Reproduction, growth, and migration of fishes in a regulated lowland tributary: potential recruitment to the river Meuse

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Abstract

Many European rivers are characterized by a canalized main channel, steep stony embankments, the absence of aquatic vegetation, regulated flow dynamics, reduced hydrological connectivity to the floodplains and a lack of spawning and nursery areas for many fish species. In such regulated rivers, tributaries may be particularly important for recruitment of fish populations in the main channel. This paper describes the reproduction, growth and migration of fishes in the Everlose Beek, a regulated lowland tributary stream of the river Meuse (The Netherlands), using bi-weekly sampling from January to December 2002. A total of 8615 fishes were caught, belonging to 13 different species. The fish species were classified into three groups, viz., residents, migrants and transients, based on the presence of various life-stages in the tributary. Size-frequency data suggest that each group uses the Everlose Beek differently: (i) Stone loach (*Barbatula barbatula*), Gudgeon (*Gobio gobio*) and Three-spined stickleback (*Gasterosteus aculeatus*) were resident species using the tributary as a spawning, nursery and adult habitat; (ii) Bream (*Abramis brama*), Roach (*Rutilus rutilus*), Rudd (*R. erythrophthalmus*), Tench (*Tinca tinca*), and Pike (*Esox lucius*) were migratory species, using the tributary as a spawning area, as well as a nursery habitat during their first year of growth, but migrating towards the river Meuse typically at a length of 5–15 cm; and (iii) Bleak (*Alburnus alburnus*), Sunbleak (*Leucaspius delineatus*), Carp (*Cyprinus carpio*), Crucian carp (*Carassius carassius*), and Perch (*Perca fluviatilis*) were transient species, characterized by an absence of reproduction, and the occurrence in very low densities of >age-1 juveniles and adults only. Lowland tributaries, such as the Everlose Beek, can contribute to the recruitment of particularly migrant species, hence contributing to fish populations of the regulated river Meuse.

Introduction

Natural river systems consist of a main (braided) channel, providing longitudinal linkage within the corridor (River Continuum Concept; Vannote et al., 1980) and transversal linkages to floodplain water bodies (Flood Pulse Concept; Junk et al., 1989). Along the longitudinal axis, however, the

canalization of many north-west European low-land rivers has resulted in a severe loss of habitat heterogeneity. Since spatial and temporal variation in structural habitat complexity is one of the most important conditions for the existence of well balanced aquatic riverine communities, this has generally resulted in impoverished communities in the main channel (Gorman & Karr, 1978; Schlosser, 1991; Jungwirth et al., 1993; Townsend & Hildrew, 1994; Jurajda, 1995; Nilsson et al., 1997; Ward et al., 2002; Aarts & Nienhuis, 2003). Moreover, European large rivers have an important transport function. The intense shipping traffic has, both directly and indirectly, detrimental impacts on the fish fauna. The continuous wave action has a direct negative impact on the survival of fish eggs and larvae (Arlinghaus et al., 2002; Wolter & Arlinghaus, 2003). Indirectly, the wave action and heavy eutrophication together with the resulting turbidity of the water column, prevent the establishment of aquatic vegetation in the main channel (Admiraal et al., 1993). Since, macrophyte beds serve as obligate spawning substrates for phytophilic species, as shelter for juveniles and as rich foraging habitats for adults, shipping traffic also (indirectly) exerts an effect on the fish fauna by rendering the main channel unsuitable for many fish species (Arlinghaus et al., 2002; Wolter & Arlinghaus, 2003). Along the transversal axis of the main river channel, the physical and ecological interactions (Schiemer, 1985; Ward, 1989; Calow & Petts, 1994; Van den Brink, 1994; Allan, 1995; Welcomme, 1995; Petts & Amoros, 1996; Ward et al., 2002) have become disrupted by the placement of dikes, dams and weirs (Dynesius & Nilsson, 1994). This regulation of flow has led to a decline in natural water level variations. As a consequence, floodplain lakes and other off-channel water bodies have effectively become isolated from the main channel and the ecological functioning has become disrupted (Bain et al., 1988; Ward & Stanford, 1995; Van den Brink et al., 1996; Aarts et al., 2004). The reduced habitat heterogeneity, the intense shipping traffic and the disrupted ecological function of floodplains have had severe adverse consequences for the availability of spawning and nursery habitats for many fish species in large rivers (Jungwirth et al., 1993; Vriese et al., 1994; Jurajda, 1995; Copp, 1997; Jurajda, 1999).

When studying fish ecology in regulated rivers, the importance of lowland tributaries is commonly overlooked, as attention is focused on the main channel and its immediate off-channel habitats, such as flood-plains or man-made secondary side channels (Simons et al., 2001; Buijse et al., 2002; Grift et al., 2003). However, in regulated rivers with reduced availability of spawning and nursery habitats, potential recruitment from tributaries may be particularly important. Unfortunately, natural free-flowing lowland tributaries are hardly found anymore in the Netherlands (Verdonschot & Nijboer, 2002) and other Western European countries (Wolter, 2001, Verdonschot & Nijboer, 2002; Nienhuis et al., 200b). Nevertheless, although most lowland tributaries are regulated (Verdonschot & Nijboer, 2002), they are often characterized by abundant aquatic vegetation and extensive or even no shipping traffic. As a result, regulated lowland tributaries often harbour a diverse fish fauna (Delmastro, 1982; Steinberg, 1992; Vandelannoote et al., 1998; Crombaghs et al., 2000), from which fishes can be recruited for populations in the main river, either through drift of larvae (Robinson et al., 1998; De Graaf et al., 1999; Reichard et al., 2002) or through migration of juveniles (Borcherding et al., 2002). Surprisingly, however, although most lowland streams have been influenced by man, little is known about the ecological function of such regulated stream ecosystems. Very few studies have focused on the ecology of fishes in regulated lowland streams, and quantitative data describing ecological links between regulated tributaries and the main channel are largely lacking.

To gain a better insight into the ecology of fishes in regulated tributaries and their links to the main river channel, size-frequency data were collected from the fish fauna of the Everlose Beek, a regulated lowland tributary of the river Meuse (the Netherlands), during January–December 2002, using a single standardized sampling technique. The first objective of the present study was to determine whether, and if, which species use the lowland stream as (i) a reproduction habitat, (ii) a nursery area for larval and juvenile 0+ stages, and (iii) as an adult habitat. Since, recruitment of fishes is largely

determined by survival and growth over the first year (Kirjasniemi & Valtonen, 1997), our second objective was to study the growth of 0+ fishes in the Everlose Beek. We furthermore hypothesized, that due to the shallow nature of the Everlose Beek, it would not necessarily provide a suitable habitat for larger (adult) individuals. Therefore, as a third objective, we assessed whether certain species display ontogenetic migration, from the tributary stream towards the river Meuse.

Materials and methods

Study area

The western bank of the river Meuse, in the province of Limburg (The Netherlands), features many regulated lowland tributary streams, with a total estimated length of >500 km, which discharge into the river (Fig. 1). The tributaries are characterized by an unnatural hydrology because they are
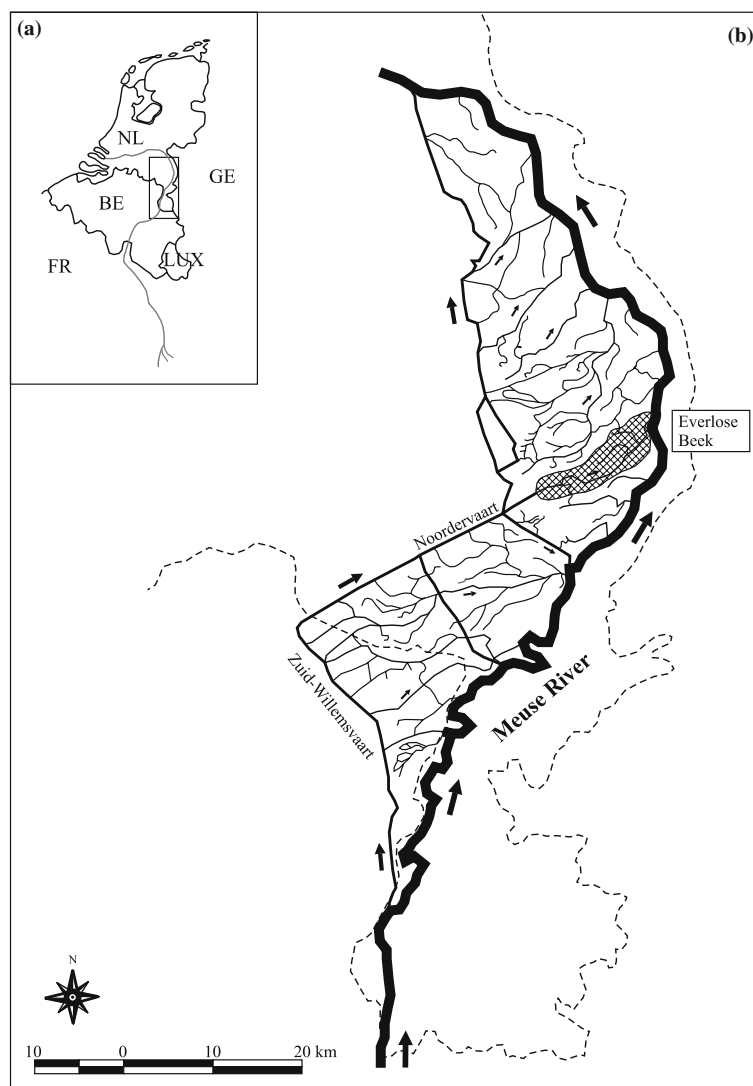

Figure 1. (a) The river Meuse, flowing through France, Belgium and the Netherlands, where it discharges into the North Sea. (b) Map of the river Meuse in the Province of Limburg (The Netherlands), showing the lowland tributary streams on its western bank. These lowland streams are supplied by water originally deriving from the river Meuse. The black arrows indicate the flow direction and the hatched out area indicates the study area, the Everlose Beek.

indirectly supplied with water from the river Meuse itself, via canals. Water enters the Zuid-Willemsvaart canal near Maastricht, which in turn supplies water to the tributaries, ultimately discharging back into the Meuse further downstream (Fig. 1). Fishes can only access these streams from upstream reaches near Maastricht, whereas movement in the tributaries is restricted to unidirectional migration in a downstream direction, due to the presence of a large number of weirs.

The Everlose Beek was chosen because it is a typical regulated lowland tributary of the Meuse, closely resembling other lowland streams in the Province of Limburg (Fig. 1) in terms of morphology, hydrology, vegetation, and fish fauna (Crombaghs et al., 2000). It is characterized by a shallow water depth (0.1–0.6 m), low stream velocities (0.1–0.5 m s^{-1}), a width of 1–10 m, a variety of substrates (silt, mud, sand, and stony bottoms), and locally dense vegetation (featuring, e.g. *Potamogeton perfoliatus, P. natans, Myriophyllum spicatum, Ceratophyllum demersum, Elodea canadensis, Ranunculus circinatus, Sparganium emersum, Sagittaria sagttifolia, Sium latifolium, Glyceria maxima, Mentha aquatica*, and *Myosotis scorpioides*).

Sampling procedure

Due to the shallowness of the tributary, fishes are most effectively sampled with hand nets (Crombaghs et al., 2000). Sampling gear consisted of a small round dip net (diameter 17.5 cm; mesh size 1.0×1.0 mm^2) for collecting fish embryos and larvae, and two types of D-shaped landing nets (60×40 cm^2; mesh sizes 1.0×1.0 mm^2 and 70×50 cm^2; 3.0×3.0 mm^2) for collecting larvae, juveniles, and adults. During 2002, fishes were sampled weekly to biweekly (a total of 36 sampling days). On each sampling day, several river stretches (mean $\pm$ SE of 4.5 ± 0.3 locations per sampling day) were sampled according to the following standardized procedure. Two fishermen were positioned in the stream, facing upstream, holding the straight side of the D-shaped nets on the bottom. A third person waded towards them from an upstream position, while holding the D-shaped net on the bottom. This allowed mobile fish species that normally swim away at the first sign of danger (typically in a downstream direction), to be captured. Next,

the three fishermen walked the same stretch again in the upstream direction, specifically sampling the more structurally complex habitats, such as dense vegetation, overhanging tree roots and stony bottoms (using their feet to turn over the stones, while keeping the mouth of the net behind the stones facing upstream). This allowed them to capture the remaining fish species, which utilize complex habitats for shelter rather than escaping by swimming away quickly. Embryos, larvae and small juveniles were taken to the laboratory for identification, using the key by Pinder (2001). Larger juveniles (>4 cm) and adults were identified and measured in the field, and subsequently released. Fork length was measured to the nearest mm for fishes smaller than 20 cm and to the nearest cm for larger fish. Fish densities were expressed as numbers of fish collected per 100 m^2 of sampled area.

Growth model

The growth of 0+ fish was followed by regularly sampling the fish fauna from the Everlose Beek. Observed lengths were plotted against sampling date, showing the length increase over time. The average growth of 0+ fishes in a population was described by the Gompertz equation (Molls, 1997; Gamito,1998):

$$L_{(t)} = K * e^{-e^{-r(t-M)}}$$

In this equation, $L(t)$ represents the length of the fish at time t ($t=0$ being the time of first appearance of larvae), K the upper asymptotic growth, M the time of maximum growth and r a growth related parameter. For each sampling date, the average length was calculated and regressed against predicted values of the Gompertz equation, by means of nonlinear regression using STATISTICA version 6.0 (StatSoft Inc., Tulsa, Oklahoma, U.S.A.). The program uses a least squares estimation procedure (Levenberg–Marquardt) to minimize the sum of squared deviations of the observed values from those predicted by the model (StatSoft Inc., Tulsa, Oklahoma, U.S.A.).

Classification

Fish species were classified into different groups, based on the absence or presence of different

life-stages. The analysis was based on a distinction between five different life-stages (Table 1): (i) larval stage, defined as length at birth up to the length at ontogenetic transition to the juvenile stage, (ii) 0+ juvenile stage, defined as the length at ontogenetic transition to the juvenile stage up to the average length attained after one year, (iii) >1+ juvenile stage, defined as the average length attained after one year up to the length at sexual maturity, (iv) small adults and (v) large adults. Length ranges of these life-stages for each species were mainly based on ranges found in the Netherlands (Table 1). Species were grouped by means of cluster analysis, using Bio Diversity Professional Beta 1 (McAleece, 1997). The classification, based on presence–absence data of the different life-stages (Table 1), was performed by calculating Jaccard coefficients. The complete linkage algorithm was used, as this algorithm is most suitable for the derivation of discrete groups (Jongman et al., 1995).

Results

Seasonal dynamics

A total of 8615 fishes belonging to 13 different species were caught in the Everlose Beek. Monthly length-frequency distribution data for the eight dominant species are presented in Fig. 2, showing seasonal variation in fish densities and length classes. These eight species, i.e. Three-spined stickleback, Stone loach, Gudgeon, Roach, Bream, Tench, Rudd, and Pike, showed fish densities that were high during the summer and low during the winter, primarily caused by a sudden increase in the number of larvae during spring and summer. Juveniles and adults of Three-spined stickleback, Stone loach, and Gudgeon were present throughout the year. Roach, Bream, Tench, Rudd, and Pike were mainly represented by larvae and juveniles. Small adults were occasionally captured, typically in spring and in low densities, whereas larger adults were notably absent throughout the year (Fig. 2). The remaining five species that were caught in the Everlose Beek, i.e. Bleak, Sunbleak, Carp, Crucian carp, and Perch, were rarely captured (not shown in Fig. 2), and the absence of larvae and juveniles suggests that these species did not reproduce in the tributary. For these species, no seasonal trend in either densities or size classes could be inferred.

Reproduction and growth

Larvae and 0+ juveniles were observed for eight of the 13 species. The presence of recently hatched

Table 1. Size-classes (in cm) representing the five life-stages for each species, used for the Jaccard clustering

Species	Life Stages				
	I	II	III	IV	V
Stone loach (*Barbatula barbatula*)	0.35–1.8	1.9–4.5	4.6–5.5	5.6–8.0	8.1–10.0
Gudgeon (*Gobio gobio*)	0.5–1.3	1.4–5.0	5.1–8.0	8.1–10.0	10.1–14.0
Three-spined stickleback (*Gasterosteus aculeatus*)	0.4–1.5	1.6–4.0	*	4.1–5.0	5.1–6.0
Bream (*Abramis brama*)	0.45–1.9	2.0–4.5	4.6–15.0	15.1–40.0	40.1–85.0
Pike (*Esox lucius*)	0.9–2.6	2.7–20.0	20.1–35.0	35.1–60.0	60.1–120.0
Tench (*Tinca tinca*)	0.35–1.9	2.0–4.5	4.6–17.0[5]	17.1–45.0	45.0–70.0
Roach (*Rutilus rutilus*)	0.6–1.7	1.8–6.0	6.1–17.0	17.1–30.0	30.1–40.0
Rudd (*Rutilus erythrophthalmus*)	0.45–1.7	1.7–6.0	6.1–15.0	15.1–30.0.	30.1–45.0
Bleak (*Alburnus alburnus*)	0.5–1.4	1.5–5.5	5.6–8.5	8.6–15.0	15.1–25.0
Sunbleak (*Leucaspius delineatus*)	0.45–1.5	1.6–2.0[6]	2.1–5.0	5.1–7.5	7.5–10.0
Carp (*Cyprinus carpio*)	0.5–1.7	1.8–10.0	10.1–40.0[7]	40.1–70.0	80.1–100.0
Crucian carp (*Carassius carassius*)	0.5–1.7	1.8–4.0	4.1–15.0	15.1–35.0	35.1–50.0
Perch (*Perca fluviatilis*)	0.5–2.1	2.2–7.0	7.1–15.0	15.1–30.0	30.1–45.0

*Three-spined stickleback attained sexual maturity in its first year. Life-stages: I. Larval stage[1]; II. 0+ juveniles[1,2]; III. > 1 + juveniles[2,3,4]; IV. Small adults[3,4]; V. Large adults[3,4] (length ranges are based on: [1]Pinder (2001), [2]Pollux et al. (2004), [3]De Nie (1996), [4]Crombaghs et al. (2000), [5]Brylińska et al. (1999), [6]Gozlan et al. (2003) and [7]Baruš et al. (2002)).

Length (cm)

Density (Numbers per 100 m²)
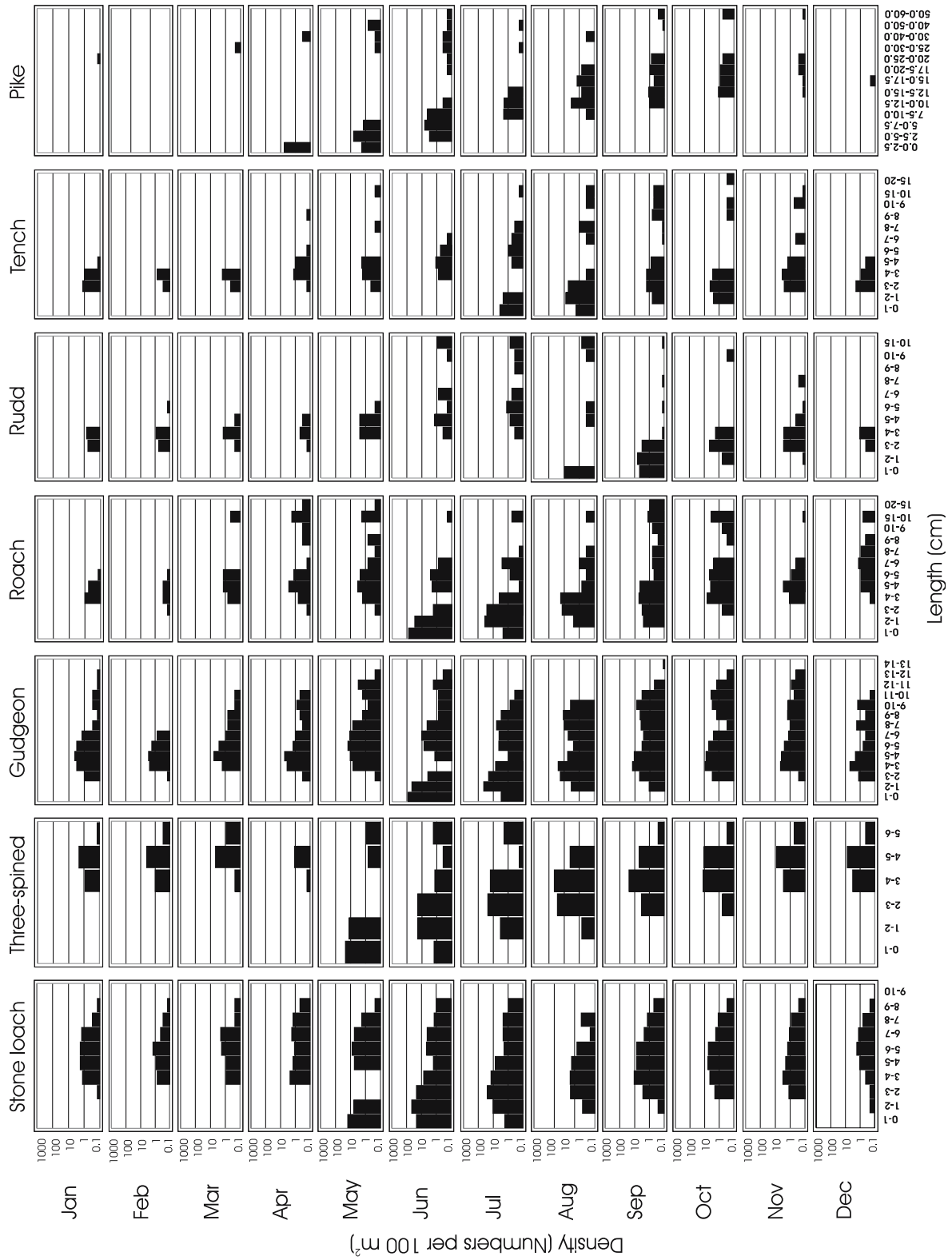
Figure 2. Monthly size-frequency distributions of Stone loach (*Barbatula barbatula*), Three-spined stickleback (*Gasterosteus aculeatus*), Gudgeon (*Gobio gobio*), Roach (*Rutilus rutilus*), Rudd (*Rutilus erythrophthalmus*), Tench (*Tinca tinca*), Pike (*Esox lucius*) and Bream (*Abramis brama*) from the Everlose Beek in 2002. Fork length on the *x*-axis (only observed size classes are presented) and numbers of fish per 100 m² on the *y*-axis (note the log-scale).

larvae (Fig. 3a), suggests that reproduction occurred in the Everlose Beek (cf. Nunn et al., 2002). Plots of observed lengths against sampling dates (Fig. 3a) show differences between species with respect to the beginning and duration of larval occurrences. Larvae of Pike were observed earliest (from April), those of Rudd last (until September). Stone loach had the longest period in which larvae were found (during May–July). Average growth curves and Gompertz growth equations are presented in Figure 3b. The consistent growth patterns, derived from regularly sampling larvae and juveniles, indicate that the eight species use the Everlose Beek as a nursery area during their first year.

Classification and migration

The cluster analysis, based on the presence of life-stages in the Everlose Beek (Table 1) revealed three different groups (Fig. 4). Group 1 consists of the three smallest species (maximum lengths ranging from 5 to 15 cm), for which all life-stages (from larvae to adults) were found in the tributary (Fig. 5). This group represents the numerically dominant species, accounting for 69% of all collected fishes in this study (Fig. 6c). The species in Group 2 are characterized by the predominant presence of larvae and juveniles (Fig. 5), suggesting that when they reach a certain size these species leave the tributary and migrate to the main river channel. The cut-off lengths at the *x*-axis (indicated by a black arrow) give an approximate indication of the size at migration (Cocheret de la Morinière et al., 2002): 5–15 cm for Bream, Tench, Rudd and Roach (coinciding with the size at sexual maturity) and 20–60 cm for Pike (Fig. 5). This group accounts for 30% of

all collected fishes in this study (Fig. 6c). Group 3 consists of species of which predominantly larger juveniles and adults were captured in the tributary (Fig. 5). Here, the absence of larvae and small juveniles suggests that these species originate from upstream areas. This group represents the numerically rare species, accounting for less than 1% of all collected fishes in this study (Fig. 6c).
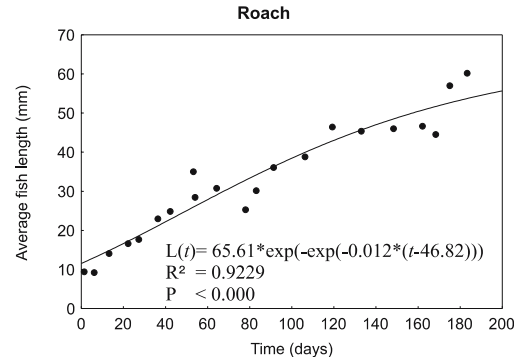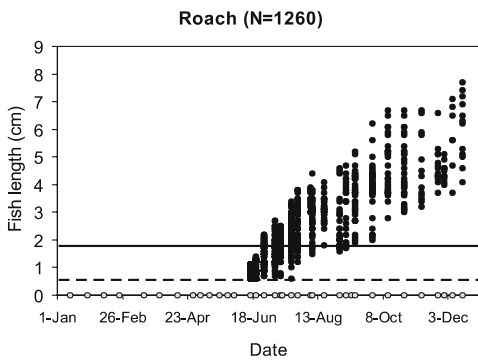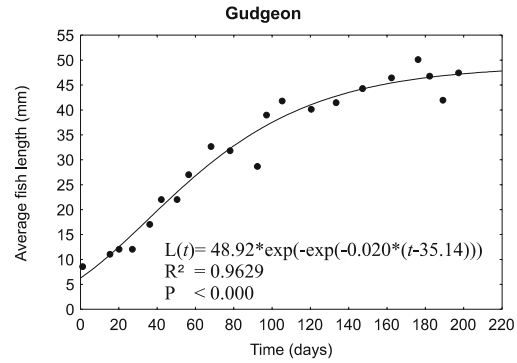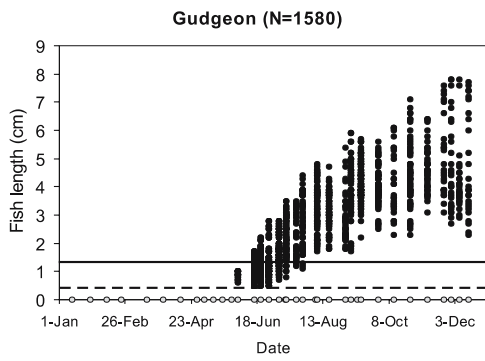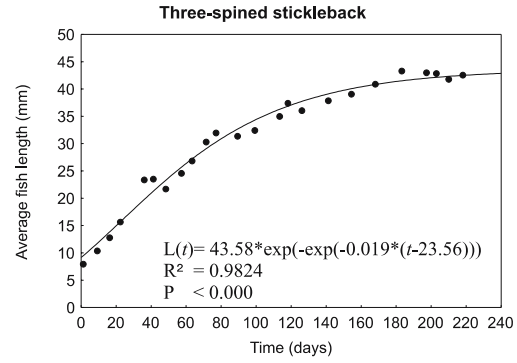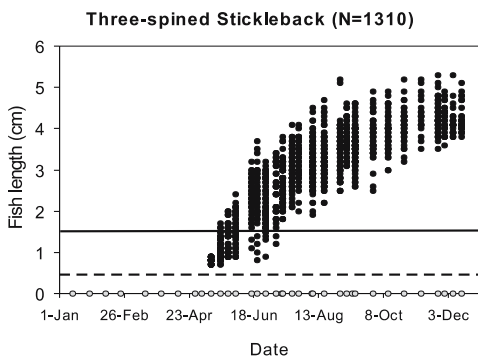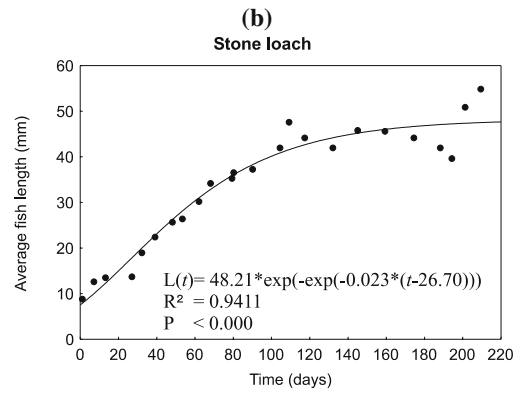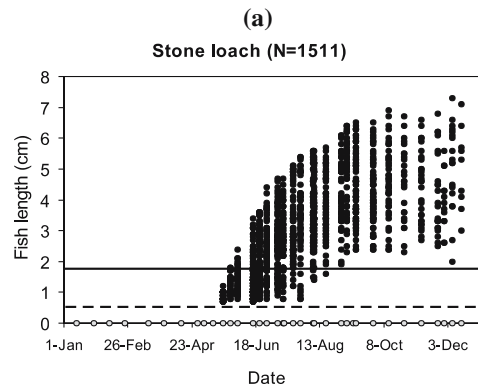
Discussion

Fish species can use tributaries during different life-stages (as larvae, juveniles, adults) for different reasons (e.g. reproduction, growth, food, shelter) and at different periods (e.g. different seasons). The results of the present study show that the fish species of the Everlose Beek can be roughly classified into three groups, viz. residents, migrants and transients, each group using the tributary in a different way (Fig. 6).

Residents (Group I)

Residents are species that complete their whole life cycle in the tributary, using it as a spawning, nursery and adult habitat (Fig. 6a). They are among the most abundant species (comprising 69% of the total catch in the Everlose Beek (Fig. 6c)). The results show that Stone loach, Gudgeon and Three-spined stickleback in the Everlose Beek are resident species. Although it cannot be excluded that some individuals in the Everlose Beek move downstream, either by drift or migration, the monthly size-frequency distributions show that fish densities of residents remain stable throughout the year, though gradually

▶

Figure 3. Growth of Stone loach (*Barbatula barbatula*), Three-spined stickleback (*Gasterosteus aculeatus*), Gudgeon (*Gobio gobio*), Roach (*Rutilus rutilus*), Bream (*Abramis brama*), Rudd (*Rutilus erythrophthalmus*), Tench (*Tinca tinca*), and Pike (*Esox lucius*): (a) 0-age fishes captured in the Everlose Beek during January–December 2002. Each black dot represents one or more 0-age fishes, the gray dots on the *x*-axis indicate the sampling dates, the dashed lines indicate length at hatching (Pinder, 2001), the continuous lines indicate length at transition from larval to juvenile stage (Pinder, 2001) and N signifies the total number of 0-age fishes that were captured. Note the different scales on the *y*-axis for each species. (b) Average 0-age growth curves calculated by regressing average fish length at each collection date (black dots) against predicted values of the Gompertz growth function.

(a)

Stone loach (N=1511)

Three-spined Stickleback (N=1310)

Gudgeon (N=1580)

Roach (N=1260)

(b)

Stone loach

$L(t) = 48.21 * exp(-exp(-0.023 * (t - 26.70)))$
$R^2 = 0.9411$
$P < 0.000$

Three-spined stickleback

$L(t) = 43.58 * exp(-exp(-0.019 * (t - 23.56)))$
$R^2 = 0.9824$
$P < 0.000$

Gudgeon

$L(t) = 48.92 * exp(-exp(-0.020 * (t - 35.14)))$
$R^2 = 0.9629$
$P < 0.000$

Roach

$L(t) = 65.61 * exp(-exp(-0.012 * (t - 46.82)))$
$R^2 = 0.9229$
$P < 0.000$

(a)

Bream (N=68)

Rudd (N=212)

Tench (N=208)

Pike (N=224)

(b)

Bream

$L(t)= 41.80*\exp(-\exp(-0.019*(t-7.67)))$
$R^2 = 0.9096$
$P < 0.000$

Rudd

$L(t)= 34.36*\exp(-\exp(-0.029*(t-17.53)))$
$R^2 = 0.9686$
$P < 0.000$

Tench

$L(t)= 34.98*\exp(-\exp(-0.044*(t-14.63)))$
$R^2 = 0.8759$
$P < 0.000$

Pike

$L(t)= 182.96*\exp(-\exp(-0.020*(t-61.60)))$
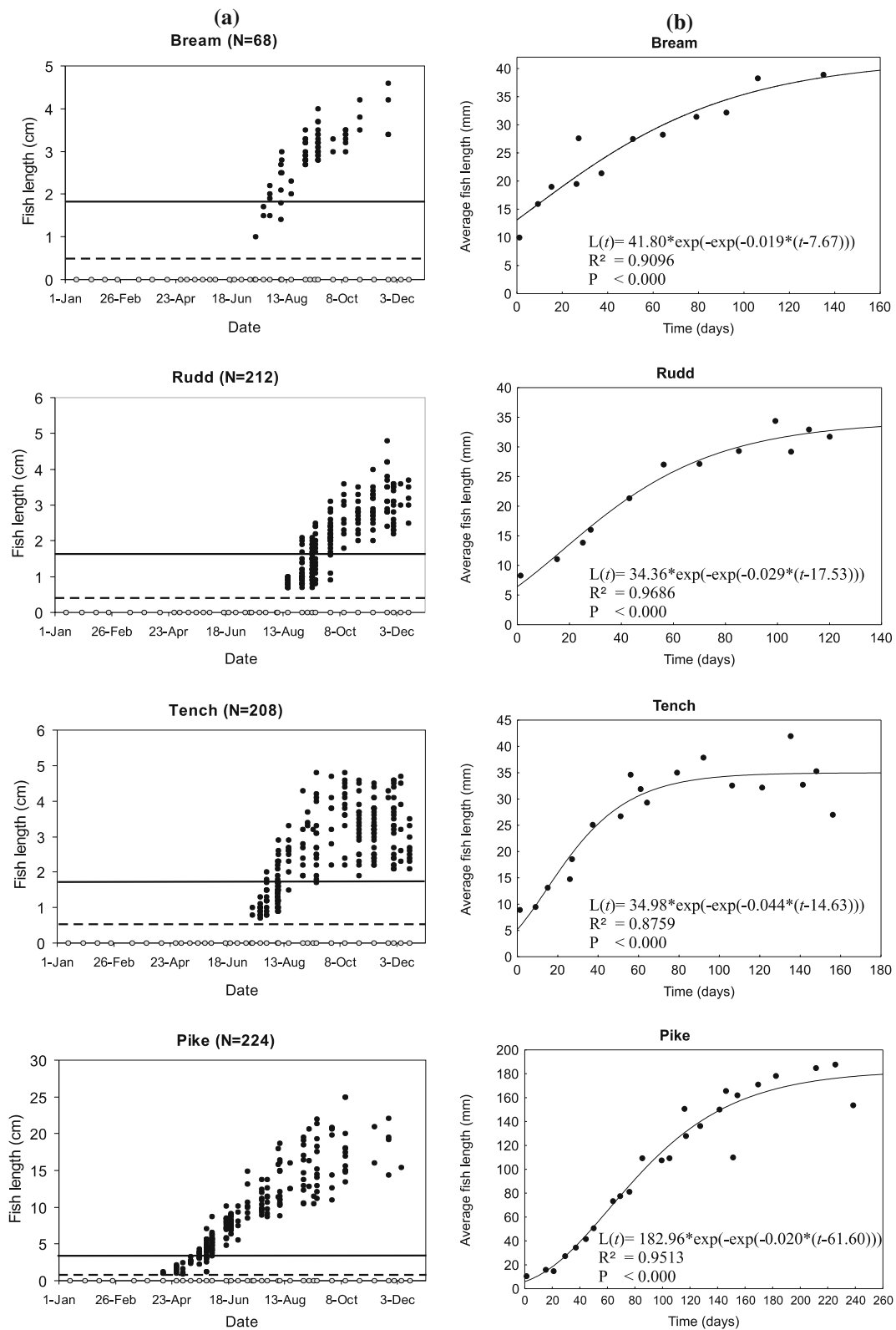$R^2 = 0.9513$
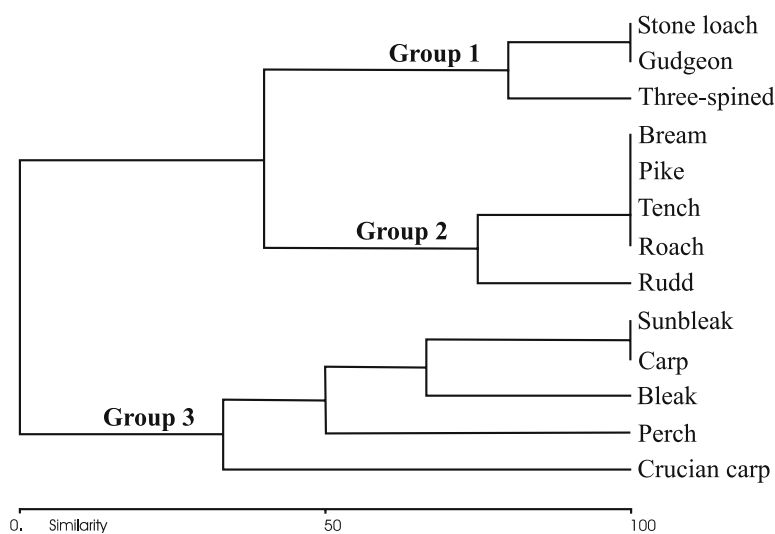$P < 0.000$

Figure 3. (Continued)

Figure 4. Complete linkage of presence–absence data for the different life-stages (Table 1), using Jaccard coefficients.

decreasing somewhat during fall and winter, indicating winter mortality rather than migration. Other studies have reported that resident species, such as Gudgeon, occupy a 'home range' (Gerking, 1953) and exhibit only restricted movements over small geographical distances, although a relatively small part of the population may sometimes display more migratory behaviour (Stott, 1961, 1967; Bănărescu,1999). In the Everlose Beek, residents are species which find suitable spawning and nursery habitats in the slow-flowing and densely vegetated lowland streams (i.e. phytophilic, phytolithophylic or psammophilic species according to Balon, 1975, 1981). Moreover, they will most likely be small species (with a maximum size range of approximately 5–15 cm), enabling them to find sufficient food and wintering habitats in the shallow streams (see below). Apart from the Stone loach, Gudgeon and Three-spined stickleback found in the Everlose Beek (in the present study) this group may also include species like Nine-spined stickleback (*Pungitius pungitius*), Spined loach (*Cobitis taenia*), and Eastern mudminnow (*Umbra pygmaea*), which have not been observed in the Everlose Beek but have been found in some of the other tributaries shown in Fig. 1 (Crombaghs et al., 2000).

Migrants (Group II)

Migrant species are characterized by the absence of larger adult size-classes (Fig. 5). Although it is known that the sampling technique, deployed in this study, tends to underestimate the presence of larger size-classes, compared to e.g. electro-fishing (Dorenbosch et al., 2000), it is unlikely that the absence of adult migrant individuals >15 cm is solely due to sampling selectivity. The capture of large adult individuals of highly mobile transient species, such as Carp (~30–40 cm), Crucian carp (~35 cm) and Perch (~20–40 cm) argues against this. Moreover, the capture of a specific size-class of Bream (~30–40 cm; Fig. 5), during a restricted period of the year (i.e., spring Fig. 2), strongly suggests that Bream >15 cm are simply absent during most of the year. Therefore, it is suggested that the absence of individuals >15 cm is not due to sampling selectivity, but the result of ontogenetic migration. Larvae and juveniles of migrant species use the tributary as nursery habitat, however, at some moment during their life cycle, typically as juveniles or small adults, they leave the tributary and migrate to the River Meuse (Fig. 6a), resulting in a low abundance or even absence of adults in the tributary during most of the year (Fig. 6d). The results suggest, that this ontogenetic migration occurs at a length of approximately 5–15 cm for Bream, Roach, Rudd and Tench, and around 25 cm for Pike.

Ontogenetic migration is generally associated with (i) ontogenetic changes in resource use (i.e. diet shifts), (ii) reduced protection from piscivores due to increased body size (i.e. the aquatic
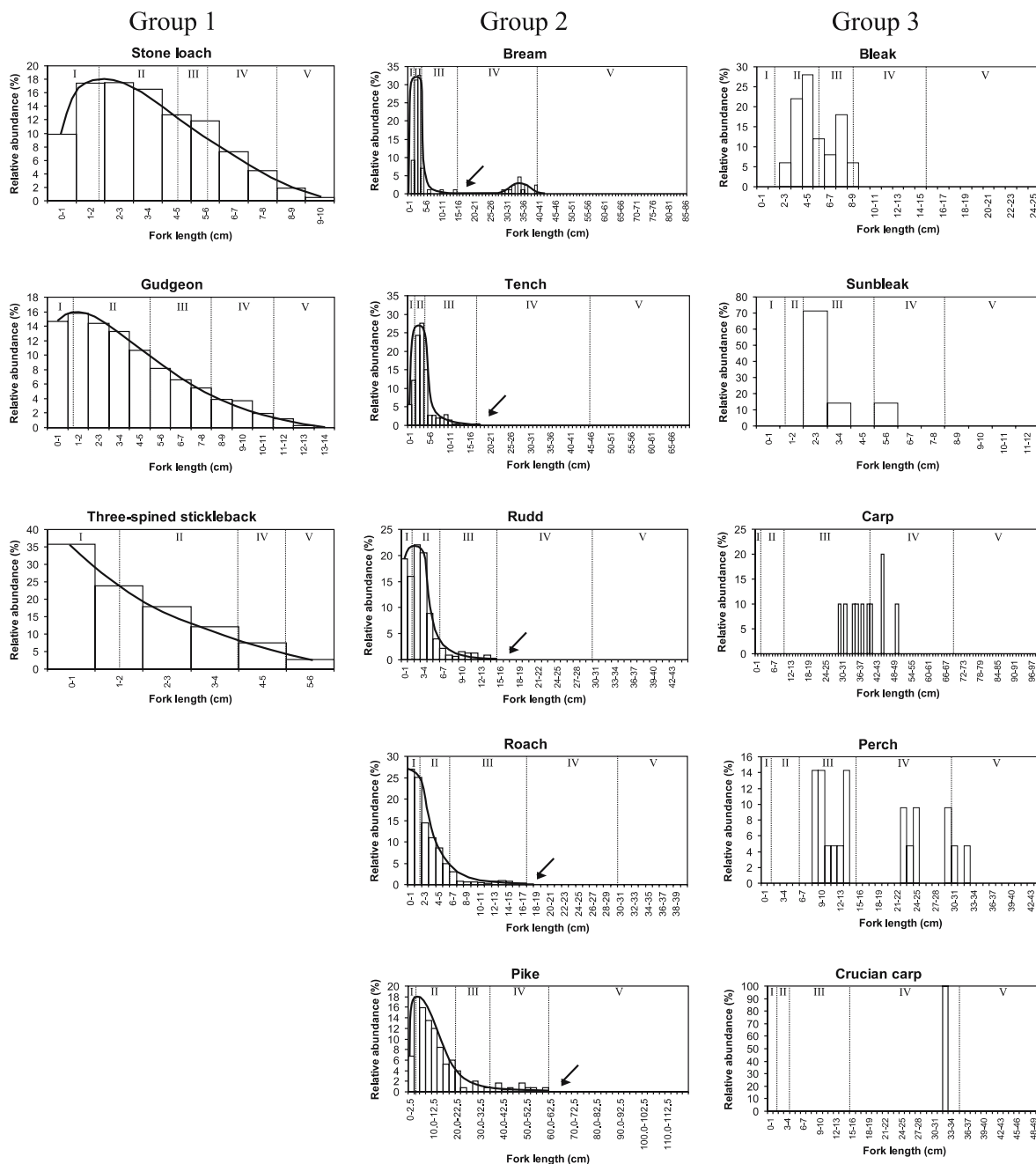
Figure 5. Relative abundance (%) of size-classes found in the Everlose Beek during 2002. The *x*-axes give the length ranges found in the Netherlands (based on De Nie, 1996; Crombaghs et al., 2000). The vertical dashed lines represent the borders of the different life-stages (see Table 1). The black arrows in Group 2 indicate the approximate length at ontogenetic migration from the tributary to the River Meuse.

vegetation no longer provides sufficient protection) or (iii) avoidance of intra-specific competition (Persson & Crowder, 1998; Cocheret de la Morinière et al., 2003). The ontogenetic migration from

the tributaries to the main river is most likely initiated by seasonal environmental changes in the tributaries. During summer, the lowland tributaries on the western bank of the river Meuse are (like
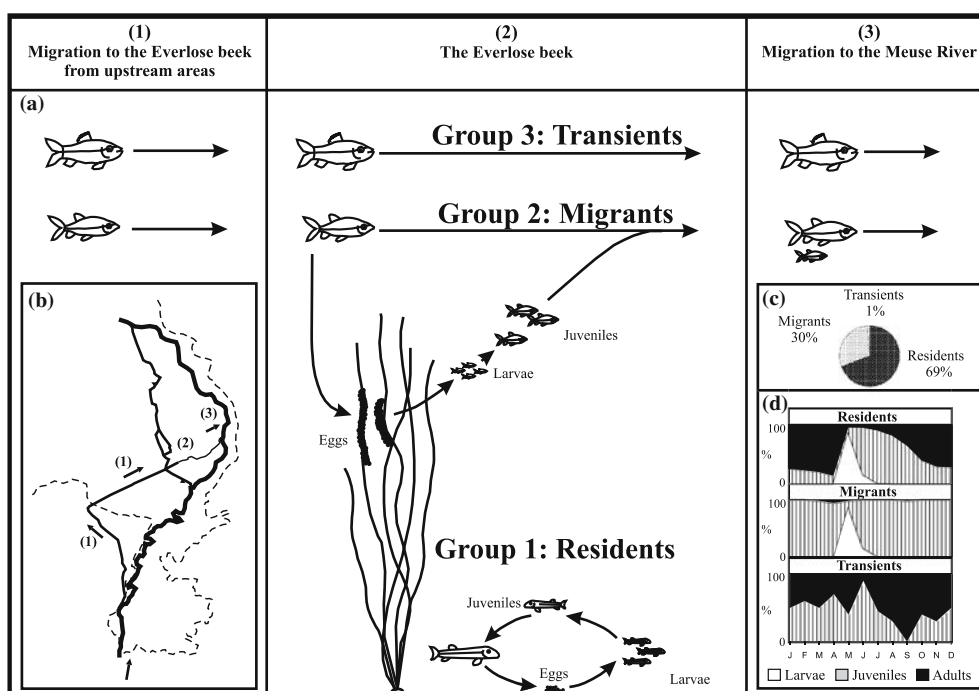
116

Figure 6. Schematic representation of the way in which resident, migrant, and transient fish species utilize the lowland tributary streams on the western bank of the river Meuse. (a) Residents complete their entire life-cycle in the tributary streams, migrants are born in the tributary streams but display ontogenetic migration towards the river Meuse and transients merely pass through the systems of canals and tributary streams without reproducing within the streams. (b) Adult migrant and transient fishes originate from upstream areas (i.e., the Zuid-Willemsvaart or Noordervaart canals), migrate towards the Everlose Beek and ultimately migrate farther downstream towards the river Meuse, displaying only unidirectional migration due to the presence of weirs. (c) Total catch (%) of resident, migrant and transient species in the Everlose Beek. (d) Composition (%) of life-stages (i.e. larvae, juveniles and adults) throughout the year (note the absence of adults for migrant species and the absence of larvae for transient species).

many lowland streams in north-west Europe) characterized by abundant aquatic vegetation, which provides structurally complex habitats offering refuge and rich foraging areas for small fishes (Rozas & Odum, 1988; Diehl & Koinijów, 1998; Grenouillet & Pont, 2001; Grenouillet et al., 2001). However, during the late fall and winter, the aboveground macrophyte biomass rapidly disappears, reducing refuge potential for fishes. In addition, flow velocity increases and water temperatures display larger and more rapid fluctuations, causing severe metabolic stress in fishes (Schlosser, 1991). Consequently, fishes (particularly larger >1+ individuals) migrate from the shallow tributaries in the fall and move to deeper water in the main channel which has a lower flow velocity and shows smaller temperature fluctuations (Nikolsky, 1963; Northcote 1978; Schlosser, 1991). Smaller individuals, up to a size of 15 cm, survive the winter (just like residents) in small

coves in the riverbank, depressions in the riverbed, among overhanging tree roots or, like Tench and Rudd, under leaves or in mud.

Transients (Group III)

Transients are characterized by very low densities (Fig. 6c) and the absence of larvae in the tributary (Fig. 6d). Transient species most likely originate from upstream areas, i.e. the Zuid-Willemsvaart or Noordervaart canals (Fig. 6b), and do not use the Everlose Beek for their reproduction (Fig. 6a). They may dwell in the tributary for a while but ultimately migrate further downstream towards the Meuse, most likely during late fall and winter, when conditions in the tributaries change rapidly and densities of these species are lowest.

The results suggest that Bleak, Sunbleak, Perch, Carp, and Crucian carp can be considered to be transient species. These transients are species

for which the shallow, slow-flowing, lowland tributaries do not provide suitable spawning and nursery habitats or optimal adult habitats. Carp and Crucian carp prefer stagnant water bodies, such as isolated floodplain lakes, both for their reproduction and as adult habitats (Baruš et al., 2002), while adult Perch and Bleak prefer the deeper and more open waters of the main channel of the river Meuse (Lelek & Buhse, 1992), where they find ample spawning and nursery habitats (Vriese et al., 1994). The Sunbleak constitutes a notable exception, finding its optimal habitat in slow-flowing, densely vegetated ditches, canals and narrow streams (Lelek & Buhse, 1992). The Everlose Beek therefore provides a very suitable habitat for this species. In the present study, very few Sunbleak were caught and reproduction was not observed. An earlier study by Akkermans (1996), however, found a large number of Sunbleak during fish sampling (using the same standardized methodology), including larvae and small juveniles (Akkermans, pers. comm.). Populations of Sunbleak are known to show extreme fluctuations in size across years, with densities varying from sporadic in one year to explosively abundant in another (Lelek & Buhse, 1992; Crombaghs et al., 2000). Therefore, despite the absence of larvae in 2002, the Sunbleak is more likely to be a resident species, since it is able to reproduce in the Everlose Beek, has a small adult size (<10 cm) enabling it to survive the winter in the shallow tributaries, and is also known elsewhere, as a non-migratory species (http://www.fishbase.org).

Potential recruitment from lowland tributaries

During the last two centuries, modifications to the geomorphology of the large lowland rivers Rhine and Meuse have resulted in steep and fortified stony embankments and a severe lack of aquatic vegetation in the main channel (Nienhuis et al., 1998; Rant, 2001; Nienhuis et al., 2002a, b), leading to a greatly reduced or even absent recruitment potential for limnophilic and rheophilic species (Vriese et al., 1994). In addition, former floodplain areas directly adjacent to regulated rivers have been turned into agricultural land, greatly reducing the total floodplain area along large rivers (Nienhuis et al., 2002a, b; Buijse et al., 2002) agree with the change. Simulta-

neously, flow regulation by means of dams and weirs has led to a decline in natural water level variations effectively leading to the isolation of the remaining floodplain water bodies (Bain et al., 1988; Dynesius & Nilsson, 1994; Ward & Stanford, 1995; Aarts et al., 2004). The few remaining floodplain lakes often have a depaupered fish fauna, dominated by a few eurytopic species, such as Bream, White bream and Roach (Van den Brink et al., 1996; Grift et al., 2001; Buijse et al., 2002). Newly created man-made habitats, such as gavel-pit lakes and excavated secondary side-channels connected to the main river, are mainly used by eurytopic species, to a lesser degree by rheophilic species, yet rarely by limnophilic species (Neumann et al., 1994; Staas & Neumann, 1994, 1996; Simons et al., 2001; Grift et al., 2003). Not surprisingly, the fish fauna of the large lowland rivers Rhine and Meuse in the Netherlands is currently dominated by eurytopic species (Van der Velde et al., 1990; Admiraal et al., 1993; Van den Brink et al., 1996; Raat, 2001).

What is surprising, however, is that despite the apparent lack of spawning and nursery areas for limnophilic species in the main channel, floodplain lakes, gravel-pit lakes and secondary side-channels, a few limnophilic species, particularly Pike, Tench and Rudd are still found in the river Meuse, and although they are generally found in small numbers, their occurrences have been quantified as common to locally common by Admiraal et al. (1993) and Crombaghs et al. (2000), respectively. This has given rise to the hypothesis that the recruitment sources for these predominantly phytophylic spawners are situated elsewhere in the river basin. The results of the present study suggest that regulated lowland tributaries may act as such recruitment sources, preventing the total extinction of these species in the River Meuse.

In the Netherlands, the Meuse is connected to over a 100 lowland streams (Maris et al., 2003). The lowland streams on the western bank of the Meuse in the Province of Limburg (Fig. 1) alone already have an estimated total length of over 500 km, with an average width of approximately 5–10 m (the eastern bank of the river Meuse also features a number of tributary streams, not shown in Fig. 1). Although most of these lowland streams are to some degree regulated (natural free flowing lowland rivers and streams can hardly be found in

the Netherlands anymore; Verdonschot & Nijboer, 2002), they comprise an area of considerable size consisting of slow-flowing, shallow-water habitats with locally abundant vegetation, hence providing suitable spawning and nursery habitats for many species. The present study shows that phytophylic (e.g. Rudd, Tench, Pike, and Three-spined stickleback), psammophilic (Stone loach and Gudgeon), and polyphilic (Roach and Bream) spawners can reproduce in these regulated streams. A few species spend their entire lives in the shallow streams (the residents), but other species display ontogenetic migration to the river Meuse (the migrants). We suggest that regulated lowland tributaries, such as the Everlose Beek, may function as important recruitment sources for many limnophilic species in large rivers. We further suggest that the persistence of the severely reduced populations of limnophilic species in heavily modified rivers in north-western Europe, such as the river Meuse, may be attributed to recruitment from regulated lowland tributary streams.

Acknowledgement

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