gape size limited for these taxa. Between doy 148 and doy 167 perch and burbot cold both ingest large copepods but were still gape size limited for large daphnids and predatory cladocerans (>1.6 mm), and between doy 167 and 178 only perch had overcome this limitation. After doy 178 perch as well as burbot could ingest all prey taxa. Because the gape size limitations were similar for perch and burbot between doy 147 and doy 167 and after doy 178, in these periods higher rates of diet similarity/overlap were expected.

Model of potential diet overlap

The comparison of observed patterns of diet overlap within the five periods to a hypothetical model allows to observe deviations and evaluate their causes. Hence, the following considerations were formulated into Equation 6.3:

Consider two predators P(erch) and B(urbot) eating a certain number of prey taxa, which have equally probability to be ingested. Under these conditions the potential diet overlap of perch and burbot depends on the number of consumed prey taxa taken by both predators (overlap) as well as the total number of taxa consumed by the predator with the wider diet spectrum (in this case perch). The more taxa are eaten by a predator with no selectivity, the lesser the probability for a single taxon to become ingested. If a predator consumes only one taxon, the probability for this taxon to be found in its stomach is 1, but if a predator eats eight taxa, the probability to find a certain taxon is 0.125 (=1/8). Hence, the probability that the common taxon i will be found in the stomach of perch and burbot (Pi_{PB}) will depend on the number of common taxa (i) and the number of taxa exclusively eaten by perch (j). The probability of a taxon i to be found in a perch and a burbot stomach (Pi_{PB}) can be expressed as follows:

$$Pi_{PB} = (1-\sum_j P_j) * \sum_i P_i \qquad \text{(Eq.6.3)}$$

where P_j is the probability of taxon i being eaten by perch and burbot alike and P_j is the probability of a prey to be only eaten by perch. Pi is calculated as

$$P_i = Ri_p * Ri_B \qquad \text{(Eq.6.4)}$$

where Ri_P and Ri_B are the relative abundances of taxon i in the stomach of perch and burbot. Pj is calculated as

$$P_j = Rj_P \qquad \text{(Eq.6.5)}$$

where Rj_P is the relative abundance of taxon j (only consumed by perch) in a perch stomach.

Table 6.1: Summary of hypothesised diet overlap probability (Pi_{PB}) of perch and burbot during their early life history. Doy refers to day of year counted continuously from 1st of January. Taxa are the taxa which can be ingested by perch and burbot according to the gape size model. P_i is the probability of taxon i being eaten by perch and burbot alike, P_j is the probability of taxon j being eaten exclusively by perch. Pi $_{PB}$ is calculated after equation 6.3.

Period [Doy]	*Taxa* $_{Perch}$	*Taxa* $_{Burbot}$	P_i	$1-\Sigma P_j$	Pi_{PB}
< 138	NAUP CYC<0.8 CAL<0.8	NAUP CYC<0.8 CAL<0.8	0.333	0	0.333
138-147	NAUP CYC<0.8;CYC>0.8 CAL<0.8; CAL>0.8 DS<1.6 DG<1.6 BOS	NAUP CYC<0.8 CAL<0.8	0.125	0.375	0.047
148-167	NAUP CYC<0.8; CYC>0.8 CAL<0.8; CAL>0.8 DS<1.6 DG<1.6 BOS	NAUP CYC<0.8;CYC>0.8 CAL<0.8;CAL>0.8 DS<1.6 DG<1.6 BOS	0.125	0	0.125
168-178	NAUP CYC<0.8; CYC>0.8 CAL<0.8; CAL>0.8 DS<1.6; DS>1.6 DG<1.6; DG>1.6 BOS BYT LEPT	NAUP CYC<0.8;CYC>0.8 CAL<0.8;CAL>0.8 DS<1.6 DG<1.6 BOS	0.083	0.666	0.055
> 178	NAUP CYC<0.8; CYC>0.8 CAL<0.8; CAL>0.8 DS<1.6; DS>1.6 DG<1.6; DG>1.6 BOS BYT LEPT	NAUP CYC<0.8;CYC>0.8 CAL<0.8;CAL>0.8 DS<1.6; DS>1.6 DG<1.6; DG>1.6 BOS BYT LEPT	0.083	0	0.083

Statistics

For all analysis of stomach content, biomass stomach data were used. The stomach compositions by wet weight of perch and burbot were compared with ANOSIM and SIMPER analysis using Primer-E 6.0. The absolute biomass data of stomach contents were standardized to relative amount of biomass per stomach and subsequently rank transformed to calculate a Bray-Curtis rank similarity matrix used for the ANOSIM (Clarke & Gorley, 2006, Clarke & Warwick, 2001).

Square-root transformed and standardized biomass data were also used for SIMPER analysis to investigate the similarity of stomach contents between individual perch and burbot and the dissimilarity between perch and burbot stomach contents within the five defined time periods.

The diet overlap (C) between perch and burbot for the five periods was calculated after Schoener (1971):

$$C = 100 * \left(1 - 0.5 * \sum \left| r_{bi} - r_{pi} \right| \right) \tag{Eq. 6.6}$$

where r_{bi} is the mean proportion of prey [wet weight stomach contents] item i in the stomach of burbot and r_{pi} is the mean proportion of food item i in the stomach of perch.

Results

Stomach contents composition

As perch grew and their gape size increased during summer their diet spectrum diversified, and after doy 167 all prey taxa except for copepod nauplii could be found in the perch stomachs. Before doy 138 larval YOY perch fed exclusively on small cyclopoid copepods (Fig.6.2). From doy 138 onward daphnids became increasingly abundant in perch stomach contents until after doy 167 even larger daphnids were ingested and daphnids accounted for more than 66 % of all consumed biomass. After doy 167 also large cladocerans (*B. longimanus* and *L. kindtii*) as well as *B. longirostris* contributed to about 10 % of perch diet, whereas copepods became less dominant: before doy 167 copepods contributed about 66 % to the consumed biomass, but after perch overcame the gape size limitation for large daphnids, copepods contributed less than 20 % to perch stomach biomass.

Similar to perch, the diet of burbot became more diverse as they grew, however, not as many different prey taxa were consumed (Fig 6.2., Perch = 11 prey taxa, burbot = 7 prey taxa after doy 178). Burbot fed mainly on small cyclopoid copepods before doy 147, but to a small extent also consumed nauplii during this time (Fig.6.2). From doy 147 onwards, large cyclopoid copepods constituted at least 40 % of the diet, which suited well with the predicted ending of gape size limitation for this taxa. The regression model between TL and gape size predicted a gape size of > 1.6 mm at doy 180, and in accordance, large daphnids were not found before doy 179. However, small daphnids (< 1.6 mm carapace length) were only consumed in minimal proportions during the entire summer. After doy 178 also a small number of *B. longimanus* was consumed, indicating that during their pelagic stage burbot overcame gape size limitation for even the largest crustacean zooplankton.

Table 6.2: Results of SIMPER analysis on square-root transformed, standardized biomass data of perch and burbot stomach contents.

Period [Day of year]	*Similarity Perch [%]*	*Similarity burbot [%]*	*Dissimilarity [%]*
< *138*	100.00	92.84	4.04
138-147	54.64	77.17	38.68
148-167	42.28	57.36	53.69
168-179	26.52	42.92	93.36
> *179*	27.98	47.00	76.06

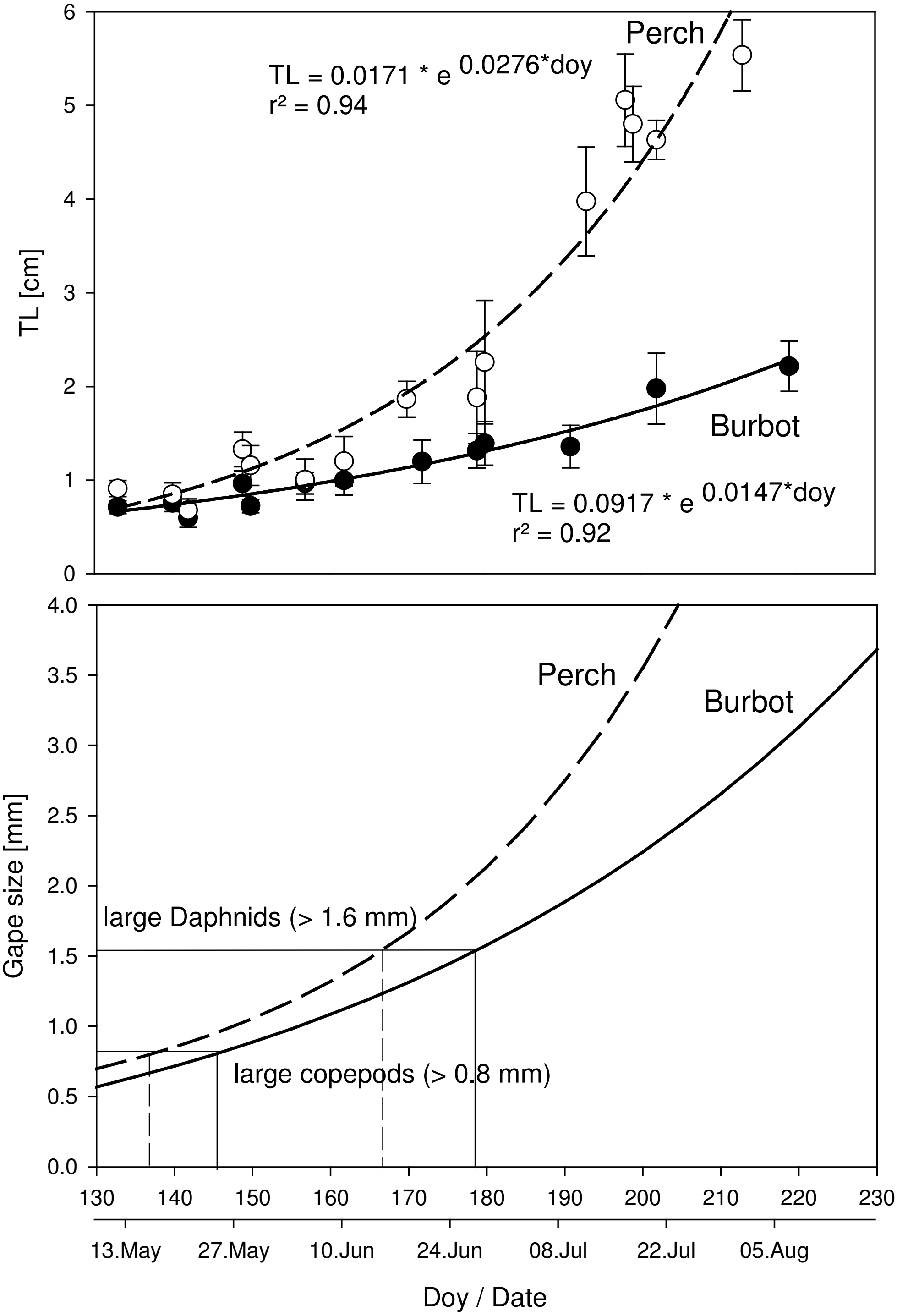

Figure 6.1: The growth of YOY perch and burbot during spring and summer in Lake Constance. **Upper)** The relationship between day of the year (doy) and total length (TL). The equations and r²-values for both regression lines are presented, with both regression being significant ($P < 0.001$). **Lower)** Changes of both species' gape size during spring and summer. Black lines indicate the estimated time for the overcoming of gape size limitation for large copepods (> 0.8 mm carapace length) and large Daphnids (1.6 mm carapace length) for perch (hatched line) and burbot (straight line).

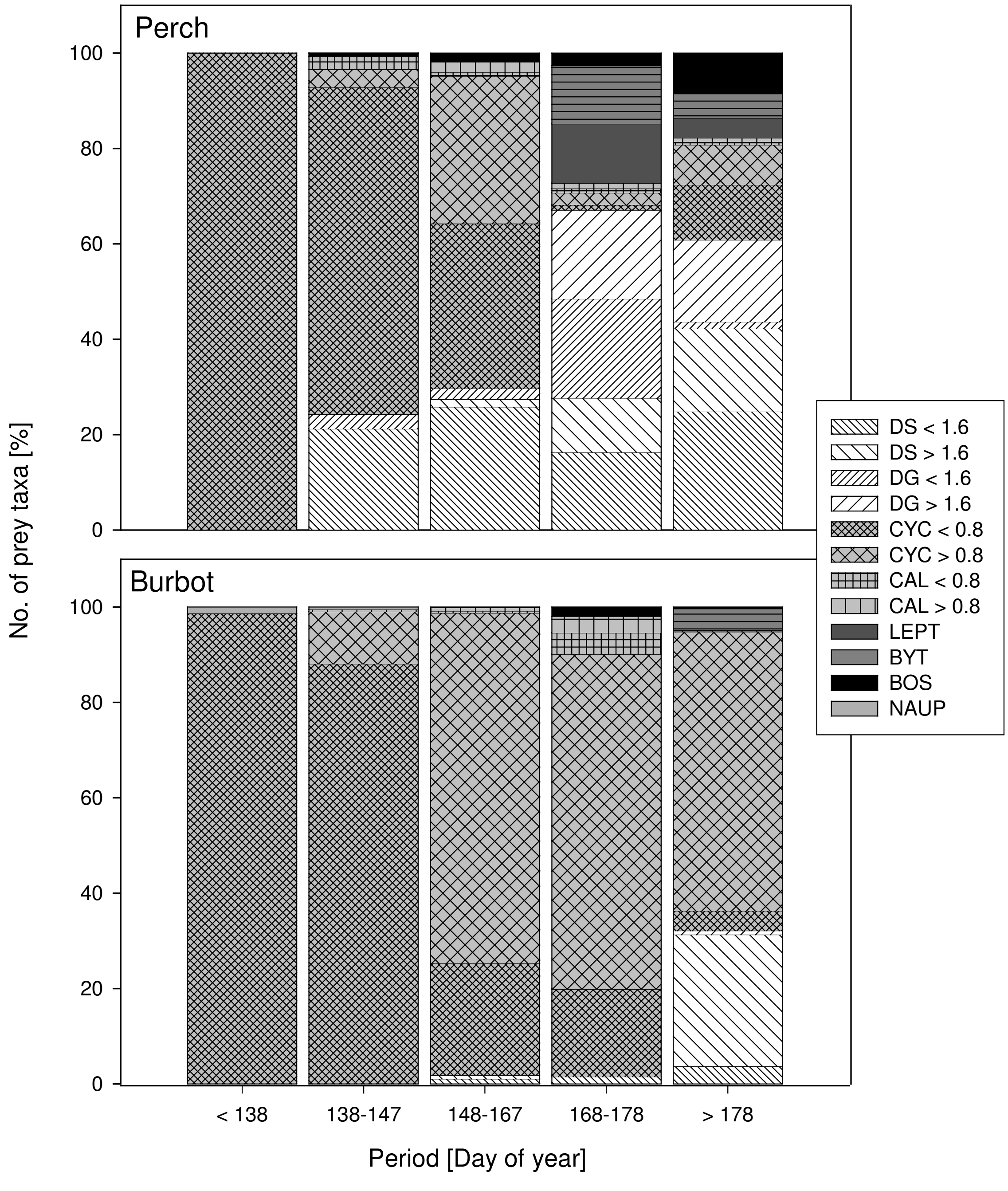

Figure 6.2: Relative composition of stomach biomass of perch (**upper**) and burbot (**lower**) during the five investigation periods with different gape size limitations. Zooplankton taxa are abbreviated as DS = *Daphnia sp.*, DG = *Daphnia galeata*, CYC = cyclopoid copepods, CAL = calanoid copepods, LEPT = *Leptodora kindtii*, BYT = *Bythotrephes longimanus*, BOS = *Bosmina longirostris.* Numbers behind abbreviations refer to carapace length in mm.

Diet overlap

The stomach dissimilarities between perch and burbot increase until doy 178 to 93.36 %, but decrease after doy 178 to 76.06 % (Table 6.2). Until doy 147, the interspecific differences in stomach composition were mostly attributable to copepod nauplii, small cyclopoid copepods, and small *Daphnia sp.* (Table 6.3). After doy 147, however, the stomach contents of both species also differed as a result of different amounts of consumed large cyclopoid copepods and after doy 178 large *Daphnia sp.* contributed 16.7 % to the observed dissimilarity.

Comparing the trajectory of observed Pi $_{PB}$, Schoener's C, and SIMPER dissimilarity during the periods of varying gape size limitation between perch and burbot, the observed values of all methods indicate similar trends in diet overlap (Fig.6.3). However, there was a general deviation from hypothesised Pi $_{PB}$-values for the periods between doy <138, 138-147 and 148-167. During the first two periods the number of ingested prey taxa was smaller than predicted by the gape-size model. During the period between doy 148-167 the diet overlap between both species did not increase compared to the previous period (doy 138-147), which was mostly due to the fact that burbot rarely ingested daphnids until doy 178, even after they should have overcome gape size limitation for small daphnids during the period between doy 147 and 167. The subsequent increase in diet overlap after doy 178 was attributable to the diet switch of burbot feeding on large cladocerans.

The intraspecific similarity of perch stomach contents decreased until doy 178, but remained at 28 % after doy 178, when large cladocerans and *Bosmina sp.* became an important constituent of perch diet (Fig.6.3). The ingested prey taxa, which accounted most often for the similarity of perch stomach contents, were small cyclopoid copepods until doy 167 and small daphnids after doy 167 (Table 6.4). The relative contributions to similarity of single taxa decreased constantly over time, reflecting the diversification of perch diet.

Similar to perch the intraspecific similarity between burbot stomach contents decreased during the summer (Table 6.2). However, the relative similarity of burbot stomach contents remained twice as high as for perch. The intraspecific stomach content similarity of burbot was caused exclusively by cyclopoid copepods, which always contributed more than 50 % to the calculated total similarity (Table 6.4).

Table 6.3: Main taxa responsible for interspecific dissimilarities between perch and burbot stomach contents during the five periods of various gape size limitations. Av. abundance = average square-root transformed abundance of prey taxon in stomach data, av.diss. = average dissimilarity between pair wise comparisons of perch and burbot stomach data, diss./SD. = av. dissimilarity/standard deviation of pair wise comparisons, contrib. = relative contribution to interspecific dissimilarity value (Table 6.2). Cum. = cumulative contribution. Prey taxa are abbreviated as CYC = cyclopoid copepods, NAUP = nauplii, DS = *Daphnia sp.*, DG = *Daphnia* galeata, BOS = *Bosmina longisrostris*, numbers behind taxa abbreviations indicate size class. The list of contributing prey taxa was cut off, when the cumulative contribution achieved > 50%.

Period	*Prey taxa*	*Av.Abund. Perch*	*Av.Abund. Burbot*	*Av.Diss [%].*	*Diss./SD.*	*Contrib. [%]*	*Cum. [%]*
< 138	*CYC<0.8*	100.00	95.96	2.02	0.53	50.00	50.00
	NAUP	0.00	4.04	2.02	0.53	50.00	100.00
138-147	*CYC<0.8*	68.93	86.90	16.84	1.00	43.53	43.53
	DS<1.6	15.77	0.00	7.88	0.55	20.38	63.90
148-167	*CYC<0.8*	57.16	56.66	21.36	1.29	40.00	40.00
	CYC>0.8	20.09	39.28	19.05	1.21	35.68	75.68
168-178	*CYC>0.8*	3.25	49.93	24.54	1.24	26.28	26.28
	CYC<0.8	3.33	38.49	18.80	0.97	20.14	46.42
	DG<1.6	22.08	0.00	11.04	0.87	11.82	58.24
> 178	*CYC>0.8*	13.00	54.78	24.27	1.58	31.91	31.91
	DS>1.6	18.21	17.05	12.70	0.95	16.69	48.60
	CYC<0.8	16.24	12.50	8.65	1.00	11.38	59.98

Discussion

Competition occurs only for limited resources (Begon *et al.*, 1996). While the evidence for top-down regulating effects of fish on zooplankton populations is controversial, young-of-the-year fishes may exert some pressure especially on larger cladocerans (Mehner & Thiel, 1999, Mehner *et al.*, 1995). Due to lower densities of zooplankton in oligotrophic lakes, the competition between YOY fishes for zooplankton resources may be more severe in these systems (Guillard *et al.*, 2006). Because Lake Constance has undergone re-oligotrophication since the 1990s, the competition between YOY perch and burbot may have increased.

During the period, when YOY perch and burbot simultaneously inhabit the pelagic zone of Lake Constance, perch are more abundant by one or two orders of magnitude (Probst, personal data, Wang & Appenzeller, 1998). Because of their numerical dominance and the sooner overcoming of various gape size limitations, perch can be regarded as the superior competitor exerting considerable competitive pressure on burbot. The relative compositions of stomach content biomass indicate that the potential for exploitive competition between both species exists mainly before doy 138, which was also the time when the interspecific dissimilarities between stomach contents of perch and burbot were lowest. However, by the middle of June the abundance of burbot decreases to such low numbers, that perch may rather be subject to intraspecific competition than to interspecific competition with burbot.

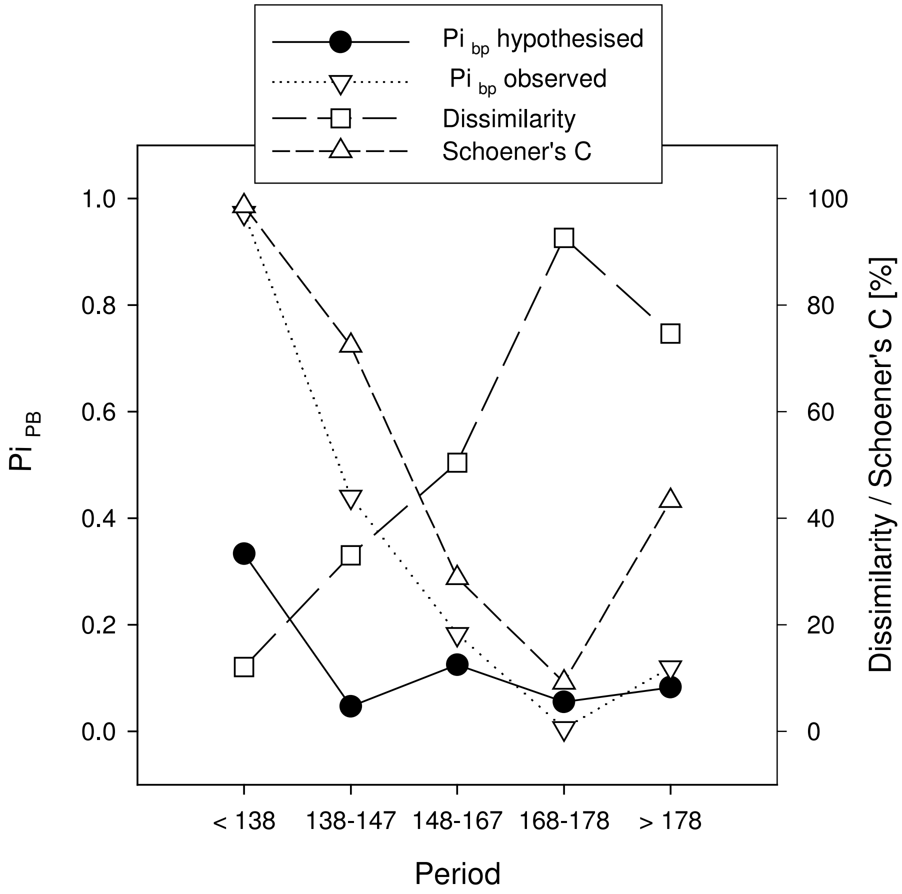

Figure 6.3: The trajectories of SIMPER-dissimilarity, hypothesised and observed P_i (see Table 6.1) and Schoener's C index for diet overlap between perch and burbot during the five periods of differing gape size limitation.

Table 6.4: Main taxa accounting for at least 50 % of intraspecific similarities (Sim.) of perch and burbot stomachs during five time periods of differing gape size limitation. Av. abundance = average square-root transformed abundance of prey taxon in stomach data, av.sim. = average similarity between pair wise comparisons between individual stomach data, sim./S.D. = av. similarity/standard deviation of pair wise comparisons, contrib. = relative contribution to similarity value of Table 2 Cum. = cumulative contribution. Prey taxa are abbreviated as CYC = cyclopoid copepods, DS = *Daphnia sp.*, DG = *Daphnia* galeata, numbers behind taxa abbreviations indicate size class. The list of contributing prey taxa was cut off, when the cumulative contribution was > 50%.

Sim. between…	*Period*	*Prey taxa*	*Av. Abund. [%]*	*Av. Sim. [%]*	*Sim./SD.*	*Contrib. [%]*	*Cum. [%]*
…Perch	*< 138*	*CYC<0.8*	100.00	100.00		100.00	100.00
	138-147	*CYC<0.8*	68.93	49.60	1.40	90.79	90.79
	148-167	*CYC<0.8*	57.16	34.68	0.96	82.03	82.03
	168-178	*DG<1.6*	22.08	8.83	0.62	33.30	33.30
		DS<1.6	19.97	8.13	0.66	30.65	63.95
	> 178	*CYC<0.8*	16.24	6.69	0.66	23.90	23.90
		DS<1.6	14.85	6.30	0.64	22.51	46.41
		DS>1.6	18.21	5.18	0.40	18.51	64.92
…Burbot	*< 138*	*CYC<0.8*	95.96	92.38	10.04	99.50	99.50
	138-147	*CYC<0.8*	86.90	75.93	2.30	98.40	98.40
	148-167	*CYC<0.8*	56.66	36.87	1.29	64.29	64.29
	168-178	*CYC>0.8*	49.93	25.92	0.78	60.39	60.39
	> 178	*CYC>0.8*	54.78	36.09	1.23	76.79	76.79

The similarity in stomach biomass of perch decreased continuously until doy 178, with similarities remaining at 28 % during the last period of their pelagic stage. By overcoming the various gape size limitations, the decreasing intraspecific similarity values suggest, that individual perch became specialized on a limited number of prey taxa and thereby reduce intraspecific competition (Bolnick *et al.*, 2003). This was evident from the fact that before doy 168 more than 50 % of similarity resulted mostly from small cyclopoid copepods. After doy 168, however, values of similarities were less than 10 %. Intraspecific competition for declining zooplankton resources may have induced the ontogenetic habitat shift frequently observed in juvenile perch (Treasurer, 1988, Wu & Culver, 1992, Urho, 1996), which in Lake

Constance usually return to the littoral zone by the middle of July (Wang & Eckmann, 1994a). Accordingly, the habitat shift of juvenile perch coincided with the decline of pelagic zooplankton in the present study years (Probst, unpublished data).

The intraspecific diet overlap of burbot remained high even after the overcoming of gape size limitation for large daphnids. However, considering the low densities of YOY burbot in the pelagic zone of Lake Constance in summer (between 3.8 Ind. m^{-3} in middle of June to less 0.01 Ind. m^{-3} by the middle of July; Probst, unpublished data) intraspecific competition may affect burbot growth or survival only during spring.

Hartmann (1986) described the feeding strategy of larval perch and burbot, both species being mostly limited in prey type selection by their gape size. The present results partly confirm this pattern, but also indicate that in spite of similar feeding strategies during the larval stage, the feeding strategies of both species diverged in late summer. Whereas only a total of 7 different prey taxa were found in all burbot stomachs after doy 178, perch consumed all classified taxa. By contrast, the intraspecific similarity between perch stomachs decreased to less than 30 %, but remained at approx. 50 % in burbot. Thus, perch seem to become individual specialists, whereas burbot continue to feed on a common resource.

The limited spectrum of ingested prey taxa by burbot may be the result of the diel vertical migrations. As described in Chapter 5, burbot feed mainly around dusk when they are still below or within the thermocline. Hence, burbot may be confined to migrating zooplankton taxa, which they meet in a crepuscular light window. Contrary, perch are well known to feed on many prey types (Schleuter & Eckmann, 2007, Guma'a, 1978), and due to their faster growth they could utilize all available (non-migrating and migrating) zooplankton resources since the middle of June. Because of the dominant abundance and competitive superiority of perch, the diel vertical migration may help burbot to reduce interspecific interference competition with perch (see Chapter 5).

The restriction of burbot diet during their ontogeny also explains the observed deviation of diet overlap indices from the hypothesized pattern between doy 148-167. During this period small daphnids (<1.6 mm carapace length) should have become edible for burbot, but were only found in perch stomachs. Thus, burbot feeding was not determined by gape size limitation, but by other feeding constraints. Among these, the aforementioned spatial overlap with zooplankton during periods of increased visibility during dusk (Chapter 4) or the dependence on copepods as a essential part of burbot diet may be discussed. Marine copepods are considered to contain essential nutrients for the survival, development and growth of many fish larvae (Koven, 2003, Malzahn *et al.*, 2007), and strong dependencies on food quality have also been found in freshwater systems (Kolkovski *et al.*, 2000, Coutteau & Sorgeloos, 1997). The consistent presence of copepods in the diet of burbot may thus reflect the nutritional dependency of burbot on fatty acids or phospholipids contained in their copepod diet.

Because of their dependency on small cyclopoid copepods during their early life history, both perch and burbot can be expected to react sensitive to absolute changes in abundance of cyclopoid copepods. However, due to extended dependency of burbot on cyclopoid copepods, their year-class strength should be particularly affected by this zooplankton taxon. Contrary, the abundance and population dynamics of single prey taxa should have less impact on the survival, growth, and condition of YOY perch. Under this light, the changes in the zooplankton community as a result of re-oligotrophication may affect the ontogeny of YOY perch and burbot differently. When copepods densities remain at similar levels, but cladocerans decrease in abundance, re-oligotrophication may have more severe impacts on the population of Lake Constance perch. Contrary, a total decline in copepods abundance may affect burbot more severely, because they rely longer on this zooplankton taxon and do not seem to be able to utilize other prey taxa as flexible as perch.

Acknowledgements

Svein Hetland, Alexander Moßbrucker, Caitlin Lyman, Timo Basen and Markus Pehr helped to catch larval and juvenile perch and burbot and to count the stomach samples. Stefan Werner and Martin Mörtl provided a brief introduction to E-Primer.

7. General conclusions

The previous chapters gathered new insights into the ecology of perch and burbot in Lake Constance. Special focus of this thesis was directed towards the knowledge of the precise temporal and spatial distributions of the two species, which allowed to explain the shoaling behaviour of juvenile perch and the DVM of larval and juvenile burbot.

Chapter 2 describes how the spawning behaviour of perch is influenced by ship and wind induced waves. Regular wave exposure may indirectly affect the duration of egg incubation by forcing perch to spawn in deeper areas with cooler water temperatures. As the load of boat traffic in Lake Constance cannot be assumed to reduce in the near future, the impacts of ship-induced waves on perch reproduction require consideration in further research and conservation efforts.

In Chapter 3 the application of a new echosounding technique revealed that after metamorphosis YOY perch formed shoals below the lake surface. Shoaling during the day may be interpreted as an antipredation behaviour and may have implications for the intraspecific food competition of perch.

The incomplete knowledge on the diel vertical migration (DVM) behaviour of burbot lead to speculative conclusions on their spatial and temporal distribution during their pelagic stage (Fischer, 1999, Miler & Fischer, 2004). Only the detailed knowledge on the distribution of YOY burbot during the circadian cycle allowed to relate the DVM to environmental factors such as light and predator/prey distribution.

Many organisms, which perform DVM, have evolved this behaviour as a mechanism to evade visually orientated predators. Consequently, their DVM amplitude is affected by light (Hays, 2003, Scheuerell & Schindler, 2003, Scheuerell & Schindler, 2001). According to the “anti predation window”-hypothesis (Clark & Levy, 1988) the DVM of burbot is strongly related to ambient light levels. The preferred light levels of burbot alter with increasing body length and pigmentation and hence burbot seem to asses their predation risk in relation to their own morphology. The size-related light preference (and risk assessment) may be mediated by increased visual acuity during burbot ontogeny.

While the evasion of competition and/or predation (e.g. with/by YOY perch) through DVM may provide an important adaptation for juvenile burbot, their DVM may also be helpful to follow their prey and save on respirations costs during the day. The DVM behaviour of burbot may thus be the optimal strategy with multiple adaptive values for an organism in the middle of the food web, which similar to its prey faces predation in the epilimnion.

During the cause of this thesis, the DVM behaviour of burbot emerged as a central issue. Due to the limited amount of available time, laboratory experiments assessing the influence of single environmental factors on burbot DVM could not be conducted. This work is presently performed by Michael Donner and his results will eventually lead to a comprehensive understanding of burbot DVM in Lake Constance.

The potential for exploitative competition for zooplankton resources between perch is confined to a short period in spring, when both species are abundant and feed on small cyclopoid copepods. However, intraspecific competition between YOY perch may exert some constraints on their growth and survival, which may affect the timing of the ontogenetic habitat shift towards the littoral zone. The qualitative and quantitative assessment of the bottom-up influences of zooplankton on YOY perch appears to be another promising research topic. However, to approach this objective, long term data sets of yearly perch and zooplankton abundance are needed, both of which may be aggregated within the near future by the research groups of the SFB 454. Yearly abundances of YOY perch and burbot in the littoral zone of Lake Constance are collected since 1997 (Rejyol *et al.*, 2005) and may be related to the abundance of copepods and daphnids when a period of 12 to 15 years is covered.

Changes in perch and burbot ecology as result of re-oligotrophication?

The comparison with data by Wang & Appenzeller (1998) and Wang (1994b) do not indicate any significant deviation in behaviour and distribution of the early life-history stages of perch and burbot since the early 1990s. The ontogenetic habitat shift of perch occurred in the middle of July in the 1990s as well as today. Wang & Appenzeller (1998) already describe the DVM of burbot (though the full amplitude was not investigated). The decreasing catch rates of burbot in the study by Wang & Appenzeller (1998) since the beginning of July are in accordance with the observations by Miler and Fischer (2004) as well as with my personal observations. Hence the majority of burbot disappear from the pelagic zone by the end of June or the beginning of July. However, a small proportion of burbot remain in the pelagic zone until August. The reasons for this diverging behaviour are uncertain, but may be the combined effects of an extended spawning season (February - April), different growth rates or behavioural plasticity in the settlement behaviour of burbot.

Perch and burbot rely on cyclopoid copepods during May and June. Therefore the abundance and behaviour of this zooplankton taxon can be expected to play a key role for the survival success of perch and burbot. As a result of the re-oligotrophication, the zooplankton community of Lake Constance is changing and may further alter within the next decade. Due to the limitation in nutrient supply a general decline in zooplankton biomass has become evident (Bürgi *et al.*, 2006). Furthermore, copepods are expected to become the dominant taxon in Lake Constance (Straile, personal com.) and thus the food abundance for larval fish in the pelagic zone may remain at similar levels. However, the abundance of cladocerans during the juvenile stage of perch and burbot may become a more limiting factor and influences the survival, growth and time of return to the littoral zone of both species.

Since the early 1990, neither the sequence of taxa, which perch and burbot consume during their ontogeny nor the size during their pelagic stage was different (Wang & Appenzeller, 1998). On the other hand, Eckmann *et al.* (2006) found a decreasing trend in perch size by the end of their first summer, which was attributed to the combined effects of re-oligotrophication and increasing prevalence of the pike tapeworm *Triaenophorus nodulosus* (Pallas, 1781). The latter, however, affects perch mostly after their ontogenetic habitat shift to the littoral zone, as tapeworm prevalence is increasing with age. The similar growth rates observed by Wang & Appenzeller (1998) and the present study support this assumption and suggest that until now, the re-oligotrophication did not affect perch growth during their pelagic stage. However, to assess the impacts of re-oligotrophication on the perch or burbot populations of Lake Constance, studies on long term data sets are desirable (similar to Thomas & Eckmann, 2007 on lake whitefish). This has been partly attempted by Eckmann *et al.* (2006), but continuous data since the 1950s on growth and abundance of perch (not to mention burbot!) were lacking. Hence, the various influences of re-oligotrophication, pike tapeworm infection and competition with ruffe on perch growth could not be separated. Alternative methods to acquire long-term data on the abundance and growth of perch may yield valuable insights into the influences of trophic status on the growth and survival of perch and burbot.

The future of perch and burbot - a speculative outlook

Climate change has already caused changes in the seasonal abundance of copepods in Lake Constance (Seebens *et al.*, 2007) and shifts in the seasonal peak abundance of nauplii and copepodits may affect the temporal match/mismatch of perch and burbot larvae. It is difficult to predict to which extent warming water temperatures induce a mismatch between fish larvae and their prey. Warmer water temperatures may shift the spawning of perch and burbot towards earlier periods of the year (Noges & Jarvet, 2005), but this may also be the case for zooplankton taxa (Seebens *et al.*, 2007). For perch as littoral spawners changes in water temperature may cause a more obvious temporal shift (Gillet & Dubois, 2007) than for burbot, which spawn in the profundal zone in late winter and early spring at water temperatures of 4 – 5 °C. However, the influence of climate on the hypolimnetic water and their impact on winter spawning whitefish has already been demonstrated by Straile *et al.* (2007) and thus climate change may also affect the timing of burbot hatch.

The rate of introduced non-native species to Lake Constance is accelerating as new invasive benthic invertebrates are now discovered almost every year (Gergs & Rothhaupt, 2008, Hanselmann & Gergs, 2008, Werner & Rothhaupt, 2007). It is unknown, how these species affect the benthic food web and whether they are beneficial or detrimental to the nutrition of littoral fish. One example is the recently introduced gammerid *Dikerogammarus villosus*, which is well eaten by adult perch and burbot, but which may also introduce another link into the benthic trophic food web (Eckmann *et al.*, 2008). Whether the replacement of the detritus eating native gammerid *Gammarus roeseli* (Gervais, 1835) by the invasive, omnivorous *D. villosus* will result in reduced or enhanced allocation of benthic production towards benthivorous fish is uncertain and remains to be assessed. An invasion with similar potential impact on the feeding ecology of Lake Constance fishes occurred in 2007, when the mysid *Limnomysis benedeni* spread over the entire littoral zone of Lake Constance. Preliminary investigations suggest, that *L. benedeni* is also accepted as food by perch (Eckmann, personal communication), and may thus provide a new resource for fish. However, *L. benedeni* inhabits the littoral as well as pelagic areas of the lake while foraging on pelagic zooplankton. Hence, the influence of invasive species in Lake Constance may extend into the pelagic food web, even more so if the more pelagic mysid *Hemimysis anormala* was introduced to Lake Constance. *H. anormala* has already been found in other large prealpine lakes (Wittman & Ariani, 2008) and is a likely candidate for the invasion of Lake Constance.

The presence of such large zooplankton may further reduce the amount of available food for YOY perch and burbot and aggravate the decline of commercial perch yields in the long run.

The research on the impact of wave events on fish communities of large lakes is still in its infancy. Stoll et al. (2008) demonstrated, that wave-exposure reduced the somatic growth of juvenile fishes in the littoral zone, but not the daily otolith increment. Their results suggest that juvenile fish have to spend more energy on swimming and movement and can allocate less energy to somatic growth. The here presented investigation on the spawning depth preference of female perch confirm the adverse influences of anthropogenic waves, which should be considered for all life-history stages of littoral fishes. The boat traffic on Lake Constance is constantly increasing and ship induced waves reach shore lines, which are sheltered from wind induced waves. Thus the hydrodynamic forces exerted on many parts of the littoral zone of Lake Constance become much stronger and more frequent, while the total area of calm, low impact zones is declining. It is uncertain, to which extent anthropogenic induced waves affect the population dynamics of littoral fish species and once again, long term data sets may allow to address this question. Nonetheless, it seems advisable, to consider wave impacts in conservation efforts. For private boats the restricted passage at a closer distance than of 300 m to the shore line already aims to protect sensible littoral communities, however, it seems doubtful, whether this restriction is implemented rigorously. In accordance with private boating the intensity of commercial traffic is constantly increasing. Just in September 2008 the maiden voyage of a new passenger cruise ship, the MS "Sonnenkönigin" is scheduled on Lake Constance. This boat is 69 m long and is equipped with a 2466 hp engine. According to the ship manufacturer it is among the largest ships in European inland waters. Another example for increasing boat traffic is the high-speed catamaran, which commutes every hour between the harbours of Konstanz and Friedrichshafen since 2005. Though the MS "Sonnenkönigin" and the catamaran are designed to create low wave turbulence, they represent an increasing demand for commercial boat traffic on Lake Constance. The frequency and intensity of commercial boat waves have been observed to travel long distances and therefore will most certainly affect even remote areas of the littoral zone (Hofmann *et al.*, 2008). If the number of private and commercial boats on Lake Constance will increase further, the frequency and intensity of ship-induced wave events on the littoral zones will also increase. The majority of boats cruise on the lake in spring and summer at times, when the shallowest littoral areas are used as nursery areas by many larval and juveniles fishes (Fischer & Eckmann, 1997). Adverse effects of ship-induced waves must therefore be expected for fishes during their most vulnerable life-history stages as eggs, larvae and juveniles.

8. Summary

This thesis gathered new information on the ecology of the two dominant young-of-the-year (YOY) fish species Eurasian perch *Perca fluviatilis* L. and burbot *Lota lota* (L.) in the pelagic zone of Lake Constance. Five investigations on **1)** the spawning depth selection of female perch, **2)** the near-surface distribution of juvenile perch, **3)** the diel vertical migration of larval and juvenile burbot, **4)** the ultimate causes for this migration behaviour, and **5)** the diet overlap between perch and burbot intend to provide new insights into the biology of both species, allowing a better understanding of their population development in a large lake affected by re-oligotrophication, climate change, and the invasion of new species.

1) The selection of spawning depth by perch was investigated in an experiment using artificial substrata in Lake Constance during the spawning season of 2007. The experiment compared spawning behaviour at substrata between 0.5 and 15 m depth at two sites exposed to different regimes of ship-generated wave action. The total abundance of egg ribbons did not differ significantly between the two sites, but the preferred spawning depth was deeper at the wave exposed site (5 m) compared to the sheltered site (2 m). While water temperatures could not account for the observations, differences in wave exposure may explain the different spawning depth preferences. At both sites, large egg ribbons were generally found in deeper water, and large egg ribbons occurred more frequently at the sheltered site. Because the egg ribbons of perch are likely to have a size-dependent susceptibility to hydrodynamic stress, large females may select deeper spawning locations where the effects of surface waves are considerably attenuated.

2) The near surface distribution of YOY perch was observed with a towed upward beaming transducer system (SIMRAD EK60 with a circular 7° transducer). Perch aggregated in dense shoals between the surface and five meters depth during daytime and dispersed evenly at the same depth during night. Shoaling commenced in late June when perch metamorphosed from larval to juvenile stage. Average shoal width was 6.6 m and average shoal height was 2.35 m in July when perch were observed in the pelagic zone for the last time. Upward echosounding revealed the presence and fine-scale distribution of pelagic juvenile perch. This method may be used as complementary survey tool to get more precise information about distribution, behaviour and abundance of near-surface fish.

3) The behaviour of YOY burbot in the pelagic zone of Lake Constance was investigated with split beam echosounding and net catches. Their vertical distribution was compared to light intensity at the surface and to the light intensity at their mean depth. Burbot larvae were detected since the beginning of May until the end of August. From early June, after the stratification of the water column, burbot performed DVM between the hypolimnion and the epilimnion. The amplitude of DVM increased constantly during the summer and reached 70 m by the end of August. Burbot started their ascent to the surface after sunset and descended into the hypolimnion after sunrise. As the YOY burbot grew from May to August, they experienced decreasing diel maximum light intensities: In May and early June burbot spend the day at light intensities > 40 W m^{-2}, but they never experienced light intensities above 0.1 W m^{-2} since the end of June. From this time, burbot experienced brightest light intensities during dusk and dawn, suggesting feeding opportunities at crepuscular hours. The present study implies that YOY burbot on the pelagic zone of Lake Constance increased their DVM amplitude during the summer to counteract a perceived predation risk related to body size and pigmentation.

4) DVM are commonly assumed to provide three possible ultimate adaptations: the evasion of predators, foraging, or bioenergetic optimisation. To resolve the ultimate causes for the DVM of YOY burbot their vertical distribution during their DVM cycle was compared with the depth of predators, zooplankton prey and ambient temperature. There was a high spatial overlap between zooplankton prey and burbot depth, but not with the depth of potential predators. However, stomach analyses indicate that burbot do not feed intensively during the day, but during their ascent towards the surface at dusk. With increasing depth burbot also experienced cooler temperatures, thus facing a temperature gradient of up to 19 °C during their DVM. The present results suggest a multiple adaptation of burbot DVM to the conditions in a temperature-stratified lake. At day, the food abundance in the epilimnion is low, whereas the abundance of potential predators is high. By performing DVM, burbot efficiently avoid the encounter with predators during day while saving energy in cool hypolimnetic waters.

5) The diet overlap as a measure of exploitative competition between YOY perch and burbot during spring and summer was investigated in relation to gape size limitation. Because perch were larger and grew faster than burbot during their early life-history in the pelagic zone, perch overcame gape size limitation for various zooplankton taxa always earlier than burbot. All zooplankton taxa could be found within perch stomachs by the middle of June, when perch overcame gape size limitation for large cladocerans. However, there was a tendency for individual diet specification as the similarity between perch stomachs decreased. Contrary, the similarity between burbot stomachs remained at almost 50 % until the end of August, indicating that all burbot rely on the same zooplankton resource, mostly cyclopoid copepods and large daphnids. Because YOY perch are about two orders of magnitude more abundant by July in the pelagic zone than burbot, it can be assumed that YOY perch are more affected by intraspecific competition than by competition with burbot. Burbot, on the other hand, may evade strong competition with YOY perch by performing DVM, thus being restricted to feed on migrating zooplankton prey.

9. Zusammenfassung

Im Rahmen dieser Doktorarbeit wurden neue Erkenntnisse über die Ökologie des Flussbarschs *Perca fluviatilis* L. und der Trüsche *Lota lota* (L.) im Bodensee gewonnen. Fünf Untersuchungen über **1)** die Laichtiefenpräferenz von Flussbarschweibchen, **2)** die oberflächennahe Verteilung von juvenilen Flussbarschen, **3)** die tagesperiodische Vertikalwanderung von larvalen und juvenilen Trüschen, **4)** die Ultimatfaktoren dieser Vertikalwanderungen und **5)** die Nahrungsüberlappung zwischen einsömmrigen Flussbarschen und Trüschen im Pelagial ermöglichen ein vertieftes Verständnis für die Verteilung und die Bestandsentwicklung beider Arten im Bodensee.

1) Anhand eines Experiments mit künstlichen Laichsubstraten wurde die bevorzugte Laichtiefe von Flussbarschen im Frühjahr 2007 untersucht. In diesem Experiment wurden Laichsubstrate zwischen 0.5 und 15 m Tiefe an zwei Stellen mit unterschiedlicher Wellenexposition ausgebracht. Die gesamte Anzahl an Laichbändern war zwischen den beiden Versuchsstandorten gleich, jedoch war die Hauptlaichtiefe an der wellenexponierten Stelle war tiefer (5 m) als an der geschützten Stelle (2 m). Die Wassertemperaturen an beiden Versuchsstandorten konnten die unterschiedliche Laichbandverteilung nicht erklären, der Einfluss von Wellenexposition bietet jedoch eine mechanistische Erklärung. An beiden Versuchsstandorten wurden große Laichbänder generell in größeren Tiefen gefunden und mehr große Laichbänder wurden an der geschützten Versuchsstelle beobachtet. Unter der Annahme, dass größere Laichbänder hydrodynamischem Stress stärker ausgesetzt sind als kleine Laichbänder, legen die Ergebnisse dieses Experiments nahe, dass große Weibchen grundsätzlich tiefere Laichplätze bevorzugen. Dort ist der Einfluss von Oberflächenwellen stark abgeschwächt. Flussbarsche scheinen daher ihre Laichplätze auch in Abhängigkeit von hydrodynamischem Stress auszuwählen.

2) Die oberflächennahe Verteilung von einsömmrigen Flussbarschen wurde mit einem nach oben gerichteten Echolotschwinger beobachtet (einem zirkulären Schwinger mit 7° Öffnungswinkel an SIMRAD EK 60). Die Flussbarsche schlossen sich am Tag zwischen der Oberfläche und 5 m Tiefe in engen Schwärmen zusammen und verteilten sich nachts gleichmäßig unterhalb der Wasseroberfläche. Die Schwarmbildung begann im späten Juni und fiel in die Zeit, in der die Flussbarsche vom larvalen zum juvenilen Habitus metamorphosierten. Im Juli, als die Barsche zum letzten Mal im Pelagial beobachtet wurden, betrug die durchschnittliche Schwarmbreite 6.60 m und die durchschnittliche Schwarmhöhe 2.35 m. Aufwärtsgerichtetes Echoloten erwies sich als eine effektive Methode zur Beobachtung der kleinräumigen Fischverteilung unterhalb der Oberfläche und könnte als ergänzende Methode zur Bestandserhebung tiefer gehende Erkenntnisse über die Verteilung, das Verhalten und die Abundanz von oberflächennahen Fischen liefern.

3) Tagesperiodische Vertikalmigration (DVM) mit einer Amplitude von 50 m und mehr ist ein bekanntes Phänomen, das bei vielen marinen Fischlarven beobachtet wurde. In dieser Arbeit wird erstmals die detaillierte Verteilung larvaler und juveniler Trüschen, den einzigen Süßwassergadiden der Nordhemisphäre, im Laufe ihrer DVM beschrieben. Das Verhalten der Jungtrüschen im Pelagial des Bodensees wurde mit einem Splitbeam-Echolot untersucht und mit der Lichtintensität über der Oberfläche und in der Durchschnittstiefe der Trüschen korreliert. Trüschenlarven konnten von Anfang Mai bis Ende August im Bodenseepelagial beobachtet werden. Ab Anfang Juni, nachdem sich eine temperaturgeschichtete Wassersäule ausgebildet hatte, zeigten die Trüschen ein ausgeprägtes DVM - Verhalten. Die Amplitude der DVM nahm kontinuierlich zu und erreichte bis Ende August 70 m. Die Trüschen begannen ihren Aufstieg an die Oberfläche nach Sonnenuntergang und stiegen in der Morgendämmerung wieder zu ihrer Tagestiefe hinab. Während ihres Wachstums von Mai bis August verbrachten die Trüschen den Tag in zunehmend dunklen Wassertiefen: Im Mai verbrachten sie den Tag bei Lichtintensitäten > 40 W m^{-2}, aber ab Ende Juni mieden sie Lichtintensitäten > 0.1 W m^{-2}. Ab dieser Zeit erlebten die Trüschen die höchsten Lichtintensitäten während der Abend- und Morgendämmerung, was mit optimierten Fressbedingungen während den Dämmerungsstunden zusammenhängen könnte. Die Ergebnisse dieser Studie legen nahe, das einsömmrige Trüschen die DVM-Amplitude im Laufe ihrer pelagischen Phase erhöhen, um einem steigendem Prädationsrisiko, welches in Zusammenhang mit ihrer zunehmenden Körpergröße und -Pigmentierung stehen mag, entgegen zu wirken.

4) Als Ultimatfaktoren von DVM werden grundsätzlich drei verschiedene Hypothesen diskutiert: Die Vermeidung von Räubern, die Optimierung der Nahrungsaufnahme durch das Verfolgen der Beute oder die Optimierung des bioenergetischen Budgets. Um zu klären, welche dieser drei Möglichkeiten die DVM der einsömmrigen Trüschen im Bodensee begünstigt, wurde die Tiefenverteilung der Trüschen mit der vertikalen Verteilung von potentiellen Räubern, Beutezooplankton und Wassertemperaturen verglichen. Die Trüschen zeigten starke räumliche Überlappung mit ihrer Beute, jedoch nicht mit potentiellen Räubern. Mageninhaltsanalysen von Jungtrüschen legen nahe, dass der größte Teil der Nahrungsaufnahme während des Aufstiegs in der Abenddämmerung erfolgt und somit die Aufenthaltstiefe der Trüschen am Tag nicht ursächlich durch ihre Beute bedingt ist. Mit zunehmender Tiefe waren die Trüschen kälteren Wassertemperaturen ausgesetzt, so dass sie einen Temperaturgradienten von bis zu 19 °C während ihrer DVM erfuhren. Die DVM der pelagischen Trüschen im Bodensee kann daher eine Mehrfachanpassung an die Lebensbedingungen in einem geschichteten See der gemäßigten Zone darstellen, indem die Trüschen den Kontakt zu Räubern während des Tages vermeiden und ihre metabolischen Kosten durch den Aufenthalt im kühlen Hypolimnion reduzieren.

5) Die Nahrungsüberlappung zwischen Flussbarschen und Trüschen wurde in Verbindung mit der Maulspaltengröße analysiert und als Schätzwert für potentielle Ressourcenkonkurrenz verwendet. Aufgrund ihres schnelleren Wachstums und ihrer größeren Ausgangsgröße überwanden Flussbarsche die Maulspaltenlimitierung für diverse Beutetaxa stets früher als Trüschen. Ab Mitte Juni fraßen Flussbarsche alle klassifizierten Beutetaxa, jedoch wiesen verringerte intraspezifische Similaritätswerte der SIMPER-Analyse auf eine individuelle Nahrungs-Spezialisierung der Barsche hin. Im Gegensatz dazu ähnelten sich die Mageninhalte der Trüschen bis Ende August zu fast 50 %, so dass alle Trüschen auf cyclopoide Copepoden und Daphnien als gemeinsame Nahrungsressource angewiesen waren. Während der pelagischen Koexistenz von Flussbarsch und Trüsche kommen Flussbarsche fast 100 mal häufiger vor als Trüschen. Daher sind Flussbarsche stärker durch intraspezifische als interspezifische Konkurrenz beeinflusst. Trüschen hingegen können durch DVM die Konkurrenz zu den Flussbarschen verringern, bleiben dabei jedoch auf wandernde Beutetaxa beschränkt.

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11. Plate I

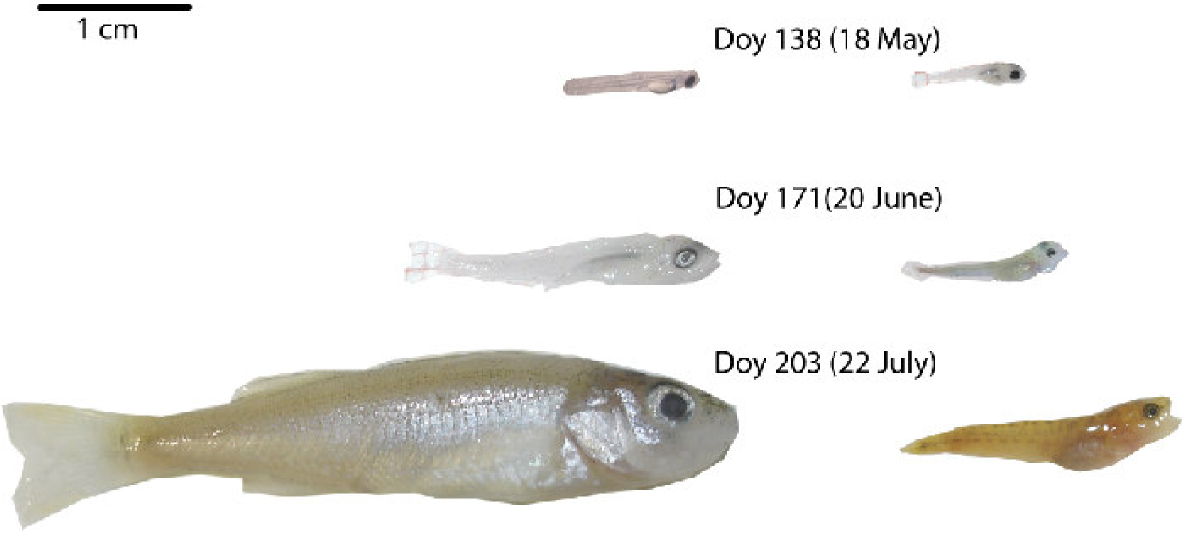

Plate I: Size relationships and morphological development of perch and burbot during their pelagic life history. In the middle of May (138 day of year = doy) both species are in their larval stage. By the middle of July both species have transformed in to juveniles with fully developed fins and pigmentation.

12. Acknowledgements

To many people I am very obliged in the completion of this thesis. Without their help, it would have impossible to get finished:

Reiner Eckmann supervised this thesis and provided valuable advice and comments on this thesis. I am especially grateful for his introduction to hydroacoustics and many fruitful discussions about the here presented research topics. He also acquired the funding for my PhD-position within the **CRC 454 "The littoral zone of Lake Constance"** financed by the **German Research Foundation (DFG)**.

My colleagues at the Limnological Institute kept my spirits high. Amongst them especially **Stefan Stoll**, **Gregor Thomas**, **Diana Schleuter**, **Jasminca Behrmann-Godel**, **John Hesselschwerdt**, **Rene Gergs**, **Bern Köder**, **Oliver Miler**, **Stefan Werner**, **Hilmar Hofmann, Manuel Hirning, Phillip Hirsch, Florian Kundinger, Christian Michel, Daniela Harrer, Michael Donner, Karsten Rinke** and **Arnd Weber** need to be mentioned.

Florian Kundinger, **Timo Basen**, **Markus Pehr**, **Alexander Moßbrucker**, **Katja Lamm**, **Milene Santos-Stangler**, **Caitlin A. Lymann**, **Matthias Lohr, Lars Frederik Martinussen**, **Svein Roald Hetland, Joachim Böhler, Michael Puffer, Arnd Weber, Alfred Sulger, Heiner Probst** and **Karl Fütterer** helped on the boat during the surveys and provided a lot of patience and good company.

For assistance in the analysis of zooplankton samples I thank **Pia Mahler** and **Miriam Schmidt**.

Martin Wolf, **Jürgen Gans-Thomsen**, **Beatrix Rosenberg**, **Ursula Haake** and **Joseph Halder** provided technical support.

Silvia Berger and **Karin Huppertz** helped me to keep track of my administrative obligations, which became a particularly delicate task during the last months prior to the submission of this thesis.

Special thanks are also due to **Helge Balk** from the University of Oslo, who provides up-to date freeware versions of SONAR5_Pro for download (www.fys.uio.no/~hbalk/sonar4_5/ Downloads.htm). Without this program, a great part of this work could not have been analysed.

I also thank the scientific dive team of the University of Konstanz, amongst them **Martin Mörtl**, **Andreas Nisch**, **Manuel Hirning**, **John Hesselschwerdt**, **Stefan Werner**, **Martin Wolf**, **Philipp Fischer** and **Nicole Bohnenberger** for assistance during the dive campaigns and for the contracts to buffer financial short comings.

Mentioning financial support, I also thank the Arbeitsagentur Konstanz, which made the completion of this thesis possible by granting Arbeitslosengeld I for 7 months.

Wilfried and **Sigrid Probst, Sandra Hahn, Gregor Thomas** and **Julia Mohs** provided advice and comments on the earlier versions of this thesis.

I am especially grateful to my parents **Sigrid** and **Wilfried** who gave me empathy, mental and material support during my studies and research. I also thank my sister **Anne** and my brother **Heiner**.

And finally, I thank **Julia**, who I met during my stay in Konstanz. She made this town become a real home. Hopefully we will find a new one in the near future!

13. Erklärung

Ich erkläre hiermit, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus anderen Quellen direkt oder indirekt übernommenen Daten und Konzepte sind unter Angabe der Quelle gekennzeichnet. Weitere Personen, insbesondere Promotionsberater, waren an der inhaltlich materiellen Erstellung dieser Arbeit nicht beteiligt. Die Arbeit wurde bisher weder im In- noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

Konstanz, den 11.08.2008

(W.N. Probst)

14. Record of achievement / Abgrenzung der Eigenleistung

Chapter 2:	I contributed to the design, installation and conduction of the experiment. I analysed the collected data in conjunction with Stefan Stoll.
Chapter 3:	I conducted the hydroacoustic surveys in conjunction with Gregor Thomas and I exclusively analysed the collected data.
Chapter 4, 5, 6:	I conducted the hydroacoustic surveys and sampling campaigns with assistance of various students and research assistants. I contributed significantly to the analysis of stomach and zooplankton samples and exclusively analysed the collected data.

15. Curriculum vitae

Name: Wolfgang Nikolaus Probst

Date of birth: 11. November 1975

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Education: Diplom-Biologist (MSc Biology)

Family status: not married

Since August 2008	Employee at the Young Scholar Research Fund project “Fish induced turbulences”
January 2008- August 2008	Dissertation
October 2004 – December 2007	Employee at the collaborate research centre “The Littoral zone of Lake Constance”, PhD, planned submission of thesis August 2008
26. February 2004	Graduation MSc(German Diplom) in Fisheries Science Zoology and Physical Oceanography
February 2003 – June 2003	MSc thesis under supervision of Dr. E.A. Trippel and Dr. G. Kraus „Parental effects on the early life-histroy traits of haddock *Melanogrammus aeglefinus* L.”
October 1997 – February 2004	Study of Biology, Fisheries Science, Zoology and Physical Oceanography at the Christian-Albrechts-Institut (CAU) and the IfM-GEOMAR, Kiel
August 1996 – August 1997	Civilian service at Artefact e.V.(Glücksburg)
1986 – 1996	Fördegymnasium Flensburg, Abitur (High School equivalent)

16. Publications

Peer reviewed publications:

PROBST, W.N., KRAUS, G., RIDEOUT, R., TRIPPEL, E.A. 2006. Parental effects on early-life history traits of haddock *Melanogrammus aeglefinus*. *ICES Journal of Marine Science* **63**: 224-234

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PROBST, W.N, ECKMANN, R. (in press). The influence of light on the diel vertical migration of young-of-the-year burbot *Lota lota* in Lake Constance. *Journal of Fish Biology*

PROBST, W.N, THOMAS, G., ECKMANN, R. (in press) Hydroacoustic observations of surface shoaling behaviour of young-of-the-year perch *Perca fluviatilis* (Linnaeus, 1758) with a towed upward-facing transducer. *Fisheries Research*

Non-peer reviewed publications:

PROBST, W.N., ECKMANN, R. 2006. Hydroakustische Untersuchungen über das Verhalten juveniler Flussbarsche *Perca fluviatilis* und Trüschen *Lota lota* im sommerlichen Bodenseepelagial. DGL Tagungsbericht 2006, 131-135