Feeding range of age 1+ year Eurasian perch *Perca fluviatilis* in the Baltic Sea

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(Received 20 September 2016, Accepted 30 January 2017)

Using the widespread Eurasian perch *Perca fluviatilis* as a model organism, feeding ranges were investigated using stable-isotope ratios ($\delta^{15}$N and $\delta^{13}$C) and body condition. Differences were found between closely located sampling sites in a littoral area without obvious migration barriers, indicating that individual fish had small feeding ranges. Body condition differences between sampled stations were consistent over 4 years. Such sedentary behaviour is important to consider in, e.g. fisheries management and environmental monitoring, as local catch regulations may be meaningful or geographic stability in sampling locations may reduce noise in data.

Key words: body condition; food web; littoral; sedentary; spatial scale; stable isotopes.

INTRODUCTION

The spatial scale at which trophic interactions occur is essential in ecology (Rooney *et al.*, 2008), influencing food-web structure and stability (de Roos *et al.*, 1998; Rooney *et al.*, 2008) and population dynamics (Bertrand *et al.*, 2011). Individual feeding ranges are important indicators of these spatial scales, determining the range of possible trophic interactions (Bertrand *et al.*, 2011) and can be of relevance to fisheries management, e.g. in deciding on the adequate size of aquatic protected areas. If fishes are sedentary on a rather small scale, management such as a minimum landing size can be meaningful even if it is only applied locally. Knowledge about limited migration is also of relevance to environmental monitoring. In sedentary species and where prey abundances differ at a small geographical scale, differences among sampling sites can potentially contribute to noise or false trends in, e.g. tissue concentrations of contaminants, growth and body condition.

Although perch *Perca fluviatilis* L. 1758 can perform spawning migrations, tagged individuals are generally recaptured within 10–30 km from where they were released (Collette *et al.*, 1977; Thorpe, 1977a, b) and even tend to return to their home area if translocated (Willemsen, 1977). Genetic studies have, however, documented differences over shorter distances (0.3–2 km; Bergek & Björklund, 2009; Bergek *et al.*, *Author to whom correspondence should be addressed at present address: Swedish University of Agricultural Sciences, Department of Aquatic Resources, SE 178 93 Drottningholm, Sweden. Tel.: +46 704601265; email: ida.ahlbeck.bergendahl@slu.se*
2010) than suggested from the tagging studies. It is also possible that even within a genetically homogenous population, different individuals or parts of the population have different behaviour, e.g. using different habitats, foraging areas or specializing in different prey types (Schindler et al., 1997; Iguchi et al., 2001; Barry et al., 2016). Such specialization could then result in geographically small-scaled phenotypic differences, such as variation in growth or body condition.

*Perca fluviatilis* display ontogenetic diet shifts. Young-of-the-year fish typically feed on zooplankton, but as they grow they switch to benthos and later on become piscivorous (Thorpe, 1977a, b). This diet transition has been described also from the Baltic Sea by Hansson (1985), Koli et al. (1988), Lappalainen et al. (2001) and Mustamäki et al. (2014) and the age 1+ year *P. fluviatilis* that are in focus for this study feed primarily on mysid shrimps and benthic invertebrates.

Stable-isotope ratios can be used as natural markers (McMahon et al., 2013) as isotopes are incorporated into the animal’s tissue via its diet (Hobson, 1999). Stable isotopes can hence indicate migratory routes, trophic levels and geographic origin of fishes and other animals (Post, 2002; Zimmo et al., 2012; Hoffman, 2016). The stable-isotope ratio of nitrogen ($\delta^{15}$N) is most often used to trace the trophic level of an individual due to the stepwise trophic enrichment of the heavy isotopes (Hobson & Wassenaar, 2008). The stable-isotope ratio of carbon ($\delta^{13}$C) can, on the other hand, be used to some extent to trace diets as different plants fractionate carbon differently. So called C4 and Crassulacean acid metabolism (or CAM photosynthesis) results in a lower fractionation than C3 photosynthesis (Karasov & Martinez del Rio, 2007). In aquatic ecosystems, pelagic primary production has a lower carbon isotope signature than production from benthic macrophytes (Fry & Sherr, 1984).

Nitrification and denitrification processes in municipal sewage treatment plants result in discharge water comparatively rich in inorganic $^{15}$N (Heaton, 1986). This can result in a spatial gradient in isotope composition, with high $\delta^{15}$N values close to the discharge, labelling both benthic vegetation (Savage & Elmgren, 2004) and higher levels of the food web (Hansson et al., 1997; Holliand et al., 2012).

Site fidelity may make fishes respond to local environmental conditions and has been reported to induce morphological differences in *P. fluviatilis* (Svanbäck & Persson, 2004; Olsson & Eklöv, 2005; Olsson et al., 2006; Faulks et al., 2015) due to differences in diet (Hjelm et al., 2001; Svanbäck & Eklöv, 2003; Mustamäki et al., 2014) and predation pressure (Eklöv & Svanbäck, 2006). Hence, body condition can be an important tool when studying feeding ranges as *P. fluviatilis* easily adapt to local conditions.

In this study an anthropogenically induced $^{15}$N gradient in a Baltic Sea bay (Hansson et al., 1997; Savage & Elmgren, 2004) was used in combination with measures of fish body condition (length and mass relation) to investigate the feeding ranges in age 1+ year *P. fluviatilis*. If fish have limited feeding ranges, differences in fish $\delta^{15}$N ratios between stations along this gradient could be expected. Furthermore, if the fish are reasonably sedentary this may be associated with differences in local feeding conditions. Local abundance or shortage of food can influence body condition, as can differences in the degree of exploitation of benthic $\nu$. pelagic food sources. The use of more pelagic prey could be associated with a slenderer body (Hjelm et al., 2001; Svanbäck & Eklöv, 2003) and lower $\delta^{13}$C values as described above.
STUDY AREA

The study was conducted in Himmerfjärden, a relatively large bay on the Swedish coast of the northern Baltic Sea proper (Fig. 1). There are no physical barriers to fish movement within the bay. The inner Himmerfjärden basin, where most of the stations were located, is c. 11 km long, has an average depth of 17 m and a salinity of 6–7 (Engqvist, 1996). Late summer (15 August to 15 September) Secchi disc depth and surface temperature are c. 4 m and 17°C, respectively (Hajdu et al., 2015). In the northern end of the bay a municipal sewage treatment plant discharges processed waste water from a population of c. 280 000 inhabitants. Owing to denitrification in the sewage treatment plant, the discharged water is comparatively rich in 15N, resulting in a pronounced north–south gradient in δ15N in the sessile vegetation (Fucus vesiculosus; Savage & Elmgren, 2004) and also in the pelagic food web (Hansson et al., 1997; Holliland et al., 2012).

SAMPLING

Collection of fish

All fish were caught in gillnets of the type referred to as Nordic nets (Appelberg et al., 1995), which are 30 m long and 1.5 m deep and containing twelve 2.5 m long panels of different mesh size (5.0, 6.25, 8.0, 10.0, 12.5, 15.5, 19.5, 24.0, 29.0, 35.0, 43.0, 55.0 mm). Thirty stations were sampled and fishing took place annually in late August to early September in the years 2008–2011. Each station was fished one night per year; hence, 120 gillnet nights were fished. To restrict the sampling to the littoral zone, nets were as far as practically possible, set perpendicular to the shore. Average starting depth for the nets was 2 m (80% of the sets started within 1–2.5 m) and the largest depth at a station was on average 4 m (80% range 2–6 m, but on one occasion the net reached 10 m). Fish sampling in this project was approved by the relevant animal-care agency under the supervision of the Swedish Board of Agriculture, decisions 2007-11-12S181-07 and 2011-06-21S116-11. Fish that were not already dead when the nets were collected were killed by a blow to the head followed by decapitation.

Stable-isotope measurements

From the 2011 fishery, eight 1+ P. fluviatilis (total length, L_T, range: 101–146 mm, mean ± s.d.: 117 ± 10 mm) were sampled from each of 10 stations that were evenly distributed along the shoreline of the study area (Fig. 1). From each fish (n = 80), muscle samples for C and N isotope analyses were taken from the back of the fish, just behind the head. Samples were freeze dried and ground to a fine powder before being sent for analysis.

For the baseline signature, at each station where fish were sampled for stable-isotope analysis (Fig. 1), five new growth tips (c. 2 cm) from the perennial brown macroalgae F. vesiculosus were also collected in 2011, merged into one sample per station and the 10 samples were processed in the same way as the fish samples.

Samples were analysed at University of California Davis stable isotope facility, using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd; https://serconlimited.com/). The results are expressed according to the equation Δx = [(R_sample × R_reference⁻¹) – 1] × 1000, where x = 15N or 13C and R = 15N/14N or 13C/12C⁻¹. The reference materials used were atmospheric N₂ and PeeDee belemnite, respectively. Regularly during the analyses, two working standards (fish tissue, local standard) were analysed, as well as analytical and method blanks to control for possible analytical drift as well as contamination during laboratory work.

Measurements on fish

Each fish caught during the 2008–2011 fishery was weighed with a precision of 0.1 g (M) and measured for L_T to the closest mm from the tip of the nose to the end of the caudal fin (Le Cren, 1947). The L_T distribution of P. fluviatilis showed a consistent and clearly distinguishable peak around 100–120 mm, which corresponds to late summer L_T of P. fluviatilis of age 1 year.
FEEDING RANGE OF 1+ *P. FLUVIATILIS* 2063

Fig. 1. Map of sampling stations (→) from which *Perca fluviatilis* were collected for stable isotope analyses: ○, station 0; ▲, stations on the western shore of Himmerfjärden; ■, eastern shore stations; ●, stations not associated with any particular side of the bay; ——, 10 m depth contour.

(Hansson, 1985). All *P. fluviatilis* from this *L*_T frequency peak were included in the statistical analyses of body condition described below (peak ranges: 94–135 mm, *n* = 330; 94–125 mm, *n* = 539; 90–130 mm, *n* = 330; 98–135 mm, *n* = 438 in 2008–2011 respectively).

**STATISTICAL ANALYSES**

Unless stated otherwise, statistical tests were conducted in SYSTAT for Windows 11.00.01 (www.systatsoftware.com).

Spatial trends in δ^{15}N and δ^{13}C were explored using general linear modelling (GLM) with distance from station 0 (Fig. 1) as a continuous variable (distances measured as the crow flies) and side of the bay as a categorical variable.

To explore differences in body condition between stations, the linear model \( \ln(M) = a_y + b_y \ln(L_T) \) was fitted to the length (*L*_T) and mass (*M*) data. This was done separately for each year (*y*).
Table I. Results from general linear modelling (GLM) analyses on effects of total length ($L_T$, continuous variable) and sampling station (categorical factor) on *Perca fluviatilis* muscle tissue $\delta^{13}C$ and $\delta^{15}N$.

<table>
<thead>
<tr>
<th>GLM</th>
<th>$\delta^{13}C$</th>
<th>$\delta^{15}N$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$L_T$ Station</td>
<td>$L_T$ Station</td>
</tr>
<tr>
<td>$F$</td>
<td>0.47 8.14</td>
<td>0.63 10.5</td>
</tr>
<tr>
<td>d.f.</td>
<td>1.67 9.67</td>
<td>1.67 9.67</td>
</tr>
<tr>
<td>$P$</td>
<td>$&gt;$0.05 $&lt;$0.001</td>
<td>$&gt;$0.05 $&lt;$0.001</td>
</tr>
</tbody>
</table>

By analysing each year separately, the influence of interannual variation in body condition was removed. The residual ($R_i$) value for each fish was calculated as $\ln(M_i) - a_y + b_y \ln(L_T)$, where $M_i$ and $L_T$ denote mass and length of a fish $i$, while $a_y$ and $b_y$ are derived from the linear model described above; a positive residual indicates a heavier fish than average and a negative residual indicates a leaner fish than average. To investigate if there were differences in the frequency of heavy and lean fish among stations the number of positive and negative residuals was recorded for each station and homogeneity in the frequency distributions were tested by using $\chi^2$ analyses. This test was done both for each year separately and for data merged over the 4 years.

To further investigate if there were certain stations that generally produce heavier or leaner fish than average, the mean residual value ($R_{sy}$) was calculated separately for each station (s) and year (y). An $R_{sy} > 0$ indicates that the mass of fish at that combination of station and year are on average heavier than expected from their $L_T$ and $R_{sy} < 0$ indicates fish slimmer than average. By using $R_{sy}$ values in statistical analyses, equal numbers of observations per station are obtained. Differences in $R_{sy}$ among stations were explored using ANOVA. This analysis was followed by two ANOVAs, one for stations from the eastern side and one for those from the western side.

A spatial correlation in body condition among stations along each shoreline was conducted, exploring effects of vicinity on body condition. In these analyses, distance measures were the minimum swimming distance between two stations. These analyses were done separately for each year and side of the bay using Moran’s I-measure of spatial autocorrelation (available in the ape library in the R software package; www.r-project.org).

The relationship between body condition and *P. fluviatilis* abundance (measured as catch per unit effort, CPUE) was analysed using GLM with $R_{sy}$ as response variable and CPUE (continuous variable) and year (categorical variable) as explanatory variables. Two measures of abundance were used: CPUE of age 1+ year *P. fluviatilis* and CPUE of all *P. fluviatilis* age 1+ and older. Year was entered in the model to remove effects of catch differences among years, since other factors than fish abundance may influence catches.

RESULTS

STABLE ISOTOPES

There were highly significant differences in *P. fluviatilis* isotope signatures among stations in both $\delta^{15}N$ and $\delta^{13}C$, but $L_T$ (range 101–146 mm) had no influence on the isotope ratios (Table I). *Perca fluviatilis* tissue showed significant north–south gradients in $\delta^{15}N$ and $\delta^{13}C$ (Figs 2 and 3 and Table II). For $\delta^{13}C$, but not for $\delta^{15}N$, this gradient differed between the eastern and western side of the bay (Table II) and further analyses of $\delta^{13}C$ were done separately for the two bay sides (Table III). *Perca fluviatilis* caught on the western side of the bay generally had higher $\delta^{13}C$ values than those from the eastern side (Fig. 3). The $\delta^{13}C$ values at the stations on the western side of the bay
Fig. 2. $\delta^{15}$N in *Perca fluviatilis* muscle tissue from stations at different distances from sampling station 0. ○, station 0; ▲, stations on the western shore of Himmerfjärden; ■, eastern shore stations. The regression line has a slope that is statistically significant: $y = 17.10 - 0.21x$; $r^2 = 0.34$, $F_{1,78} = 50.1$, $P < 0.001$.

Fig. 3. $\delta^{13}$C in *Perca fluviatilis* muscle tissue from stations at different distances from sampling station 0. ○, station 0; ▲, stations on the western shore of Himmerfjärden (---, $y = 21.6 + 0.27x$; $r^2 = 0.33$, $F_{1,30} = 14.9$, $P < 0.001$); ■, eastern shore stations (----, $y = -21.4 + 0.15x$; $r^2 = 0.25$, $F_{1,30} = 10.6$, $P < 0.01$). The western stations were spread over a larger geographical range than the eastern stations and to allow for comparisons between results from the two sides, only sampling stations within the range of 3–10 km from sampling station 0 were included in these analyses.
Table II. Results from general linear modelling (GLM) analyses on effects of distance from sampling station 0 (continuous variable) and bay side (categorical factor) on *Perca fluviatilis* muscle tissue $\delta^{13}$C and $\delta^{15}$N

<table>
<thead>
<tr>
<th>GLM</th>
<th>$\delta^{13}$C</th>
<th>Bay side</th>
<th>$\delta^{15}$N</th>
<th>Bay side</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Distance from station 0</td>
<td>4.4</td>
<td>Distance from station 0</td>
<td>0.8</td>
</tr>
<tr>
<td>$F$</td>
<td>27.8</td>
<td>4.4</td>
<td>46.6</td>
<td>0.8</td>
</tr>
<tr>
<td>d.f.</td>
<td>1.77</td>
<td>1.77</td>
<td>1.77</td>
<td>1.77</td>
</tr>
<tr>
<td>$P$</td>
<td>&lt;0.001</td>
<td>&lt;0.05</td>
<td>&lt;0.001</td>
<td>&gt;0.05</td>
</tr>
</tbody>
</table>

decreased significantly with the maximum depth for the gillnet (linear regression with depth at the outer end of the net as independent variable and station average $\delta^{13}$C as dependent: $F_{1,3} = 78, P < 0.01, 95\%$ c.i. for the slope $-0.67$ to $-0.32$).

The stable isotope composition in *F. vesiculosus* showed no spatial trend for $\delta^{13}$C, but a significant southward decrease in $\delta^{15}$N (linear regression: $F_{1,8} = 9.0, P < 0.05, 95\%$ c.i. for the slope $-0.80$ to $-0.10$; Fig. 4). There were no significant differences in isotope signature between the eastern and western sides of the bay. The gradient for *F. vesiculosus* $\delta^{15}$N was steeper ($-0.45$) than the corresponding gradient for *P. fluviatilis* tissues ($-0.23$), but the difference was not statistically significant ($P > 0.05$ for $b = 0$ when fitting the model $\delta^{15}$N = $a + (b - 0.23) \times$ distance).

Pearson correlation between isotope values in *F. vesiculosus* and *P. fluviatilis* muscle (averaged per station) were statistically significant (Pearson correlation 0.65, Bartlett $\chi^2$ statistic, $P < 0.05$) for $\delta^{15}$N, but not for $\delta^{13}$C (Pearson correlation 0.65; Bartlett $\chi^2$ statistic $P > 0.05$).

**BODY CONDITION**

In all 4 years, there were significant differences in fish body condition, *i.e.* the frequency distribution of positive and negative residuals (actual fish mass relative to expected mass), differed between stations (Table IV, within year). Although the differences among stations were rather small (within $\pm 10\%$ of average mass at a given length), consistent differences among stations were found across years (Table IV, across years). Thus, there were stations at which the fish generally, over the years, had low or high body condition (Fig. 5).

There were significant differences in condition ($R_{sy}$) between the western and eastern sides of the study area (ANOVA, $F_{1,92} = 7.2, P < 0.01$, bay-side as factor), with generally leaner fish on the eastern shore stations. When comparing stations along the same side of the bay, significant differences in condition were found among fish from the stations located on the eastern shore (ANOVA, $F_{11,36} = 2.1, P < 0.05$, station as factor), but not among stations along the western shore (ANOVA, $F_{11,34} = 1.8, P > 0.05$, station as factor).

The analyses of spatial autocorrelation between stations along each shoreline of the study area revealed that of the resulting eight tests (4 years, two sides), only one was weakly significant (Moran’s $I$, $P < 0.05$). The general absence of spatial autocorrelation indicates that *P. fluviatilis* at more closely located stations did not have more similar body condition than distantly located stations along the same shoreline.
Table III. Results from linear regression analyses on effects of distance from sampling station 0 on Perca fluviatilis muscle tissue δ¹³C and δ¹⁵N, including 95% c.i. for the slopes. For δ¹³C each bay side was analysed separately as bay side affected δ¹³C significantly (Table II).

<table>
<thead>
<tr>
<th>Distance from station 0</th>
<th>δ¹⁵N</th>
<th>δ¹³C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole bay</td>
<td>10·6</td>
<td>14·9</td>
</tr>
<tr>
<td>East side</td>
<td>1·30</td>
<td>0·13</td>
</tr>
<tr>
<td>West side</td>
<td>1·30</td>
<td>0·41</td>
</tr>
</tbody>
</table>

There were no correlations between body condition (Rₛᵧ) and P. fluviatilis abundances, either for CPUE data based on age 1+ year P. fluviatilis (GLM, F₁,86 = 0·04, P > 0·05) or when total P. fluviatilis catches were used (GLM, F₁,86 = 0·03, P > 0·05).

**DISCUSSION**

In this paper, the extent of the foraging area exploited by individual 1+ year P. fluviatilis was studied in an open, shallow-water seascape. Based on stable-isotope
Table IV. Summary of statistical analyses of the body condition of *Perca fluviatilis* within year showing results from $\chi^2$ analyses of the frequencies of positive and negative weight residuals, *i.e.* the probability of equal body condition at all stations in the area during that year, and across years showing ANOVA results based on the station and year-specific average residuals ($R_{xy}$) and the significance indicates stations with consistently heavy or lean fish.

<table>
<thead>
<tr>
<th></th>
<th>2008</th>
<th>2009</th>
<th>2010</th>
<th>2011</th>
<th>Sum</th>
<th>Across years</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\chi^2$</td>
<td>65.0</td>
<td>58.2</td>
<td>56.9</td>
<td>42.6</td>
<td>222.6</td>
<td>F = 2.2</td>
</tr>
<tr>
<td>d.f.</td>
<td>27</td>
<td>28</td>
<td>28</td>
<td>28</td>
<td>111</td>
<td>d.f. 29.87</td>
</tr>
<tr>
<td>$P$</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.05</td>
<td>&lt;0.001</td>
<td>$P &lt; 0.01$</td>
</tr>
<tr>
<td>$n$</td>
<td>331</td>
<td>535</td>
<td>290</td>
<td>455</td>
<td>1611</td>
<td>n = 117</td>
</tr>
</tbody>
</table>

Signatures and body-condition measurements it is concluded that 1+ year *P. fluviatilis* have home ranges on the km scale or less. As the effluent water from the sewage treatment plant creates a north–south $\delta^{15}$N gradient in the study area (Hansson *et al.*, 1997; Savage & Elmgren, 2004) and as 1+ year *P. fluviatilis* feed primarily on sedentary benthos (Hansson, 1985; Koli *et al.*, 1988; Lappalainen *et al.*, 2001) a spatial trend in $\delta^{15}$N was predicted if the *P. fluviatilis* had reasonably limited feeding ranges. There are several previous studies showing that *P. fluviatilis* are reasonably sedentary (Bergek & Björklund, 2009; Bergek *et al.*, 2010) and may specialize on a demersal or more pelagic life (Hjelm *et al.*, 2001; Svanbäck & Eklöv, 2003; Mustamäki *et al.*, 2014).

The significant $\delta^{15}$N gradient found in *P. fluviatilis*, not differing significantly from that of the sessile benthic plant *F. vesiculosus*, supports strong site fidelity for *P. fluviatilis*, and also that they feed at the same trophic level across the system. The differences in body condition, however, indicate that *P. fluviatilis* respond to local differences in, *e.g.* food availability, quality and composition (Hjelm *et al.*, 2001; Svanbäck & Eklöv, 2003).

The significantly lower $\delta^{13}$C values in fish from the eastern side of the bay could be explained by *P. fluviatilis* on that side of the bay feeding more on prey grown on pelagic primary production (Fry & Sherr, 1984). This explanation is consistent both with the topography of the bay’s eastern shore, where the littoral zone drops off sharply allowing for a stronger influence of pelagic production and the significant decrease in $\delta^{13}$C with increasing depth on the western side of the bay. In addition to differences between bay sides, there is also a southward trend of increasing $\delta^{13}$C for both sides of Himmerfjärden, indicative of a more littoral diet further south, which is consistent with the larger littoral areas in the south of the bay. An alternative explanation to the differences in *P. fluviatilis* $\delta^{13}$C could be differences in benthic algal $\delta^{13}$C, but this was unsupported by the sessile *F. vesiculosus* isotope data which show no spatial trend in $\delta^{13}$C.

In addition to the differences found in isotopic signature there were also consistent differences in *P. fluviatilis* body condition among stations over the years. *Perca fluviatilis* from the eastern side of Himmerfjärden had significantly lower body condition (slenderer) than fish from the western side. Based on findings by Svanbäck & Eklöv (2003), this could indicate that *P. fluviatilis* are more pelagic on the eastern side than on the western side of Himmerfjärden. This is consistent with the $\delta^{13}$C finding and also
with morphological differences between the two bay sides (narrow littoral zone along the eastern shore and more extensive shallow bottoms on the western shore).

The results from the analyses of isotopic signatures and body condition leads to the conclusion that even in open coastal habitats, without obvious dispersal barriers, age 1+ year *P. fluviatilis* show high site fidelity with limited feeding range. Stable isotopes and body condition only reflect that the *P. fluviatilis* were sedentary within a growth season, but provide no information about movements between years. Restricted movements also between years, however, have been shown by genetic differences over short distances (Bergek & Björklund, 2009; Bergek *et al*., 2010).

This sedentary behaviour makes *P. fluviatilis* responsive to local environmental conditions. Knowledge about feeding range may be of great importance in food-web
analysis, as it may affect energy flow, connectedness, population dynamics and food-web stability (Rooney et al., 2008; Bertrand et al., 2011). Furthermore, restricted feeding ranges may suggest that local fishing regulations, such as closing areas for fishing, can be expected to influence local abundances and size distributions (Murawski et al., 2000; Bergström et al., 2007). It is further concluded that it is important to consider, for fisheries management and environmental monitoring, that fish caught at one site may not be representative of the entire population of the studied system even at relatively small scales.

B. Larsson, P.-E. Erlandsson and B. Svangren gave very valuable assistance and support, as did numerous fishing right owners. Thanks to L. Enhus, C. Amid, M. Jalmlöv, K.-M. Johansson, K. Landeström and C. Ek for helping out with sampling. Anonymous reviewers have provided very valuable and constructive comments on earlier versions of the manuscript. The study was funded by the Foundation Baltic Sea 2020 as part of the project 'Pikeperch in Himmerfjärden' and the Sweden–America Foundation.

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