An Individual-based Approach to Depict the Influence of the Feeding Strategy on the Population Structure of Roach (*Rutilus rutilus* L.)

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With 7 Figures and 3 Tables

Key words: Individual-based model, functional response, consumption, ontogenetic shift, food composition

Abstract

We used an individual-based modelling strategy to simulate the growth of a roach population. Individual growth is based on food utilization, bioenergetics, spatial distribution, and seasonal influences. With this approach, it is possible to connect the animals' activity pattern with the energetic needs required for this activity. This allows investigating the role of spatial heterogeneity and individual variability for the dynamics of fish growth. The parameterisation is based on laboratory measurements and field studies performed at Lake Belau (Schleswig-Holstein, Northern Germany). The interactions of the behavioural repertoire, growth processes, and food preferences emerge in the context of a decreasing proportion of zooplankton in the food composition of simulated roach. Roach feeding on molluscs grow faster. The ontogenetic shift is related to the necessity to switch to larger prey as a consequence of the increase of energetic demands with body size.

Introduction

Bioenergetic models have frequently been used to predict fish growth under given sets of environmental conditions, to estimate the effects of fish on their prey community, to evaluate the importance of fish on nutrient turnover in lakes, and to improve management strategies (KITCHELL et al. 1977; ADAMS & BRECK 1990; HEWETT & JOHNSON 1992; HANSON et al. 1997). The precision of the output depends on accurate estimation of food consumption, growth and respiration rates (JOBLING 1994; TANG & BOISCLAIR 1995). Most of these models assume that individuals within a population or age class are equivalent. However, a key to understand fluctuations in fish populations is whether, and to what extent, connections exist between population dynamics and the differences among individuals in the population (CHAMBERS 1993). In this context it is important to know how individual fish allocate resources and time among activities related to maintenance, growth and reproduction in a changing environment (WOOTTON 1990). Therefore, individual-based models offer considerable advantages to estimate the role of individual variability in influencing population dynamics. They provide a framework to conceptualise the natural processes, design the sampling strategy, analyse results, and combine empirical studies and modelling in a synergistic manner (DEANGELIS & ROSE 1992; VAN WINKLE et al. 1993).

The motivation to develop an individual-based model for roach (*Rutilus rutilus*) was based on two aspects.

1. Roach is a successful generalist fish in Central European freshwater habitats (SCHIEMER & WIESER 1992), and is therefore a well-studied species. This allows to meet the high information requirements of individual based models, and
2. roach is one of the dominant fish species besides bream and perch in Lake Belau (Schleswig-Holstein, Germany) which is the main research area of the ecosystem research project, Kiel (PÁC 1989; PFEIFFER 1999).

The roach model we developed for Lake Belau is now in a state in which it provides a valuable base for fish ecological studies. It is possible to use a 3-dimensional habitat representation to extrapolate short time observations of individuals to the population level and to connect spatial behaviour with the energetic needs required for this activity (HÖLKER 1999).

Due to the integration into a large ecosystem research project (HÖRMANN 1995), we had access to the data of other projects working at Lake Belau, e.g. data on zooplankton and zoobenthos abundance, microclimate data and maps from the Geographic Information System (GIS). In 5 years of labora-
In laboratory studies, it was achieved to measure all major components of the energy budget of roach (HÖLKER 1999). The growth and food composition serve as interface between the field investigations and the laboratory findings. Here we present the simulated food consumption, emerging properties on the individual level and the influence of the feeding strategy on the population structure of roach.

Material and Methods

Program system

The program is written in SIMULA (DAHL et al. 1968). It was compiled with CIM, a public domain SIMULA-to-C conversion program under LINUX. A set of classes represents the various structural and functional aspects of the system. Each of these parts is operating on an independent updating schedule. The model is organized in two domains; one to specify the environment consisting of the process classes NIGHT AND DAY, TEMPERATURE and SET SIGHT RANGE, the other one to describe the fish biology (process classes: READ FISH INDIVIDUAL DATA and FISH). The fish class contains a detailed set of rules (behavioural repertoire) used to determine the activity of an individual fish as a response to the internal condition, the environmental situation and the reaction to conspecifics (HÖLKER & BRECKLING 1998).

The simulation program reads several input data sets including a grid map of the lake, data about the habitat structure, weather conditions (light, temperature) and food availability, as well as data dealing with the initial values of each individual fish (sex, bioenergetics, behaviour) at the simulation start (Fig. 1).

Modelling the environment

The environment consists of a habitat representation using a 3-dimensional grid map, microclimate data, and data sets about the available food. The grid map is derived from the Geographical Information System of the Ecosystem Research Centre (Kiel). The grid elements have a surface area of 2500 m² each and describe the water column down to the bottom of the lake (Fig. 2). It is possible to work with grid maps from other lakes or artificial habitats as well. The littoral shore zone is defined as the area with a water depth of less than 5.5 m. The meteorological information consists of data on temperature (°C) in a water depth of 1 m on a weekly basis and data on global radiation (J cm⁻²) 1 m above the surface on an hourly basis. A standard year with the identical resolution was calculated by using the mean meteorological data of the years 1991–1995.

The food organisms are resumed as grid element specific density variables. They consist of two categories: zooplankton (N l⁻¹) and zoobenthos (N m⁻²) shown for a standard year in Fig. 3. The zoo-
plankton size fraction larger than 100 μm is attractive for roach (Pfeiffer, pers. comm.). In Lake Belau, this fraction consists mainly of Cladocera and Copepoda (Fleckner, pers. comm.). An average zooplankton organism with a mean weight was calculated for each fortnight of the year using the data set of Fleckner (pers. comm.). The energy and water content are supposed to be 21.45 kJ g⁻¹ dw and 89.9% (Hepper 1988). The data set includes the period 1991–1994 with a resolution of 14 days. Zoobenthos comprises the categories benthic insect larvae and mollusks, which are mainly found in the littoral zone. Benthic insect larvae play an important role as a food source of cyprinids in Lake Belau. Especially chironomid larvae are essential food organisms (Dienemann 1997; Pfeiffer 1999). The data set of Dienemann (1997) was used to calculate the seasonal abundance alterations and the mean individual weight of chironomid larvae. The seasonal fluctuations in the density of Trichoptera and Ephemoptera larvae were calculated by Pfeiffer (1999) who used empirical data from Otto (1991). The calculated data set for insect

**Fig. 3.** Abundance of zooplankton (N l⁻¹, fat line) and insect larvae (N m⁻², narrow line) in a standard year in Lake Belau.

**Fig. 4.** Basic structure to simulate an individual roach. The class FISH provides all rules and variables, which specify a fish individual.

**PROCESS CLASS FISH BEGIN**

Declaration of a process class to describe the properties of an individual

**Declaration of activity PROCEDURES**

**Behavioural repertoire**
- Habitat selection
- Shoaling
- Food searching
- Straight swimming
- Spawning

**Energetics**
- Test if hungry
- Consumption
- Digestion
- Excretion
- Respiration
- Somatic growth
- Reproductive growth
- Starvation

**Life loop**
Selection and call of activity procedures

While alive do
  - Examine seasonal and internal status
  - Choose activity
  - Execute activity and calculate activity costs
  - Update energetic state
  - Check life state

If alive
  Execute activity
Else
  End of while

END OF FISH
larvae represents only the seasonal fluctuations of one standard year with a resolution of 1 month. The mean energy and water content was assumed to be 21.91 kJ g$^{-1}$ dw and 82.8% (HESSEY 1988). Bivalvia and Gastropoda comprise the second benthic group. The mean benthic biomass of molluscs in Lake Belau was between 11.7 and 30.2 g dw m$^{-2}$ (ASSHOFF 1990). No adequate data set exists about seasonal variations in abundance and biomass. As an estimation, a mean mollusc biomass of 21 g dw m$^{-2}$ was supposed to be constant throughout the year. The mean individual weight was about 1 mg (PFEIFFER 1999 using data from ASSHOFF 1990). The mean energy and water content was assumed to be 16.28 kJ g$^{-1}$ dw and 32.2% (HESSER 1988).

Modelling the FISH

The fish part of the program consists of the process class FISH. This class provides all rules and variables, which specify a fish individual. It consists mainly of bioenergetic parameters, energy allocation and reallocation rules, physiological activities and the scheduling of behavioural activities (Fig. 4). In the context of this paper, we want to present the regulation of the food consumption. A full description of the model is given in HOLKER (1999).

An essential element of the class FISH is the so called ‘life loop’. As long as the FISH life-state variable is ‘true’, the program will execute this loop and calls appropriate activity procedures (Fig. 4). A HOLD procedure interrupts the execution of the FISH life loop and leaves a notation in the internal execution timetable to continue execution one time-increment forward.

Spatial behaviour

Our intention was to specify the behavioural variability and activity pattern of individuals by integrating specific biological information known from literature and assumptions that are based on own observations of Lake Belau roach. We use a type of choice behaviour in which the individual responds to a set of environmental stimuli (light, temperature, habitat type) by showing a preference for staying in an area that can provide the set. The internal physiological status is controlled by Boolean variables, which cause the corresponding habitat selection and activity mode (Table 1). If the fish find themselves outside of their preferred area they increase their swimming speed. In the simulation a fish switches to a higher swimming speed and reduces the moving angle until the fish reaches the preferred area. In preferred areas the fish switches to a lower swimming speed and enlarges the moving angle. The resulting behaviour is connected with the energetic requirements for this activity (HOLKER & BRECKLING 1998).

The movement of a simulated roach is a ‘correlated random walk’. This means that swimming direction and moving angle are calculated stepwise with a certain random deviation. The diet pattern of light and dark strongly influence the spatial behaviour. According to PFEIFFER (1999) and the local fisherman at Lake Belau the roach population is active mainly at day, dusk and dawn. During day and night the fishes prefer the pelagic area of the lake. At dusk and dawn they prefer the littoral zone. Benthic food items are only available in the latter area. The simulated roach have the status ‘hungry’ only during day, dusk and dawn (Table 1). This causes a specific food searching behaviour, which costs more energy than e.g. straight swimming (WIESER 1991; HOLKER & BRECKLING 1998). The probability to feed mainly on benthic prey is higher at dusk and dawn than during the day. The chance to feed primarily on plankton is higher during daytime.

Consumption

We assume that roach capture the resource following a Holling type II functional response (HOLLING 1959). The relationship between prey density and capture rate was obtained from an approximate version of the Holling II equation given by PERSSON (1987):

\[
C = \frac{aN}{1 + ahN}
\]

where C is the capture rate (prey s$^{-1}$), a is the attack coefficient, h is the handling time (s), and N is the prey density (l$^{-1}$ or m$^{-2}$ respectively).

This function was used to predict the consumption rate of fish on zooplankton and insect larvae. Due to the incomplete data set, it was impossible to define a functional response formula for consumption on molluscs. In Lake Belau, roach shifts at a length of about 13 cm from zooplankton and insect larvae to molluscs as an additional food item (PFEIFFER, pers. comm.). The ingestion of molluscs for roach

| Table 1. The internal physiological status of individual roach is controlled by Boolean variables, which are used to select the corresponding habitat preferences and activity mode. Littoral is defined as the lake area with a water depth equal or below 5.5 m, pelagial as the lake area with a water depth of more than 5.5 m. |
|-----------------|-----------------|-----------------|-----------------|
| Physiological status (Boolean variable) | Time of the day | Habitat selection | Activity mode (procedure) |
| "hungry := true" | Night            | Pelagial         | Straight swimming |
|                  | Day              | Pelagial         | Food searching   |
|                  | Dusk and Dawn    | Littoral         | Food searching   |
| "hungry := false" | Night            | Pelagial         | Straight swimming |
|                  | Day              | Pelagial         | Straight swimming |
|                  | Dusk and Dawn    | Pelagial         | Straight swimming |
| "spawning := true" | Night            | Pelagial         | Straight swimming |
|                  | Day              | Littoral         | Spawning         |
|                  | Dusk and Dawn    | Littoral         | Spawning         |
| "winter := true" | Night            | Pelagial         | Straight swimming |
|                  | Day              | Pelagial         | Straight swimming |
|                  | Dusk and Dawn    | Pelagial         | Straight swimming |
larger than 13 cm follows a linear relationship between consumption rate and body length. In the model roach shows a preference for benthic prey about zooplankton in the littoral.

A roach tries to achieve its maximum daily ration capacity \( (C_{\text{max}}) \). The simulated fish has the status ‘hungry’ as long as it has not achieved \( C_{\text{max}} \). For roach \( C_{\text{max}} \) (g ww) is described as an allometric function of fish biomass from ad libitum feeding experiments with chironomid larvae within a temperature range from 5 °C to 20 °C (HÖLKNER 1999). The temperature dependence follows an exponential function.

\[
C_{\text{max}} = 0.016 \times W^{0.84} \times e^{(0.11) \times T}
\]

\( W \) is the fish biomass (g ww) and \( T \) is the temperature (°C). During the short spawning season, roach consumes only a small proportion of \( C_{\text{max}} \). During winter, roach in Lake Belau nearly stop their food intake. Even in March 88% of the population had empty guts (PFEIFFER 1999). STEINMANN (1996) found a similar situation in backwaters of the River Sieg (Germany), where the roach population stops food intake almost entirely during winter. At temperatures below 5 °C in aquarium experiments roach stop their food intake, too (STEINMANN 1996). It is therefore assumed in the model that roach does not feed at water temperatures below 5 °C.

Energy budget

A correct representation of the energetic state is one of the most important parts of the model. Therefore we divided roach energetics into different compartments with specific functions to simulate the flow and storage of energy (HÖLKNER 1999). The considered compartments are the stomach, a short-term storage (carbohydrates), a medium-term storage (fat), a long-term energy storage (protein) and a reproduction fraction. The food energy flow follows the path from the stomach to the physiological processes of energy absorption and assimilation as well as respiration. This results in growth processes and different energy allocation and reallocation rules. Though the reproductive fraction consists of carbohydrates, fat and protein as well, it was modelled as a separate compartment due to its high dynamic. To take the costs for activity into consideration, the model is able to connect spatial behaviour with the energetic needs required for this activity.

The processes correspond to the different components of a typical energy budget and are integrated into the model as procedures of the class FISH. An important constraint on a fish’s capacity to regulate the allocation of energy to maintenance, activity and feeding is the effect of changes in the biotic and abiotic environment. The primary effects on the physiological components in the model are therefore fish weight, food supply, season, temperature, and light.

Parameterisation

The model covers the major aspects of a roach’s life starting at the end of the first growth season. It was parameterised for a standard year. To start a simulation run, 100 roach are placed into a starting area. Dependent on the internal physiological status and daytime each simulated roach tries to reach the preferred habitat using a corresponding activity mode (Table 1). For example, as long as a roach has not achieved its maximum daily ration \( (C_{\text{max}}) \) during dusk or dawn the fish has the status ‘hungry’, switches to the activity mode ‘food searching’ and tries to reach the littoral zone. The resulting consumption rate follows the corresponding functional response curves in dependence of the prey density in the present habitat. If the rate of food consumption is sufficiently high, the roach can, in addition to meeting the energy costs of maintenance and activity, synthesise new tissue.

In order to calibrate and connect the spatial behaviour and the energetic needs with the growth and food composition of roach in Lake Belau we used the following criteria (Fig. 5):

![Fig. 5](image-url)

**Fig. 5.** Parameterisation of the individual-based roach model by connecting food consumption (energetic needs for simulated growth and spatial behaviour) with empirical data (growth and food composition) in an iterative process. The parameter \( a \) is the attack coefficient and \( h \) the handling time from the Holling type II functional response curve presented by PERSSSON (1987).
• Start values are the length, weight (November 1991, 1992) and the food composition (autumn 1991) of 0+ roach in Lake Belau (BERTRAM, subm.).
• Target values are the growth of Lake Belau roach over 6 years and the food composition of adult roach (PAC 1989; PFEIFFER 1999).
• The attack coefficient \( a \) and the handling time \( h \) (s) from the Holling type II functional response curve serve as search parameters. They were computed in an iterative process starting with values given by PERSSON (1987).

In a first step, the consumption rate of roach up to a length of 13 cm was adjusted. At this size, Lake Belau roach feed mainly on zooplankton and insect larvae. In a second step, the consumption rate of molluscs was integrated up to the age class 6+. To validate the resulting parameters of the functional response curves we discuss the model results in the context of values known from literature (Fig. 5).

### Results

#### Parameterisation

Because the seasonal fluctuations of the zooplankton abundance were much higher than the seasonal changes of the insect larvae (Fig. 3), the calibration of zooplankton intake proves to be very sensitive. In Table 2 the values for \( a \) and \( h \) are summarized. The consumption rate on zooplankton is located between 0.31 and 0.33 prey \( s^{-1} \) with a handling time of 3.0 s and an attack coefficient \( a \) of 0.36.

To adjust the consumption rate of roach on insect larvae we assume an increase of the consumption rate following a functional response curve, too. In Table 2 the computed values for \( a \) and \( h \) are summarized at a concentration of 300–7500 N \( m^{-2} \). The consumption rate on insect larvae was between 0.0014 and 0.0183 prey \( s^{-1} \) with a handling time of 6.9 s and an attack coefficient \( a \) of 0.0000028.

Due to the incomplete data set, it was not reasonable to define a functional response formula for molluscs. We assumed for the ingestion of molluscs by roach larger than 13 cm a linear relationship between consumption rate and body length. A starting value for the consumption rate on molluscs of 0.002 prey \( s^{-1} \) was assumed. The iterative computation results in:

\[
C \text{ (prey } s^{-1} \text{)} = 0.0047 \times \text{body length (cm)} - 0.058
\]

This means that simulated roach consume between 0.0031 and 0.032 molluscs per second.

#### Food composition

Fig. 6 summarizes the mean length and the corresponding food composition of 100 simulated roach over 6 years. In comparison the figure presents the start and target values between 0.0014 and 0.0183 prey \( s^{-1} \) with a handling time of 6.9 s and an attack coefficient \( a \) of 0.0000028.

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\]

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### Table 2. Results from the simulation runs to estimate the parameters of the Holling type II functional response curve. \( C \) is the capture rate (prey \( s^{-1} \)), \( a \) is the attack coefficient, \( h \) is the handling time (s), and \( N \) is the prey density (1 \( \text{m}^2 \) or \( \text{m}^3 \) respectively).

<table>
<thead>
<tr>
<th>Food item ((N))</th>
<th>Consumption rate ( C ) (prey ( s^{-1} ))</th>
<th>Attack coefficient ( a )</th>
<th>Handling time ( h ) (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zooplankton ((10–400 \text{ ml}))</td>
<td>0.31–0.33</td>
<td>0.36</td>
<td>3.0</td>
</tr>
<tr>
<td>Insect larvae ((300–7500 \text{ m}^2))</td>
<td>0.0008–0.0183</td>
<td>0.0000028</td>
<td>6.9</td>
</tr>
</tbody>
</table>

Fig. 6. Mean fish length and food composition of 100 simulated roach during their ontogeny over 6 years. In the first 3 simulated years, there is a continuous decrease of zooplankton in the consumed food, which results as a consequence of larger swimming distances when individuals grow. On the right the figure presents the start and target values for parameterisation based on data about growth and diet composition of roach in Lake Belau. Start values are length and food composition of 0+ roach in Lake Belau in autumn (BERTRAM, subm.). Target values are the growth over 6 years and the food composition of adult roach (PFEIFFER 1999).
haviour. Larger roach are able to swim longer distances per time unit than the smaller ones. Therefore, they are able to scan a larger area for suitable feeding grounds. This connection of spatial behaviour and feeding strategy can be interpreted as an emergent property (MÜLLER et al. 1997). In the third simulated year, the roach reach the required size of 13 cm that enables them to feed on molluscs. The increase of molluscs in the diet follows the linear increase of the consumption rate with the body length of roach and is implemented in the model and therefore not an emergent property.

Population structure

The consequences of different feeding strategies on the growth rate of roach are illustrated in Fig. 7. Here, the population profile of 100 simulated roach in the second simulated standard year is plotted. At the end of the year, only a few roach (> 13 cm) were able to feed on molluscs and to use this additional food source for growth which resulted in a stunted cohort of non-molluscivorous with a few larger molluscivorous. The length frequency became positively skewed.

Discussion

Parameterisation

When we try to understand the dynamics of interacting populations of predators and prey, the critical linkage is the predator functional response to changes in prey density (FRYXELL & LUNDBERG 1998). To validate if the parameterisation of the presented model results in reasonable values of the functional response curves, we compare the model results with results for roach (> 5 cm) known from literature. Experimental tests of functional responses, in which roach consume zooplankton, are common in the literature. Table 3 summarizes all results known to the authors. The consumption rate measured by PERSSON (1987) is 4 to 6 times higher than the rate given by WINKLER & Orellana (1992). The computed rate of our study lies within these limits (0.31–0.33 prey s⁻¹). In contrast, the handling time in the investigation of Winkler & Orellana (1992) was longer than the calculated one given by Persson (1987). The computed handling time of the simulation model lies in between the results of these investigations (3 s prey⁻¹).

Experimental tests, in which roach consume insect larvae, are quite rare. Persson (1987) found a minor ability of roach to use chironomid larvae regardless of prey density (300–3000 m⁻²). However we assume an increase of the consumption rate with prey density. The handling time of 6.9 s prey⁻¹ given by Persson (1987) was valuable for computing the consumption rate. This results in a rate of 0.0008 to 0.0079 insect larvae per second at a concentration of 300–3000 N m⁻². Diehl (1988) found at a concentration of about 700 N m⁻² a handling time of 18.1 s prey⁻¹. The mean number of captured chironomid larvae decreased markedly
Table 3. Results from the simulation runs to estimate the parameters of the Holling type II functional response curve in comparison with values for roach (> 5cm) from literature. \( C \) is the capture rate (prey s\(^{-1}\)), \( a \) is the attack coefficient, \( h \) is the handling time (s), and \( N \) is the prey density (1 m\(^{-2}\) or m\(^{-3}\) respectively).

<table>
<thead>
<tr>
<th>Food item (N)</th>
<th>Consumption rate ( C ) (prey s(^{-1}))</th>
<th>Attack coefficient ( a )</th>
<th>Handling time ( h ) (s)</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Zooplankton (10–100 l(^{-1}))</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copepoda</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclops sp.</td>
<td>0.7–0.9</td>
<td>0.36</td>
<td>1.1</td>
<td>Persson (1987)</td>
</tr>
<tr>
<td>Cyclops sp.</td>
<td>0.13–ca. 0.20*)</td>
<td>4.8</td>
<td>Persson (1987)</td>
<td></td>
</tr>
<tr>
<td>Cladocera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daphnia magna</td>
<td>1.6–1.8</td>
<td>2.92</td>
<td>0.6</td>
<td>Persson (1987)</td>
</tr>
<tr>
<td>Bythotrephes longimanus</td>
<td>0.25–ca. 0.28*)</td>
<td>3.6</td>
<td>Winkler &amp; Orellana (1992)</td>
<td></td>
</tr>
<tr>
<td>Daphnia magna, no vegetation</td>
<td>1.1**)</td>
<td></td>
<td>Winkler &amp; Orellana (1992)</td>
<td></td>
</tr>
<tr>
<td>Daphnia magna, vegetation</td>
<td>0.2**)</td>
<td></td>
<td>Winfield (1986)</td>
<td></td>
</tr>
<tr>
<td>Literature range</td>
<td>0.13–1.8</td>
<td>0.36–2.92</td>
<td>0.6–4.8</td>
<td></td>
</tr>
<tr>
<td>Model results</td>
<td>0.31–0.33</td>
<td>0.36</td>
<td>3.0</td>
<td></td>
</tr>
<tr>
<td><strong>Insect larvae (300–3000 m(^{-3}))</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chironomus plumosus</td>
<td>0.001–0.002</td>
<td></td>
<td>6.9</td>
<td>Persson (1987)</td>
</tr>
<tr>
<td>Chironomus anthracinus, no vegetation</td>
<td>ca. 0.014*</td>
<td>18.1</td>
<td>Diehl (1988)</td>
<td></td>
</tr>
<tr>
<td>Chironomus anthracinus, Vegetation</td>
<td>ca. 0.0028*</td>
<td>18.1</td>
<td>Diehl (1988)</td>
<td></td>
</tr>
<tr>
<td>Literature range</td>
<td>0.0010–0.0140</td>
<td>–</td>
<td>6.9–18.1</td>
<td></td>
</tr>
<tr>
<td>Model results</td>
<td>0.0008–0.0079</td>
<td>0.0000028</td>
<td>6.9</td>
<td></td>
</tr>
</tbody>
</table>

*) Calculated from figures, **) at 2.35 l\(^{-1}\).

with increasing vegetation density. In a non-vegetated habitat, roach had a consumption rate of ca. 0.014 N s\(^{-1}\). In a \( Chaco \) habitat, they had a consumption rate of about 0.0028 N s\(^{-1}\) (Tab. 2). Neither Diehl (1988) nor Persson (1987) considered ontogenetic changes of foraging rates. In our study, we did not take different prey size classes into consideration as well. Laboratory studies have shown that even large roach utilize sizes of zooplankton prey down to 0.4 mm (Lessmark 1983). Therefore, a constant functional response curve is likely to simulate the intake of zooplankton and insect larvae appropriately. In order to be able to include a size dependent functional response curve, data sets with a higher resolution would be necessary.

Information about the consumption rate of roach on molluscs are rare (Nagelkerke & Sibbing 1996). Additionally, the data availability for this food type in Lake Belau is incomplete. Due to the high variability in weight and energy content of different mussel species, it is problematic to assemble the different taxa to one group. In future, a further differentiation in several taxa would be desirable. The food intake of molluscs is strongly related to body size starting at minimum lengths between 13 and 15 cm (Westphalen 1956; Lammens et al. 1987). Nagelkerke & Sibbing (1996) found that the handling time increases with the size of \( Dreissena polymorpha \) and is inversely related to fish size. Especially roach is superior in static crushing hard and brittle material like zebra mussel shell (Nagelkerke & Sibbing 1996). The computed linear relationship between consumption rate and body length considers these circumstances.

**Food composition**

Most of the ontogenetic changes in the diet composition of fishes are probably caused by morphological changes, particularly the increase in mouth size and the improvement in locomotory ability (Wootton 1990). One result of the modelled foraging strategy is the decrease of zooplankton in the food, which is a consequence of ontogenetic changes in the scaling of spatial behaviour. Though the feeding strategy did not change during this time, larger roach are able to swim longer distances than the smaller ones. Therefore they can scan a larger area for suitable feeding grounds. When the fishes have the physiological state ‘hungry’ and the connected behavioural repertoire ‘food searching’ is executed at dusk or dawn, the probability of larger roach to visit littoral areas of the lake increases.

In the third year the simulated roach reached the minimum size of 13 cm to feed on molluscs. Pfeiffer (1999) states that
adult roach in Lake Belau prefer molluscs as food items. RASK (1989) reported that roach could feed successfully on zebra mussels, eating more molluscs than e.g. common bream (Abramis brama) and white bream (Blicca bjoerkna), suggesting that it is the more efficient molluscivore. This may be explained by the conclusions of NAGELKERKE & SIBLING (1996) that roach can process larger mussels than the other two species. In eutrophic Lake Sniardwy (Poland) zebra mussels accounted for 6% of the food mass in fish of 160–179 mm and for over 95% of the food mass in fish over 280 mm (PREJS et al. 1990).

### Population structure

For the simulated roach the switch to molluscs results in better growth (Fig. 7). At the end of the year only a few roach (> 13 cm) were molluscivorous and used the additional food source for growth. This is in agreement with results from WESTPHALEN (1956). In his investigations in different lakes of Northern Germany, roach populations which switched to benthic food items, especially molluscs, grew faster. KEMPE (1962) speaks of a minor revolution for part of the roach when a lake contains large amounts of molluscs. The author found in a summary of different investigations that roach, which are capable of feeding on molluscs, obtain an increased growth rate. Therefore the ontogenetic shift can be related to the necessity to switch to larger prey in order to compensate for increased energetic demands with increasing body size.

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