

# The influence of light on the diel vertical migration of young-of-the-year burbot *Lota lota* in Lake Constance

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The diel vertical distribution of young-of-the-year (YOY) burbot *Lota lota* in the pelagic zone of Lake Constance was compared to light intensity at the surface and to the light intensity at their mean depth. *Lota lota* larvae inhabited the pelagic zone of Lake Constance from the beginning of May until the end of August. From early June, after the stratification of the water column, fish performed diel vertical migrations (DVM) between the hypolimnion and epilimnion. The amplitude of DVM increased constantly during the summer and reached 70 m by the end of August. *Lota lota* started their ascent to the surface after sunset and descended into the hypolimnion after sunrise. As the YOY fish grew from May to August, they experienced decreasing diel maximum light intensities: in May and early June *L. lota* spent the day at light intensities  $>40 \text{ W m}^{-2}$ , but they never experienced light intensities  $>0.1 \text{ W m}^{-2}$  after the end of June. From this time, *L. lota* experienced the brightest light intensities during dusk and dawn, suggesting feeding opportunities at crepuscular hours. The present study implies, that YOY *L. lota* in 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.

Key words: gadoid; hydroacoustics; larvae; ontogeny; pelagic; predator evasion.

## 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 fishes (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 h'. The common pattern of DVM comprises the ascent at dusk and the descent at dawn, but this pattern can be reversed (Levy, 1990; Sims *et al.*, 2005).

The amplitude of larval and juvenile fish DVM can range from a few metres (Cech *et al.*, 2005; Hensler & Jude, 2007) to  $>50$  m (Harden Jones, 1968; Scheuerell & Schindler, 2003; Auth *et al.*, 2007; Voss *et al.*, 2007). Among freshwater fishes, the deep DVM of larval and juvenile sockeye salmon

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*Oncorhynchus nerka* (Walbaum) is one of the best known examples and has been studied extensively (Narver, 1970; Brett, 1971; Levy, 1987).

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

In large lakes of the northern hemisphere, larval 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 swimbladder (McPhail & Paragamian, 2000). After swimbladder inflation, larval *L. lota* inhabit the pelagic zone, feeding on plankton (Ryder & Pesendorfer, 1992). In Lake Constance, pelagic *L. lota* larvae have been observed to perform DVM by Miler & Fischer (2004) and Wang & Appenzeller (1998). The precise DVM behaviour and the duration of the pelagic stage of young-of-the-year (YOY) *L. lota*, however, remained speculative, as in both studies only data from net catches were used. After spending between 2 and 3 months in the pelagic zone of the lake, *L. lota* are assumed to settle to the profundal zone (Miler & Fischer, 2004). From the profundal zone, they presumably migrate along the slope of the lake bottom towards the littoral zone where they arrive as juveniles (Fischer, 1999). The earliest juveniles come to the littoral zone in late June (Fischer, 1999), but the majority of the YOY arrives in August or September (Fischer & Eckmann, 1997).

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

In the present study, the relationship between light and the DVM behaviour of YOY *L. lota* was investigated. A prerequisite for this objective was the knowledge of the fine-scale temporal and spatial distribution of *L. lota*, which was investigated by split-beam echosounding. The observed depth of the fish 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 *L. lota* during their pelagic stage in Lake Constance.

## MATERIALS AND METHODS

### RESEARCH AREA

All data were sampled from Upper Lake Constance (ULC; 47°35' N; 9°28' E), a warm monomictic pre-alpine lake situated at the borders of Austria, Germany and Switzerland. ULC has an average water depth of 101 m and a surface area of 476 km<sup>2</sup>. During the summer, the lake stratifies and a thermocline is established at c. 10 m depth. Data were sampled in the western part of the main basin of ULC and in Lake Ueberlingen, a fjord-like bay in the north-western part of ULC. All the data presented here were obtained from lake areas, where the lake was deeper than 100 m (Fig. 1).

### LIGHT INTENSITY

Light intensities above the water surface ( $I_0$ , W m<sup>-2</sup>) were measured by a stationary light sensor on the roof of the Limnological Institute, Konstanz, Germany. The sensor recorded light intensities every 30 s. Arithmetic mean light intensities for 10 min time intervals were calculated, which corresponded to the time interval of the hydro acoustic transects analysed. Light intensities ( $I_z$ , W m<sup>-2</sup>) at the mean depth of *L. lota* ( $Z_{MD}$ , m) were calculated after Uhlmann & Horn (2001):

$$I_z = I_0 e^{-(k Z_{MD})} \quad (1)$$

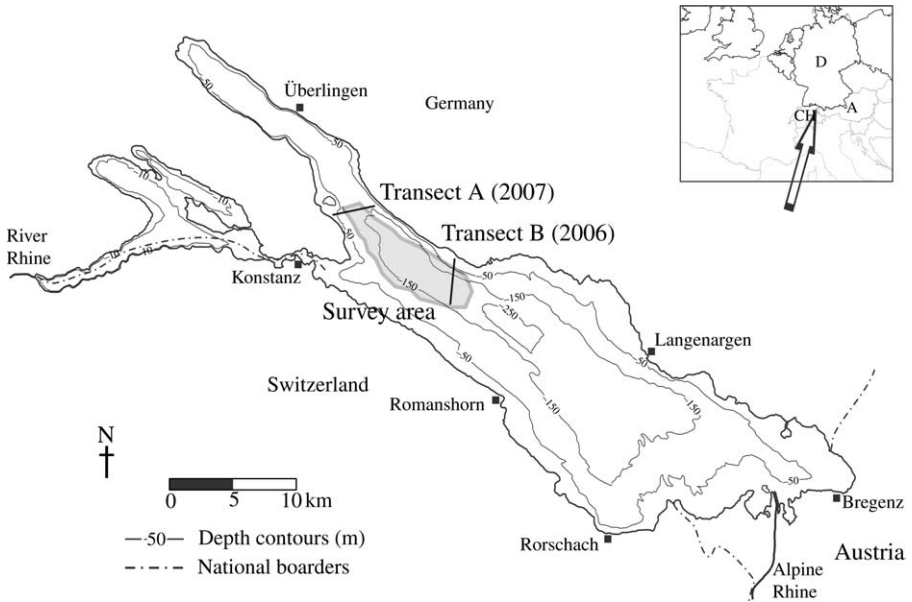


FIG. 1. Location of Lake Constance (⇒⇒) and the survey areas for hydroacoustic observations of vertical distribution of *Lota lota* in 2006 and 2007. The transects were regularly surveyed by hydroacoustics at day, dusk and night. Transect A was monitored in 2007 and transect B in 2006. Additional recordings at various times of the day were performed in both years randomly within the survey area (◐). For dates and times of surveys refer to Table I. Net catches were obtained in the vicinity of the transects within the survey area.

where  $k$  is the extinction coefficient.  $K$  was determined from *in situ* measurements of light intensity in the water column with a waterproof luxmeter (LTM, Berlin, Germany) during each survey. The values for  $I_Z$  were corrected for sun inclination related changes in surface albedo by calculating the sun inclination in degrees ( $I_s$ ) at Konstanz at the given date and time. A regression between water surface 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 ( $I_{Z\text{corr}}$ ):  $I_{Z\text{corr}} = [1 - (77.481e^{-0.0752I_s})100^{-1}](I_Z)$ , where the term in the parentheses 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 2 week intervals from the beginning of May until the beginning of September in 2006 and end of August in 2007 (Table I). The surveys were conducted in the western part of ULC following standard

TABLE I. Dates and locations (see Fig. 1) of mean *Lota lota* depth determined in 2006 and 2007. (SA, survey area; TA, transect A; TB, transect B). Times of day were defined as dawn between 0430 and 0630 hours, day between 0630 and 2000 hours, dusk between 2000 and 2200 hours and night between 2200 and 0430 hours

Date	Day of year	Location	Total number of observations	Number of samples at			
				Dawn	Day	Dusk	Night
04 May 2006	123	SA	3	1	2		
22 May 2006	141	TB	1		1		
01 June 2006	151	SA, TB	5	1	2		2
19 June 2006	169	SA, TB	4		2		2
26 June 2006	176	SA, TB	6		3	1	2
04 July 2006	184	SA, TB	6		5		1
10 July 2006	190	SA, TB	9		6	1	2
24 July 2006	204	SA, TB	8		4	2	2
31 July 2006	211	SA, TB	5		1	2	2
07 August 2006	218	SA, TB	5		3	1	1
21 August 2006	232	SA, TB	10		8	1	1
05 September 2006	247	SA	4		2		2
03 May 2007	122	SA	1		1		
12 May 2007	131	SA	2		2		
14 May 2007	133	SA	2		2		
16 May 2007	135	SA	1		1		
21 May 2007	140	SA, TA	5		2	1	2
31 May 2007	150	SA, TA	7	1	3	1	2
12 June 2007	167	SA, TA	5		2	1	2
22 June 2007	172	SA	2		2		
29 June 2007	179	SA, TA	12	2	5	1	4
11 July 2007	191	SA	1		1		
22 July 2007	202	SA, TA	6		3	1	2
18 August 2007	229	SA, TA	3		2		1
27 August 2007	238	SA	1		1		
$\Sigma$			114	5	66	13	30

$\Sigma$ , sum of observations.

transect routes at day (Fig. 1), dusk and night and cruising randomly on the lake in the meantime. For the analysis of mean *L. lota* depth only hydroacoustic data from lake areas with more than 100 m depth were used.

Surveys were usually performed from noon or afternoon until nightfall. On four occasions (4 May 2006, 1 June 2006, 31 May 2007 and 29 June 2007) the hydroacoustic surveys were extended until the next morning to observe the descent of YOY *L. lota*.

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 100 W, a pulse length of 0.256 ms and 8.71 kHz bandwidth. Ping intervals during the surveys ranged from 0.2 to 1.3 s per ping and were adjusted to avoid false bottom echoes. Data were stored on a laptop computer that 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 (TS) (at 1490 ms<sup>-1</sup> sound speed) according to the manufacturer's manual.

Hydroacoustic data were analysed with SONAR5\_Pro 5.9.5 and 5.9.6 (Balk & Lindem, 2006). To estimate the number of *L. lota* at depth single echo counting was used. A single echo is defined as the echo energy attributed to a single target. 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 *L. lota* at a given time and day, a pelagic transect (water depth >100 m) containing at least 500 pings (corresponding to c. 5 min) 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 and wind waves). Echoes were attributed to *L. lota* by their TS and depth distribution. When SED were below a depth of 10 m during day and where within a TS range between -80 to -58 dB they were considered to result from YOY *L. lota*. Any other fish species would not occur below 10 m depth (e.g. YOY *P. fluviatilis*; see Table II) or would have considerably larger TS. For *L. lota* echoes, the range of minimum and maximum TS at a given date was determined, which was then used for the calculation of SED volume density ( $D_v$ , where  $D_v$  = number of SED m<sup>-3</sup>) by counting the number of SED per volume within this TS range. TS outside the determined TS range was excluded from the volume density calculation. To obtain the number of SED per volume, the analysed transect was divided into 1 m 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 was calculated by SONAR5\_Pro) in each 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 *L. lota* until the end of the summer.

Mean ( $Z_{MD}$ ) and s.d. ( $Z_{SD}$ ) of *L. lota* depth were calculated as the weighted mean and s.d. of class-grouped data:

$$Z_{MD} = \left[ \sum_1^i (z_i D_{vi}) \right] \sum D_{vi}^{-1} \quad (2)$$

and

$$Z_{SD} = \left( \left\{ \sum_1^i [D_{vi}(z_i - Z)^2] \right\} (\sum D_{vi} - 1)^{-1} \right)^{0.5} \quad (3)$$

TABLE II. Catches of young-of-the-year (YOY) *Lota lota* in 2006 and 2007. Time of day defined as in Table I. Number caught refers to the number of caught *L. lota* within each haul and per cent of catch refers to relative number of *L. lota* 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 total length ( $L_T$ ) was calculated from all caught individuals within the 12 sampling campaigns

Date	Day of year	Time of day	Depth (m)	Number caught	Catch density (individuals $1000\text{ m}^{-3}$ )	Per cent of catch	Mean $L_T \pm \text{s.d.}$ (mm)
23 May 2006	142	Day	0	0	0	0	$6.0 \pm 1.0$
			5	2	2.3	1	
			10	30	49.8	91	
			20	7	8.7	100	
07 June 2006	157	Night	0	3	4.03	2	$9.7 \pm 1.2$
20 June 2006	170	Dusk	5	4	13.9	10	$11.0 \pm 1.6$
			10	1	2.1	10	
11 July 2006	191	Dusk	8	15	6.6	100	$13.6 \pm 2.3$
08 August 2006	219	Dusk	20	7	1.9	100	$22.1 \pm 2.7$
14 May 2007	133	Day	15	10			$7.1 \pm 0.7$
21 May 2007	140	Day	13	3			$7.6 \pm 0.9$
		Dusk	17	9			
		Night	13	12			
30/31 May 2007	149/150	Dusk	0	9			$9.6 \pm 1.4$
			20	20			
		Night	5	8			
		Dawn	0	9			
			27	8			
12 June 2007	162	Day	27	12			$10.0 \pm 1.6$
		Dusk	2	17			
		Night	4	21			
22 June 2007	172	Day	35	13			$12.0 \pm 2.3$
29/30 June 2007	179/180	Dusk	0	14			$13.1 \pm 1.8$
		Night	0	12			
		Dawn	0	5			
22 July 2007	202	Dusk	28	4			$19.8 \pm 3.8$
			5	4			

$L_T$ , total length.

with  $z_i$  as the depth of the layer  $i$  (m),  $D_{vi}$  as the volume density (number of SED  $\text{m}^{-3}$ ) within layer  $i$ .

## NET CATCHES

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

Larvae and juveniles were caught with 3 m long ichthyoplankton nets with a circular opening of 1.4 m diameter and mesh-sizes of 1200 and 800  $\mu\text{m}$  and 1600 and 1200  $\mu\text{m}$

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 metre 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 (Hydro-bios, Kiel, Germany) 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 *L. lota* echoes displayed by the echosounder. Depending on tow depth and weather conditions, the nets were trawled with a speed of 0.7–1.5 m s<sup>-1</sup>. The speed was adjusted to maintain a consistent depth but was held as fast as possible.

Fish caught were anaesthetized and killed in trichloromethyl-propanol (2 g l<sup>-1</sup>) directly after catch and subsequently preserved in 4% formalin or put on ice. Within 6 h, all fish that had been put on ice were stored in a freezer at -18° C until they were further processed. In the laboratory, the total length ( $L_T$ ) of frozen fish was measured to the nearest 0.1 mm under a dissecting microscope.

## STATISTICS

Mean depth of *L. lota* calculated from echograms from 24 survey days and at various daytimes in 2006 and 2007 (Table I;  $n = 114$ ) were combined with data on light for the same times and days, which was used to model the influence of surface light intensity and day of the year ( $D_{oy}$ ); counted continuously from 1 January as  $D_{oy} = 1$  on mean *L. lota* depth ( $Z_{MD}$ ) using a non-linear regression:

$$Z_{MD} = (D_{oy} + m)[alog_{10}(I_0) + Z_N], \quad (4)$$

$D_{oy}$  was used as a proxy for  $L_T$ , which was significantly correlated (mean  $L_T = 0.099e^{0.0143 D_{oy}}$ ,  $n = 12$ ,  $r^2 = 0.93$ ,  $P < 0.001$ ). 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 (Statsoft Inc., Tulsa, OK, U.S.A).  $Z_N$  is an estimate of the depth of *L. lota* (at night), the term  $m$  accounts for the increasing influence of the day of the year and  $(D_{oy} + m)$  describes the slope of the light and 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 *L. lota* ( $I_{Z_{corr}}$ ):

$$I_{Z_{corr}} = (ce^{bD_{oy}})e^{\{-0.5[(t-p)q^{-1}]^2\}} \quad (5)$$

with  $t$  as the daytime (hhmm) and  $b$ ,  $c$ ,  $p$  and  $q$  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 1),  $p$  and  $q$  are the coefficients of a Gaussian bell-shaped curve, which is suitable to describes the light intensity in relation to daytime (Fig. 2).

Both non-linear-regressions were fitted with a Levenberg–Marquard least-squares algorithm with a maximum numbers of 1000 iterations and a 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 ( $b$ ,  $c$ ,  $p$  and  $q$ , respectively).

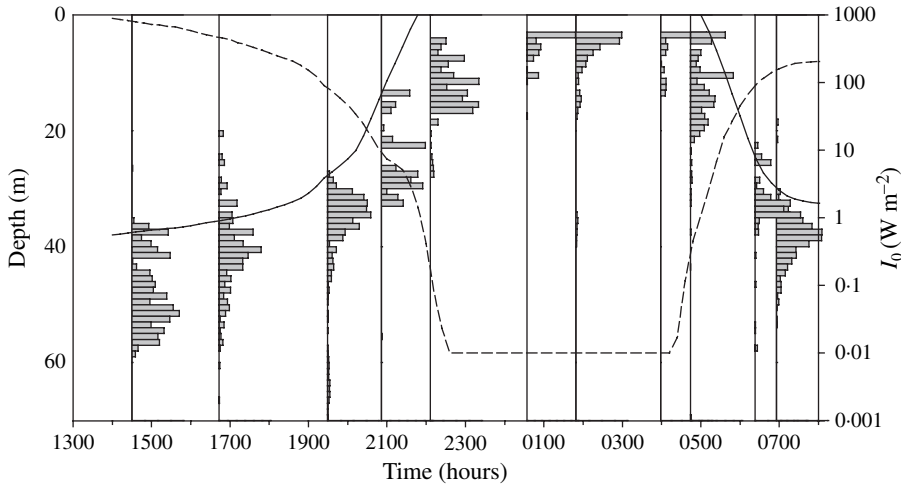


FIG. 2. Diel vertical migration of *Lota lota* on 29 June 2007: the relative abundance at depth of young-of-the-year *L. lota* at the various times of the day (■). (—), the depth of the  $0.01 \text{ W m}^{-2}$  isolume; the ----, light levels above the surface ( $I_0$ ).

## RESULTS

### LOTA LOTA DISTRIBUTION

During the 2 years of the investigation, only one *C. lavaretus* and two cyprinid larvae were caught. The rest of the catch consisted of YOY *P. fluviatilis* and *L. lota*. The first *L. lota* larvae were caught at the middle of May and pelagic juveniles could be caught until August (Table II). From the middle of August, juvenile *L. lota* were difficult to catch but could still be observed by echosounding and identified by their TS. The observed TS of *L. lota* ranged from  $-80$  to  $-70$  dB in May to  $-69$  to  $-58$  dB in August. The SED of YOY *L. lota* could be observed in the echograms from 4 May 2006 and 3 May 2007 until 5 September 2006 and until 27 August 2007 in 2006 and 2007, respectively.

During May, *L. lota* daytime and night-time depths were similar (Fig. 3). From June onwards, the fish performed pronounced DVM, staying in the epilimnion (between 5 and 10 m depth) at night and at the metalimnion or hypolimnion during the day. *Lota lota* ascended to the epilimnion at dusk and descended to the hypolimnion at dawn (Fig. 2). By August, *L. lota* DVM reached amplitudes of 70 m (Fig. 3). Day-time mean depths of fish increased from May to August and were strongly correlated to the day of the year (Fig. 3). Night-time depths of *L. lota* decreased during May and early June and remained constantly above 10 m depth after the middle of June.

### THE RELATIONSHIP BETWEEN LIGHT AND *L. LOTA* DVM

Within the 114 *L. lota* observations from 25 surveys performed in 2006 and 2007, the light intensity above the surface ranged from 0.0 (several occasions at night) to  $922.8 \text{ W m}^{-2}$  on 22 July 2007 at 1342 hours. A maximum light



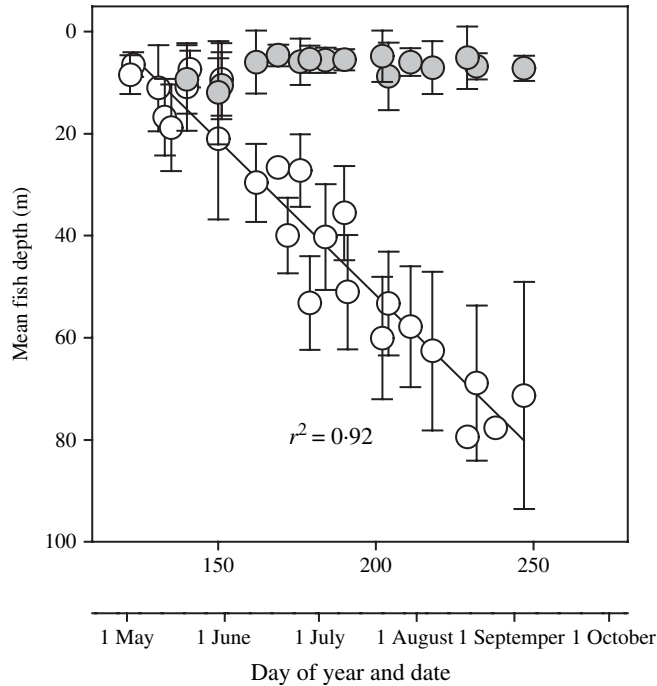


FIG. 3. The maximum (at day, ○) and minimum (at night, ●) mean depth ( $\pm$ s.d. calculated from equation 3) of young-of-the-year *Lota lota* at a given survey date between May and September. Mean depth of *L. lota* was calculated from equation 2. Data from hydroacoustic surveys performed in 2006 and 2007 are shown. The curve was fitted by:  $y = 0.607x - 69.751$ .

intensity of  $116.0 \text{ W m}^{-2}$  experienced by larval *L. lota* was calculated on the 3 May 2007 at 1036 hours at a mean depth of 8.4 m.

The ascent and the descent of *L. lota* was related to the light intensity at the surface, because the highest changes in depth occurred at sunrise and after sunset (Fig. 4). Furthermore, the mean *L. lota* depth was significantly related to surface light intensities, which increasingly affected the mean depth of fish as the summer progressed [Fig. 5(a)]. The model of equation 4 provided a good fit to the observed data ( $r^2 = 0.91$ ), with all estimated coefficients contributing significantly to the model (Table III). The model also provided an adequate value for the minimum depth of *L. lota* of 4.5 m ( $\pm 2.4$  m CI), which was similar to the depth at night observed by hydroacoustic and net catches (Fig. 3 and Table II). The regression model confirmed the increasing influence of  $I_0$  on the DVM of YOY *L. lota* during the progression of the summer.

The second non-linear regression model equation 5 indicated that *L. lota* lived in illuminated water layers until *c.* 180  $D_{\text{oy}}$  (which was 30 June), but afterwards did not inhabit water layers with light intensities  $>0.1 \text{ W m}^{-2}$  [Fig. 5(b) and Table IV]. In other words, the amplitude of the *L. lota* DVM became so high by the end of June, that YOY *L. lota* experienced low light intensities  $<0.1 \text{ W m}^{-2}$  during the entire day.

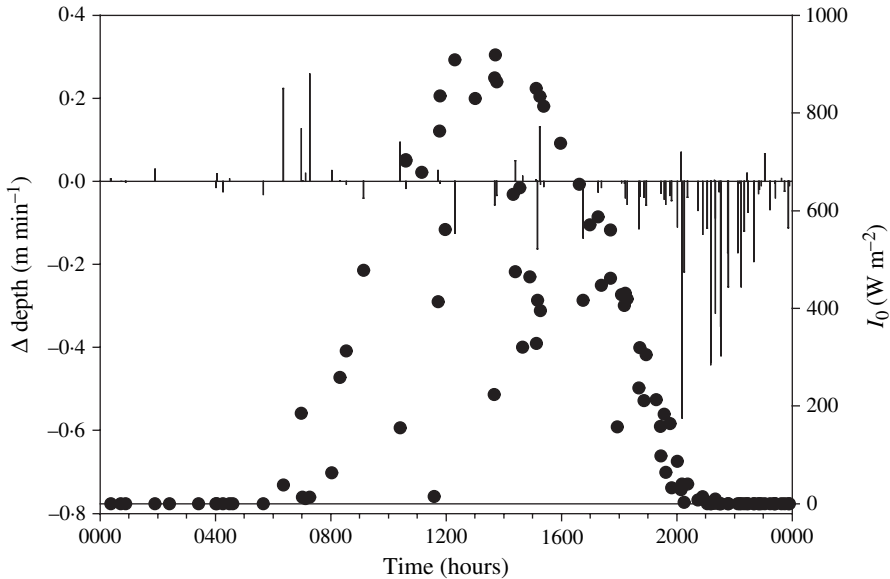


FIG. 4. The relationship between light intensity above the surface ( $I_0$ , ●) and the change in depth ( $\Delta$  depth, ■) of young-of-the-year *Lota lota*. Data are from 114 measurements at 25 survey dates, but recordings from dawn were performed on just five occasions, resulting in a lower number of samples at dawn.

In May and until mid-June,  $I_{Z_{\text{corr}}}$  was highest during daylight hours, but from the end of June (176  $D_{\text{oy}}$ ) there was evidence for *L. lota* to experience the highest light levels during crepuscular hours (Fig. 6). Thus, the appearance of crepuscular light ‘windows’ in the diel light cycle experienced during the DVM of *L. lota* coincided with the avoidance of bright light levels in the day. The  $I_{Z_{\text{corr}}}$  at these crepuscular light windows decreased by more than two orders of magnitude during the summer (from  $0.016 \text{ W m}^{-2}$  on  $D_{\text{oy}}$  176 to  $0.0001 \text{ W m}^{-2}$  on  $D_{\text{oy}}$  232).

The mean light intensity at depth ( $I_{Z_{\text{corr}}}$ ) at a given  $D_{\text{oy}}$  was significantly correlated with mean  $L_T$  at the same day of the year ( $n = 12$  catch dates; see Table II,  $r^2 = 0.93$ ,  $P < 0.001$ ; Fig. 7). Thus, the larger *L. lota* grew, the lower the light intensities they experienced.

## DISCUSSION

The DVM of Lake Constance *L. lota* is an example for the importance of hydroacoustic methods to observe fine-scale distributions of fishes. YOY *L. lota* were present in the pelagic zone from the beginning of May until the end of August, which is much longer than previously assumed (Wang & Appenzeller, 1998; Miler & Fischer, 2004). Miler & Fischer (2004) were the first to discover the daytime distribution of YOY *L. lota* below the thermocline in Lake Constance. The precise temporal and spatial distribution patterns, however, remained unknown and consequently, the great amplitude of *L. lota* DVM exceeding 70 m was not detected.

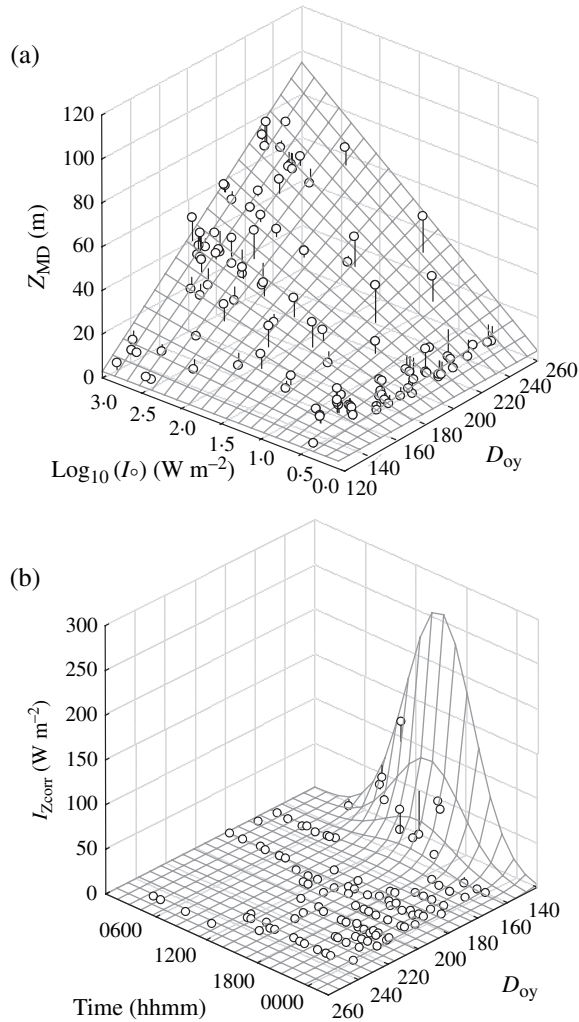


FIG. 5. The relationship between *Lota lota* diel vertical migration and light intensity at the surface ( $I_0$ ), day of the year ( $D_{oy}$ ) and daytime estimated by non-linear regressions. (a) The influence of  $D_{oy}$  year and  $I_0$  on the mean depth of young-of-the-year (YOY) *Lota lota* ( $Z_{MD}$ ) (see also Table III). (b) The influence of daytime and  $D_{oy}$  on the light intensity at depth ( $I_{Z_{corr}}$ ) experienced by YOY *L. lota* (see also Table IV) [○, data points; —, the reference line to the three-dimensional model fit (grey grid)].

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). Lough & Potter (1993), however, 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 *L. lota* as a transition between the pelagic larval and demersal juvenile stage has also been discussed by Miler & Fischer (2004). The YOY *L. lota* in Lake Constance, however, migrated to the surface

TABLE III. Results from the non-linear regression modelling the influences of day of the year ( $D_{oy}$ ) 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

Model-equation	$r^2$	$F$	$P$	No. it.
$Z_{MD} = (D_{oy} + m) [a \log_{10} (I_0) + z_N]$	0.908	1021.067	<b>&lt;0.001</b>	6
Coefficient	Estimate	CI	$t$	$P$
$m$	-120.648	$\pm 7.698$	-31.054	<b>&lt;0.001</b>
$a$	0.214	$\pm 0.018$	23.385	<b>&lt;0.001</b>
$z_N$	4.501	$\pm 2.239$	3.982	<b>&lt;0.001</b>

CI, the 95% CI for the coefficient estimate;  $F$ , the  $F$ -value from the model-validating ANOVA, which compares the variance explained by the model against the variance within the residuals; No. It., to the number of iterations, until the convergence criteria of  $10^{-6}$  were met;  $P$ , the significance values from the  $F$ -statistics and  $t$ -statistics printed bold when  $<0.5$ ;  $r^2$ , the amount of variance explained by the regression model;  $t$ ,  $i$  the value from the  $t$ -statistic to confirm significant contribution of the coefficient to the regression model.

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 *L. lota* 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 *L. lota* seems to be regulated by the light intensity above the surface, because the fish commenced their ascent after sunset and descended to their daytime depth with sunrise. Light intensity regulates the DVM behaviour of many organism (Appenzeller & Leggett, 1995; Lampert & Sommer, 1999; Cech *et al.*, 2005) because DVM is commonly regarded as an antipredation behaviour (Stich, 1989; Hays, 2003; Scheuerell & Schindler, 2003; Hrabik *et al.*, 2006; Stratton & Kesler, 2007), and the risk of predation is directly

TABLE IV. Results from the non-linear regression modelling the influences of daytime ( $t$ ) and day of the year ( $D_{oy}$ ) on the experienced light intensity at depth ( $I_{Z_{corr}}$ ) of young-of-the-year *Lota lota*.  $C$ ,  $b$ ,  $p$  and  $q$  are the coefficients of the model equation estimated by a Levenberg–Marquardt least-squares algorithm (see Table III)

Model-equation	$r^2$	$F$	$P$	No. It.
$I_{Z_{corr}} = (ce^{bD_{oy}})e^{-0.5[(t-p)q^{-1}]^2}$	0.92	333.321	<b>&lt;0.001</b>	101
Coefficient	Estimate	CI	$t$	$P$
$c$	$1.336 \times 10^9$	$\pm 2.740 \times 10^9$	0.967	0.336
$b$	-0.129	$\pm 0.273$	-16.171	<b>&lt;0.001</b>
$p$	0.615	$\pm 0.025$	49.664	<b>&lt;0.001</b>
$q$	0.163	$\pm 0.019$	17.329	<b>&lt;0.001</b>

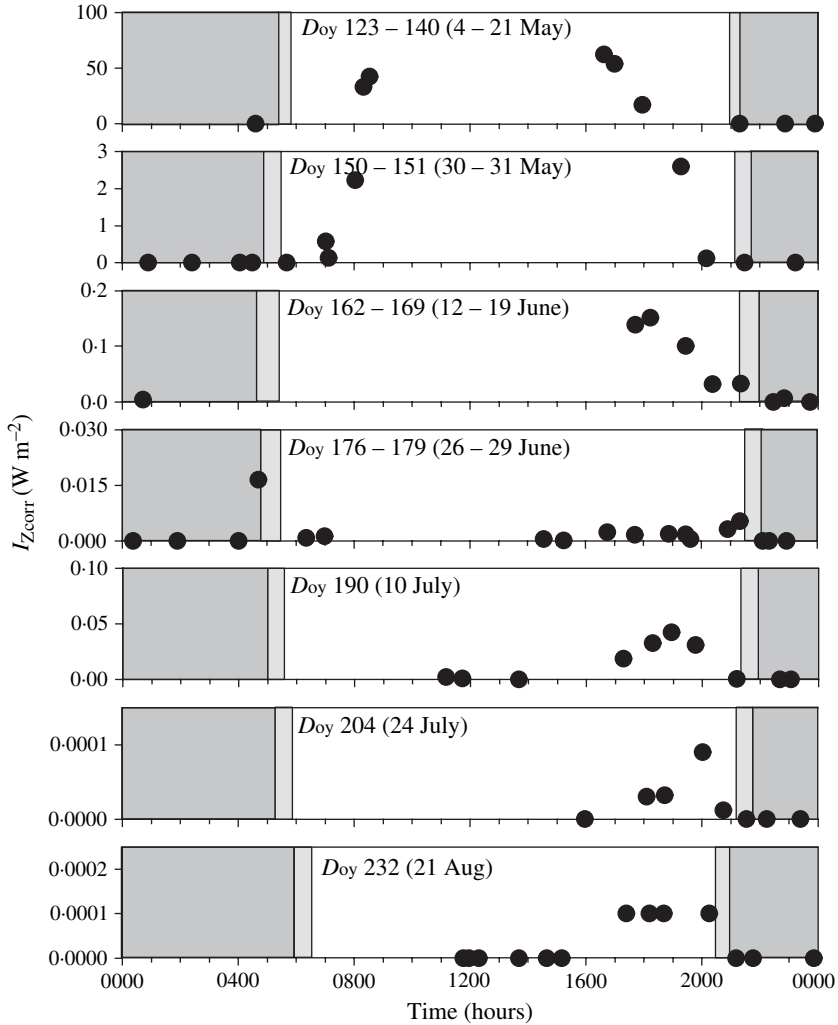


FIG. 6. Evidence for crepuscular light ‘windows’ at dusk and dawn from day of the year ( $D_{oy}$ ) 176. Before, light intensities ( $I_{zcorr}$ ) at the mean depth of *Lota lota* were following the diel light cycle, as shown in Fig. 5(b). Note the different scale on the y-axis (■, night; □, crepuscular hours).

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 just recently been suggested to be a genetically inherent trait (Mehner *et al.*, 2007). Because no evidence for the acute predation of YOY *L. lota* was found (neither in stomach of *P. fluviatilis* nor *C. lavaretus* the two most abundant species in the pelagic zone of Lake Constance; W. N. Probst, pers. obs.; G. Thomas, pers. comm.), the DVM behaviour of YOY *L. lota* may represent a genetic fixation from ‘a ghost of the predation past’ (Gliwicz & Jachner, 1992).

The DVM of *L. lota* is very strictly related to the day of the year, which also correlated strongly with the size of YOY fish. It seems therefore plausible, that

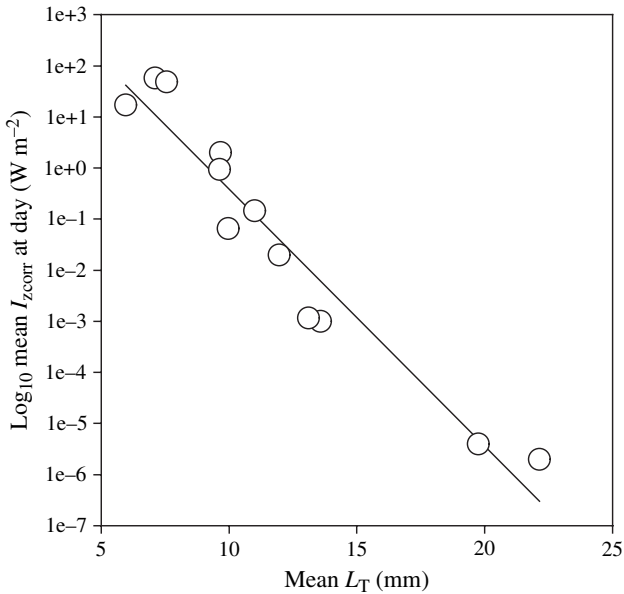


FIG. 7. Relationship between the total length ( $L_T$ ) from net catches in 2006 and 2007 and the ambient light intensity at mean depth of *Lota lota* ( $I_{zcorr}$ ).  $I_{zcorr}$  was averaged for all daytime values within a day, and  $L_T$  was averaged for all *L. lota* caught on the same day of the year (see Table II). Note the logarithmic scale on the y-axis. The curve was fitted by:  $y = -5.024x + 4.605$  ( $r^2 = 0.93$ ).

the increasing amplitude of *L. lota* DVM is a result of the increasing body size and pigmentation, which in turn may increase their perceived predation risk. Accordingly, *L. lota* do not commence their DVM before the beginning of June. At this time of the year, fish are still in the larval stage without significant skin pigmentation and an average  $L_T$  of <10 mm (Wang & Appenzeller, 1998). Larval *L. lota* remain in well-illuminated water layers, where they experience high light intensities, which are directly related to light intensities above the surface. As *L. lota* metamorphose into juveniles by the middle of June, their skin becomes pigmented and develops a golden-brown colour. Metamorphosis from the larval into the juvenile stage, which also coincides with an increasing body size, may therefore induce DVM and determine its amplitude.

When YOY *L. lota* commence their DVM, they inhabit increasingly dark water layers with low light intensities at which successful feeding may be impaired. Fig. 6 suggests that from the end of June onwards, *L. lota* adjust their DVM to experience crepuscular light ‘windows’, at which they can optimize the risk between (potential) predation and feeding (Clark & Levy, 1988; Appenzeller & Leggett, 1995; Scheuerell & Schindler, 2003). Furthermore, Hartmann (1983) observed higher stomach contents of Lake Constance YOY *L. lota* at dusk, supporting the assumption of crepuscular feeding. Whether the light intensities, which *L. lota* 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 *L. lota* could not be caught during daytime and thus their stomach contents could not be analysed. The visual

irradiance threshold for zooplanktivorous feeding of juvenile salmonids, however, lies between  $10^{-3}$  and  $10^{-4}$  W m<sup>-2</sup> (Henderson & Northcote, 1985), which is about one or two magnitudes higher than the light experienced by *L. lota* (at day in August). Hence, the low light levels experienced by deep migrating *L. lota* during the day suggest that feeding may be limited at this time of the day.

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

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