

Location and timing of the deposition of egg strands by perch (*Perca fluviatilis* L.): the roles of lake hydrology, spawning substrate and female size

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Received May 24, 2011

Revised June 22, 2011

Accepted July 25, 2011

ABSTRACT

Key-words:
SCUBA diving,
Aquatic
vegetation,
Common
stonewort,
Chara vulgaris,
Common reed
*Phragmites
communis*,
Lake
management

The reproduction biology of perch *Perca fluviatilis* was studied in relation to lake hydrology, spawning substrate and female size using SCUBA divers during late April and mid-May 2009 in Chabařovice Lake, Czech Republic. An extreme displacement of water mass, induced by a long-lasting strong wind, caused the abundance of egg strands to differ significantly between individual parts of the lake. On average, 91% of perch spawning activity occurred at depths greater than 3 m. The mean concentration of dissolved organic carbon (DOC) indicated that the lake belongs to the category where DOC influencing the penetration of ultraviolet radiation, is not responsible for the deep deposition of egg strands by perch. Most probably, the avoidance of shallow depths (<3 m) results from strong wind/waves coming from any direction. Larger perch females started to spawn earlier than their smaller conspecifics and they used shallower depths for depositing their egg strands. As a spawning substrate, perch strongly selected dead submerged vegetation, such as common reed *Phragmites communis* and worm weed *Artemisia* sp. These substrates, however, reveal signs of progressive degradation and seem likely to disappear from the lake within several years.

RÉSUMÉ

Lieu et date de la ponte des rubans d'œufs par la perche (*Perca fluviatilis* L.) : les rôles de l'hydrologie lacustre du substrat de ponte et de la taille des femelles

Mots-clés :
plongée
sous-marine,
végétation
aquatique,
Chara vulgaris,
armoise,
roseau commun

La biologie de la reproduction des perches *Perca fluviatilis* a été étudiée en relation avec l'hydrologie lacustre, le substrat de ponte et la taille des femelles par des plongeurs de la fin avril à la mi-mai 2009 dans le lac Chabařovice, République Tchèque. Un déplacement extrême de la masse d'eau, induit par un vent fort de longue durée, a provoqué une abondance des rubans d'œufs différant considérablement entre les différentes parties du lac. En moyenne, 91 % de l'activité de frai des perches est survenue à une profondeur supérieure à 3 m. La concentration moyenne en carbone organique dissous (DOC) indiquant que le lac appartient à la catégorie où le DOC influence la pénétration du rayonnement ultraviolet, n'est pas responsable du dépôt profond de rubans d'œufs par la perche. Très probablement, l'évitement des faibles profondeurs (<3 m) résulte du vent fort et/ou des vagues venant de n'importe quelle direction. Les plus grandes perches femelles

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1 ont commencé à frayer plus tôt que leurs congénères plus petites et elles ont uti-
 2 lisé des profondeurs plus faibles pour le dépôt de leurs rubans d'œufs. Comme
 3 substrat de frai, la perche a fortement sélectionné la végétation morte submergée
 4 telle que le roseau commun *Phragmites communis* et l'armoise. Ces substrats,
 5 cependant, montrent des signes de dégradation progressive et semblent suscep-
 6 tibles de disparaître du lac dans quelques années.

INTRODUCTION

2 The location and timing of perch [*Perca fluviatilis* L. in Eurasia; *P. flavescens* (Mitchill) in North
 3 America] spawning activity is influenced by many biotic and abiotic factors, among which
 4 temperature and spawning substrate seem to be the most important (e.g. Treasurer, 1983;
 5 Rask *et al.*, 1990; Gillet *et al.*, 1995; Gillet and Dubois, 1995; Sandström *et al.*, 1997; Huff *et al.*,
 6 2004; Gillet and Dubois, 2007; Čech *et al.*, 2009). Frequently lake hydrology and, especially,
 7 prevailing wind and from that resulting waves, also contributed significantly to the place and
 8 depth of egg strand depositions as well as to the length of the spawning period (Jones,
 9 1982; Newsome and Aalto, 1987; Probst *et al.*, 2009). It has also been suggested from large
 10 pre-alpine lakes (Lake Geneva, Lake Constance) that larger female perch have a tendency
 11 to spawn later than small ones and that they use deeper spawning places (Gillet *et al.*, 1995;
 12 Gillet and Dubois, 2007; Probst *et al.*, 2009). Completely opposite results have, however, been
 13 published from Klíčava Reservoir, Czech Republic (Holčík, 1969; female size only) and from
 14 an inundated quarry pit, La Gombe, Belgium (Dalimier *et al.*, 1982). More recently, Williamson
 15 *et al.* (1997) and Huff *et al.* (2004) have shown that the concentration of dissolved organic
 16 carbon (DOC) plays a crucial role in the depth distribution of egg strands. In low-DOC lakes
 17 (DOC ~1.1 mg · L⁻¹) where damaging ultraviolet radiation (UVR) penetrates to deeper layers
 18 of the water column, perch, in an effort to protect their eggs, are forced to spawn in much
 19 greater depths compared to higher-DOC lakes (DOC ≥ 4.7 mg · L⁻¹; Huff *et al.*, 2004).

20 The present study focused on the location and timing of the deposition of egg strands by
 21 perch in the newly created Chabařovice Lake. In this lake, Čech *et al.* (2009, 2010) have
 22 previously reported that 92% (year 2007) and 88% (2008) of egg strands were deposited at
 23 depths greater than 3 m which closely resembles the situation in the low-DOC Lake Giles,
 24 Pennsylvania, described by Huff *et al.* (2004; 92% of egg strands were deposited at depths
 25 greater than 3 m). In Chabařovice Lake, the concentration of DOC has never been analyzed.
 26 Moreover, it is believed that other factors such as the presence of an appropriate spawning
 27 substrate, temperature and wind (coming from all directions due to deforestation of the sur-
 28 rounding landscape) are responsible for such deep deposition of egg strands (in extreme up
 29 to more than 20 m; Čech *et al.*, 2009, 2010).

30 The main questions of the present study were: (1) Is the location of perch egg strands deposi-
 31 tion affected by the lake's hydrology, especially by a long-lasting strong wind in one direction
 32 causing water mass displacement? (2) Is the deep deposition of egg strands reported for
 33 Chabařovice Lake by Čech *et al.* (2009, 2010) a result of low DOC concentration in the lake or
 34 is it more likely a result of cumulative effect of e.g. wind/waves, temperature and the presence
 35 or absence of appropriate spawning substrates? (3) Does the size of egg strands differ dur-
 36 ing the spawning season or with depth of spawning? (4) Does the size of egg strands differ
 37 according to the spawning substrate used (dead or living submerged vegetation at least)?

38 This study is part of a long-term project focusing on succession processes in a newly created
 39 opencast mine lake (see also Čech *et al.*, 2009, 2010).

MATERIALS AND METHODS

> STUDY AREA

40 The study was carried out in the oligo- to mesotrophic Chabařovice Lake, Czech Republic
 41 (80 km north-west of Prague), which has an area of c. 200 ha, volume of 18 × 10⁶ m³ and

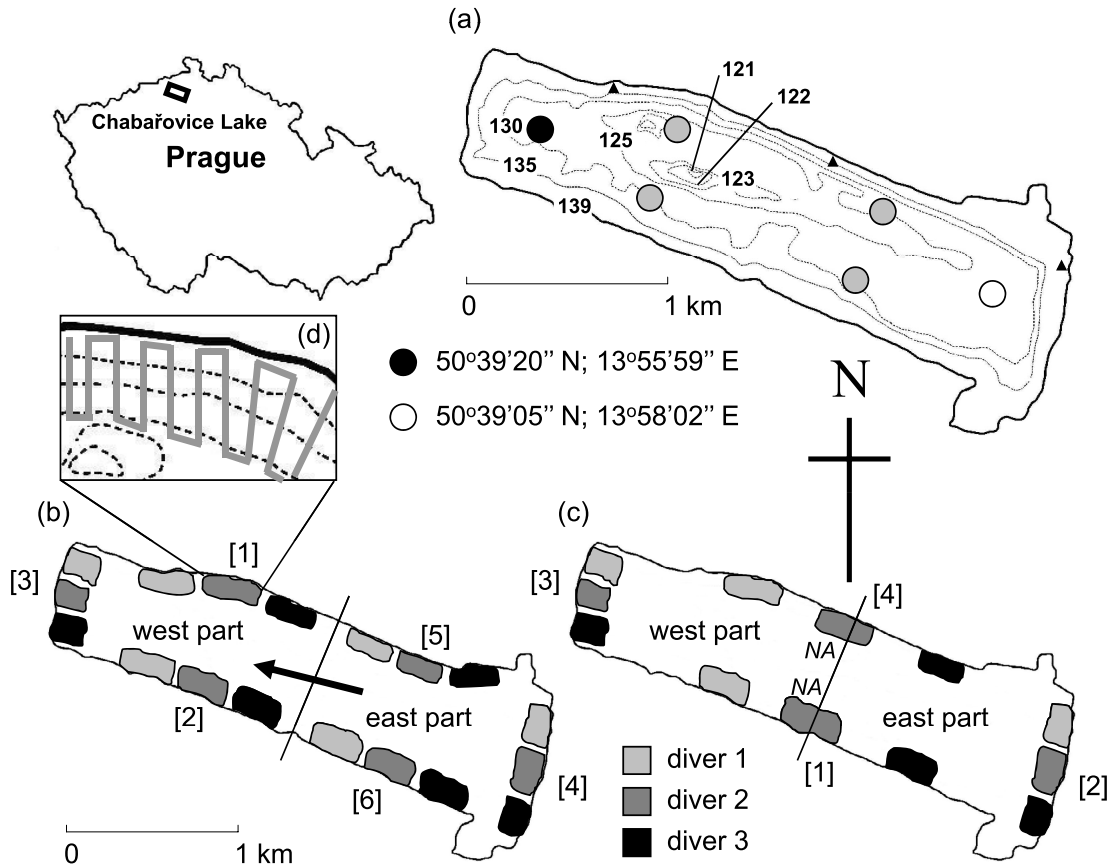


Figure 1

A map of Chabařovice Lake and its location in the Czech Republic. (a) Contour map of the lake. Numbers indicate bottom altitude in meters above sea level. Dots (black, grey, white) indicate places from which water for measurement of dissolved organic carbon was taken and where temperature as well as dissolved oxygen was measured in the whole water column on 28 April and 19 May 2009 (in May the DOC data were provided by the Elbe River Authority). At those points Secchi disc depth was also measured. Longitude and latitude of the black and white dots is given (data used in Figure 3). Black triangles indicate locations where surface water temperature was measured daily from 15 March 2009. (b, c) A schematic distribution of the individual diving localities where three divers simultaneously monitored egg strands and spawning substrates of perch. Numbers in brackets show the order of sampling. (b) 27–30 April 2009. The black arrow shows the direction of the long-lasting strong wind prior to and during the sampling period. (c) 18–20 May 2009. NA, these localities were not included into the analysis of the lake hydrology effect on the location of perch egg strands deposition. (d) An example of the systematic parallel transect sampling (diver No. 2; 10 transects) from 0 m towards the 12 m depth. The short turning trajectories at a depth of 0 and 12 m were not sampled.

maximum depth of 22 m (Figure 1a). Chabařovice Lake is a newly created, opencast mine lake where aquatic restoration started in 2001 (Čech et al., 2009, 2010). The water level did not fluctuate during the study period. This water body has no obvious limitation to perch spawning activity in terms of depth and spawning substrates, which are numerous (e.g. dead trees, dislodged branches, bushes, beds of dead common reed *Phragmites communis* and worm weed *Artemisia* sp., Eurasian water milfoil *Myriophyllum spicatum* and common stonewort *Chara vulgaris*) and some of which are present to the deepest part of the lake (Čech et al., 2009, 2010). However, especially the beds of dead common reed and worm weed, the most important substrates for perch spawning, reveal signs of progressive degradation and this substrate seems likely to disappear from the lake within several years (Čech et al., 2009, 2010).

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1 Despite the extensive stocking programme focusing on larger individuals of pike *Esox lucius*
2 L., zander *Sander lucioperca* (L.) and wels catfish *Silurus glanis* L. (years 2005–2007; for
3 biomanipulation purposes), perch is still the most abundant predatory fish in the lake, and a
4 key species, significantly affecting the whole lake ichthyofauna (Peterka *et al.*, 2009; Peterka
5 and Čech, unpubl. data).

> SAMPLING

6 Three SCUBA divers simultaneously monitored perch spawning activity in the 0–12 m depth
7 layer (systematic parallel transect sampling) during 27–30 April and 18–20 May 2009. At indi-
8 vidual localities, the divers were landed from the boat at a distance of at least 400 m (north
9 and south banks) or 200 m (west and east banks) from each other according to GARMIN
10 GPSmap 60CSx (Figure 1b and 1c). Each diver swam from a very shallow littoral zone (depth
11 0 m) towards the depth of 12 m (transect 1), sampling the space 3 m to each side of him,
12 then turned 90°, performed ten standard fin strokes (c. 15 m distance – not sampled), turned
13 another 90° and swam back from 12 m deep towards the 0 m depth (transect 2; Figure 1d).
14 In total, 168 transects were sampled during 27–30 April (18 day dives, 20 h underwater) and
15 120 transects during 18–20 May 2009 (12 day dives, 14 h underwater). In contrast to the
16 previous studies of Čech *et al.* (2009, 2010; sampling in various depth layers parallel to the
17 shore) from the years 2007 and 2008, in 2009 a different sampling scheme was used in or-
18 der to monitor all the depth layers more equally. The depths >12 m, although comprising a
19 spawning habitat for perch, especially at the end of the spawning period (*cf.* Čech *et al.*, 2009,
20 2010), were omitted from sampling because (i) depths >12 m comprised almost 60% of the
21 lake which would make the research even more demanding and because (ii) the proportion of
22 greater depths in the lake is much less equal in comparison to shallower depths (0–12 m in
23 particular). Chabařovice is a trough-like lake with more or less uniform slopes but with a moon
24 landscape with many craters of various and unpredictable depths (a result of coal mining) on
25 the main bottom (Figure 1a). In this area (depths >12 m), perch egg strands are deposited
26 on dead common reed, trees and branches, which distribution is, however, extremely scarce
27 (<1% of the ground coverage) and patchy (Čech, unpubl. data).

28 During both sampling surveys, the divers recorded the type of substrate on which individual
29 egg strands were deposited, the depth of their deposition and the sizes of the egg strands
30 (width; using a ruler). This information was noted under water on a plastic slate for each
31 individual egg strand in each individual transect. The sizes of the spawning perch females
32 were reconstructed from the width of individual egg strands using the equation of Dubois
33 *et al.* (1996).

34 A detailed substrate survey was carried out at the same time as the monitoring of perch
35 spawning activity. For the purpose of the present study, the categories of potential perch
36 spawning substrate recorded were as follow: (i) flooded terrestrial vegetation, (ii) trees and
37 branches, (iii) Eurasian water milfoil, (iv) common reed, (v) worm weed, (vi) common stonewort
38 and (vii) others. The large stands of curly pondweed *Potamogeton crispus* observed in the lake
39 in 2007 (Čech *et al.*, 2009) were much less abundant in year 2008 (<<5% of the 2007 situation;
40 Čech *et al.*, 2010), and had completely vanished from the lake in 2009. The actual ground
41 coverage occupied by individual spawning substrates, with a clear dominance of common
42 stonewort, especially in the 3–11 m depth layers (fourfold increase in abundance compared
43 to 2007 situation) is given in Figure 2.

44 Temperature and dissolved oxygen in the whole water column were measured using a cali-
45 brated YSI 556 MPS probe on 28 April and 19 May (midday). Surface water temperature was
46 measured daily (morning) from 15 March at three separate locations around the lake shore
47 (Figure 1a) in order to catch the beginning of the perch spawning period at 8–10 °C (Kubečka,
48 1992). Water for DOC measurement was taken from the epilimnion, 30 cm below the water
49 surface, at 6 places equally distributed around the lake (Figure 1a). This water was filtered in
50 the field, cooled and transported to the laboratory. DOC was analyzed in the samples filtered
51 through GF-5 filters with a TOC 5000A analyzer (Shimadzu, Japan).

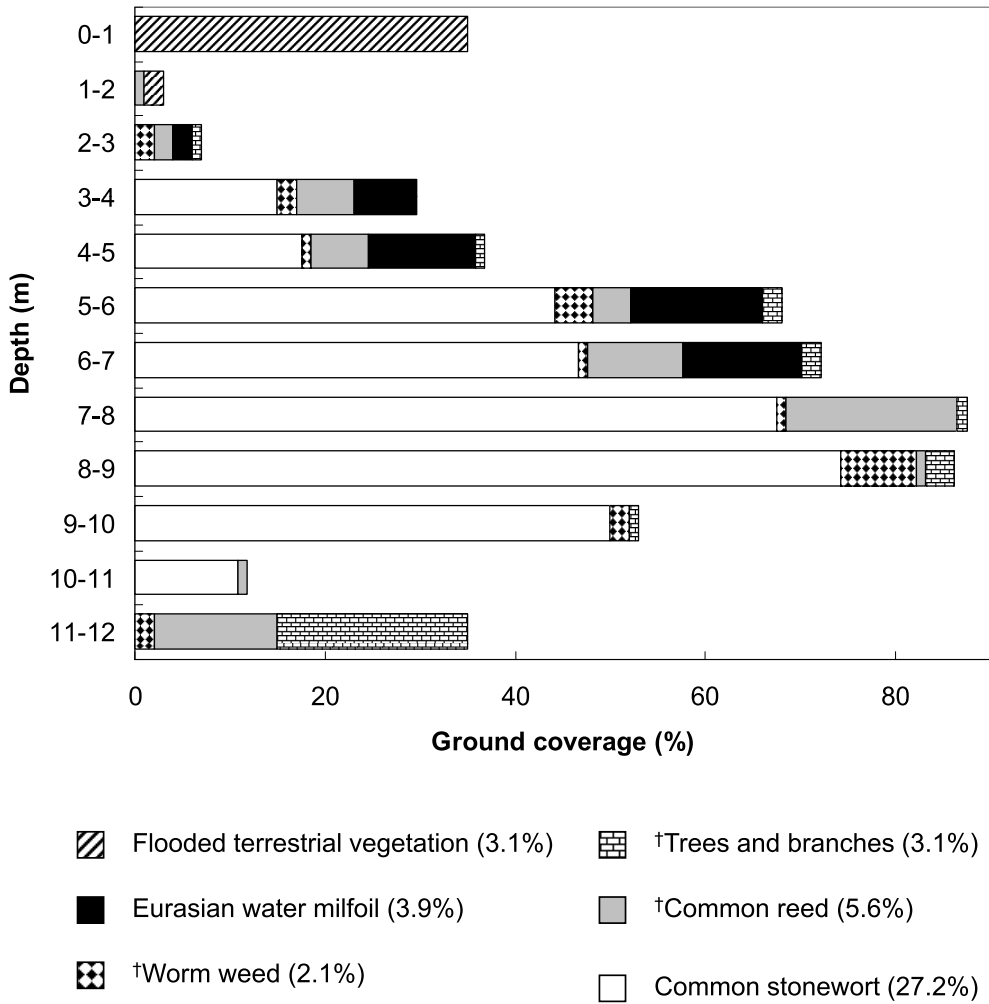


Figure 2
 Distribution of potential spawning substrates for perch in Chabařovice Lake in spring 2009 in 0–12 m depth layers. Mean ground coverage of individual spawning substrates for the whole vertical profile sampled is given in parentheses (total ground coverage composed of submerged vegetation in the 0–12 m depth layers was 44.9%; bare bottom, especially mud and boulders, covered the rest).

The data were tested using the Mann-Whitney *U*-test (lake hydrology effect on location of egg strands deposition), Kruskal-Wallis test (site and period related depth distribution of egg strands; size of egg strands in individual sampling periods), one-way ANOVA for unequal *n* (size of egg strands according to the spawning substrate exploited), regression analysis (relationship between the size of egg strands and the depth of deposition) and χ^2 -test (spawning substrate preferences – dead vs. live submerged vegetation). The selection by perch females of appropriate spawning substrate was evaluated using the Ivlev index (Ivlev, 1961).

>RESULTS

During and prior to the first sampling survey (27–30 April) a strong wind coming from the East (12–15 m s⁻¹; Czech Hydrometeorological Institute, unpubl. data) prevailed in the Chabařovice area. Large waves transported the warm, surface water to the west part of the lake (mean temperature in the upper 8 m of the water column 12.9 °C; Figure 3). Consequently, these water masses pushed the cold, deep water to the east part of the lake (mean temperature in the upper 8 m of the water column only 8.2 °C; Figure 3). This temperature

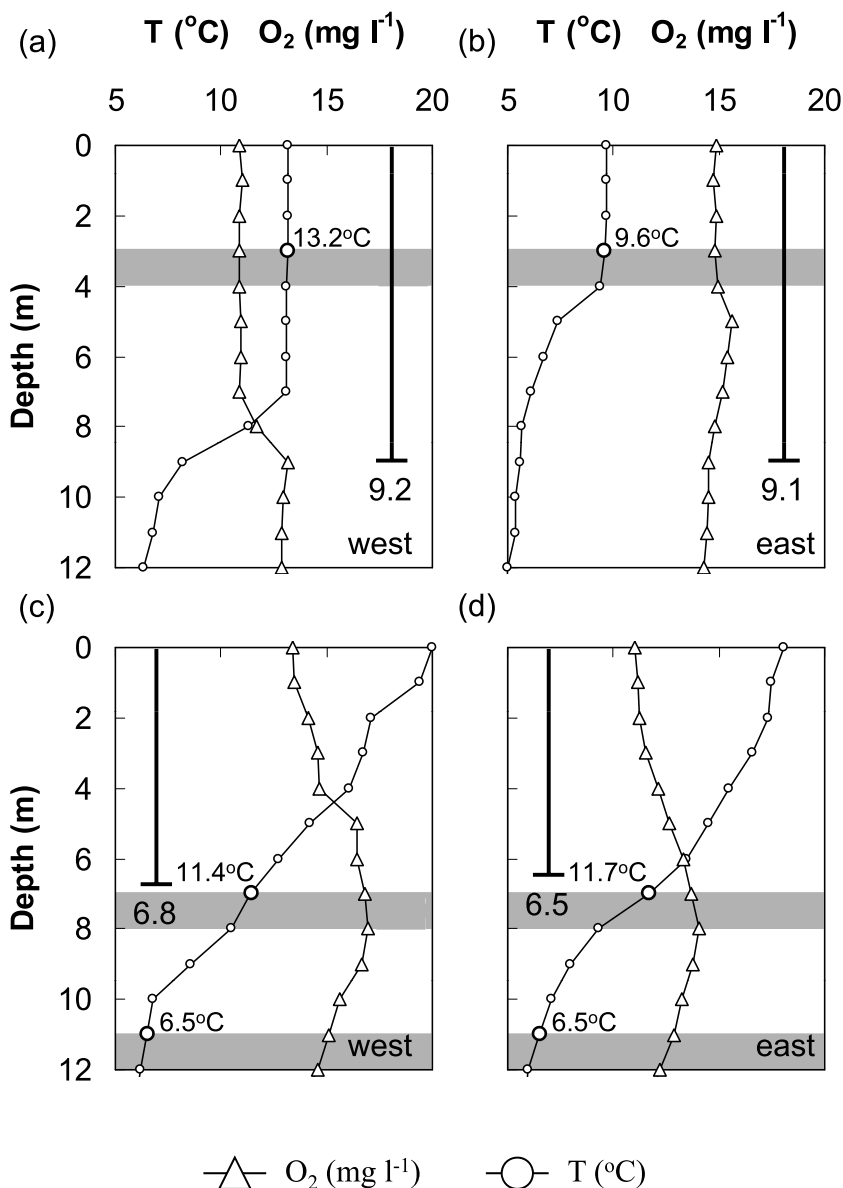


Figure 3

Comparison of the vertical profiles of temperature and dissolved oxygen measured at noon on (a, b) 28 April and (c, d) 19 May 2009 in Chabařovice Lake in the west and east parts of the lake (cf. Figure 1). The horizontal grey bars indicate the depth layers where most egg strands occurred during the first (27–30 April) and the second (18–20 May) sampling surveys (whole lake peak; cf. Figure 4). The vertical bars show the Secchi disk depths.

- 1 difference caused the abundance of egg strands of perch to differ significantly between the
- 2 west and the east parts of the lake (Mann-Whitney *U*-test; $P < 0.01$) being, on average,
- 3 0.56 egg strands · transect⁻¹ in the warmer west part and only 0.16 egg strands · transect⁻¹
- 4 in the colder east part of the lake. The mean depth of egg strands deposition, however, did
- 5 not differ between the west and the east part of the lake (Kruskal-Wallis test; $P = 0.42$) being
- 6 4.3 m and 4.2 m, respectively.
- 7 During the second sampling survey (18–20 May), a long period of calm weather had caused
- 8 stabilization of the water column in the whole lake. The temperature was similar in both parts
- 9 of the lake (mean temperature in the upper 8 m of the water column 15.3 °C in the west and
- 10 14.9 °C in the east part of the lake; mean temperature in the upper 12 m of the water column

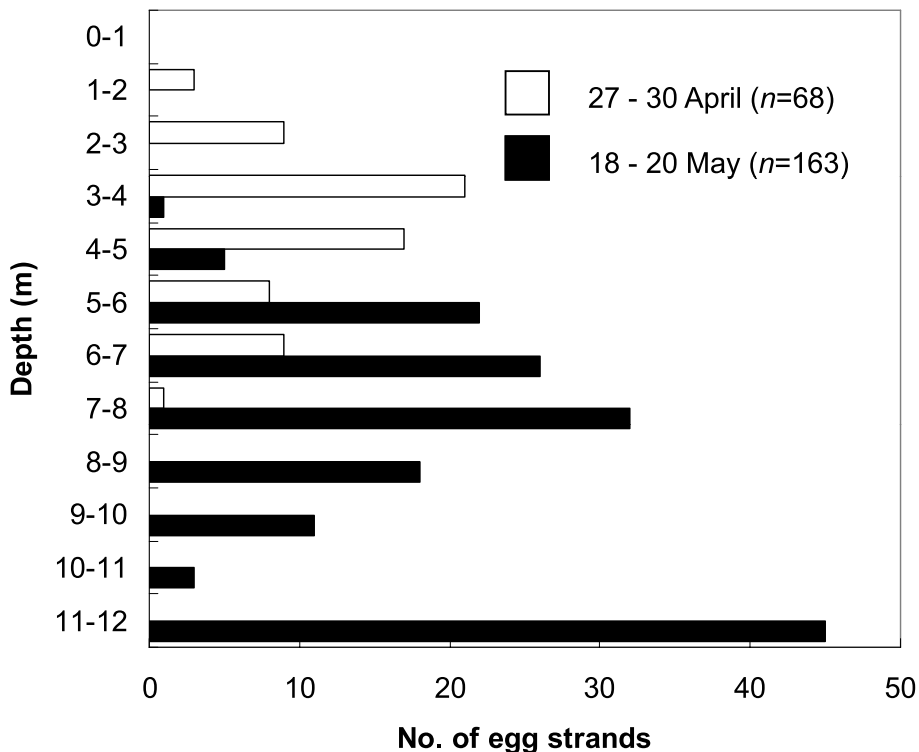


Figure 4

Depth distributions of egg strands of perch in Chabařovice Lake in spring 2009 during 27–30 April (mean depth 4.2 m) and 18–20 May (mean depth 8.6 m). Note that only 0–12 m depth layers were sampled and that in Chabařovice Lake, according to previous results of Čech et al. (2009, 2010), up to ~10% of egg strands is usually spawned at depths >12 m. n, total number of egg strands found during individual sampling surveys.

12.8 °C in the west and 12.4 °C in the east part of the lake; Figure 3). This stabilization of the water column meant that there was no longer any significant difference in the abundance of egg strands between the two parts of the lake (on average 2.1 and 1.5 egg strands · transect⁻¹ in the west and east parts of the lake respectively; Mann-Whitney *U*-test; *P* = 0.25).

The depth distributions of the egg strands differed dramatically between the two sampling dates (Kruskal-Wallis test; *P* < 0.001; Figure 4), being much shallower in late April when the peak of perch spawning activity was in the 3–4 m depth layer, compared to mid-May when the peak was in the 7–8 m and 11–12 m depth layers. On the same dates, continuous warming of the upper layers of the water column was recorded (a temperature increase of 3.2–6.5 °C in the 3–4 m depth layer from late April to mid-May when considering individual parts of the lake; cf. Figure 3). Only during the first sampling survey were 12 egg strands found in water <3 m in depth (*i.e.* 17.6%; Figure 4), but even at this time no egg strands were found in water shallower than 1 m.

The mean concentration of *DOC* in the lake was 6.2 mg · L⁻¹ (min.-max., 5.7–7.6 mg · L⁻¹) indicating that according to the classification of Huff et al. (2004) Chabařovice Lake belongs to the category of higher-*DOC* lakes, *i.e.* to the category where *DOC* (penetrating UVR in fact) is not responsible for deep deposition of egg strands of perch.

The size (width) of the egg strands differed significantly between the two sampling dates (Kruskal-Wallis test; *P* < 0.001; Figure 5) being on average 10.7 cm in late April and 8.7 cm in mid-May. In other words, larger perch females were spawning during the first compared to the second sampling survey. During each sampling date, there was no trend in the increase or decrease of the size of egg strands with the depth of deposition (regression analysis 27–30 April; *P* = 0.20; regression analysis 18–20 May; *P* = 0.77; cf. Figure 5), however, when both

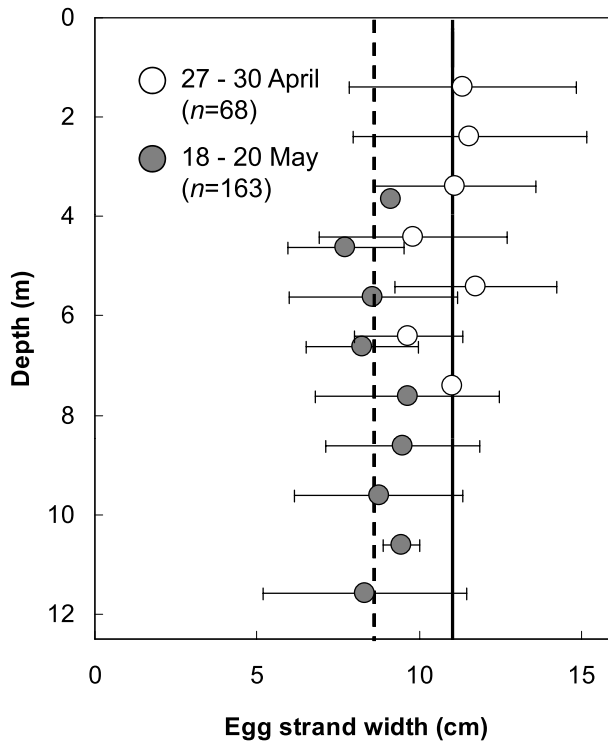


Figure 5

Sizes of egg strands (mean \pm S.D.) of perch in individual depth layers of Chabařovice Lake in spring 2009 during 27–30 April and 18–20 May. The black line shows the average width of the egg strands during the first sampling survey (10.7 cm), and the dashed line during the second sampling survey (8.7 cm).

- 1 sampling dates were combined, the size of the egg strands clearly decreased with the depth
 2 of deposition (regression analysis; $P < 0.001$).
- 3 Although common stonewort comprised $>60\%$ of the submerged vegetation in the 0–12 m
 4 depth layers of Chabařovice Lake (cf. Figure 2), the substrate most frequently used for perch
 5 spawning was common reed, worm weed and trees and branches (82.4% of egg strands during
 6 the first survey and 80.4% of egg strands were deposited on those substrates during the
 7 second survey; Figure 6). Clearly, the perch did not use live and dead submerged vegetation
 8 in proportion to their presence in the lake (χ^2 -test 27–30 April; $P < 0.001$ and χ^2 -test 18–20
 9 May; $P < 0.001$). According to the values of the Ivlev index, perch strongly selected dead
 10 submerged vegetation (Ivlev index from 0.5 to 0.66 for dead common reed, worm weed and
 11 trees and branches; the only exception being in the case of trees and branches in late April,
 12 when these substrates were mostly too deep, *i.e.* still in a cold water, to be chosen for spawn-
 13 ing) and avoided live submerged vegetation (Ivlev index from -1.00 to 0.26 for live Eurasian
 14 water milfoil, common stonewort and flooded terrestrial vegetation). Moreover, significantly
 15 larger egg strands were found to be deposited on dead submerged vegetation compared to
 16 those on live submerged vegetation (ANOVA; $P < 0.01$). Especially in the case of common
 17 stonewort, very small egg strands were observed to be laid in between their dense stalks.

DISCUSSION

- 18 There is no doubt that wind and waves affect perch reproduction and survival in lakes. Clady
 19 and Hutchinson (1975) reported that, as a result of high winds, large quantities of eggs of
 20 yellow perch were washed ashore at a number of localities on the windward shoreline of
 21 Oneida Lake. A severe wave action caused damage to almost one percent of the estimated
 22 egg potential of the lake's perch population within a single day. Similarly, Newsome and Aalto

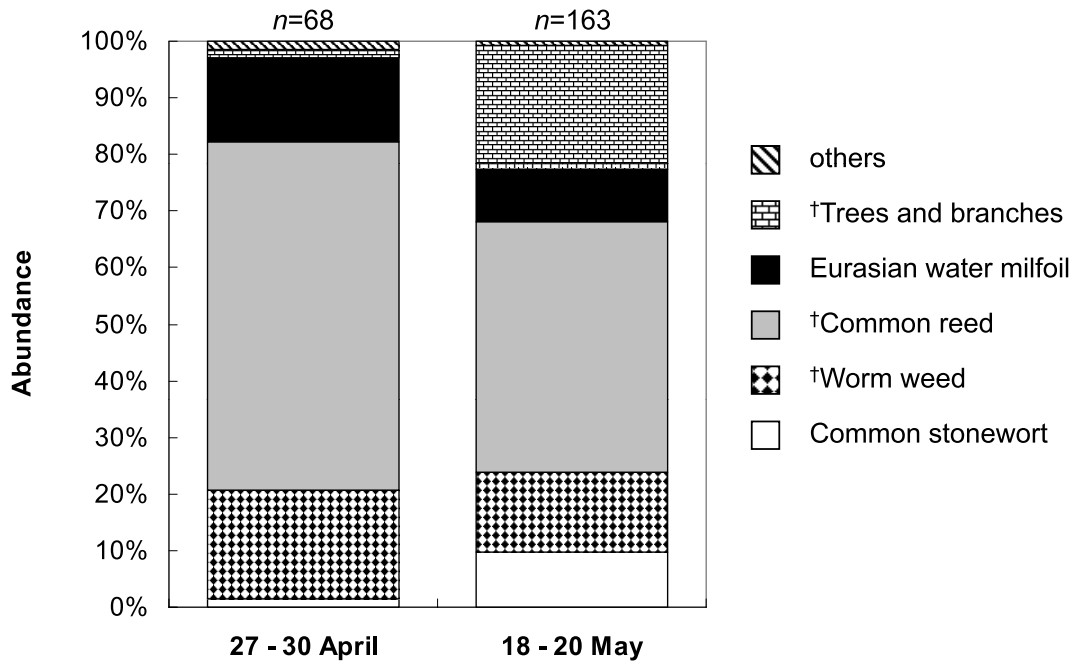


Figure 6

The composition of spawning substrate for perch in Chabařovice Lake in spring 2009 during the first days of spawning and at the end of spawning when most of the spawning events occurred in deeper parts of the lake (cf. Figure 4). † indicates dead plants, bushes or trees (for details see also Čech et al., 2009). “Others” category includes: terrestrial vegetation and fence wire-cloth.

(1987) have shown that wind-generated internal seiches in Lochaber Lake, Nova Scotia, (water temperature changed as much as 7 °C in 15 min) may result in thermal shocking of perch embryos and cause abnormal gill and jaw development, smaller body size and smaller pectoral fins. Severe deformities lead to immediate death, while intermediate deformities lead to greater susceptibility to predation.

The violent water movements might be responsible not only for mechanical damage to eggs but abrasive wave action could impose the danger of silt and other forms of deposit, which would adversely affect the development of perch eggs. These factors are of considerable importance, especially in the shallows. For that reason, in many lakes, female perch select sheltered spawning areas or deeper layers where hydrodynamic stress is of low importance (Jones, 1982; Gillet and Dubois, 1995, 2007; Probst et al., 2009).

In Chabařovice Lake, large waves generated by a long-lasting strong wind coming from the East caused drastic water mass displacement, with warm water in the west part of the lake and cold water in the east. This situation led to a significantly greater abundance of perch egg strands in the west part of the lake. It seems that female perch selectively avoided the cold, east part of the lake where the water temperature only just reached the lower limit for the usual onset of perch spawning (Kubečka, 1992; Gillet and Dubois, 2007) and they greatly preferred the warmer, west part of the lake where the water temperature was almost optimal for perch spawning (Gillet and Dubois, 1995, 2007). Moreover, nowhere in the lake were the egg strands observed in water shallower than 1.2 m and, in total, 91% of egg strands were deposited at depths greater than 3 m. This finding corresponds well to the previous results from Chabařovice Lake, for 2007 and 2008 when 92% and 88% of egg strands were deposited at depths greater than 3 m (Čech et al., 2009, 2010). Very similar results have been published by Huff et al. (2004) from Lake Giles, Pennsylvania, where the authors have provided evidence that such a deep deposition of egg strands by yellow perch was a result of low DOC concentration in the lake and thus an evolutionary response of spawning perch females to the penetrating UVR. According to the work of Williamson et al. (1997) and Huff et al. (2004), UVR has a severe damaging effect on the eggs of perch.

1 In Chabařovice Lake, however, the concentration of *DOC* was relatively high (mean
2 $6.2 \text{ mg} \cdot \text{L}^{-1}$), suggesting that the lake belongs to the category of higher *DOC* lakes (for classi-
3 fication see Huff *et al.*, 2004), *i.e.* to the category where *DOC* (penetrating UVR, in fact) does
4 not evoke an avoidance reaction to shallow habitats in spawning perch and so that it is not re-
5 sponsible for deep deposition of egg strands. Most probably, avoidance of depths shallower
6 than 3 m is a result of strong wind/waves coming from any direction, which is in accordance
7 with previous findings of Jones (1982) from Loch Leven, Gillet and Dubois (2007) from Lake
8 Geneva, and Probst *et al.* (2009) from Lake Constance. Also, in very shallow water the rapid
9 increase of temperature during a period of calm sunny weather should not be omitted as a
10 possible factor affecting the depth selected for deposition of egg strands. Guma'a (1978) has
11 demonstrated that in temperatures $>14 \text{ }^\circ\text{C}$ a significant proportion of perch eggs die prior to
12 hatching. In Chabařovice Lake during the period of perch spawning, the temperature in the
13 shallow water regularly exceeds $14 \text{ }^\circ\text{C}$ (Čech *et al.*, 2009, 2010), which may cause a significant
14 risk for successful egg development.

15 Several studies have shown that, according to the size of egg strands, in large lakes like
16 Lake Geneva and Lake Constance, larger perch females spawn later in the season than the
17 small ones and that they use deeper spawning places (Gillet *et al.*, 1995; Gillet and Dubois,
18 2007; Probst *et al.*, 2009). In Chabařovice Lake, within each sampling period, there was no
19 relationship between the size of the egg strands and the depth of deposition. However, larger
20 females spawned significantly earlier than the smaller ones and used shallower depths (as
21 shown by the relationship when the data from both sampling periods were pooled together).
22 The later corresponds well with the findings of Dalimier *et al.* (1982) from an inundated quarry
23 pit La Gombe, and of Holčik (1969) from Kličava Reservoir. It seems that perch populations
24 behave differently in small water bodies (opencast mine lake, inundated quarry pit, valley
25 reservoir) compared to large water bodies (pre-alpine lakes).

26 The results of the present study have also indicated that larger perch females selected dead
27 submerged vegetation and that, in general, this substrate was used much more for spawning
28 (on average 81.4% of egg strands were deposited on this substrate) than was living sub-
29 merged vegetation. This is particularly interesting because live submerged vegetation com-
30 prised the majority of the relevant perch spawning substrate in the lake. This finding does,
31 however, correspond to the findings of Čech *et al.* (2009, 2010) from the same lake where,
32 in 2007 and 2008 on average 64.7% and 91.0% of all egg strands were deposited on dead
33 submerged vegetation. A strong preference for dead submerged vegetation could be clearly
34 seen, especially during the second sampling period. At this time, spawning perch rather chose
35 dead worm weed, common reed, trees and branches in the depth layer of 11–12 m in a tem-
36 perature around $6.3 \text{ }^\circ\text{C}$ (a suboptimal temperature for perch spawning and egg development;
37 Guma'a, 1978; Gillet and Dubois, 2007) than the abundant common stonewort and Eurasian
38 water milfoil in shallower depth layers in much more suitable temperature conditions (13.1 –
39 $8.3 \text{ }^\circ\text{C}$ in the 6–9 m depth layers; *cf.* Figures 2 and 4). Following the suggestion of Reyes *et al.*
40 (1992), Nash *et al.* (1999) and Čech *et al.* (2009) it appears that dead submerged vegetation,
41 such as common reed, worm weed and trees and branches, represents an ideal spawning
42 substrate for perch because (1) it is a hard three-dimensional structure and, (2) there is much
43 less oxygen requirement during night hours. Both factors are of crucial importance for the
44 deposition of perch egg strands and their further development.

CONCLUSION

45 The present study has shown that the location and timing of perch spawning is not easy to
46 predict even in a relatively simple system such the trough-like Chabařovice Lake, described
47 in the recent history of this water body as without any 'obvious limitation to perch spawning'
48 (*cf.* Čech *et al.*, 2009, 2010). The important roles played by lake hydrology, temperature and
49 the presence of appropriate spawning substrates, in particular the presence of hard three-
50 dimensional structures, have become apparent.

Since perch is the key species in Chabařovice Lake, the progressive degradation of appropriate spawning substrates mentioned by Čech *et al.* (2009, 2010; further documented in this study) is not good news for overall lake management. Due to the continuous filling of the lake the rest of the dead common reed, worm weed and trees and branches are now mostly situated in very deep water in inappropriate temperature conditions, at least at the beginning of the perch spawning period. As the presence of live submerged vegetation is less predictable in time, moreover, it is not much suitable spawning substrate for perch (Čech *et al.*, 2009, 2010), the installation of an artificial spawning substrate (Gillet and Dubois, 1995; Dubois *et al.*, 1996; Nash *et al.*, 1999; Pedicillo *et al.*, 2008; Probst *et al.*, 2009), preferentially in depth layers of 3–8 m, would, in the near future, be an important means of both sustaining the stock of perch, the main predatory fish in the lake, and for overall management of the lake's ichthyofauna.

The results from the above mentioned attempt (artificial spawning substrate installation) on the population of perch in Chabařovice Lake would be of crucial importance for other large water bodies forming in the region of North-West Bohemia, such as the opencast mine lake Most–Ležáky (area 311 ha; filling started in 2008), Medard–Libík (area 486 ha; filling started in 2010) or Jiří–Družba (area 1322 ha; filling will start in 2036). According to the most recent state of knowledge (Kubečka *et al.*, pers. obs.), also in these lakes it can be expected that perch will have a key role in the initial formation of the lake's ichthyofauna, and that there will be progressive degradation of its most suitable spawning substrate in the near future.

ACKNOWLEDGEMENTS

The authors thank M. Morris for careful reading and correcting the English, and two anonymous referees for valuable comments on the manuscript. The study was supported by the Grant Agency of the Czech Republic (project No. 206/09/P266) and the Palivový kombinát Ústí, státní podnik. The Elbe River Authority kindly provided the data on *DOC* in May.

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