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Early piscivory in 0+ perch (*Perca fluviatilis* L.) implications for trophic position and whole ecosystem dynamics

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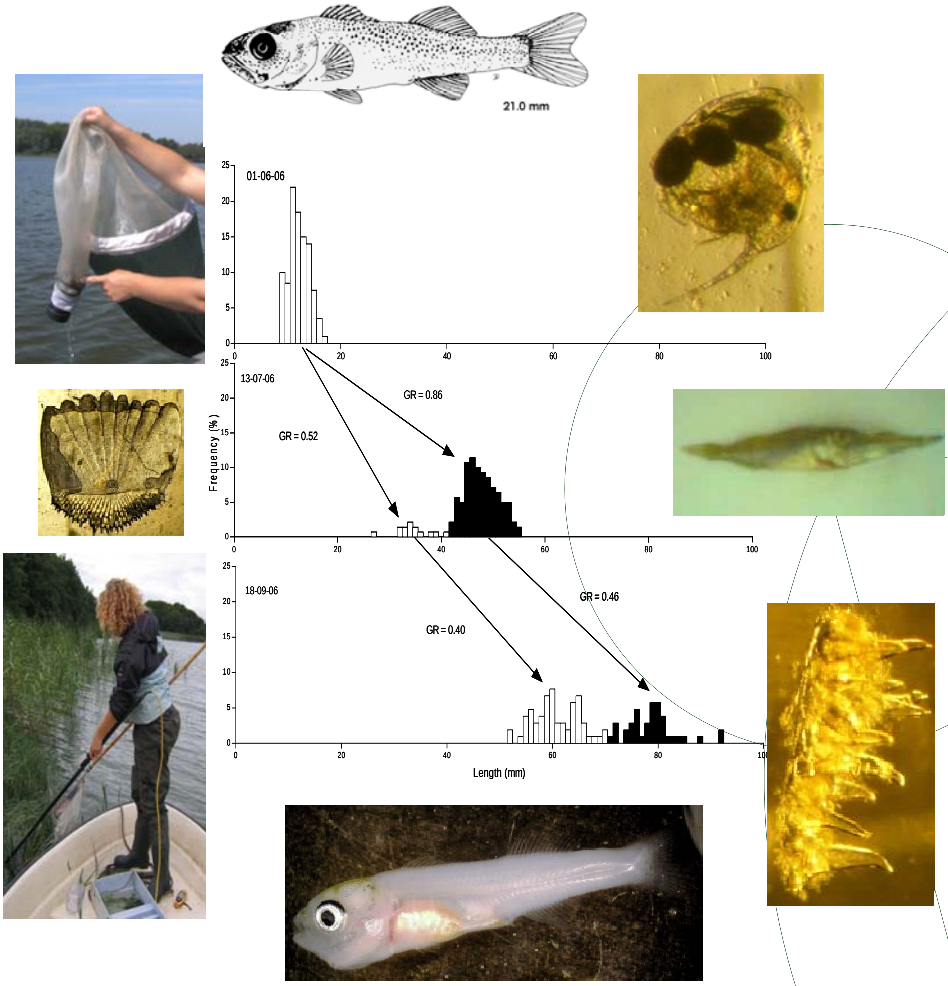

Technical University of Denmark
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Master thesis

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Front page: Length frequencies of 0+ perch from Lake Gødstrup on three dates. Field photos: Martin Andersen and Morten Tønsberg Limborg. Photos from the laboratory: Maria Karm

Preface

This thesis is part of my master degree in biology from the University of Copenhagen (KU) and has been completed in conjunction with DTU Aqua, National Institute of Aquatic Resources at the department of Inland Fisheries (Lake ecology group).

I am sincerely grateful to my supervisors Klaus P. Brodersen (KU) and Søren Berg (DTU Aqua) for guidance, enlightening and inspiring discussions and pleasant company throughout the study.

Furthermore, I wish to show my gratitude to Martin Andersen, without his help and company the field work would have been extremely difficult to carry out.
I also wish to thank everybody at DTU Aqua for a pleasant and fascinating environment during field and laboratory work, especially Christian Skov and Lene Jacobsen who always had time for questions.

I also want to thank Liselotte Sander Johansson (National Environmental Research Institute, University of Aarhus) for guidance in laboratory work concerning stable isotopic signature.

Last, but not least, special and loving thanks to my family, friends and Morten for support and sympathy when I got frustrated, interest when everything was going in the right direction, and just every day support.

Copenhagen, February 2008

Maria Karm

Contents

Summary

One of the currently most important tasks in freshwater ecology is restoration and maintenance of good water quality in lakes. One of the most used methods to obtain this is biomanipulation. This includes restocking with piscivorous fishes and/or removal of zooplanktivorous (e.g. cyprinids) because clearer water conditions are assumingly best gained through a top-down manipulated ecosystem with high concentrations of predatory fish. Many ecological mechanisms are not yet fully understood and good results are not obtained in all cases of biomanipulated lakes. One problem in restocking with 0+ predatory fish, for example, is that the 0+ fish often feed on zooplankton in the first years, and thus there will be no immediate effect on the zooplanktivorous fish community.

Laboratory experiments on 0+ perch have shown that they are capable of consuming substantial quantities of 0+ bream and roach (cyprinids). If 0+ perch are able to consume the same quantity under natural conditions, as they were in laboratory experiments (3-12 bream per. day), they can potentially control the population. Subsequently it has further been shown in a gravel pit lake characterized by a small littoral zone and steep slopes (i.e. atypical conditions for most natural lowland lakes). This study showed that 0+ perch in periods were able to consume large quantities of 0+ bream and in that way keep the population down.

In this study I tested whether 0+ piscivory occurs, and to what extend, in completely natural Danish lakes covering a turbidity gradient from “clear” to “turbid” water. If it does occur, which mechanisms control this shift and how big is the impact? To what extend is the 0+ perch population affected and will cohorts of 0+ cyprinids be significantly affected?

What I discovered was that early piscivory is not restricted to clear nor turbid lakes although it seemed to be more pronounced in turbid lakes. A possible reason for this could be that perch in turbid lakes had higher growth rates early in the season compared to clear lakes. This might be due to higher macroinvertebrate intake. Perch from turbid lakes also had higher proportions of macroinvertebrates in their stomachs than perch from clear lakes. Perch from turbid and clear lakes had significant different diets. Large 0+ perch in the cohort are also more likely to shift to piscivory earlier in the season than smaller perch, due to the fact that larger perch have a more favourable size advantaged over prey fish compared to small perch.

It was possible to detect the 0+ perch habitat shift from the pelagic to the littoral zone by increased values of the stable isotope $\delta^{13}C$. The expected diet shift from predominantly zooplankton and small macroinvertebrates to predominantly larger macroinvertebrates and fish

was not observed in comparative analyses of the stable isotope $\delta^{15}N$. $\delta^{15}N$ values might not be useful to state trophic position of 0+ perch.

Dansk resumé

En af de vigtigste opgaver inden for ferskvands økologi lige nu, er restaurering til og bibeholdelse af klarvandede tilstande i hovedsageligt søer. En af de meget brugte metoder for at opnå dette er biomanipulation, hvor der enten udsættes rovfisk og/eller opfiskes fredfisk da klarvandet tilstand opnås bedst hvis der er en overvægt af piscivore fiskearter. Der er dog stadig mange mekanismer der ikke forstås til fulde, og gode resultater observeres ikke i alle tilfælde fordi andre faktorer også påvirker resultatet. Et af problemerne med udsætninger af 0+ rovfisk er, at de oftest ernærer sig ved planktivori i de første leveår og derfor ikke har en effekt på fredfiske bestanden.

Forsøg har vist, at 0+ aborrer kan indtage store mængder af 0+ skaller og brasen, hvis de eksponeres for disse. Hvis 0+ aborre i naturlige søer kan spise de samme mængder 0+ fredfisk pr. dag, som det er blevet observeret i laboratorieforsøg (3-12 brasen pr dag), vil det kunne gøre et væsentligt indhug i bestanden af disse. Efterfølgende er det blevet observeret, i en grusgravs sø med specielle betingelser, som en lille litoralzone og stejle skrænter, at 0+ aborrer i perioder konsumerer betragtelige mængder 0+ brasen og derved regulere bestanden.

I dette studie blev det undersøgt hvorvidt 0+ piscivori også forekommer, og i hvilket omfang, i naturlige danske søer karakteriseret som både klarvande og uklare? Hvis dette finder sted, hvilke mekanismer er styrende, og hvor stor er effekten af piscivori? Hvordan påvirkes 0+ aborre populationen og bliver 0+ bestanden af fredfisk overhovedet påvirket af dette? Ydermere blev det undersøgt om fødeskift kan detekteres ud fra analyser af stabil isotop sammensætning i muskelvævet?

Det blev vist, at selvom tidligt piscivori ikke er begrænset til klare eller uklare søer, så ser det ud til, at piscivori er mere udtalt i søer med uklart vand. Dette skyldes muligvis at aborrerne i disse søer har en høj vækstrate først på sæsonen pga. rigelige mænger af fødeemner som makroinvertebrater, hvorimod det er lige omvendt i de mere klarvandede søer. Der er også en højere procentdel af invertebrater i aborremaver fra uklare søer, sammenlignet med aborremaver fra mere klarvandede søer. Aborre fra uklare og mere klare søer havde signifikant forskellige diæter. Store aborre i kohorten er mere tilbøjelige til at skifte til piscivori end små aborre da størrelsesforholdet ofte er mere fordelagtigt for store 0+ aborre i forhold til bytte fisken.

Det var også muligt at detektere 0+ aborrernes habitat skift fra den pelagiske til den littorale zone ved en øget δ^{13}C. Derimod var det ikke muligt at detektere et forventet diætskifte fra overvejende zooplankton og små makroinvertebrater til en diæt domineret af større

makroinvertebrater og fisk, hvilket burde afspejles i en forøgelse af δ^{15}N værdierne. Det betyder at 0+ aborres tropiske position ikke kan bestemmes ud fra δ^{15}N værdierne alene.

Chapter 1

General Introduction

General Introduction

The purpose of this general introduction is to present some important aspects of freshwater ecology, and how this study applies to general lake ecology. I also present the five lakes used in this study. Hereafter, I will give a brief introduction to the study organisms, Eurasian perch (*Perca fluviatilis* L.), biology and behaviour especially during the fist growing season which is of particular interest to this study. A general introduction is given to some of the practical and mathematical methods used in this study. Finally, I describe the objectives and an overall conclusion of this study and some perspectives of my results and potential further studies.

Background and objective of this study

In an investigation on 0+ perch in Lake Speldrop, a gravel pit lake in Germany, bimodal length distributions and high 0+ piscivory was discovered (Beeck *et al.* 2002; Beeck 2003). Even though, high abundance of 0+ bream was observed in spring, the adult fish community was dominated by piscivorous species, and in September abundance of 0+ bream was extremely low. Stomach content analysis and bimodal length distributions showed that large 0+ perch started preying on the smaller 0+ bream thus giving the largest fraction of the 0+ perch a high growth rates. However, the smaller perch remained on a diet composed of zooplankton giving them lower growth rates. The larger 0+ perch predation had a high impact on the 0+ bream that they hampered the recruitment of bream considerably.

The objective of this study is to examine:

- Whether early piscivory in 0+ perch is a general phenomenon.
- Whether the high and controlling effect of 0+ perch on 0+ bream density described by Beeck (2003) is detectable in natural lowland lakes, or if this was a product of the special conditions in the artificial gravel pit lake examined by Beeck (2003).
- Whether the extent of piscivory is the same in both clear and turbid lakes.
- Whether there is time displacement in onset of piscivory and other differences between large and small 0+ perch.
- Whether this ontogenetic shift to 0+ fish prey can be detected in the stable isotopic composition in 0+ perch tissue (^{13}C and ^{15}N).

The concentration of ^{15}N increase with trophic position and the ^{13}C concentration of benthic living organisms is higher than pelagic living organisms (Hecky and Hesslein 1995). Thus, organisms at higher trophic levels (piscivores) are expected to deviate from lower trophic organisms (herbivores) with higher ^{15}N concentrations, and benthic/littoral feeding organisms are expected to have higher ^{13}C concentrations than pelagic feeding.

Lowland lakes

Lowland lakes (e.g. all lakes in Denmark) are in general shallow (Jeppesen 1998) and eutrophic. Lakes having high nutrient contents are described as being eutrophic (Kalff 2002) and both nitrate and phosphate are responsible for large summer algae blooms in temperate lakes (Kalff 2002). Especially phosphate has a large effect on algae blooms (Schindler *et al.* 1973), and is often the limiting nutrient (Moss 1998). Most important contributors to the increasing concentrations of nitrate and phosphate through time have been fertilizers from agriculture and waste water (Kalff 2002). The level of nutrient contents in Danish lakes is, indeed, due to the often close proximity of agricultural and/or densely populated areas (Søndergaard and Jeppesen 2007). Even though nutrient load from these sources have been reduced markedly over the last decades, the "damage has been done" so to speak, and high concentrations of nutrients, especially P, are stored in lake sediments (Søndergaard *et al.* 2003). Every summer nutrients recycle between the sediment and water column leading to annually repeated algae blooms (Kalff 2002). This is in general a serious problem in Danish lakes (Søndergaard *et al.* 2007), delaying the recovery to a good environmental quality.

Restoration of lakes with the intention of improving water clarity and environmental quality and is a still ongoing task, but several factors complicate the recovery of lakes and it is rarely sufficient to simply reduce the nutrient loading (Moss 1998). This is partly due to the prevalence of high densities of planktivorous fish and hence high predation pressures on zooplankton. This causes a concomitantly low grazing rate on phytoplankton, preventing a shift towards clearer water and lower algae biomass (Moss 1990). Reduction of the density and/or biomass of the planktivorous fish community is called biomanipulation and in theory this should lead to higher abundance of zooplankton and reduced levels of phytoplankton biomass (Mehner *et al.* 2004). A further release of predatory fish to a three-level ecosystem may cause a decrease in planktivorous fish and phytoplankton and an increase in zooplankton (Persson 1988).

Biomanipulation through top-down food web control can be an effective method for improving water quality (McQueen *et al.* 1989; Benndorf 1995). There is often an immediate effect with improving water clarity but most biomanipulated lakes in Denmark have shifted back to unclear conditions characterized by poor visibility and fish communities dominated by planktivorous species after some years (Søndergaard *et al.* 2007). This may be due to strong year classes of planktivores (e.g. roach) and/or weak year classes of piscivores (e.g. perch) (Benndorf 1995). However, in some systems age-0 fish ,e.g. 0+ perch, (Mehner *et al.* 1996) are able to take the place (same feeding strategy) of the former abundant zooplanktivorous fish (e.g. roach) and in that way disrupt the success of long-term biomanipulation because 0+ perch increase predation on zooplankton due to reduced competition with roach (Dörner *et al.* 1999).

The five study lakes

Physiochemical data from the five lakes were taken from environmental monitoring reports published by the local county administrations and from experiments performed in the lakes by DTU Aqua Summer mean values are means from May – September (both inclusive). Parameters obtained during this study were: temperature, secchi depth, fish data and macrophyte and plant compositions in the littoral zone.

Lake Almind

Lake Almind covers an area of 53 ha and has a catchment area of only 4 km^2 covered with forest. Despite the close proximity to the city of Silkeborg, deposit of waste water in the lake is negligible. No farming occurs in the catchment area. Two small streams supply water but most originates from groundwater springs within the lake. Most of the supplied nutrients originate from precipitation. Water residence time (WRT) is 2.4 years and the lake is deep (maximum depth 20.5 m, mean depth 10.5 m) compared to most other Danish lakes. Lake Almind is clear (Fig. 1) and the high transparency of the water allows a relatively deep macrophyte depth distribution (6.5 m) and approximately 20 macrophyte species are present. The most abundant species are *Myriophyllum alterniflorum* DC., *Batrachium circinatum* Sibth. Spach, *Lobelia dortmanna* L. Ascherson, *Littorella uniflora* L. Ascherson and *Chara* spp. is represented with three species. Less abundant species include *Potamogeton* spp. represented by seven species, *Isoetes lacustris* L. The sparse littoral vegetation is dominated by *Phragmites australis* Trin. Ex.

Steudel and *Typha* sp.. *Lobelia*, *Littorella* and *Isoetes* are all species restricted to clear water lakes. Fish species are listed in Table 1. The Lake is important for recreational fisheries and a popular swimming lake.

Lake Thor

Lake Thor covers 69 ha with a catchment area of 9.5 km^2 in a hilly terrain dominated by woodlands. In the north-eastern corner is a small village (Virklund) but there is no current waste water load. Water sources into the lake originate from a small stream and diffuse springs. WRT is 156 days, the lake has a maximum and mean depth of 7.9 m and 4.2 m respectively. The secchi depth is also relatively high compared to other Danish lakes (Fig. 1, Table 2). Macrophyte depth distribution is 2.5 m and the following seven species are present: *Scirpus lacustris* L., *Sparganum emersum* Rehman, *Littorella uniflora, Potamogeton praelongus* Wulf, *Potamogeton crispus* L., *Elodea Canadensis* L.C. Rich. and *Nuphar lutea* (L.) Sm. The sparse littoral vegetation was dominated by *Phragmites australis* and *Typha* sp. Fish species are listed in Table 1. The lake is important for recreational fisheries and is also subject to public swimming.

Lake Ørn

Lake Ørn covers 42 ha with a catchment area of 56 km^2. The lake is positioned on the outskirts of Silkeborg but the catchment area is sparsely populated. The main water supply is from the Funder stream and a groundwater spring near the west shore named Arnakke Kilden. The supply of phosphor is from upstream fish farms near Funder stream, the ground water also have high concentrations of phosphor. WRT is 18 days and the lake has a maximum depth of 10.5 m and a mean of 4 m. Due to the low water transparency (Fig. 1, Table 1) there are no submerged macrophytes present. Reed belts in the littoral zone is dense and dominated by *Phragmites australis* and *Typha* sp., while more sparsely occurring species include *Nuphar lutea*, *Scirpus lacustris* and *Eleocharis palustris* L. Roemer & Schultes. Fish species are listed in Table 1. The lake is important for recreational fisheries.

Lake Hinge

Lake Hinge covers 91.4 ha with a catchment area of 53.8 km^2 of which 50 km^2 consist of cultivated farmland. The lake is highly eutrophic due to washout from farm land and a high internal recirculation. The main water sources are from different streams (Mausing Møllebæk, Haurbæk and Skjellegrøften). Despite the large size the lake has a high turnover rate with a WRT of only 18.25 days. Mean and maximum depth is 1.2 m and 2.6 m respectively. Water clarity is very low (Fig. 1, Table 1) however, nine macrophyte species are found: two species of *Batrachiun* sp., *Myriophyllum spicatum* L., *Elodea canadensis*, four species of *Potamogeton* sp. and *Sparganium emersum*. Most of these have floating leafs and the macrophyte depth distribution is only 1.5 m. There are also very dense reed belts in the littoral zone dominated by *Phragmites australis*, *Typha* sp. and *Scirpus lacustris*. Fish species are listed in Table 1. The lake is occasionally used for swimming.

Lake Gødstrup

Lake Gødstrup covers 46 ha with a present catchment area of only 1.5 km^2 which mostly consist of meadow, garden and small woodland. In 1993 the River Herningholm was diverted from the lake. Until 1993 a substantial amount of waste water for the city of Herning was discharged into the lake, and even though this has been reduced, the lake is still hypertrophic, due to internal phosphorous loading. WRT is 1 year. Mean and maximum depth is 1.8 m and 4.0 m respectively. Transparency is very low (Fig. 1, Table 1) and due to this practically no submerged macrophytes are present, *Nuphar lutea* covers small parts of the shallow areas outside the emergent vegetation. The littoral zone is dominated by very dense *Phragmites australis*, *Typha* sp. and *Scirpus lacustris* reed belts. Fish species are listed in Table 1.

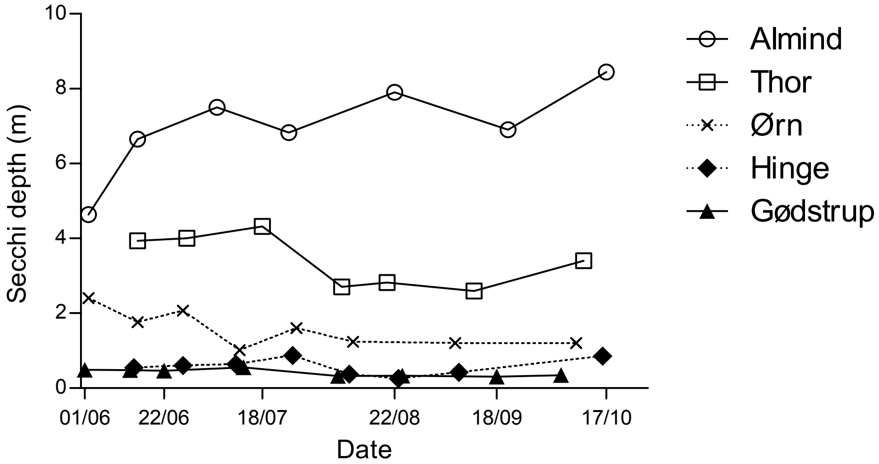

Figure 1. Secchi depth in the five study lakes from June to October 2006.

Table 1. Distribution of fish species in the five lakes. Mean summer secchi depth June to October 2006 and mean summer total phosphor (TP) May to October 2003 and 2004.

Fish species	Almind	Thor	Ørn	Hinge	Gødstrup
Perch (*Perca fluviatilis* L.)	x	x	x	x	x
Roach (*Rutilus rutilus* L.)	x	x	x	x	x
Rudd (*Scardinius erythrophthalmus* L.)	x	x	x		x
Pike (*Esox lucius* L.)	x	x	x	x	x
Bream (*Abramis brama* L.)	x	x	x	x	x
Eel (*Anguilla anguilla* L.)	x	x	x	x	x
Zander (*Stizostedion lucioperca* L.)		x	x		x
Three-spined stickleback (*Gasterosteus aculestus* L.)		x	x	x	
Ruffe (*Gymnocephalus cernuus* L.)		x		x	x
Crucian carp (*Carassius carassius* L.)		x			
Burbot (*Lota lota* L.)			x		
Belica (*Leucaspius delineatus* Heckel),				x	
Gudgeon (*Gobio gobio* L.)				x	x
Tench (*Tinca tinca* L.)				x	
Mean summer secchi depth (m)	6.98	3.40	1.56	0.57	0.41
Mean summer total phosphor (mgPl-1)	0.011	0.034	0.064	0.154	0.360

Selection criteria for the study lakes

The five Study lakes were selected to cover a gradient of phosphorous contents or degree of eutrophication, resulting in a water clarity gradient from clear to turbid. According to O.E.C.D. (1982) the five lakes are divided into following lake categories Lakes Almind and Thor are mesotrophic, Lake Ørn are eutrophic and Lakes Hinge and Gødstrup are hypertrophic. In this study Lake Almind and Thor are considered the two clear lakes, with Almind having the highest secchi depth and lowest TP. Lake Hinge and Gødstrup are considered the two turbid lakes, with Gødstrup having the lowest secchi depth and highest TP. Lake Ørn is intermediate in terms of these parameters (Fig. 1, Table 1).

It was also crucial that 0+ perch had some potential prey fish. Roach and bream were selected as the two main prey species, mainly because they have higher spawning temperatures compared to perch. This means that perch larvae hatch earlier in the season compared to their potential prey species. Also rudd and three-spined stickleback contributed to the perch diet, but they were not present in all of the lakes.

Study organism: Perch

Eurasian perch (*Perca fluviatilis* L.) belongs to the order Perciformes and the family Percidae it is widely distributed all over Europe and Asia (Thorpe 1977) and is a very common freshwater species in northern Europe (Karås 1987). Perch is an opportunistic and ubiquitous species and it inhabits most freshwaters and in addition some brackish habitats (Karås 1987). The dorsal fin is split into two, the first have 13 – 17 hard fin rays and a black spot at the back, the second fin have 2 hard and 13 – 15 soft fin rays (Thorpe 1977). It has a greenish colour with dark cross bands (Fig. 2). Spawning takes place in early April when water temperatures reach approximately 6-9 °C (Thorpe 1977).

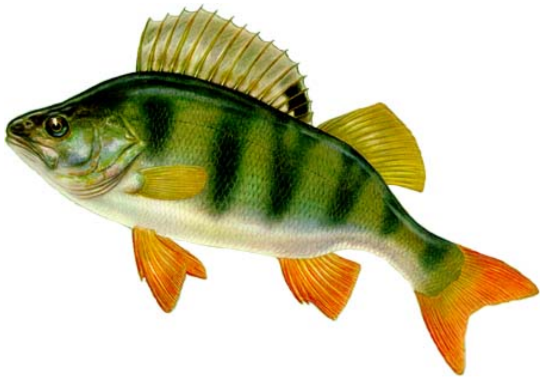

Figure 2. *Perca fluviatilis*.

Eggs are spawned in 1 – 2 m long and 2 – 2.4 mm wide (depending on the size of the female) coherent egg bands which get entangled in submerged branches and vegetation in shallow waters (Thorpe 1977). Multiple males fertilize the eggs of a female which subsequently protects the eggs for a few days (Thorpe 1977). Eggs hatch after 2 – 3 weeks and the larvae are 5 – 6 mm long when they hatch (Thorpe 1977). Soon after hatching the larvae are found in the pelagic zone where they feed predominantly on zooplankton (Gumaá 1978; Keast and Eadie 1985). They gradually develop into juveniles and at a size of approximately 20 mm they shift habitat and become more littoral, but continue to feed mainly on zooplankton (Smyly 1952; Craig 1978; Gumaá 1978; Keast and Eadie 1985), as they grow they begin to consume a diet dominated by benthic invertebrates (Smyly 1952; Il'ian 1973; Gerstmeier 1985). When they reach a total length of 110 – 160 mm corresponding to ages from 2+ to 5+ they become predominantly piscivores (Persson 1983; Keast and Eadie 1985; Buijse and Houthuijzen 1992). When following this strict pattern it has been hypothesized that perch need the intermediate bentivorus state before they can switch over to the final piscivorous state (Gerstmeier 1985). The early occurrence of piscivori and cannibalism has previously been observed for 0+ perch (Smyly 1952; Il'ian 1973; Gumaá 1978; Beeck *et al.* 2002; Chapter 2). Perch are generally omnivorous (generalists) (Graeb *et al.* 2005) and they are able to feed on almost any prey (Hammer 1985; Persson *et al.* 1999). However, positive selection for some prey items compared to others occurs but this is also depending on perch length (Gumaá 1978; Treasurer 1990). Juvenile perch have often been shown to prefer copepods compared to e.g. *Daphnia* sp. (Gumaá 1978; Treasurer 1990) and this was also observed in the present study (Fig. 3 in Chapter 2). Other studies, however, show an exactly opposite pattern (Mills and Forney 1983; Murtaugh 1985). Mehner *et al.* (1998) showed that type of prey and prey size only depends on perch size, and that growing perch predominantly ingested the most profitable prey size (with the lowest handling cost and highest energy gain) corresponding to the optimal feeding strategy proposed by Werner and Hall (1974). Naturally food selection also corresponds with availability of any given prey type (Mehner and Thiel 1999) and Dörner *et al.* (2001) found relationship between diet composition of age 1+ perch and the availability of *Daphnia galeata* and perch even switch back to *D. galeata* when they again became dominant in autumn. At the end of the first growth season perch reach sizes of 40 – 60 mm (Smyly 1952) but larger sizes have been found for 0+ individuals (103 mm; Chapter 2 and 120 mm; Beeck *et al.* 2002). When perch reach ages of 8 years they reach a mean length of approximately 39 cm, maximum size for adult perch is ~62 cm (Thorpe 1977).

The occurrence of stunted growth in perch populations is not unusually (Alm 1946). In stunted populations, growth can be fairly good during the first years only to decrease rapidly at some intermediate size. There seem to be two superior reasons for stunted growth: 1. Too large and dense populations in proportion to the supply of food, consequently few attain the size where they begin to feed on small fish. 2. Unsuitable environment conditions (e.g. low pH and poor oxygen concentrations). There is a tendency to the occurrence of stunted perch populations in smaller lakes, whereas large lakes usually attain normal sized perch populations (Alm 1946) probably due to limitations in food supply and maybe also denser populations.

Adult perch inhabit most habitats within a classic low-land lake (littoral zone, pelagic zone, surface, metalimnion and bottom water layers (Horppila *et al.* 2000)). Even though piscivory increases with length, perch still have a mixed diet (zooplankton, zoobenthos and fish) at sizes between 155-184 mm (Horppila *et al.* 2000). They are furthermore able to switch among different prey items depending on their relative abundance (Dörner *et al.* 2001). Perch have high intraspecific competition, different year-classes compete for food and habitat (Persson and Greenberg 1990; Horppila *et al.* 2000). There is also a high degree of cannibalism in perch populations (Diehl and Eklöv 1995). Most common predators on perch in European lakes are pike and zander (references in Thorpe 1977). The allopatric yellow perch (*P. flavescens* Mitchill) occurs in North America and is a subspecies of Eurasian perch (Thorpe 1977). It is very similar in morphology, physiology, behaviour and ecology and can be considered as biologically equivalent (Thorpe 1977).

In this study I found niche overlapping of 0+ and 1+ perch, and had to examine scales to separate small 1+ perch from large 0+ perch. Winter bands are easily detected on the scales (Fig. 3) and scales from perch above 80 mm were examined to exclude all 1+ individuals.

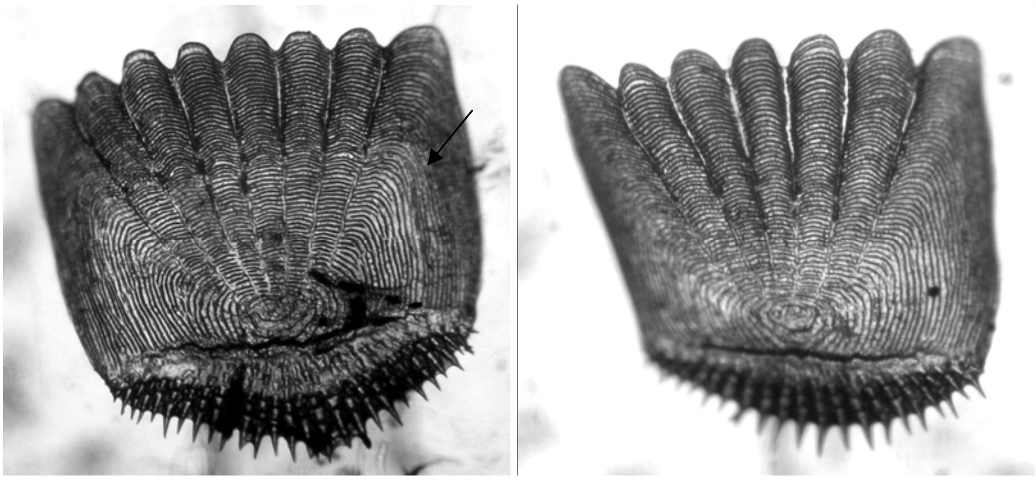

Figure 3. Picture of scales from two Lake Almind perch caught on the 17th of October 2006. Left: scale from 1+ perch (85 mm). Arrow indicates winter band. Right: scale from 0+ perch (77 mm).

Sampling methods

There are many different fish sampling methods, I have chosen to go into detail with 3 of these. Two of them were used in this study (hoop net and electro-fishing) and the last method is very often used in other studies (gill net).

Hoop net

In order to obtain 0+ larvae in the pelagic zone the standard hoop net (2 m long, 0.4 m diameter) employed by the Danish survey programme for 0+ fish monitoring was used (Mooij 1992). The lake was divided into five equally sized zones, in every zone two transects were chosen, one along side and one abeam of the shore. Sampling was carried out from a small motorboat controlled by one person, the second person held the net in front of the boat. The centre of the hoop net was placed 0.5 m under the surface. The first half of the net has a cylindrical shape (mesh size 2 mm) the second half has a conical shape (mesh size 1 mm) and at the end a jar collected the fish (Fig. 4). By calibrating a flow meter within the net and measuring the distance travelled total volume of water sampled was determined (Skov *et al.* 2002). This method is very useful when the 0+ fish are small, relatively motionless, and consequently not able to escape the net. But when the fish get bigger, and their fins are developed, they become faster and in addition begin to migrate into the littoral zone where use of the hoop net is impossible. Especially in Lake Almind but also in Lake Thor I experienced some problems with using the hoop net, because evidently the lakes were too clear for the larvae to inhabit the pelagic zone maybe due to increased predation risk compared to turbid lakes. As a result of this pelagic 0+ perch were never caught in Lake Almind and only on the fist sampling date in Lake Thor (where there was coherence with spring algae bloom).

Figure 4. Use of hoop net in Lake Gødstrup.

Electro-fishing

Electro-fishing is more efficient in vegetated areas and in the littoral zone (Coop and Peňáz 1988). Sampling was undertaken from a small boat controlled by one person. Another person positioned in front of the boat performed the actual fishing with an anode in one hand and a dipnet in the other (Fig. 5). Approximately 50 sampling points were randomly chosen alongside the shore but covering the whole littoral zone of the lake. Every point was approached as silently as possible and the anode was rapidly immersed to a depth of 0.5 m above the sediment or 0.1 m if water depth were < 0.5 m. After 5 seconds the anode were elevated to a position just below the water surface and held there for 10 s. All visible and stunned fish were collected with the net. In order to sample fish from below the secchi depth three hauls were made with the net below the Secchi depth (in the turbid lakes) (Perrow *et al.* 1996; Skov and Berg 1999). This method was very functional in turbid lakes but again in lake Almind there were some problems in catching the fish, this were probably due to a combination of low conductivity and high visibility, which made the fish able to escape the electric field.

Figure 5. Electrofishing in Lake Hinge.

Gillnet

Gillnet sampling is a common method used in fish stock assessment. In many stock assessment studies, series of nets containing different mesh sizes target different-sized individuals with equal efficiency (Kalff 2002; Finstad and Berg 2004) (Fig. 6). Mesh sizes and duration differ corresponding to investigation and study organisms. If the fish caught are to be used for stomach content analysis the nets are set for about 4 hours (Beeck *et al.* 2002). If it is a fish stock assessment study, nets are often set over night (Skov *et al.* 2002). However, even advanced combinations of mesh sizes in gillnet series may show size-dependent selectivity and biased length distribution patterns (Finstad *et al.* 2000). Bimodal size distributions can for example be suggested from the gill-net catch while this is not truly representing the real distribution (Finstad and Berg 2004). This would be a serious problem in this type of study and therefore gillnetting was not used.

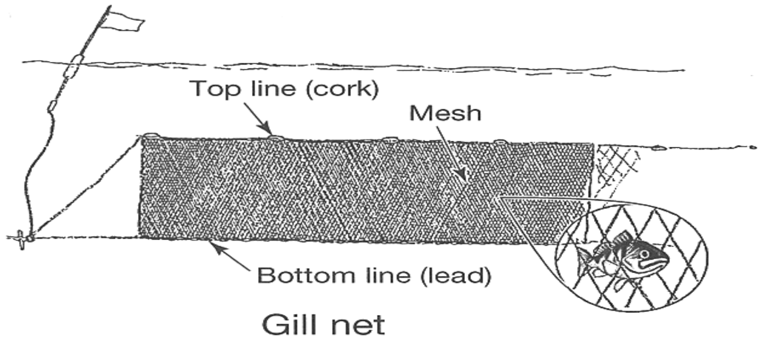

Figure 6. Picture from Kalff (2002) illustrating how gill nets work.

Calculations of bimodality

Akaike's Information Criterion (AIC) is used to estimate the relative expected K-L (Kullback-Lieber) distance between the approximating model and the true data.

$AIC = -2 \ln(\sigma 2) + 2K$,

σ^2 is the residual difference between the expected/calculated and the true data or the maximum likelihood (ML) for the given model and data, K is the number of parameters (Burnham and Anderson 1998).

In application each model is fitted to the data and an estimated AIC is calculated. One should select the model that yields the smallest value of AIC among the candidate models considered. The model with the smallest AIC value is estimated to be the best approximation for the information in the observed data (Burnham and Anderson 1998).

With inspiration from Haddon (2001) the following could be done in Microsoft Excel ©: one or two normal distributions were fitted to my data, giving some expected frequency. This made it possible to calculated maximum likelihood from ln likelihood (LL),

$$LL = \text{frequency}_{(\text{observed})} \times \text{Ln}(\text{frequency}_{(\text{expected})})$$

$$ML = \Sigma(LL) + (n_{(\text{observed})} - n_{(\text{expected})})^2$$

Then AIC was calculated

AIC = (2xML) + (2xK),

where K is either one or two normal distributions. Using the solver function in excel it was possible to find the minimum value for AIC trough an iteration process by changing the different parameters for the fitted normal distributions. This was done with both one and two normal distributions. The model solution (one or two normal distributions) with the lowest AIC was chosen. For the example shown in Fig. 6 the model solution with two normal distributions was considered to be the best. This lead to the conclusion, that there were bimodal length distributions for 0+ perch on that date.

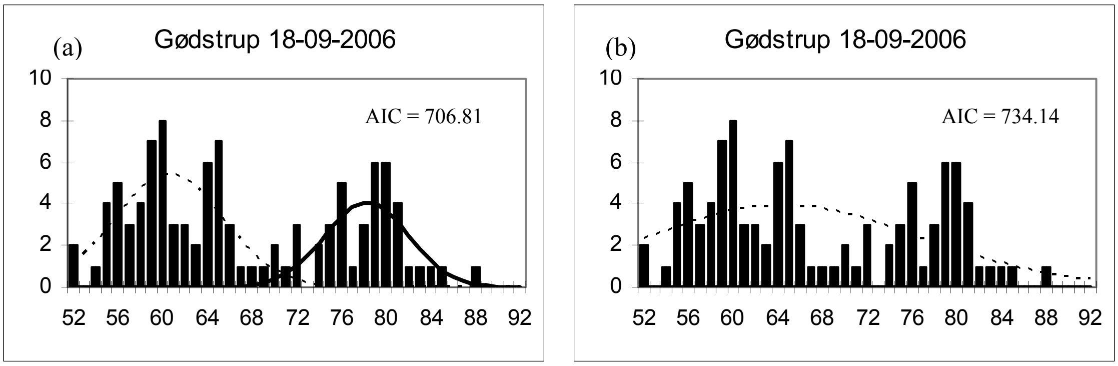

Figure 6. Length-frequency distribution from Lake Gødstrup on September 18th 2006. Bars indicate the number of perch with a given lengths (mm) caught. (a) Two normal distributions fitted to the data, the value for AIC is given in the right top corner. (b) One normal distribution fitted to the data, the value for AIC is given in the right corner.

Length distributions graphs of perch in the five lakes on all dates from May to September are shown in Appendix 1 with AIC given for both one and two normal distributions.

Additionally it was also tested whether the data had a normal distribution or not with Kolmogorov-Smirnov test for normality. Except for three dates, length distributions which were bimodal did not have a normal distribution; these three dates are indicated with ♣ in the figures in appendix 1.

Conclusions and perspectives

Over-all results with mechanisms are summarised in Fig. 7. Piscivory in 0+ perch were commonly and at times the frequency of piscivorous perch were high, but seemed to be more pronounced in turbid lakes than in clear lakes. Bimodal length distributions were observed in the turbid Lakes Hinge and Gødstrup but not in the clearer Lakes Almind, Thor and Ørn (Chapter 2 and Appendix 1). Several factors affect 0+ piscivory and in some years it might not be as pronounced as in others. Piscivory may be affected by: prey availability of suitable size early in season but also later on (Timmons *et al.* 1980; Dörner *et al.* 2001), synchronized spawning time in perch and prey fish (Mittelbach and Persson 1998; Graeb *et al.* 2005) and water temperature (Olson 1996). Opposite small 0+ perch, large 0+ perch had early onset of piscivory which probably additionally increased growth rate.

The growth pattern was also different between clear and turbid lakes; turbid lakes had highest growth rates early in the season but decreased later on the opposite pattern was observed for clear lakes (Fig. 1 Chapter 2). The growth rates correlated with temperature after the temperature maximum (Fig. 2 Chapter 2) implying that the increased growth later in the season observed in clear lakes might be caused by high temperatures in these lakes. Whereas the high growth rates observed in the turbid lakes early in the season, might be more correlated with the availability of food items. Significant differences in diet were observed between clear and turbid Lakes (Table 4, Fig. 3 and 4 in Chapter 2), and this time Lake Ørn was joint with the most turbid lakes. Differences in growth were affected by differences in diets, early or delayed onset of piscivory and temperature.

The principles and mechanisms of stable isotope signature are explained in Chapter 3. Indications of 0+ perch trophic position by $\delta^{15}N$ was not observed (Fig 1a in Chapter 3) and there were no correlation between any of the food items and $\delta^{15}N$ (Table 2 in Chapter 3). The expected change/increase in $\delta^{15}N$ values was not observed. Increased $\delta^{13}C$ values were detected in correlation with 0+ perch habitat shift (from pelagic to littoral). Positive correlation was observed between $\delta^{13}C$ values and some food items (chironomidae and other invertebrates; characteristic of the littoral zone) but negatively with cladocera (characteristic of the pelagic zone) (Fig 1b and 3, Table 2 in Chapter 3). Data from this study do not fully support the theory that if the system is already top-down controlled, the 0+ perch piscivory will contribute to the maintenance of this state. Because piscivory were less pronounced in the clear lakes.

Further studies need to be made to fully understand the mechanisms of 0+ perch piscivory and how big the effect in fact are on the prey fish community. Variation from year to year could be considerable significant, so time-series need to be taken into consideration. It would also be interesting to see if perch shows positive selection for any given food item (especially fish) in order to definitely exclude that early piscivory should just happen by chance. Further more it would be interesting to observe 0+ piscivory in perch populations in a long term biomanipulated Danish lake, to observe whether 0+ piscivory is increased or decreased.

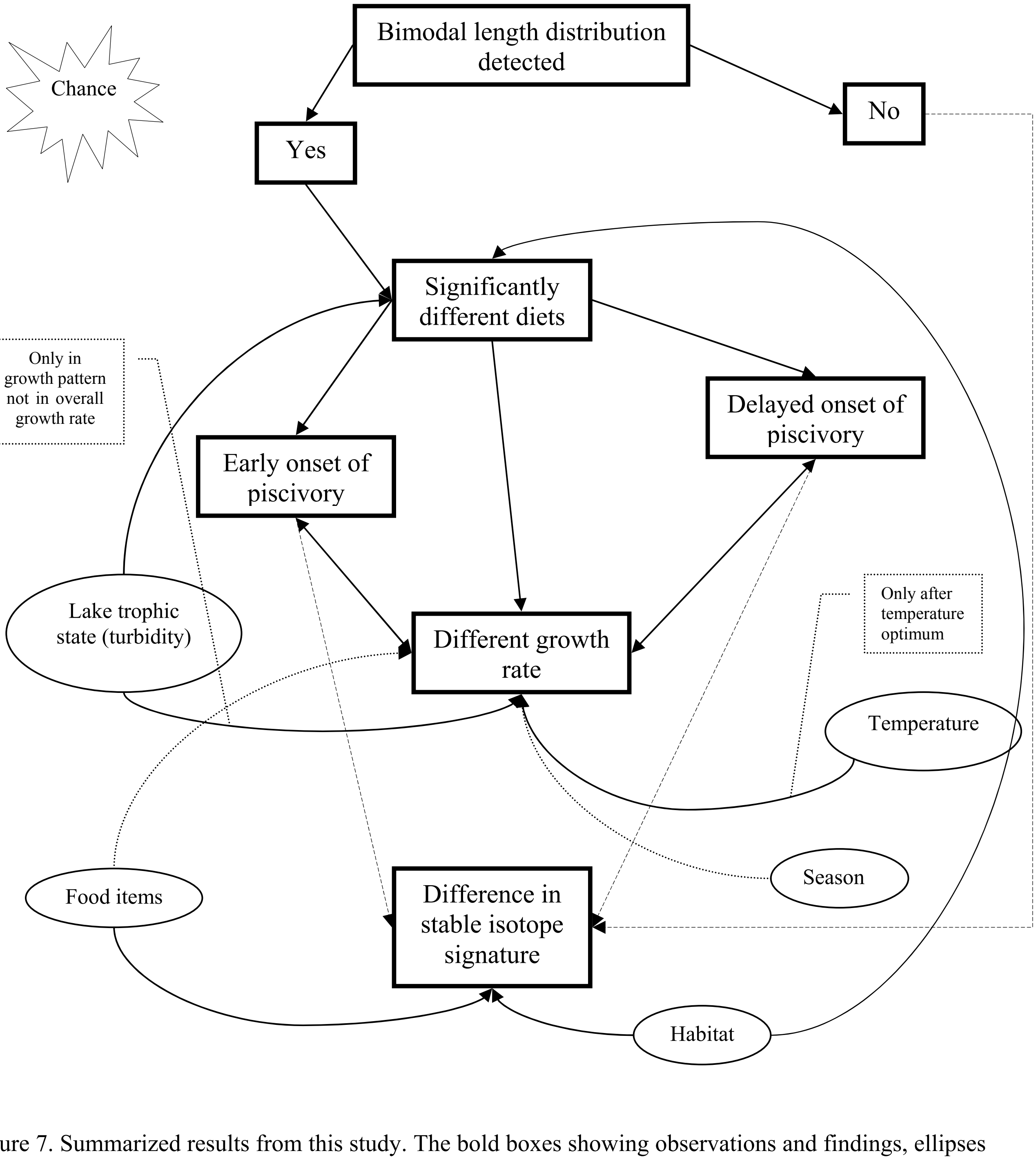

Figure 7. Summarized results from this study. The bold boxes showing observations and findings, ellipses indicate mechanisms and parameters leading to the observations, thin lined boxes are comments. Full lines (arrows) between boxes indicate actual and significant findings dotted or broken lines indicate ideas and/or findings from other studies.

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Chapter 2

Bimodality and early piscivory in 0+ perch (*Perca fluviatilis* L.) populations in five Danish lowland lakes.

Manuscript I

Bimodality and early piscivory in 0+ perch (*Perca fluviatilis* L.) populations in five Danish lowland lakes.

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Abstract

First year growth, length distributions and early piscivory were investigated for Eurasian perch (*Perca fluviatilis* L.) from May through October 2006 in five natural low-land lakes over a productivity gradient.

In the two most clear water lakes (mean Secchi depth range 3.4 – 7.0m) 0+ piscivory was observed occasionally and on more than one date in the clearest lake (Lake Almind). In neither of these lakes bimodal length distribution were observed. In the two most turbid lakes (mean Secchi depth = 0.4 range 0.6m) 0+ piscivory was more consistent and when first started, the larger perch in the cohort continued to perform piscivory. Large perch were more likely to begin piscivory than small perch. Bimodal length distributions were observed in the most turbid lakes. Overall, perch stomach contents were significantly different between clear and turbid lakes and when perch were eating fish and invertebrates, copepoda and other cladocerans contributed relatively less to the diet. Growth patterns also differed between clear and turbid lakes. High growth rates were in turbid lakes observed earlier in season compared to clear lakes. Growth rate did not correlate significantly with temperature from May through early August (prior to temperature maximum) but did from early August through October. Lake Ørn had an intermediate turbidity (mean Secchi depth 1.6 m), but 0+ perch did not show bimodal length distribution and piscivory patterns mirrored those of clear lakes. However, the overall stomach content of perch was not significant differently from the turbid Lake Hinge.

The results of this study show that 0+ piscivory is not restricted to neither clear nor turbid lakes, but early piscivory seam to be more common in turbid lakes, maybe due to the high GR early in the season.

Introduction

Is early 0+ piscivory in perch populations a general phenomenon in lowland lakes, and how are perch and prey fish populations affected by this?

Populations of fish are in general strongly size structured within each yearclass (Werner and Gilliam 1984) and divergence in size over time among individuals in the same age class has been documented (Thorpe 1977; Timmons *et al.* 1980). There are several reasons for this size divergence. Disrupted spawning (Kramer and Smith 1962), sexual differences in growth rates (Thorpe 1977) and influence of diet and prey availability (Timmons *et al.* 1980; and others listed in Keast and Eadie 1985). Prey quality and the availability at the right time in trajectory were the main reason for difference in growth and cohort splitting for largemouth bass (*Micropterus salmoides*) (Timmons *et al.* 1980; Keast and Eadie 1985), walleye (*Sander vitreus*) (Graeb *et al.* 2005), pikeperch (*Stizostedion lucioperca*) (van Densen 1985; Buijse and Houthuijzen 1992) and perch (*Perca fluviatilis*) (Borcherding *et al.* 2000; Beeck *et al.* 2002) and must be considered as being main factors explaining intra cohort size structure. Different size groups of the same yearclass may attain different trophic positions (Olson *et al.* 1995) and thus have different effects on lake ecosystems. Piscivory in 0+ perch populations is not unknown (Smyly 1952; Il'ian 1973; Mehner *et al.* 1996; Persson *et al.* 1999; Borcherding *et al.* 2000; Beeck *et al.* 2002; Heermann *et al.* 2007), but little attention has been paid to this phenomenon due to the traditional assumptions that it only occurs rarely and by chance (Gumaá 1978a; Hammer 1985). Little is known about early piscivory in natural populations of 0+ perch, but laboratory experiments have shown that perch fry can act as piscivores on both smaller siblings and on other prey fish. Perch are able to act as piscivores already at sizes of 10.3 – 30.0 mm (Brabrand 1995; Borcherding *et al.* 2000). Early piscivori has also been found in experimental enclosures and reservoirs but mostly as cannibalism (Il'ian 1973). However, few findings of early piscivory in nature exist (Smyly 1952; Persson *et al.* 1999; Beeck *et al.* 2002).

Although several authors have examined the diet of Eurasian perch (Smyly 1952; Il'ian 1973; Mehner *et al.* 1995; Borcherding *et al.* 2000) few have quantified variations in the diet between large and small individuals of the same age class (Beeck *et al.* 2002). Most studies have been conducted in lakes that to some extent are artificial and this might have intensified the degree of piscivory. Beeck *et al.* (2002) concluded that findings of bimodal length distribution in a gravel pit lake were a consequence of early piscivory for a part of the 0+ cohort on 0+ bream. The bream population was strongly regulated by 0+ perch predation.

As perch grow, they potentially undergo two ontogenetic niche shifts (Persson 1988). The first shift is from a zooplankton rich diet to one dominated by benthic invertebrates (Smyly 1952; Il'ian 1973; Gumaá 1978a) and when they reach a total length of 110 – 160 mm (corresponding to ages from 2+ to 5+) they become piscivores (Persson 1983; Keast and Eadie 1985; Buijse and Houthuijzen 1992). During the piscivorous stage they can shift back to benthic invertebrates or even zooplankton, during periods of low fish prey availability (Berg *et al.* 1994; Dörner *et al.* 2001; Jacobsen *et al.* 2002).

Perch inhabiting low productive lakes undergo the two ontogenetic niche shifts as mentioned above (Craig 1978; Persson 1988). However, in more productive lakes juvenile perch can skip the bentivorous feeding stage and switch directly from planktivory to piscivory early during ontogeny (Mehner *et al.* 1996; Beeck *et al.* 2002). The switch from planktivory to piscivory might coincide with summer decline of zooplankton (Mehner *et al.* 1996), shift to high water transparency (Wahl *et al.* 1993) and/or availability of a high density of suitable fish prey (van Densen 1985).

Biomanipulation through top-down controlled food webs can be an effective method for improving water quality of freshwater systems (Benndorf 1995). Reduction of the density and/or biomass of planktivorous fish species, have a positive effect on zooplankton (McQueen *et al.* 1986). Many large scale fish removals have failed to have that effect on zooplankton (reviewed in DeMelo *et al.* 1992). Explanations for this could be that the remaining species change their diet: Studies have shown that age-0 fish sometimes take over the planktivore role in the food chain following biomanipulation (Qin and Culver 1995) or simply a dietary change in the remaining species (Persson and Hansson 1999) therefore high growth rates and early piscivory in especially perch may enhance the efficiency of long-term biomanipulation if they for example predate on 0+ roach instead of zooplankton (Dörner *et al.* 2001).

The aim of this study was to examine if early piscivory in 0+ perch was a general phenomenon in five natural lowland lakes. We further wanted to examine whether the extent of piscivory was the same in both clear and turbid lakes, if there was time displacement in onset of piscivory, and if the shift to piscivory have any effect on the length distribution of the 0+ perch cohorts examined. Results are also discussed in the context of biomanipulation.

Material and methods

Study site

The study was conducted during spring and summer 2006 in five natural lowland lakes, all positioned in Jutland, Denmark. Mean summer Secchi depths ranged from clear to turbid (Table 1). All lakes contained populations of perch, roach (*Rutilus rutilus*), bream (*Abramis brama*) and with the exception of Lake Hinge also rudd (*Scardinius erythrophthalmus*). Physicochemical data from the five lakes were taken from environmental monitoring reports published by the local county administrations and from experiments performed in the lakes by DTU Aqua. These data include summer mean values (May – September both inclusive) of Chl a (µg L^{-1}), total phosphorus (TP) (mg P L^{-1}), depths, area and macrophyte data. All other data listed in Table 1 are values obtained from this study.

Fish sampling

Age-0+ fish were sampled from May through October 2006. All samples were taken during daylight hours (between 09:00 am and 03:30 pm). From May through July a hoop net was used to catch larvae in open water (outside vegetated areas). Ten randomly chosen sites in each lake (five along side and five abeam of the shore) were trawled for 1 minute while a flow-meter measured trawled water volume (Skov *et al.* 2002). When 0+ fish became mobile and searched cover in the littoral zone, Point Abundance Sampling by Electrofishing (PASE) was performed as described in (Skov *et al.* 2002) and (Skov and Berg 1999). Approximately 50 sampling points were randomly selected in the littoral zone. Approximately 20 perch were immediately after catch conserved in ethanol on each sampling date for subsequent diet analyses. Approximately 50 perch were killed and frozen within maximum 4 hours from catch. All other fish were measured on location and realised.

Laboratory procedures

Total length (TL) of 0+ perch was measured to nearest mm (sample sizes ranging between 32 – 215 fish). Gab width and height was measured (in mm) on 50 perch on each sampling data. Width was considered to be the widest point of the mouth when closed. Gab height was obtained by opening the mouth and when resistance was reached the height was measured. Scales from perch above 80 mm were examined to determine whether they had a winter band or not to exclude potential 1+ individuals from the samples. Length and width of (32-198) potential prey fish (roach, rudd, bream and three-spined stickleback (*Gasterosteus aculeatus*)) were measured to nearest mm on each sampling date.

Growth rates (GR) were calculated as GR = $(TL_1\text{-}TL_0)/t$, where TL_1 and TL_0 are the average of total lengths in mm of all 0+ perch (giving the whole sample, and/or if present the two growth cohorts) and t is time in days between the two sampling dates.

When analysing stomachs prey was identified to order, family or species and up to 25 prey of each category was measured using an ocular-micrometer. Length was converted to wet weight according to length-weight relations given in Mehner *et al.* (1995) and Bottrell *et al.* (1976). Organisms not mentioned in Mehner *et al.* (1995) or Bottrell *et al.* (1976) were both measured and weighed. Percent weight per stomach of each group or species of prey organisms was calculated. The following prey groups were identified: Fish, Chironomidae, other invertebrates, copepoda, predatory daphnia, other cladocera and unknown (not recognizable stomach contents). On each sampling date mean stomach contents from large and small perch were calculated separately.

Density of both perch and prey fish caught with PASE electrofishing were calculated (fish per. Dip) to compare fish density in the five study lakes.

Statistics

Length-frequency distributions were determined by using Akaike's Information Criterion (AIC). To decide whether there were one or two size-distributions, models with one or two size-distributions were fitted to observed length distributions. AIC gives the distance between the model and the real data and the model with the lowest AIC is the one best explaining the real length distribution (Burnham and Anderson 1998).

Kruskal-Wallis tests were used to detect any difference in mean lengths among lakes and sizes. Pairwise comparisons of mean length within the five lakes were tested with Kolmogorov-Smirnov Two sample test. Statistical tests were performed in the STATISTICA® computer programme. A significance level of $\alpha = 0.05$ was used for all tests.

Dissimilarities in diet were analysed by multi dimensional scaling (NMDS) of mean stomach contents. The Bray-Curtis dissimilarity coefficients (Bray and Curtis 1957) were calculated on non-transformed frequency data of food items. The dissimilarity (D) between fish stomachs *j* and *k* was calculated as:

$$\mathrm{D}_{jk} = 100\left(\frac{\sum_{i=1}^{p} | y_{ij} - y_{ik} |}{\sum_{i=1}^{p} (y_{ij} + y_{ik})}\right)$$

where y_{ij} is the *i*th food item in the *j*th fish stomach and y_{ik} is the *i*th food item in the *k*th fish stomach. The inter-stomach distances were summarised in a two-dimensional ordination plot by non-metric multidimensional scaling (NMDS; Clarke and Warwick 1994). Significant differences among groups (i.e., among lakes and between two size classes), were tested using the ANOSIM permutation procedure (Clarke and Green 1988). The correlation between dissimilarities in stomach data and corresponding pair-wise distances in environmental data and time were explored using the nonparametric BIOENV procedure (Clarke and Ainsworth 1993). Normalised Euclidean distances were calculated on log (n+1) transformed environmental data (Secchi depth, temperature, lake area, lake max depth, conductivity, pH, TP, Chl.a and Time).

Results

Length-frequency distributions and growth

Length-frequency distributions in the five lakes were in general varying, both among lakes and over time in each lake. Lakes Almind and Thor shared a similar pattern, as did Lakes Hinge and Gødstrup, but with a different pattern. Lake Ørn showed an intermediate pattern. Lakes Almind, Thor and Ørn only showed bimodal size distributions on one date each (July 6^{th} and August 8^{th} and June 2^{nd} respectively; Table 2). In Lake Hinge bimodality was observed from June 14^{th} and until the last sampling date (October 16^{th}) where the distribution was found to be unimodal. In Lake Gødstrup bimodality occurred from June 22^{nd} throughout the sampling period (Table 2). On dates with bimodal size-distribution, lengths of small and large perch were tested against each other, and on all dates in all lakes they were significantly different from each other (P<0.01).

Mean length of perch, as an indicator of growth, during the study period are shown for all five lakes in Fig. 1. Sampling dates were divided into eight time periods (Fig. 1). Within each period, pairwise comparisons between mean lengths were performed (Table 3). In period 4, 5 and 7 there were up to 14 days difference in sampling date, new lengths were calculated based on difference in days and the GR for that period, but this did not change the result and the original data were used. In the beginning, perch mean lengths from Lake Almind were lower compared to all other lakes (period 4 and 5) but became significantly higher than Lakes Ørn, Hinge and Gødstrup (period 6, 7 and 8) while remaining lower than Lake Thor in period 7 and 8. Lake Thor followed the same pattern as Lake Almind, but had larger mean lengths on all dates. In period 6 Lake Hinge and Lake Gødstrup were not different from each other. The over all pattern corresponded well with whole populations GR (Table 2). The highest GR for perch in Lake Almind was observed between period 5 to 6 (1.00 mm d^{-1}). Perch in Lake Thor had the highest GR (1.08 mm d^{-1}) going from period 4 to 5. For perch in the three most turbid lakes, the highest GR was found earlier in the season between period 3 and 4 (Lakes Ørn, Hinge and Gødstrup: 1.03, 1.02 and 1.09 mm d^{-1} respectively). Mean GR over the whole season was compared among lakes and they were not significantly different from each other ($P = 0.6609$).

There was an overall positive correlation of temperature on GR ($P < 0.001$) (dotted line in Fig 2c). But when the data was split up in dates before and after the temperature maximum in early August (arrow in Fig. 2b), there was no significant correlation between temperature and GR prior (open circles) to temperature maximum ($P = 0.354$), but only after (filled circles) ($P < 0.001$) (Fig. 2c).

Stomach contents

Stomach contents of 440 0+ perch (45 – 95 mm TL) in total were examined on 5 or 6 dates in each of the five lakes (Fig. 3). Only five empty stomachs were recorded and they were neglected in further analyses. On each date, the examined perch were divided into small and large, irrespective of the existence of bimodal length-frequency distribution or not. When no bimodality was found an almost fifty-fifty splitting was used. The diet was very diverse hence the organisms was divided into seven food categories, some of the food categories contained multiple organism groups (Fig. 3). Stomach contents in the clear lakes consisted predominantly, throughout the season, of zooplankton (Almind ≈ 80% and Thor ≈ 95%; Fig. 3). Stomachs from the more turbid lakes contained more of larger food items (fish, chironomidae and other invertebrates), and less zooplankton (Hinge ≈ 65% and Gødstrup ≈ 40%; Fig. 3). In Lake Ørn perch stomachs contained ≈ 75% zooplankton on average throughout the season (Fig. 3). Fish as prey correlated negatively with the proportion of copepoda in perch stomachs ($r = -0.42$, $P < 0.01$).

When using multivariate mapping for overall stomach contents, there were differences among lakes (Fig. 4a). Stomach contents in Lake Almind and Thor were not different from each other ($P = 0.13$), but significantly different from the three other lakes ($P < 0.05$; Table 4). Lakes

Gødstrup and Hinge did not differ significantly from each other (*P* = 0.22). Lake Ørn was significantly different from the other lakes except Gødstrup (*P* = 0.37) (Table 4) and was positioned in between the other four lakes (Fig. 4a). There was no significant correlation between stomach contents and large or small perch within each lake (*P* =0.26; Fig. 4b). When testing the effect of different environmental parameters (Secchi depth, temperature, lake area, lake max depth, conductivity, pH, TP, Chl.a.) and population characteristics (perch length, date, and density of prey fish) on this grouping, it was found that total phosphor (TP), Chl.a. and pH where the most important factors (best correlation with least variables r = 0.36) explaining the overall perch diet. Most important was TP (r = 0.32). Perch size did not seem to be an important factor for stomach contents. In Fig. 5, a clear pattern in distribution of four of the food categories are seen. When stomachs contained fish and chironomidae (Fig. 5a and b), less copepods and other cladocerans were present (fig. 5c and d).

Small perch (the smallest fraction of the 0+ perch) started piscivory late in the season, and prey fish were only present in stomachs on one or two dates in each lake (Fig. 6a). The highest percentage of piscivory for small perch was 18 % (Lake Hinge October 16th and Lake Gødstrup September 18th). The large perch became piscivorous earlier in the season (Fig. 6b), and also reached a higher percentage of piscivory; up to 45% of the sampled population (Lake Ørn, July 27th). In Lake Thor the larger perch never switched to piscivory. Perch that was 100% piscivores were almost never found (only five individuals). There was a time delay in onset of piscivory for small perch compared to large perch (Fig. 6). Correlation of this delay and perch length was not significant (*P* = 0.08) but there was a tendency (Fig. 7). There was no correlation between density of prey fish and proportion of fish in perch stomachs (r = 0.20, *P* > 0.05).

Discussion

Perch growth

In this study development of bimodality in 0+ perch cohorts was observed in the two most turbid lakes (Hinge and Gødstrup) but not in the three more clear lakes (Table 2). Availability of food may have impact on formation of bimodality. If some of the perch shift from a diet of smaller organisms (zooplankton, insect larvae) to one of larger (insect larvae, fish), they will gain increased growth (Mittelbach and Persson 1998; Beeck *et al.* 2002); while others that continue to feed on smaller organisms, will have slower growth (Il'ian 1973; Brabrand 2001). This may cause a separation in lengths. When fish shift from being planktivores to piscivores, growth is increased (Mittelbach and Persson 1998; Beeck *et al.* 2002), because fish as food provide more energy per gram wet weight than zooplankton (Keast and Eadie 1984; Mehner *et al.* 1996). High growth rate is crucial to develop and maintain a size advantage over prey fish throughout a growth season (Keast and Eadie 1985). Several other studies have found bimodal length-distribution for 0+ populations in different piscivorous fish species: largemouth bass (Shelton *et al.* 1979; Keast and Eadie 1985), yellow perch (Post *et al.* 1997) and eurasian perch (Chodorowski 1975; Beeck *et al.* 2002; Heermann *et al.* 2007). Beeck *et al.* (2002) showed that the bimodal size distribution of 0+ perch in Lake Speldrop was associated with part of the cohort preying on 0+ bream, giving them a size advantage compared to their smaller conspecifics. The high effect detected in Lake Speldrop, an artificial and clear gravel pit lake, may be due to the special conditions of that lake. The littoral zone was extremely narrow with steep slops, and there was barely detected any macroinvertebrates in the diet. Nothing in the diet of 0+ perch from Lake Thor indicated cohort splitting (Fig. 3). The lack of bimodal size distribution in lake Almind might be caused by low number of perch sampled (Table. 2), as fish actually was part of the diet especially in larger perch both in the beginning and again later in growth season (Fig. 3). Had it been possible to sample more fish, cohort splitting in Lake Almind might have been detected. Perch in Lake Ørn did not have a consistent cohort splitting but they had the potential. Fish and invertebrates were primary components of the diet, and stomach content was similar to perch from Lake Hinge. This however, had no effect on GR, but maybe if more prey fish early in the season had been available, an effect would have been recorded.

Difference in growth patterns was also found between clear and turbid lakes, but this time Lake Ørn was grouped with Lakes Hinge and Gødstrup (Fig. 1, Table 3). This difference was not correlated with temperature from May to early August, and GR may be correlated with other ecological factors, such as food availability. From August to October there was correlation between GR and temperature witch indicates that increased growth in Lakes Almind and Thor might bee caused by high temperatures in these lakes (Fig. 2, Table 1). The differences in mean lengths at the end of the growing season is not assumed to be caused by differences in hatching time since there were no difference in mean lengths on May 31st and June 1st and 2nd in Lakes Thor, Ørn, Hinge and Gødstrup. Gumaá (1978b) observed that perch in Lake Windermere had the highest GR during the first 6 – 8 weeks and growth then became slower and conclude that GR depended on temperature, food density and/or population density.

Most studies report mean lengths of approximately 55-60 mm and maximum lengths of about 61 – 85 mm in September (Smyly 1952; Hammer 1985; Mehner *et al.* 1995; Jacobsen *et al.* 2002; Dörner and Wagner 2003). There were high correspondences between max lengths from this study and studies by Gumaá (1978b) 90 mm and Beeck *et al.* (2002) 136 mm. Lake temperatures do not seem to be different in lakes with small maximum length. It is possible that in some studies large 0+ perch have been excluded due to the assumption that they were 1+ perch, maybe supported by the unrecognized finding of bimodal size distributions.

Stomach contents and piscivory

Stomach contents from perch in turbid and clear Lakes was significantly different from each other (Fig. 4a, Table 4) and 0+ perch stomach content clearly depended on lake type and trophic state (TP, turbidity). Perch in Lake Almind and Lake Thor had a higher proportion of pelagic food items compared to benthic invertebrates and fish in their stomachs. The opposite pattern was observed in turbid Lakes. This might be a consequence of lake bathymetry and productivity, since Lakes Hinge and Gødstrup are shallow giving the perch a larger littoral/benthic area to forage, also there would be higher densities of prey fish due to high production (Jeppesen 1998) compared to Lake Almind and Lake Thor. Ilían (1973) showed that feeding shifts depend on both environmental conditions (e.g. temperature) and the availability of food. If the water reaches high temperatures during the spawning period then the perch can reach bigger sizes. And if there were high densities of various prey fish then 0+ perch were more likely to switch.

Piscivory was found in all lakes at some point in time (Fig. 3), but time of the switch to piscivory was different in large and small perch (Fig. 6 and Fig.7). This was mainly due to the availability of right sized prey fish; the prey fish must be at least 50% smaller than the perch, for perch to be able to consume the prey (Brabrand 1995; Olson *et al.* 1995). 0+ perch that obtain large sizes early in season may be able to consume the later hatched prey fish e.g. roach, bream and rudd. If the supply is adequate, this will have significant effect on the growth of the perch (Borcherding *et al.* 2000; Graeb *et al.* 2005). Consequently, late hatched or slow growing 0+ perch may not achieve the necessary size advantage over the prey fish (Graeb *et al.* 2005). This might affect winter survival of the perch (Olson 1996; Mittelbach and Persson 1998). Thus larger individuals of the 0+ yearclass will more likely survive the winter than smaller conspecifics. Piscivori in this study was evidently not restricted to clear lakes as hypothesized by Wahl *et al.*

(1993) and Beeck *et al.* (2002). Water clarity was very low in Hinge and Gødstrup (Table 1), but piscivory was not reduced (Fig. 6).

In this study 0+ perch during the first growing season did not follow the strict feeding patterns for clear and turbid lakes as mentioned earlier. The ontogenetic development of perch is perhaps far more dynamic, stochastic and opportunistic than previously believed. Apparently 0+ perch piscivori is not as rare as previously assumed (Gumaá 1978a; Hammer 1985), and this study has shown that 0+ perch piscivori can occur in both clear and turbid lakes if prey fish of the right size is present. Perch are omnivorous (or generalist) predators (Graeb *et al.* 2005). When provided with suitable fish prey they will shift to piscivory. If the growth is increased adequately they will reach and maintain the necessary size advantage throughout the season, stay partly piscivores (Keast and Eadie 1985; Mehner *et al.* 1996; Olson 1996) and, instead of competing with roach and rudd for zooplankton, begin predating on them. Piscivory may be underestimated due to the difficulties in identifying fish fry in stomachs, owing to the rapid digestion of fish compared to invertebrates (unrecognizable within 5-10 minutes) (Brabrand 1995; Beeck 2003).

Due to the ontogenetic niche shift, interactions with other fish will change from competition to predation as they grow (Polis *et al.* 1989; Olson *et al.* 1995), and because only part of the 0+ cohort will perform this shift, the population can potentially be divided into distinct stages that may have very different effects on community and ecosystem level processes (Olson 1996).

In conclusion we find that 0+ piscivory is part of the opportunistic ontogeny of perch, and that it is more dynamic than previously thought. 0+ piscivory is not restricted to neither clear nor turbid water, as long as suitable prey is provided at the right time. There were a tendency to higher degrees of piscivory in turbid lakes, but this may only be due to increased food availability (which was not tested in this study). Time displacement in the onset of piscivory between small and large perch within the population was observed.

When piscivory is substantial, 0+ perch may have some effects on the density of the populations of prey fish, but in natural populations the impact may not have the magnitude proposed by Beeck *et al.* (2002). The general opinion is that if early piscivory is favoured, as suggested in long-term biomanipulated systems (Mehner *et al.* 1996), then top-down pressure on whole ecosystems is additionally increased which will enhance the effect of biomanipulation.

This is not in complete accordance with this study since piscivory is less pronounced in the clear lakes than in the more turbid ones, however, this trend might not be a direct effect of varying turbidity. Perhaps the higher availability of zoobenthos in the hypertrophic shallow lakes will increase GR and favour earlier piscivory (Gerstmeier 1985), or maybe the encounter rate with prey fish is higher in high productive lakes and these higher densities will trigger early piscivory (Il'ian 1973). If the positive correlation between 0+ piscivory and turbidity (this study) is a general pattern early piscivory will be reduced in biomanipulated lakes, as these become clearer, instead of being enhanced.

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Table 1. Physical and biological characteristics of the five study lakes. Values of Secchi depth, temperature and total phosphor (TP) are given as summer (May – October) means. TP values: Almind, Thor, Hinge (2004) and Ørn, Gødstrup (2003). Secchi depth and temperature from 2006 (this study).

Lake	Location	Surface area (ha)	Mean depth (m)	Maximum depth (m)	Secchi depth (m)	Temperature (ºC)	Total phosphor (mgPL-1)	Chl a (µgL-1)	Macrophyte depth distribution (m)
Almind		53	10.5	20.5	7.0	19.0	0.011	3.2	6.5
Thor		69	4.2	7.9	3.4	19.7	0.034	9.0	2.3
Ørn		42	4.0	10.5	1.6	16.8	0.064	29.0	<0.5
Hinge		91	1.8	2.6	0.6	18.0	0.154	96.4	<0.5
Gødstrup		46	1.2	4.0	0.4	19.5	0.360	132.0	1.5

Table 2. Mean lengths, GR, n, minimum and maximum lengths for 0+ perch in all five lakes on all sampling dates. GR1 is whole population GR. Two mean lengths and GRs (GR2) correspond with occurrence of bimodal length distribution. GR3 is whole season and population GR. Values in parentheses is for the large size group of perch.

Lake	Date	Mean length (mm)	min. Length (mm)	max. Length (mm)	GR1 (mm/d)	GR2 (mm/d)	GR3 (mm/d)	n
Almind	06-Jul	27.65±2.64 (36.24±1.93)	33	39				38
	25-Jul	41.35±4.95	27	46	0.6			44
	22-Aug	63.43±7.27	59	77	1			27
	21-Sep	78.95±8.36	67	90	0.52			30
	17-Oct	75.21±5.63	57	88	-0.14		0.44	66
Thor	31-May	11.30±1.74	7	17				270
	28-Jun	25.42±2.27	22	31	0.5			38
	18-Jul	41.82±4.87	25	50	0.82			89
	08-Aug	63.09±3.49 (71.84±2.19)	48	74	1.08	1.01 (1.43)		70
	21-Aug	69.00±4.00	54	85	0.34			140
	12-Sep	80.00±7.00	59	95	0.5			215
	11-Oct	88.99±6.81	71	100	0.31		0.58	45
Ørn	02-Jun	10.37±1.01 (13.06±1.14)	9	16				200
	15-Jun	16.50±2.74	13	23	0.42			188
	12-Jul	44.43±5.74	30	52	1.03			36
	27-Jul	49.96±4.05	40	59	0.37			156
	07-Sep	63.42±6.67	48	64	0.32			152
	09-Oct	62.81±6.70	50	83	-0.01		0.40	208
Hinge	09-May	6.68±0.97	5	8				34
	16-May	9.84±1.12	8	12	0.46			200
	23-May	12.46±1.68	8	16	0.37			200
	31-May	14.10±1.97	11	18	0.22			167
	14-Jun	15.95±1.37 (22.10±2.13)	14	26	0.49	0.13 (0.57)		180
	27-Jun	24.26±2.61 (31.57±2.68)	20	37	0.62	0.64 (0.73)		53
	11-Jul	39.54±3.25 (47.82±3.70)	33	52	1.02	1.09 (1.16)		67
	26-Jul	44.98±2.69 (51.36±2.55)	34	57	0.28	0.36 (0.24)		90
	23-Aug	53.22±4.25 (61.96±4.07)	44	78	0.31	0.29 (0.38)		126
	08-Sep	55.43±2.51 (63.23±9.50)	49	76	0.22	1.14 (0.008)		132
	16-Oct	68.33±4.97	57	87	0.23		0.39	169
Gødstrup	01-Jun	11.91±2.20	9	17				200
	13-Jun	18.80±3.59	11	24	0.71			200
	22-Jun	18.80±1.75 (29.04±2.51)	16	33	0.56	0.00 (0.85)		32
	13-Jul	33.56±2.67 (47.79±3.43)	27	55	1.09	0.70 (0.89)		140
	07-Aug	51.56±4.14 (61.83±4.59)	45	72	0.34	0.72 (0.56)		100
	24-Aug	54.84±3.79 (66.60±7.94)	48	78	0.25	0.19 (0.28)		87
	18-Sep	60.60±4.84 (78.26±3.75)	52	92	0.34	0.23 (0.47)		104
	05-Oct	58.18±2.40 (66.21±9.27)	51	103	-0.24	-0.14 (-0.71)	0.41	165

Table 3. Pairwise comparisons of perch mean lengths in all five lakes for the eight periods shown in Fig. 1. NS = no significant difference, nd indicate no data.

	Period	Thor	Ørn	Hinge	Gødstrup	period	Thor	Ørn	Hinge	Gødstrup
Almind	1	nd	nd	nd	nd	5	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
Thor		-	NS	$P < 0.01$	$P < 0.05$		-	$P < 0.01$	$P < 0.01$	$P < 0.01$
Ørn			-	$P < 0.01$	$P < 0.01$			-	$P < 0.05$	$P < 0.01$
Hinge				-	$P < 0.01$				-	$P < 0.01$
Gødstrup					-					-
Almind	2	nd	nd	nd	nd	6	NS	nd	$P < 0.01$	$P < 0.01$
Thor		-	nd	nd	nd		-	nd	$P < 0.01$	$P < 0.01$
Ørn			-	$P < 0.01$	$P < 0.01$			-	nd	nd
Hinge				-	$P < 0.01$				-	NS
Gødstrup					-					-
Almind	3	nd	nd	nd	nd	7	NS	$P < 0.01$	$P < 0.01$	$P < 0.01$
Thor		-		$P < 0.01$	$P < 0.01$		-	$P < 0.01$	$P < 0.00$	$P < 0.01$
Ørn			-	nd	nd			-	$P < 0.01$	$P < 0.02$
Hinge				-	$P < 0.01$				-	$P < 0.03$
Gødstrup					-					-
Almind	4	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	8	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
Thor		-	NS	NS	$P < 0.01$		-	$P < 0.01$	$P < 0.01$	$P < 0.01$
Ørn			-	NS	$P < 0.05$			-	$P < 0.01$	$P < 0.01$
Hinge				-	$P < 0.01$				-	$P < 0.01$
Gødstrup					-					-

Table 4. Significant differences in stomach content among lakes. Number are *P* values, NS = not significant different, *** = significant different.

	Almind	Thor	Ørn	Hinge	Gødstrup
Almind	-	0.147	0.029	0.002	0.001
Thor	NS	-	0.03	0.005	0.001
Ørn	***	***	-	0.364	0.006
Hinge	***	***	NS	-	0.244
Gødstrup	***	***	***	NS	-

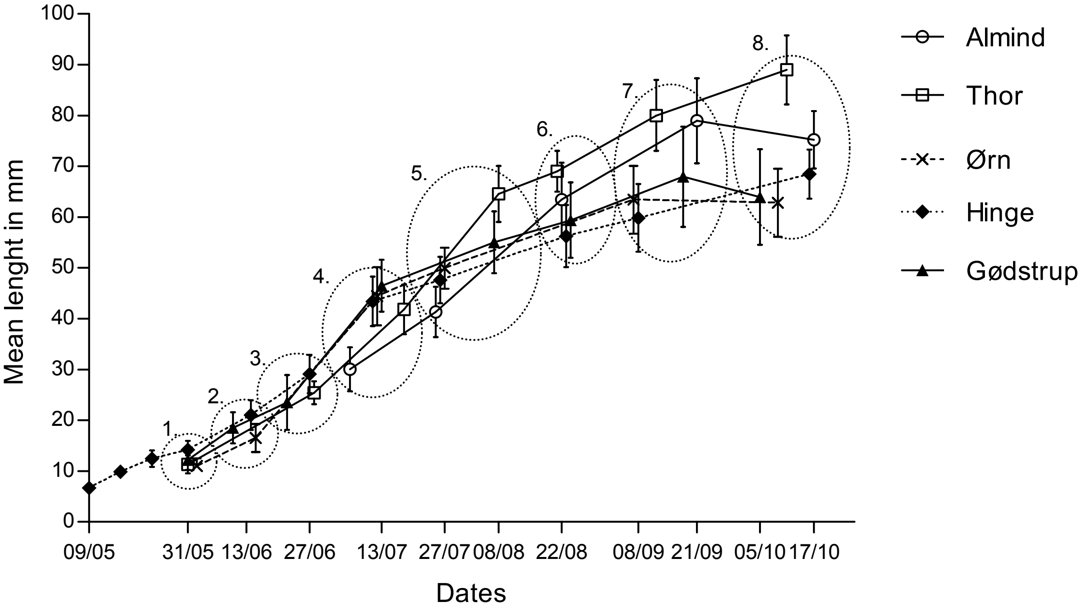

Figure 1. Mean lengths of perch in all five lakes as a function of time. Number 1-8 indicates the different groups of sampling dates being compared (see text for further explanation). Pairwise comparisons between lakes within each group are given in Table 3.

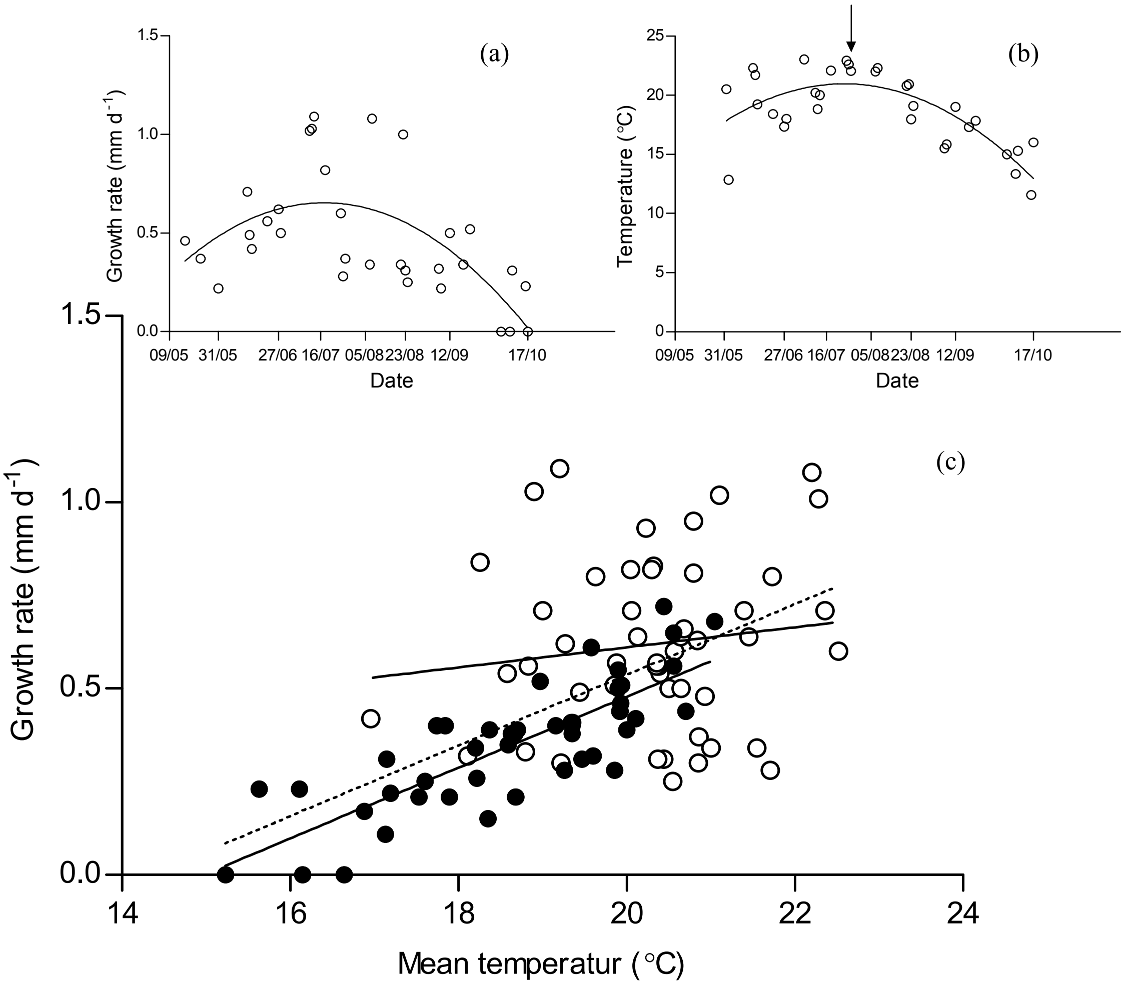

Figure 2. (a) Growth rate against time, and (b) temperature against time from the five lakes, arrow indicate temperature maximum. (c) Growth rate as a function of mean temperature. The dotted line is the regression for the whole season Y = 0.095x – 1.36; $r^2 = 0.35$, $P = 0.0001$. Open circles are values before temperature maximum, $P = 0.35$. Filled circles are values after temperature maximum, regression line: Y = 0.095x – 1.42; $r^2 = 0.66$, $P < 0.001$.

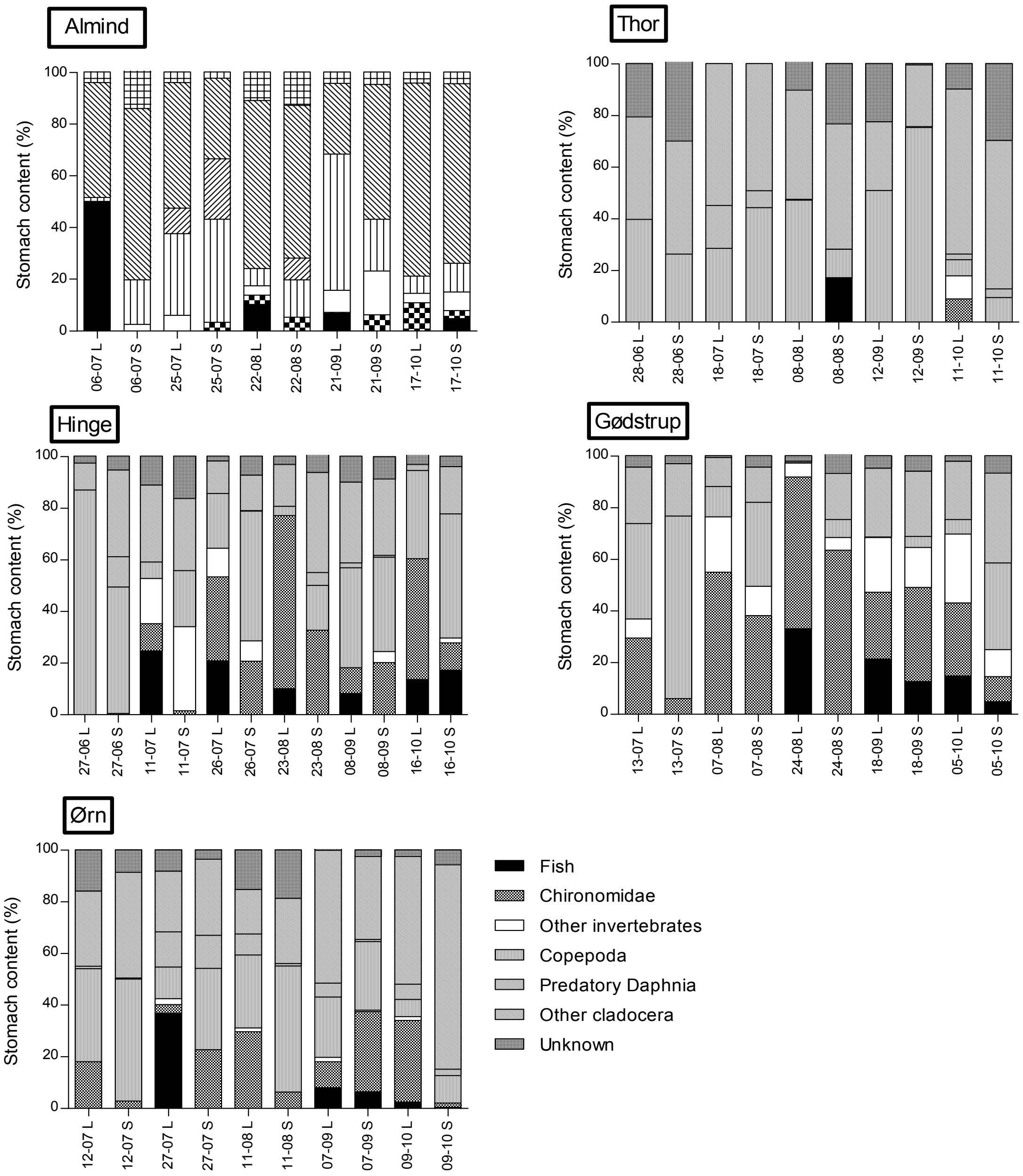

Figure 3. Proportion of prey items in the diet of 0+ perch, in all five lakes. Each sampling date is presented separate for large (L) and small (S) perch (irrespective of detection of bimodal size distribution or not) and the allocation of any given food category is given as percentage biomass of total stomach content. Fish (roach, stickleback, bream and perch), chironomidae, other invertebrates (*Ephemeroptera*, *Odonata*, *Plecoptera*, *Micronecta* sp. (*Heteroptera*), *Trichoptera*, *Coleoptera*, *Hirudinea* and *Asellus aquaticus*), *Copepoda* (calanoid and cyclopoid), Predatory daphnia (*Polyphemus* sp., *Bythotrephes* sp. and *Leptodora kindtii*) and other cladocera (*Daphina* sp., *Diaphanosoma* sp. *Ceriodaphnia* sp., *Chydoridae* sp., *Bosmina* sp., *Scapholeberis mucronata*, *Sida crystalline* and *Ostracoda* sp.).

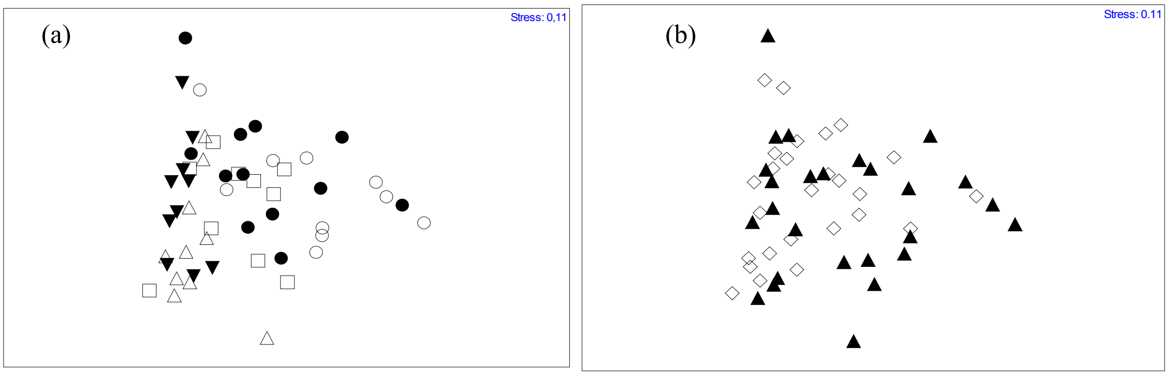

Figure 4. Multidimensional scaling (MDS) of similarity in stomach content in the five study lakes. (a) Lakes Δ: Almind, ▼:Thor, □: Ørn, ○:Hinge and ●: Gødstrup. (b) Similarity in stomach content for large▲ and small ◊ perch.

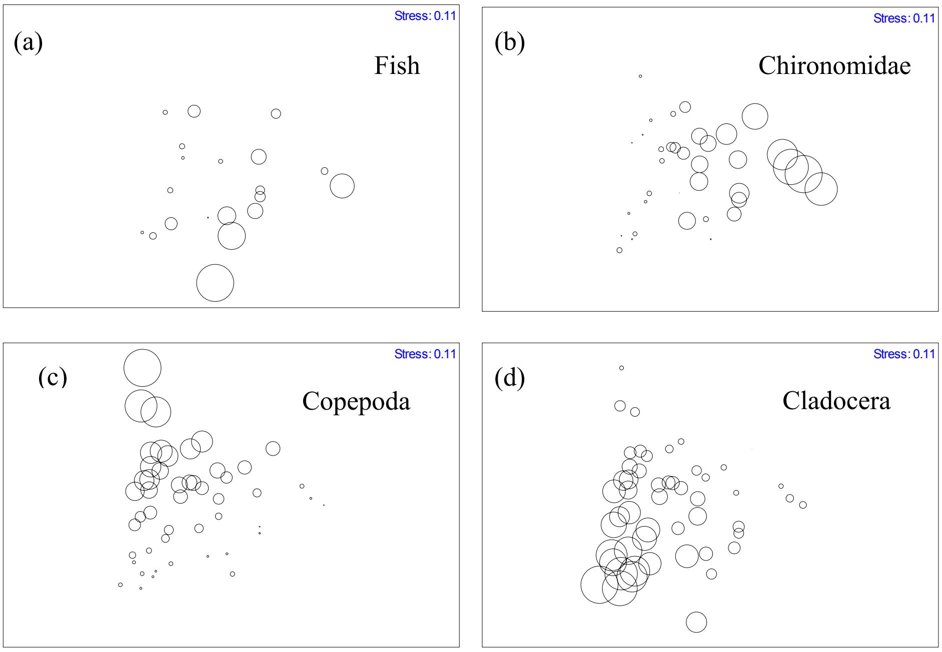

Figure 5. Distribution of four food categories in the same MDS as shown in fig. 4. (a) fish, (b) chironomidae, (c) copepoda, (d) cladocera. Size of bubble illustrate the quantity of the given prey type in the corresponding stomachs.

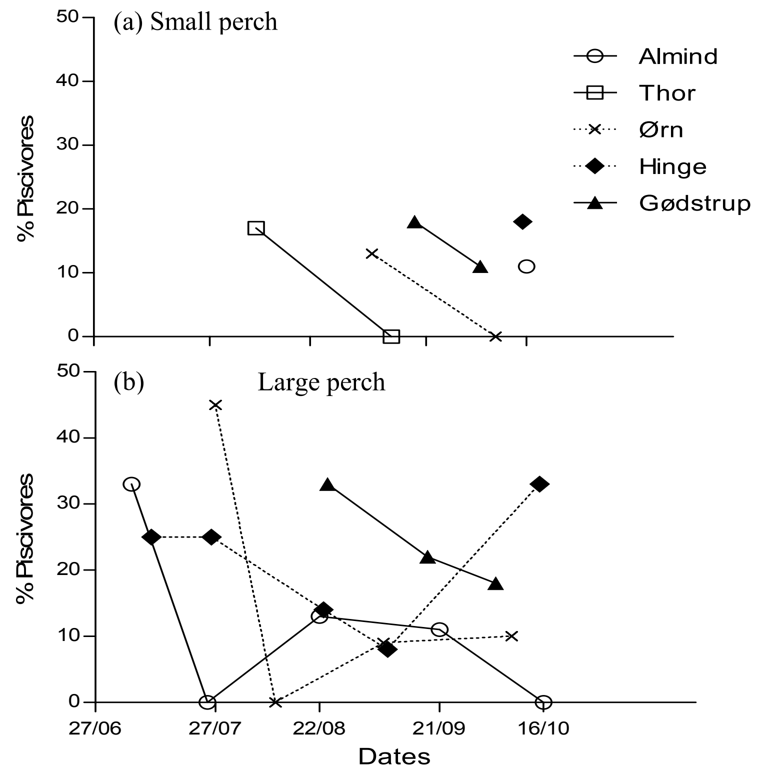

Figure 6. Proportion of perch preying on fish, in the five study lakes. a) small perch, and b) large perch (see text for definition). In Lake Thor none of the large perch had fish prey in their stomachs.

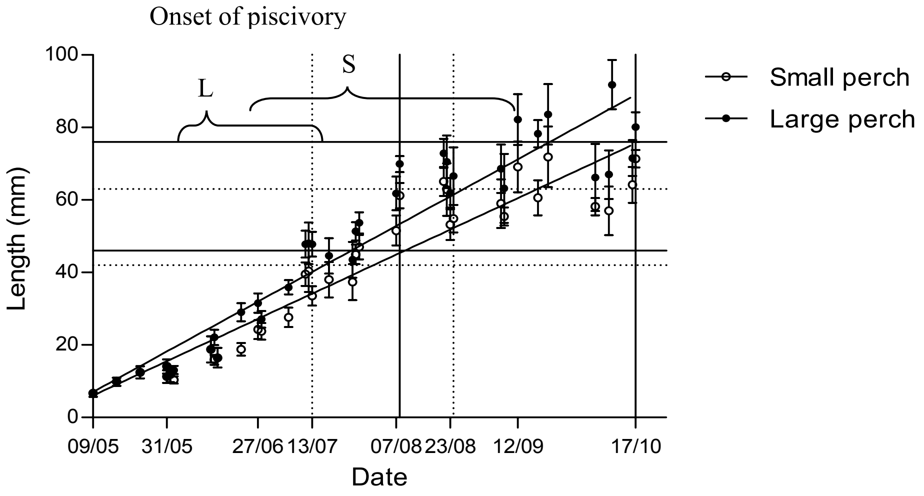

Figure 7. Mean lengths of perch for all lakes, values are split into large and small perch. Regression lines are fitted to data. $y_{small} = 0.43x + 6.05$, $r^2 = 0.89$, $P < 0.0001$. $y_{large} = 0.51x + 7.03$, $r^2 = 0.90$, $P < 0.0001$. The two regression lines were significantly different at $P = 0.053$. The vertical and horizontal lines indicate onset of piscivory, large perch (dotted) and small (solid line).

Chapter 3

Changes in stable isotope signatures (δ^{15}N δ^{13}C) in 0+ perch (*Perca fluviatilis* L.) in five lowland lakes in comparison to stomach content

Manuscript II

Changes in stable isotope signatures ($\delta^{15}N$ $\delta^{13}C$) in 0+ perch (*Perca fluviatilis* L.) in five lowland lakes in comparison to stomach content

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Abstract

Changes in values for $\delta^{15}N$ and $\delta^{13}C$ in 0+ perch mussel tissue was investigated, during spring and summer 2006 in five lowland lakes in Denmark, to examine if changes in the dietary competition, especially early piscivory, could be detected in the stable isotope composition of the fish mussel tissue.

Changes in $\delta^{15}N$ were not detected in 0+ perch in any of the five lakes, and correlation between $\delta^{15}N$ and any of the food items was not observed. In contrast a change in $\delta^{13}C$ values was detected; when 0+ perch shifted from the pelagic zone to the littoral zone $\delta^{13}C$ values increased. This was detected in all five lakes. Values of $\delta^{13}C$ correlated positively with percent of chironomidae and other macroinvertebrates in stomach content ($P = 0.008$) and negatively with percent of cladocera (not predatory daphnia) in stomach content ($P = 0.030$). The main reasons for the homogeneous values of $\delta^{15}N$ were the high growth rates and the omnivorous feeding strategy.

Introduction

Stomach contents analyses have been widely used to study the diet of fish and inter- and intraspecific trophic relationships of consumers and their food items. This type of diet analyses have traditionally been the only reliable method in analyses of trophic interactions (Hyslop 1980). However, stomach contents only provide a snapshot in time of an organism's diet. These snapshots do not necessarily represent the general diet or the average trophic position of a given population throughout the year (Vander Zanden *et al.* 1997).

Another and newer approach is analyses of stable isotope (^{15}N and ^{13}C) signatures in the tissue of organisms. This method is used to determine the trophic position and feeding structure up trough the food web (Peterson and Fry 1987; Kling *et al.* 1992; Cabana and Rasmussen 1994). The method may be very useful when examining intraspecific comparisons of 0+ fish populations due to various problems linked with dietary analysis of 0+ fish, such as identification of small (<60 μm) prey items (Vander Zanden *et al.* 1998), complete and rapid digestion of e.g. fish larva (unrecognizable within 5 – 10 minutes) (Brabrand 1995).

The stable isotope ^{15}N has been found useful to determine food chain structure and trophic position for lake trout (*Salvelinus namaycush*) (Cabana and Rasmussen 1994) and eight littoral fish species (Vander Zanden *et al.* 1997). Stable isotope ^{13}C have been used to identify foraging habitats for brown trout (*Salmo trutta*) and arctic charr (*Salvelinus alpinus*) (Jeppesen *et al.* 2002) and lake trout (Vander Zanden and Rasmussen 2001).

The ^{15}N concentration increases with trophic level in consumers. This is the result of higher excretion of the lighter ^{14}N as a by-product of protein synthesis, leaving the animal enriched in ^{15}N compared with its diet (Kling *et al.* 1992). This process results in a stepwise increase in ^{15}N with trophic level (Minagawa and Wada 1984; Fry 1991). ^{15}N is accumulated up through the food web with approximately 3.4 ‰ from one trophic level to the next (DeNiro and Epstein 1981; Minagawa and Wada 1984; Owens 1987; Peterson and Fry 1987). Top-predators thus have the highest concentrations of this stable isotope. As a consequence of this stepwise enrichment, ^{15}N in organisms will give an indication of trophic position based on energy flow along the food chain (Fry 1988; Kling *et al.* 1992).

The concentration of ^{13}C is conserved along the food chain, and do not differ significantly from one trophic step to the next, but ^{13}C can fluctuate substantial in the base of the food chain. As a consequence the ^{13}C:^{12}C ratio (δ^{13}C) can reveal the potential carbon source, since the ratio differs among different primary producers and habitats (Peterson and Fry 1987; Vander Zanden and Rasmussen 1999). Benthic algae are enriched with ^{13}C compared to planktonic algae and thus benthic consumers are ^{13}C enriched relative to planktonic consumers (France 1995; Hecky and Hesslein 1995). Stable carbon isotopes can indicate food preference and habitat choice because only little trophic variation is found from prey to predator. (Hecky and Hesslein 1995; Vander Zanden and Rasmussen 1999).

Habitat specific variation in baseline $\delta^{15}N$ and $\delta^{13}C$ values are well known in freshwater systems (Vander Zanden and Rasmussen 1999) suggesting that $\delta^{15}N$ and $\delta^{13}C$ in primary producers most likely will differ among lakes (Kling *et al.* 1992; France 1995). It is therefore difficult to find good base line values for any given system since values both vary within (between years) and among lakes (Post 2002).

If previous observations of bimodal length distributions in populations of 0+ perch (Persson *et al.* 1999; Beeck *et al.* 2002; Chapter 2) are indeed caused by early piscivori by a part of the population (larger perch), they would be expected to have different values of $\delta^{15}N$ and, depending on habitat choice, maybe also different $\delta^{13}C$ values. Juveniles are rarely studied with stable isotopes but isotope signatures of the diet can be detected within days in newly hatched fish larvae (Vander Zanden *et al.* 1998), and within 47 days for older 0+ perch (Beeck 2003). Organisms exhibiting fast growth rates should accumulate changes in isotopic composition in response to a dietary shift at higher rates (Herzka and Holt 2000). Therefore, changes in isotopic composition in 0+ perch should be detectable during the first growing season.

The aim of this study was to examine if early piscivori is detectable in tissue of 0+ perch in form of elevated $\delta^{15}N$ compared to the smaller non piscivorous 0+ perch. We further wanted to test if there were any differences in $\delta^{13}C$ levels over time and between large and small 0+ perch respectively, in order to detect shifts in food preference and habitat choice.

Materials and methods

Study sites

The study was conducted during spring and summer 2006 in five natural lowland lakes (Lake Almind, Lake Thor, Lake Ørn, Lake Hinge and Lake Gødstrup) all positioned in Mid Jutland, Denmark. Mean secchi depths range from clear to turbid (Table 1 in Chapter 2).

Fish sampling

Age-0 fish were sampled from May through October 2006 as explained in Chapter 2. Fish were caught in the pelagic zone on the first two sampling dates in Lake Thor and on the first sampling dates in Lakes Ørn, Hinge and Gødstrup (with a hoop net), on all other sampling dates perch were caught in the littoral zone by PASE electro fishing (see chapter 2 for further explanation). In Lake Almind 0+ perch was not caught in the pelagic zone only in the littoral zone. Fish for subsequent isotope signature analyses were frozen within maximum 4 hours from catch.

Laboratory procedures

Fish for stable isotopic signature analyses were defrosted but only kept at room temperature for as short a time as possible; all fish were measured and weighted to nearest mm and mg respectively. Muscle tissue (for larvae it was the whole body, but head and fins were removed) were dried at 75 ^{o}C for 50 h in small test tubes. The dried tissue was ground into a fine powder, 1-1.2 mg were packed into 4x6 mm tin capsules for subsequent stable isotopic analyses. Stable ^{13}C and ^{15}N isotope analyses were performed on the sample using a continuous flow isotope ratio mass spectrometer at the UC Davis Stable Isotope Facility, USA. Stable isotope ratios are expressed in delta (δ) notations, defined as parts per thousand (‰) deviations from standard material;

$\delta^{15}N$ or $\delta^{13}C = ((R_{Sample}/R_{standard})-1)*1000$

where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. ^{13}C standard is the PDB (Pee Dee belemnite) lime stone (Craig 1957) and atmospheric nitrogen for ^{15}N. A more positive isotopic value is said to be isotopically enriched, indicating that the sample contains proportionally more of the heavy isotopes (^{13}C and ^{15}N).

Stomach contents analyses used were taken from the experiment described in Chapter 2, each prey item is expressed in % of whole stomach content as in Chapter 2.

Statistics

Differences in $\delta^{15}N$ and $\delta^{13}C$ were tested with one-way ANOVA (Kruskal Wallis for pairs) with the dates as grouping variables in order to determine variation in $\delta^{15}N$ or $\delta^{13}C$ between dates and size classes respectively. A significance level of $\alpha = 0.05$ was used.

Results

Stable isotopes

Lake specific baseline values for $\delta^{15}N$ and $\delta^{13}C$ were not determined, as we were only interested in differences between perch size classes within lakes. Larvae from the first sampling date in all lakes (except Almind) were small (11-30 mm) and were expected to feed only on zooplankton in the pelagic zone. Thus, these could be considered as approximate baseline values for perch in the respective lakes.

In general there was little difference in $\delta^{15}N$ values throughout the study period (Fig. 1a). For all lakes almost no variation was found between large and small perch (Fig.1a and Table 1). In Lake Almind and Gødstrup no significant differences were found for any of the dates or size classes. In Lake Thor larger perch on June 28th had significant higher $\delta^{15}N$ than both size classes on August 20th. Both size classes on June 15th and July 12th in Lake Ørn had significantly lower $\delta^{15}N$ compared to both size classes on October 9th. In Lake Hinge size classes on July 11th and September 8th were significantly different from each other, but it was the smaller perch which had elevated $\delta^{15}N$ (Fig. 1(a) and Table 1).

In general there was a tendency to lower $\delta^{13}C$ values on the first sampling dates compared to later dates (Fig. 1b). Small perch caught in Lake Almind on July 6th had significantly lower $\delta^{13}C$ than perch (large and small) from August 22nd and the large ones from September 21st. In Lake Thor both large and small perch caught on June 28th had significantly lower values than perch (large and small) from August 20th. $\delta^{13}C$ values in Lake Ørn are significantly lower for both size classes from June 15th and small July 12th compared to large perch from September 7th. In Lake Hinge both size classes on June 14th had significantly lower $\delta^{13}C$ than large perch from July 11th and September 8th. $\delta^{13}C$ in Lake Gødstrup for large and small perch were significantly lower compared to large and small perch from July 13th, September 18th and October 5th. Despite the complex and varying pattern of significant differences among sampling dates within lakes there seem to be an overall trend to increasing $\delta^{13}C$ with time (Fig 1b and Table 1).

Growth for perch is shown in Fig. 2 as wet weight. During the first two months weight were doubled in 26 days, from August to October doubling took 78 days.

Stomach contents

In the overall pattern for all lakes there was significant correlation between stable isotope signature values and some of the food items (Table 2, Fig. 3). Increasing values of %

Chironomidae and other macroinvertebrates in stomachs corresponds with increasing $\delta^{13}C$ values (Fig. 3a and 3b, Table 2). The opposite pattern was observed for cladocera (not predatory daphnia) (Fig 3c, Table 2). There was almost statistic significant correlation between increasing $\delta^{15}N$ values and increasing % of Chironomidae in stomachs ($P = 0.056$) (Fig. 3d, Table 2).

Discussion

There was no overall pattern in $\delta^{15}N$ values in any of the lakes (Fig. 1a). Only sporadic differences were found, and the expected elevated levels of $\delta^{15}N$ for large or predatory fish were not detected. There were no overall significant correlations between $\delta^{15}N$ and any of the food items (Table 2). Perch with a diet consisting predominantly of chironomidae, other invertebrates and/or fish, would have been expected to have a higher $\delta^{15}N$ value this was almost the case (not significant) with chironomidae (Fig. 3d) but not for any of the other food items. In this study perch doubled their weigth in 26 days (in the first two months) (Fig. 2). As a result the diet in that time span will dominate the tissue composition. Therefore the "old" isotopic signal will continuously be blurred, especially since perch is very omnivorous and prey on zooplankton, various macroinvertebrates and fish (Persson *et al.* 1999). The $\delta^{15}N$ value as an indicator for trophic position might be vague and not as useful as anticipated. This pattern is seen for both small and large perch. As perch grow the initial nitrogen pool is diluted by the addition of newly deposited biomass (Herzka and Holt 2000). The fact that piscivori is not restricted to large perch are potential factors explaining the observed homogenous $\delta^{15}N$ values. $\delta^{15}N$ as an indicator for tropic position has also failed to provide results in other studies for 0+ and adult perch (Persson and Hansson 1999) and red drum (*Sciaenops ocellatus*) larvae (Herzka and Holt 2000)

We found lower values of early $\delta^{13}C$ compared to later in the season (Fig 1b). This corresponds with feeding habitat. Perch caught on the first sampling dates all originated from the pelagic zone, while on later sampling dates they were caught in the littoral zone. This was due to inshore migration where they generally stay throughout the rest of the season (Smyly 1952). This was observed in all lakes except Lake Almind due to no catch of 0+ perch in the pelagic zone. There were significant correlation between $\delta^{13}C$ and % chironomidae ($P = 0.008$), other invertebrates ($P = 0.001$) and cladocera ($P = 0.030$) in the diet. Higher % of chironomidae and other invertebrates in the diet results in higher $\delta^{13}C$ the opposite was observed forcladocera (Table 2, Fig. 3a, b and c). This corresponds with findings showing that zooplankton in the pelagic zone overall is depleted in carbon (lower $\delta^{13}C$) relative to benthic invertebrates in the near-shore littoral zone (Peterson and Fry 1987; Vander Zanden and Rasmussen 1999; Jeppesen *et al.* 2002).

In simple food chains where predators feed mainly on one food item, stable isotope signature may give a clear signal (Cabana and Rasmussen 1994) and $\delta^{15}N$ would indicate trophic position. Persson and Hansson (1999) concluded that stable isotope signatures cannot replace traditional dietary analysis, but only provide complementary data. But in many other studies stable isotopic signature has been found very useful. For adult fish: brown trout and arctic charr (Cabana and Rasmussen 1994; Jeppesen *et al.* 2002) and for several fish species (including yellow perch) (Vander Zanden *et al.* 1997; Vander Zanden and Vadeboncoeur 2002). In these situations the method have been useful to state the trophic position on a yearly basis for slower growing fish and/or adult life stages where growth rates are reduced compared to fry or the 0+ year class.

I found that the method is complicated in 0+ perch and increases in $\delta^{15}N$ were not detected even though some of the perch shifted to piscivori. Habitat shift, however, from the pelagic to the littoral zone was detected with $\delta^{13}C$ values. As expected higher values of $\delta^{13}C$ were found when the 0+ perch changed habitat and correspondingly also adopted a more littoral/benthic diet.

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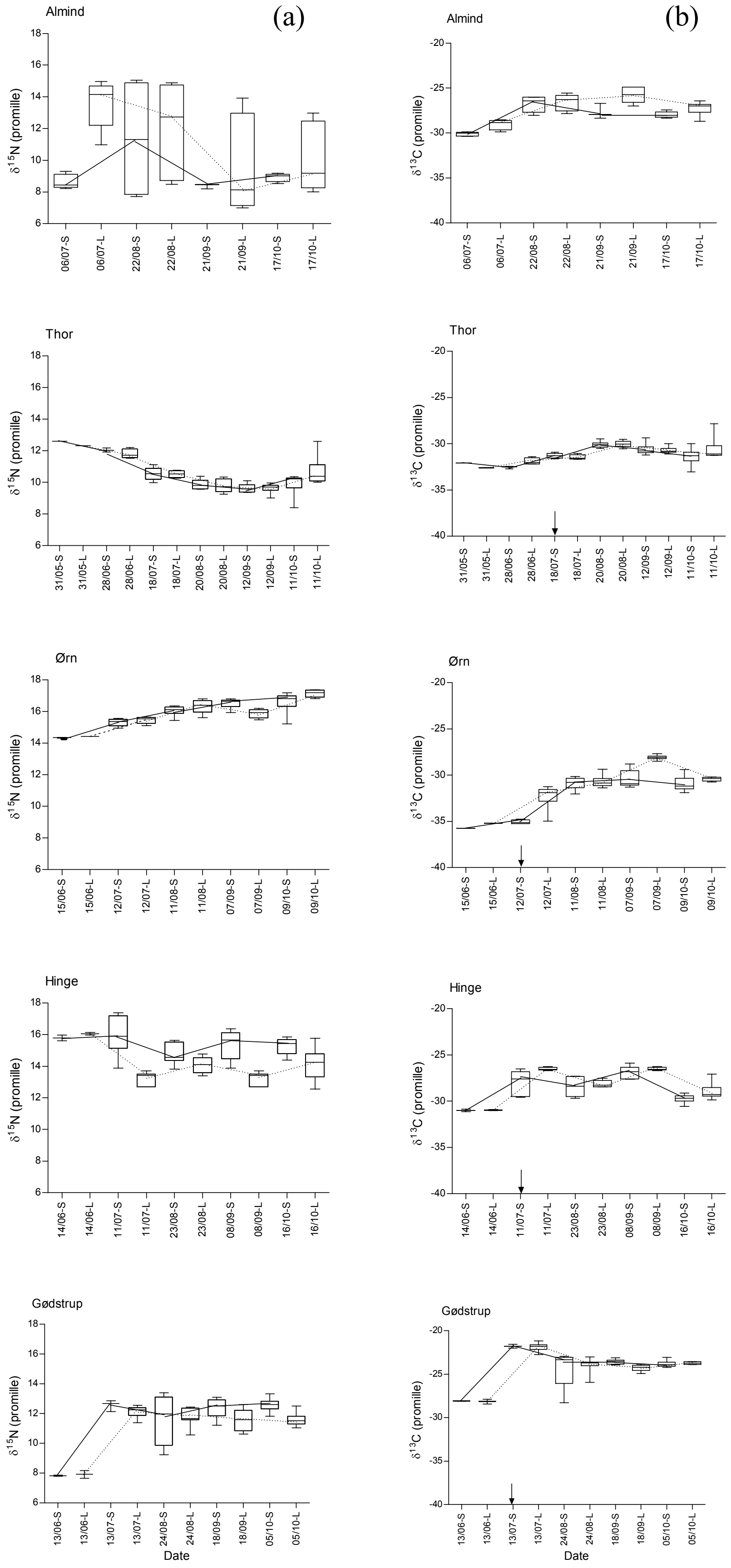
(a)
(b)
Almind
Thor
Ørn
Hinge
Gødstrup
δ15N (promille)
δ13C (promille)
Date
18
16
14
12
10
8
6
-20
-25
-30
-35
-40
06/07-S
06/07-L
22/08-S
22/08-L
21/09-S
21/09-L
17/10-S
17/10-L
31/05-S
31/05-L
28/06-S
28/06-L
18/07-S
18/07-L
20/08-S
20/08-L
12/09-S
12/09-L
11/10-S
11/10-L
15/06-S
15/06-L
12/07-S
12/07-L
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11/08-L
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07/09-L
09/10-S
09/10-L
14/06-S
14/06-L
11/07-S
11/07-L
23/08-S
23/08-L
08/09-S
08/09-L
16/10-S
16/10-L
13/06-S
13/06-L
13/07-S
13/07-L
24/08-S
24/08-L
18/09-S
18/09-L
05/10-S
05/10-L

Figure 1. (a) δ^{15}N and (b) δ^{13}C values for perch on different dates. The box presents 1st and 3rd (upper and lower) quartiles with median value in-between. Whiskers give maximum and minimum values. Arrows in b indicate when perch were first caught in the littoral zone.

Table 1. Median and range for δ^{15}N and δ^{13}C values, mean length for perch and number of samples (one sample = one perch) in all lakes on different dates.

Date-lake-size	N	TL	δ15N(‰)		δ13C(‰)	
		Mean	Median	Range	Median	Range
06-07-Almind-Small	5	28.20	8.44	8.23 to 8.95	-30.01	-29.85 to -30.37
06-07-Almind-Large	7	39.57	14.16	10.98 to 14.96	-28.82	-28.52 to -29.85
22-08-Almind-Small	4	61.25	11.32	7.72 to 15.05	-26.41	-25.99 to -28.01
22-08-Almind-Large	5	67.00	12.74	8.49 to14.88	-26.29	-25.56 to -27.81
21-09-Almind-Small	3	74.00	8.46	8.20 to 8.48	-27.92	-26.71 to -28.34
21-09-Almind-Large	6	86.83	8.14	7.00 to 13.93	-25.73	-24.88 to -25.68
17-10-Almind-Small	5	64.40	9.02	8.54 to 9.17	-28.03	-27.44 to -28.35
17-10-Almind-Large	7	79.71	9.17	8.01 to 12.97	-26.97	-26.41 to -28.69
31-05-Thor-Small	1 †	10.50	12.60		32.09	
31-05-Thor-Large	1 †	16.50	12.33		32.61	
28-06-Thor-Small	3	22.67	12.04	11.92 to 12.18	-32.51	-32.44 to -32.70
28-06-Thor-Large	4	27.25	11.72	11.54 to 12.21	-32.03	-31.41 to -32.17
18-07-Thor-Small	5	39.60	10.55	9.99 to 11.12	-31.31	-30.91 to -31.63
18-07-Thor-Large	4	46.50	10.54	10.26 to 10.76	-31.57	-31.06 to -31.67
20-08-Thor-Small	6	64.00	9.80	9.56 to 10.40	-30.10	-29.48 to -31.51
20-08-Thor-Large	6	76.00	9.72	9.25 to 10.34	-30.03	-29.53 to -30.54
12-09-Thor-Small	6	64.83	9.59	9.37 to 10.11	-30.77	-29.36 to -31.22
12-09-Thor-Large	6	88.17	9.72	9.01 to 9.96	-30.81	-29.99 to -31.09
11-10-Thor-Small	6	74.83	10.22	8.39 to 10.35	-31.30	-29.98 to -33.05
11-10-Thor-Large	6	93.67	10.38	10.00 to12.59	-31.08	-27.83 to -31.28
15-06-Ørn-Small	2 †	15.00	14.34	14.33 to 14.35	-35.73	-35.72 to -35.73
15-06-Ørn-Large	1 †	22.50	14.43		-35.18	
12-07-Ørn-Small	6	38.33	15.37	14.95 to 15.56	-35.14	-34.76 to -35.25
12-07-Ørn-Large	6	46.67	15.53	15.12 to 15.65	-31.87	-31.22 to -34.98
11-08-Ørn-Small	6	50.50	16.11	15.44 to 16.36	-30.78	-30.15 to-32.03
11-08-Ørn-Large	6	58.67	16.40	15.62 to 16.65	-30.87	-29.35 to -31.35
07-09-Ørn-Small	6	55.00	16.64	15.93 to 16.79	-30.90	-28.79 to -31.30
07-09-Ørn-Large	6	70.33	15.92	15.46 to 16.19	-28.08	-27.68 to-28.47
09-10-Ørn-Small	6	59.67	16.81	15.23 to17.17	-31.19	-29.39 to -31.89
09-10-Ørn-Large	4	71.50	17.21	16.83 to 17.11	-30.35	-30.20 to -30.74
14-06-Hinge-Small	2 †	22.00	15.80	15.62 to 15.98	-31.00	-31.13 to -30.86
14-06-Hinge-Large	2 †	25.50	16.05	15.97 to 16.14	-30.95	-30.90 to -31.01
11-07-Hinge-Small	6	37.50	15.91	13.88 to 17.40	-27.58	-26.50 to -29.56
11-07-Hinge-Large	6	50.33	13.42	12.68 to 13.71	-26.54	-26.24 to -26.68
23-08-Hinge-Small	7	51.57	14.57	13.83 to 15.64	-28.37	-27.27 to -29.68
23-08-Hinge-Large	5	67.60	14.10	13.41 to14.78	-28.26	-27.51 to -28.41
08-09-Hinge-Small	6	51.67	15.66	13.88 to 16.38	-26.79	-25.88 to -27.60
08-09-Hinge-Large	6	69.83	13.42	12.68 to 13.71	-26.54	-26.24 to -26.68
16-10-Hinge-Small	6	62.83	15.44	14.40 to 15.85	-29.69	-29.11 to -30.55
16-10-Hinge-Large	6	75.83	14.26	12.57 to 15.77	-29.27	-27.08 to -29.84
13-06-Gødstrup-Small	2 †	20.50	7.83	7.79 to 7.86	-28.07	-28.06 to -28.07
13-06-Gødstrup-Large	2 †	23.50	7.92	7.66 to 8.17	-28.15	-27.88 to -28.42
13-07-Gødstrup-Small	3	32.67	12.69	12.15 to 12.85	-21.79	-21.55 to -21.97
13-07-Gødstrup-Large	9	50.11	12.26	11.38 to 12.57	-21.77	-21.16 to -22.75
24-08-Gødstrup-Small	5	55.40	11.98	9.24 to13.41	-23.33	-22.94 to -28.28
24-08-Gødstrup-Large	7	70.86	11.67	10.55 to 12.43	-23.69	-23.00 to -25.92
18-09-Gødstrup-Small	6	57.33	12.51	11.21 to 13.11	-23.53	-23.13 to -23.93
18-09-Gødstrup-Large	6	80.50	11.59	10.63 to 12.61	-24.18	-23.84 to -24.92
05-10-Gødstrup-Small	6	55.83	12.61	11.83 to 13.33	-23.89	-23.05 to -24.23
05-10-Gødstrup-Large	6	77.67	11.51	11.05 to 11.59	-23.71	-23.56 to -23.90

† Value does not indicate number for fish but samples comprised of 5 larvae.

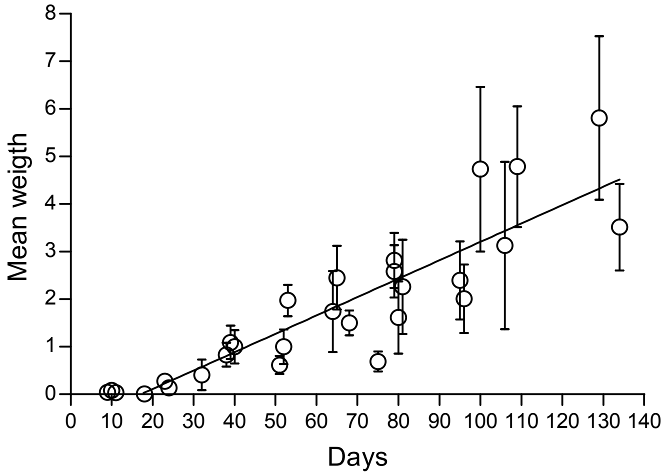


Figure 2. Mean wet weigth of 0+ perch from all five lakes in days from June 13th. Bars indicate standard deviation. Y = 0.0387x – 0.66, R^2 = 0.79.

Table 2. P values, r^2 and formula for correlations between stable isotopes and % of food item in stomachs (mean values). NS = not significant, *** = significant.

Stable isotop	Food item	P		r^2	Formula	n
δ15N	Fish	0.607	NS	0.007	Y=0.02x+12.47	42
	Chironomidae	0.056	NS	0.088	Y=0.04x+11.97	42
	Other invertebrates	0.561	NS	0.009	Y=-0.32x+12.75	42
	Copepoda	0.919	NS	0.001	Y=0.002x+12.66	42
	Predatory daphnia	0.521	NS	0.010	Y=0.08x+12.47	42
	Other cladocera	0.091	NS	0.070	Y=-0.04x+14.01	42
δ13C	Fish	0.080	NS	0.075	Y=0.08x-28.85	42
	Chironomidae	0.008	***	0.164	Y=0.07x-29.38	42
	Other invertebrates	0.001	***	0.231	Y=0.20x-29.28	42
	Copepoda	0.193	NS	0.042	Y=-0.03x-27.48	42
	Predatory daphnia	0.084	NS	0.073	Y=-0.26x-27.90	42
	Other cladocera	0.030	***	0.112	Y=-0.06x-26.17	42

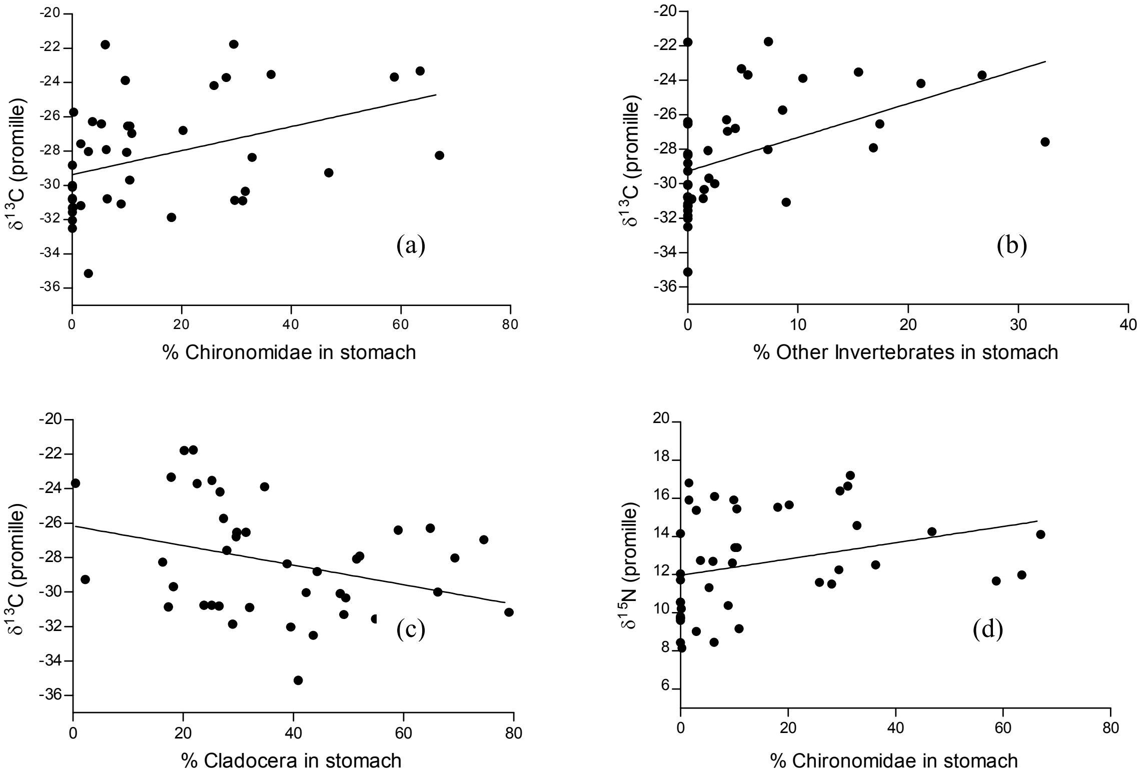
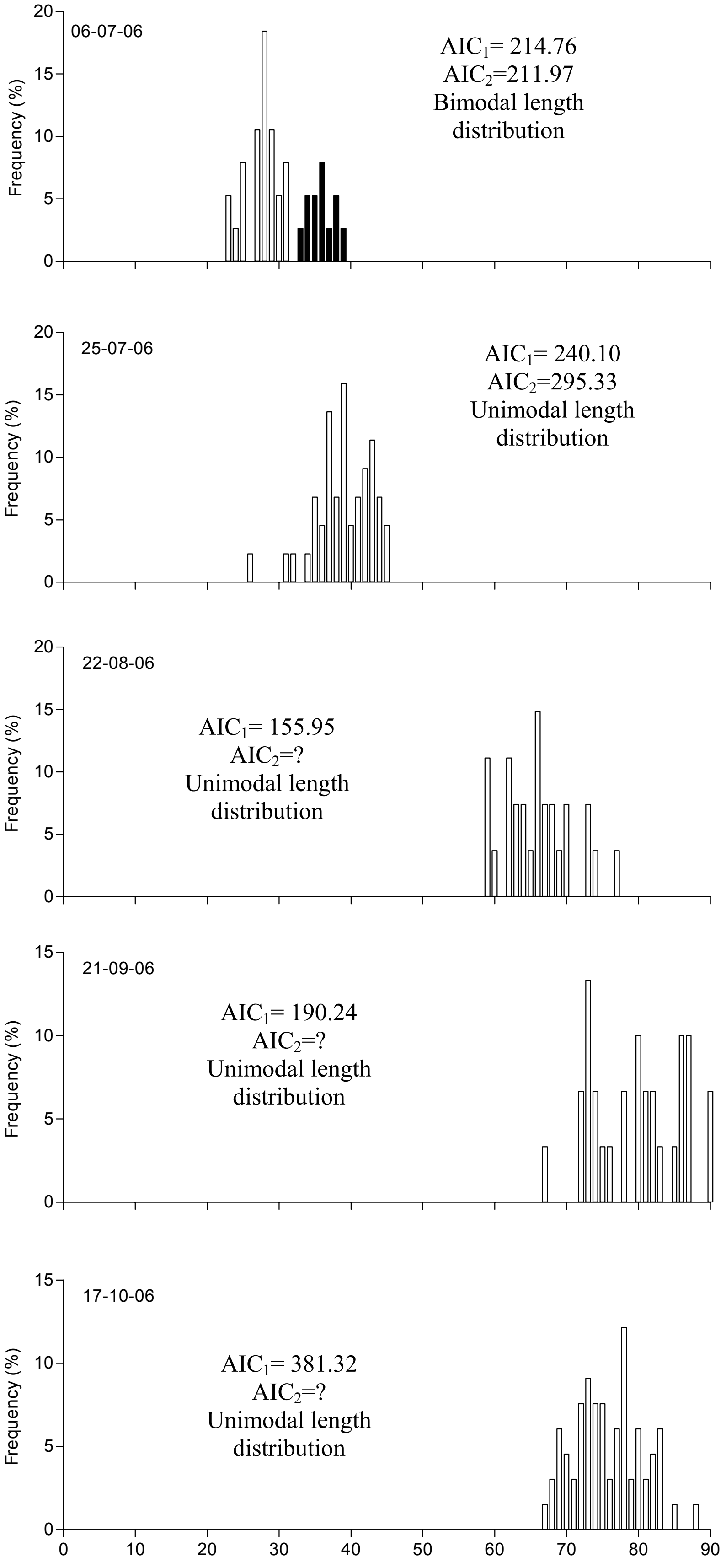


Figure 3. Correlations between % of food items in perch stomachs and stable isotope signature: (a) δ^{13}C vs. % Chironomidae in stomachs (P = 0.008). (b) δ^{13}C vs. % other invertebrates in stomachs (P = 0.001). (c) δ^{13}C vs. % cladocera (P = 0.030). (d) δ^{15}N vs. % Chironomidae in stomachs (P = 0.056). Statistic values are given in Table 2.

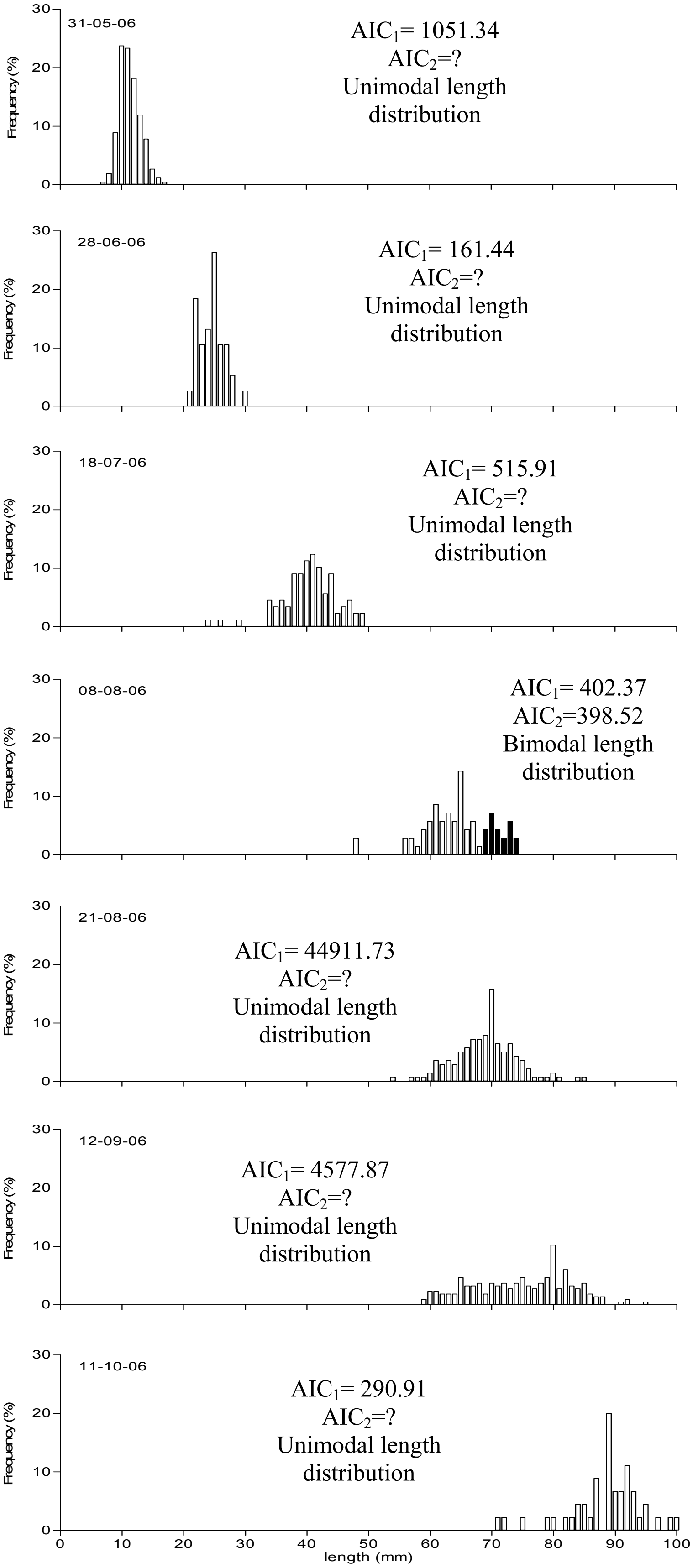
Appendiks 1

Perch length distributions from the five Lakes on all sampling dates. Whether the length distribution is unimodal or bimodal is stated every time. Black spikes indicate the large perch. AIC_1 are the value for Akaike's Information Criterion when one normal distribution curve was fitted to data. AIC_2 are the value for Akaike's Information Criterion when two normal distributions curves were fitted to data. AIC_2=? Means that it was impossible to fit two normal distributions to the data, or that it visually gave no meaning. Dates marked with ♣ indicated when there was normal distribution even though, there was bimodal length distribution.

Lake Almind from 06-07-2006 to 17-10-2006


20
15
10
5
0
Frequency (%)
06-07-06
AIC$_1$= 214.76
AIC$_2$=211.97
Bimodal length distribution
25-07-06
AIC$_1$= 240.10
AIC$_2$=295.33
Unimodal length distribution
22-08-06
AIC$_1$= 155.95
AIC$_2$=?
Unimodal length distribution
21-09-06
AIC$_1$= 190.24
AIC$_2$=?
Unimodal length distribution
17-10-06
AIC$_1$= 381.32
AIC$_2$=?
Unimodal length distribution
0
10
20
30
40
50
60
70
80
90

Lake Thor from 31-05-06 to 11-10-06


31-05-06

AIC_1= 1051.34
AIC_2=?
Unimodal length distribution

28-06-06

AIC_1= 161.44
AIC_2=?
Unimodal length distribution

18-07-06

AIC_1= 515.91
AIC_2=?
Unimodal length distribution

08-08-06

AIC_1= 402.37
AIC_2=398.52
Bimodal length distribution

21-08-06

AIC_1= 44911.73
AIC_2=?
Unimodal length distribution

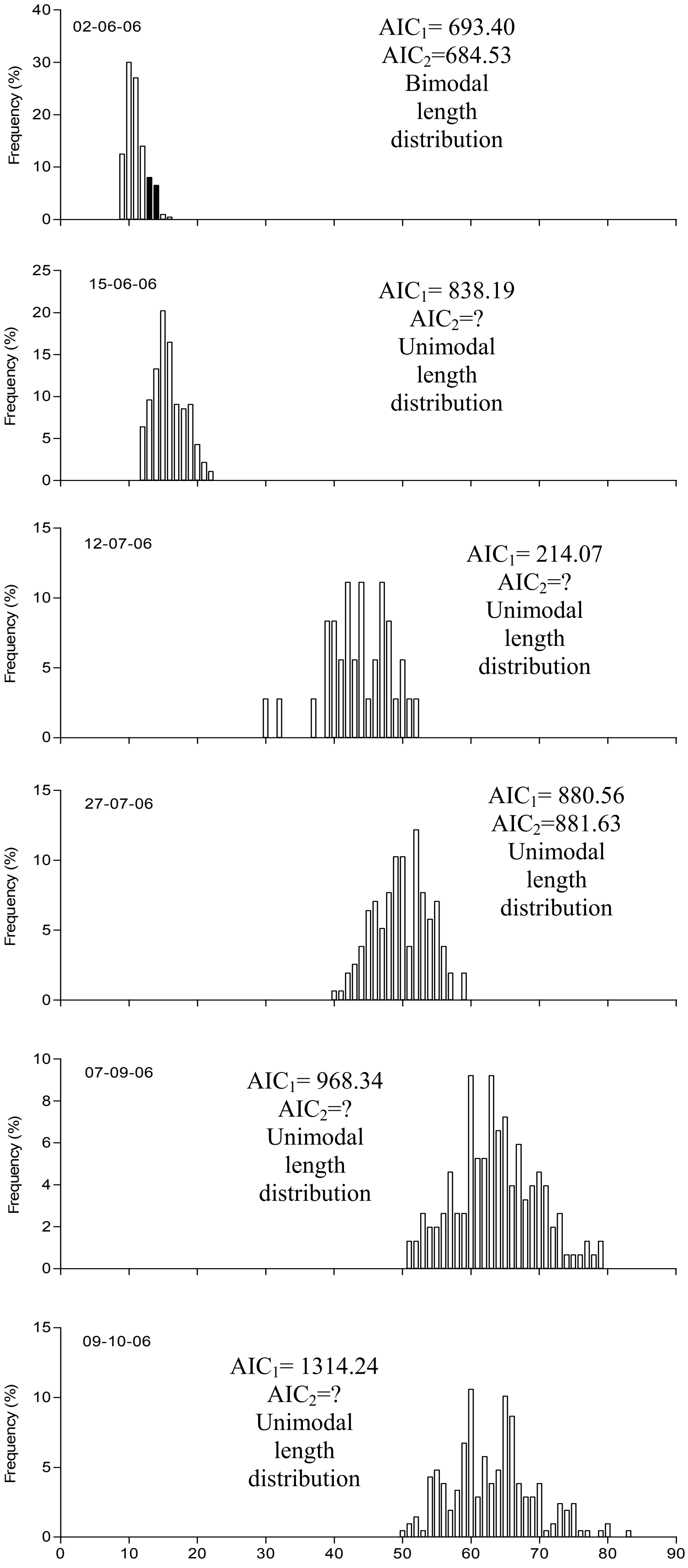
12-09-06

AIC_1= 4577.87
AIC_2=?
Unimodal length distribution

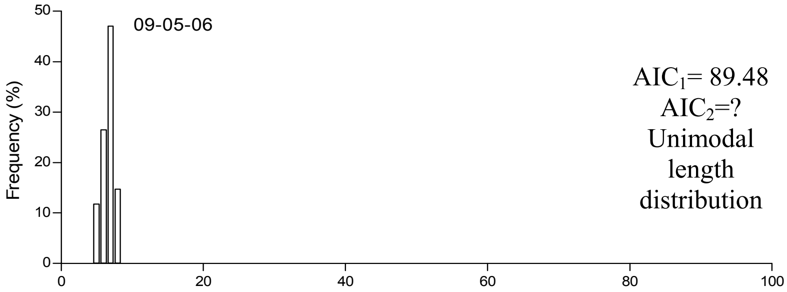
11-10-06

AIC_1= 290.91
AIC_2=?
Unimodal length distribution

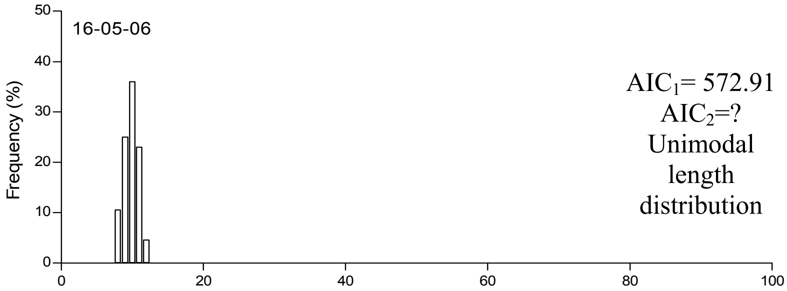
Lake Ørn from 02-06-06 to 09-10-06


02-06-06
AIC$_1$= 693.40
AIC$_2$=684.53
Bimodal length distribution
15-06-06
AIC$_1$= 838.19
AIC$_2$=?
Unimodal length distribution
12-07-06
AIC$_1$= 214.07
AIC$_2$=?
Unimodal length distribution
27-07-06
AIC$_1$= 880.56
AIC$_2$=881.63
Unimodal length distribution
07-09-06
AIC$_1$= 968.34
AIC$_2$=?
Unimodal length distribution
09-10-06
AIC$_1$= 1314.24
AIC$_2$=?
Unimodal length distribution
Frequency (%)
0
10
20
30
40
50
60
70
80
90

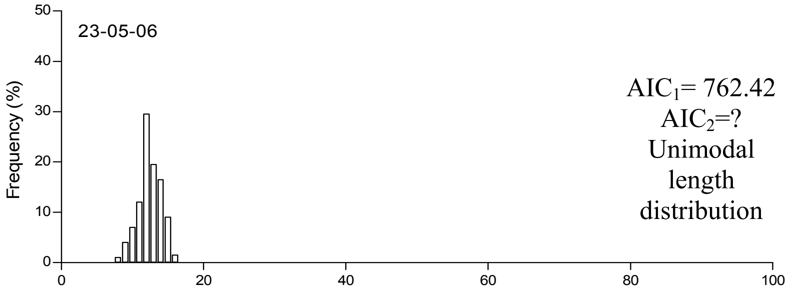
Lake Hinge from 09-05-06 to 16-10-06



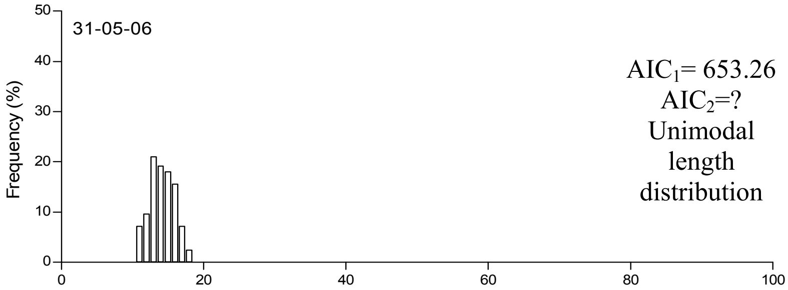
AIC$_1$= 89.48
AIC$_2$=?
Unimodal
length
distribution



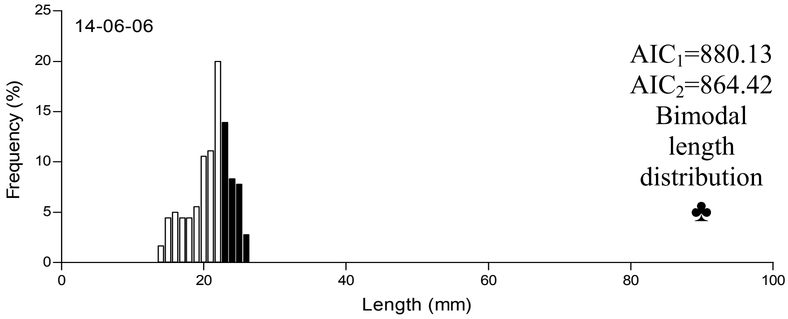
AIC$_1$= 572.91
AIC$_2$=?
Unimodal
length
distribution



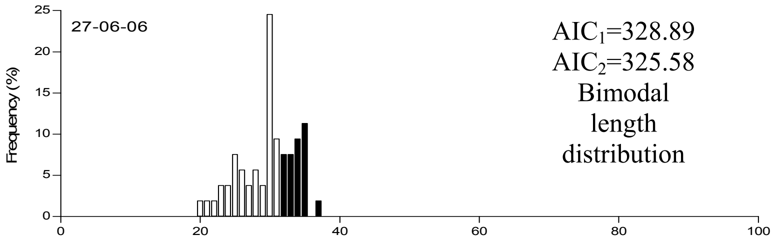
AIC$_1$= 762.42
AIC$_2$=?
Unimodal
length
distribution

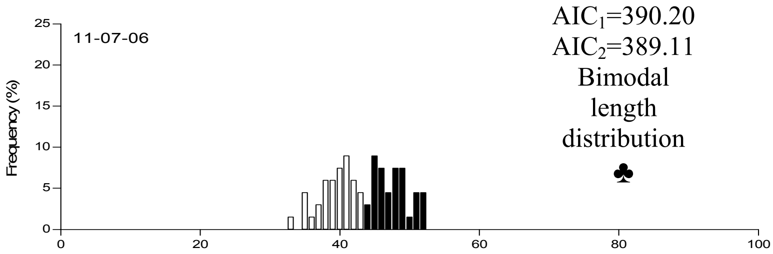


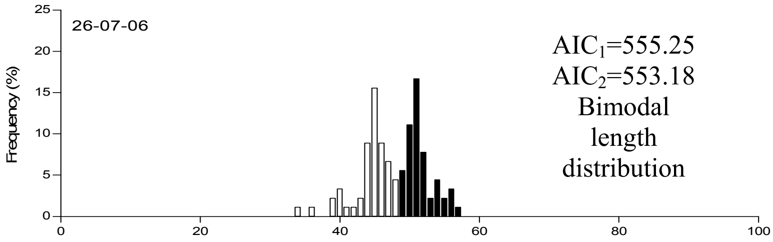
AIC$_1$= 653.26
AIC$_2$=?
Unimodal
length
distribution

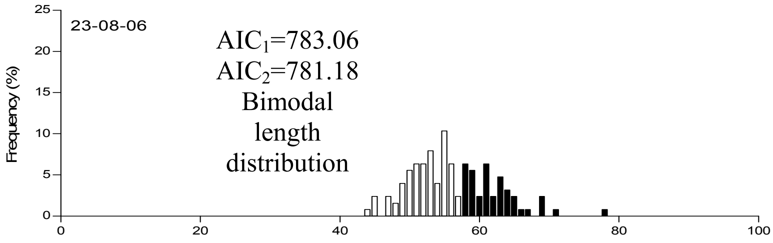


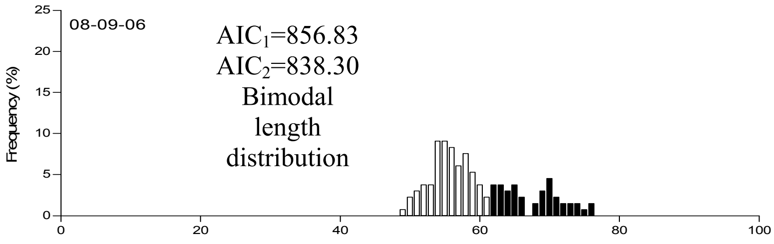
AIC$_1$=880.13
AIC$_2$=864.42
Bimodal
length
distribution
♣

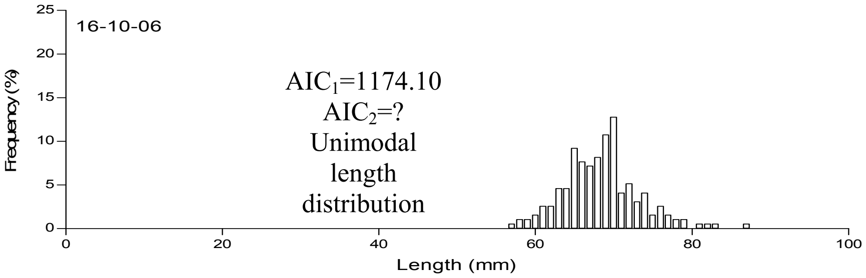

27-06-06
AIC$_1$=328.89
AIC$_2$=325.58
Bimodal
length
distribution
Frequency (%)
0
5
10
15
20
25
0
20
40
60
80
100


11-07-06
AIC$_1$=390.20
AIC$_2$=389.11
Bimodal
length
distribution
♣
Frequency (%)
0
5
10
15
20
25
0
20
40
60
80
100

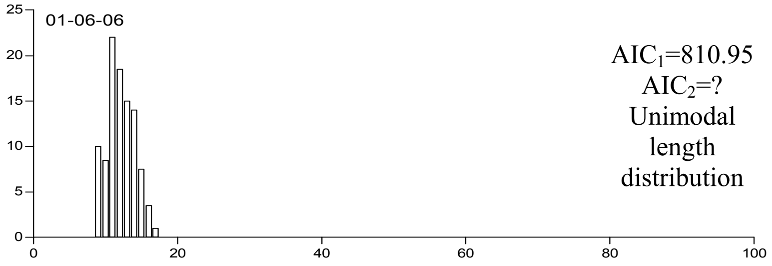

26-07-06
AIC$_1$=555.25
AIC$_2$=553.18
Bimodal
length
distribution
Frequency (%)
0
5
10
15
20
25
0
20
40
60
80
100


23-08-06
AIC$_1$=783.06
AIC$_2$=781.18
Bimodal
length
distribution
Frequency (%)
0
5
10
15
20
25
0
20
40
60
80
100

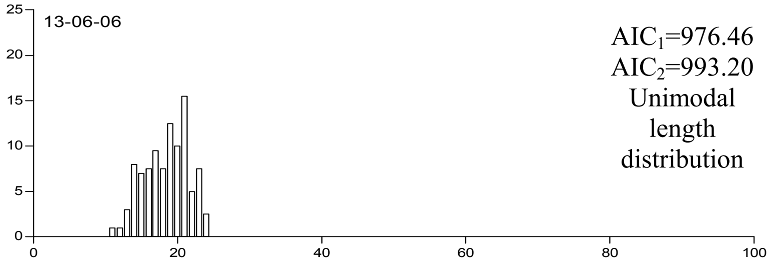

08-09-06
AIC$_1$=856.83
AIC$_2$=838.30
Bimodal
length
distribution
Frequency (%)
0
5
10
15
20
25
0
20
40
60
80
100


16-10-06
AIC$_1$=1174.10
AIC$_2$=?
Unimodal
length
distribution
Frequency (%)
0
5
10
15
20
25
Length (mm)
0
20
40
60
80
100

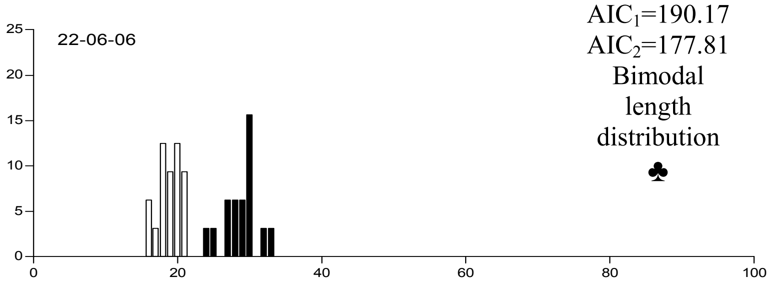
Lake Gødstrup from 01-06-06 to 05-10-06



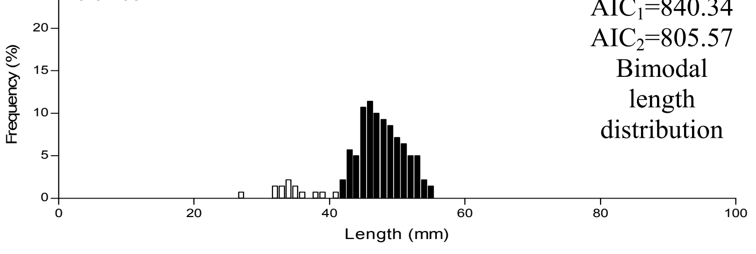
AIC$_1$=810.95
AIC$_2$=?
Unimodal
length
distribution



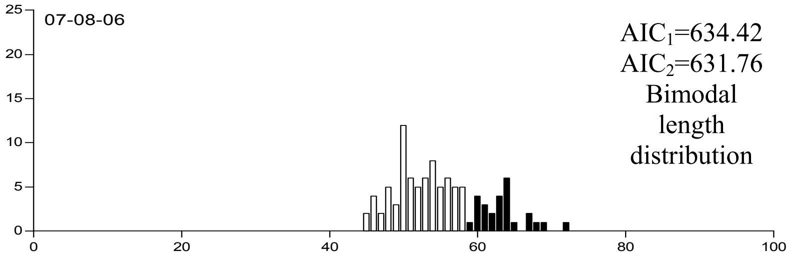
AIC$_1$=976.46
AIC$_2$=993.20
Unimodal
length
distribution



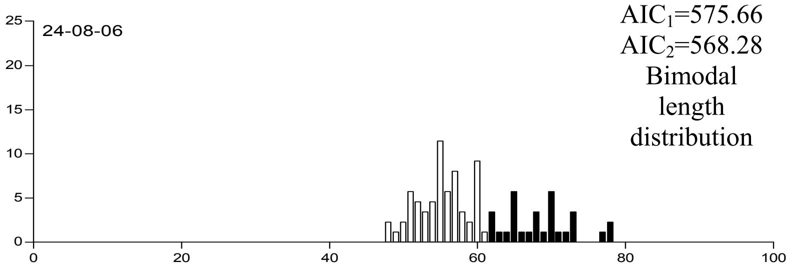
AIC$_1$=190.17
AIC$_2$=177.81
Bimodal
length
distribution
♣



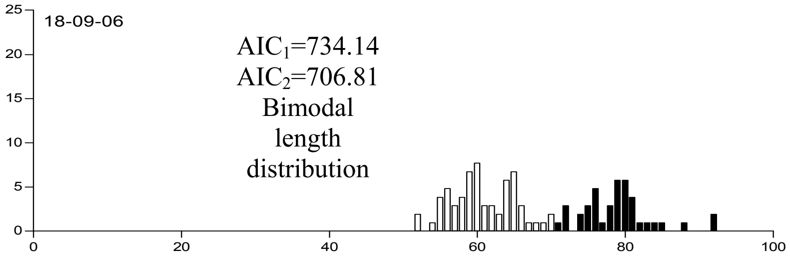
AIC$_1$=840.34
AIC$_2$=805.57
Bimodal
length
distribution



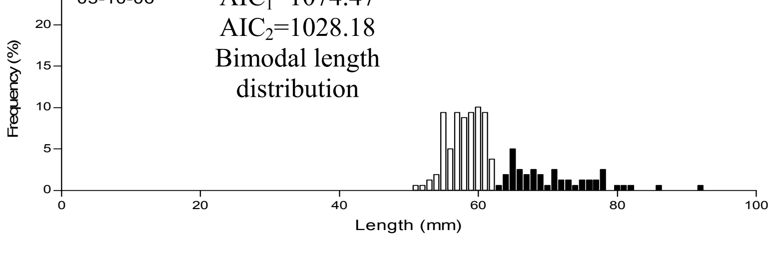
$AIC_1=634.42$
$AIC_2=631.76$
Bimodal
length
distribution



$AIC_1=575.66$
$AIC_2=568.28$
Bimodal
length
distribution



$AIC_1=734.14$
$AIC_2=706.81$
Bimodal
length
distribution



$AIC_1=1074.47$
$AIC_2=1028.18$
Bimodal length
distribution