Fødeindtag under naturlige forhold og laboratorieundersøgelser af fordøjelsesrater hos 0+ gedder (*Esox lucius* L.) mindre end 100 mm

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Forord

Dette speciale markerer afslutningen på mit studie på Århus Universitet. Specialet er udført i samarbejde med to forskere fra Danmarks Fiskeriundersøgelser, Christian Skov og Lene Jacobsen, som har fungeret som eksterne vejledere, og lektor Peter Grønkjær, Århus Universitet, som har fungeret som intern vejleder. Jeg vil gerne sige tak til alle tre for kyndig vejledning både i forbindelse med opbygning af mit specialeemne og igennem hele specialeforløbet. Det har været en lang proces med mange uforudsete problemer, hvoraf de fleste blev løst på en fornuftig måde og med et godt resultat i sidste ende.

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Specialet er bygget op omkring 2 engelsksprogede manuskripter, med en kort dansk introduktion til de behandlede emner og afsluttet med en dansk opsamling.

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Indholdsfortegnelse

Summary

Pikestocking has become a popular method of biomanipulation in resent years. However, only a few studies have shown an impact of pikestocking on biomass of 0+ planktivores. Post stocking cannibalism, lack of piscivori or anti predator behaviour have been suggested as reasons for the lack of positive results. The present M. Sc. thesis has studied several aspects of food intake and evacuation in 0+ pike and results are primarily discussed in relation to pikestocking.

Part one was an in-situ study of stomach content in stocked and native 0+ pike. The aim was to examine diel differences in food intake and possible differences between stocked and native pike. Pike were sampled by electro-fishing at 3, 16 and 37 days after stocking. At each occasion sampling was done at 5 different times within a 24-hour period – midday, sunset, night, sunrise and midday. Results showed that stomachs of pike contained food at all times of the day, but less at night – especially in the smallest pike. There were only minor differences in stomach content between stocked and native pike. Overall, piscivory was low but this could be explained by a low number of available prey fish. However, results indicated that stocked pike were less piscivorous than native pike. A result, which needs more attention in future studies. There was no significant difference in piscivory at the 5 sampling times of the day, but most fish was found in stomachs sampled at sunrise or midday.

The second part was a laboratory study of evacuation rates in 0+ pike. Evacuation rates can be used alone to estimate the potential daily evacuation or in combination with data on stomach content to estimate the actual daily consumption. Pike were starved prior to experiments to insure maximum appetite and then allowed to eat for maximum of 60 minutes. After eating, pike were removed from the feeding aquaria, divided into one of five evacuation periods, and left to digest the meal. At the end of the evacuation period, pike were preserved in alcohol and dry weight of residual stomach content was weighed. Two sizes of pike, 2-3 different temperatures and 2-3 prey species were used in the experiments. Results showed that initial intake of fish larvae were 2-3 times higher than of *G. pulex* or zooplankton. Small prey species like zooplankton and newly hatched bream larvae were evacuated in curvilinear pattern, while larger whitefish larvae and *G. pulex* was evacuated in a more linear pattern. Absolute evacuation rates were correlated to pike size and relative rates were slightly faster in small pike. However, relative rates were difficult to compare because of differences in evacuation patterns and initial meal size. No effect of temperature was found, which was in contrast to other studies. The possible causes for this result were short temperature acclimatization periods, too small temperature differences or that metabolism in small pike is only modestly influenced by temperature. Based on the evacuation rate of bream larvae, it was estimated that 24-29 mm pike could consume 20-50 bream larvae on a daily basis.

Introduktion

Gedden (*Esox lucius L.*) er det centrale omdrejningspunkt i dette speciale. Den har altid været en naturlig del af de danske søers økosystem, men i de senere år har den også fået en anden rolle, nemlig som udsætningsfisk i forsøg på biomanipulation. Her udsættes den i uklare søer for at øge prædationstrykket på nyklækket yngel af zooplankton-spisende fisk og derved hjælpe med til at ændre tilstanden fra en uklar sø til en klarvandet sø. For at geddeudsætninger skal have effekt, kræver det altså at gedderne er piscivore i et rimeligt omfang. Graden af piscivori kan bestemmes udfra undersøgelser af maveindhold og fordøjelsesrater hos gedder. De to emner danner grundlag for dette speciale.
I det følgende giver jeg først en introduktion til geddens livscyklus og fødebiologi og derefter en introduktion til problemstillingen bag brugen af geddeyngel i restaureringen af lavvandede søer.

Gedden

Gedden er udbredt over det meste af den nordlige halvkugle. I Europa findes den fra det nordlige Italien til det nordlige Sverige og Finland, og hører til blandt Europas største ferskvandsfisk sammen med den europæiske malle (*Siluris glanis*). Den tilhører familien Esocidae, som også omfatter Amurgedde (*Esox reicherti*), Muskellunge (*Esox masquinongy*), Chain pickelrel (*Esox niger*) og de 2 underarter Redfin pickerel (*Esox americanus americanus*) og Grass pickerel (*Esox americanus vermiculatus*) (Crossmann, 1996).

Livscyklus

Afhængigt af breddegrad gyder gedden i perioden februar-juni ved en vandtemperatur på 2-12 ^{o}C (Muus & Dahlstrøm, 1967). Gydningen foregår normalt på vegetationsdækkede lavvandede områder langs søens bredder eller på oversvømmede dele af vandløb og søbredder, men gedden kan også gyde sin æg på dybere områder (Bry, 1996; Farrell, 2001). Hannerne ankommer til gydeområderne først og finder en egnet gydeplads. Lige før gydningen ankommer hunnerne og lægger deres æg og de er i mange tilfælde omgivet af flere hanner under gydningen (Billard, 1996). Hunnen gyder i flere omgange og lægger i alt 8-25.000 æg pr. kg kropsvægt. Æggene på 2-3 mm i diameter er klæbrige og klistrer til vegetationen (Muus & Dahlstrøm, 1967). Gedderne har ingen yngelpleje og forlader gydeområdet efter gydningen.
Inkubationsperioden varer 11-12 dage, hvorefter de 7-9 mm store geddelarver klækkes. Geddelarverne fødes som mange andre fisk med blommesæk, som de lever af i 160-180 graddage, hvorefter de begynder at tage føde til sig (Billard, 1996).

Føde

Geddernes mave-tarm-system er ikke fuldt udviklet ved klækning. Munden udvikles 2-4 dage efter klækning og anus dannes 4-5 dage efter klækning (Balway, 1983). Indtil da lever geddelarven af blommesækken.

Mange undersøgelse tyder på at gedder er opportunistiske i deres fødeindtag (f.eks. Holland & Huston, 1984). I takt med stigende størrelse følger de sædvanligvis en bestemt rækkefølge af byttedyr: zooplankton, insekter, krebsdyr og fisk (Bry, 1996). Forskellige undersøgelser har vist, at der er stor variation i, hvornår fisk bliver det dominerende fødeemner for gedderne (tabel 1). Denne variation har stor betydning i forhold til geddernes rolle i biomanipulation (se nedenfor).

Tabel 1: Resultater fra forskellige undersøgelser af fødeindtag hos gedder. Længden i mm henviser til den længde hos 0+gedder hvor fiskeføde blev dominerende i fødeindtaget.

Geddelængde	**30-40 mm**	**70 mm**	**80 mm**	**>100 mm**	**>120 mm**
Reference	**Frost 1954**	**Hunt & Carbine 1951**	**Holland & Huston 1984**	**Skov et al. 2003**	**Grimm & Klinge 1996**

Fordøjelse

Der er ikke lavet mange undersøgelser over fordøjelsesrater hos 0+ gedder < 50 mm. Filleul & Le Louarn (1998) fodrede gedder på 29-35 mm med 1,455 mg zooplankton og fandt at ca. ¾ var fordøjet efter 5 timer ved en vandtemperatur på 15 ^{o}C. Samtidig fandt de, at kurven over fordøjelsesmønstret var bedst tilpasset en logaritmisk model.

De vigtigste faktorer der har general betydning for fordøjelsesraten hos fisk, er først og fremmest temperatur, men prædatorstørrelse, byttetype og -størrelse kan også have betydning (Bromley, 1994).

Stigende temperatur har generelt givet enslydende resultater, i form af en stigning i fordøjelseshastighed. De fleste undersøgelser har fundet en eksponentiel sammenhæng mellem fordøjelseshastighed og temperatur, men lineær sammenhænge har også været vist (Elliott & Persson, 1978; Dos Santos & Jobling, 1988; Elliott 1991; Bromley, 1994).

For prædatorstørrelse og byttetype og –størrelse er resultaterne mere forskellige. Generelt stiger den absolutte fordøjelsesrate (gram føde pr. time) med prædatorstørrelse, mens den relative (gram føde pr. gram fisk pr. time) falder (Flowerdew & Crowe, 1979), men enkelte undersøgelser har også vist at relative fordøjelseshastighed er uafhængig af prædatorstørrelse (Bromley, 1994).

Byttetypen kan have stor indflydelse på fordøjelsesraten. F.eks. er fisk langsomme til at nedbryde skjold og andre hårde dele af krebsdyr og insekter, hvilket nedsætter fordøjelseshastigheden i forhold til andre byttedyr uden skjold (Jackson et al., 1987).

Energiindholdet i byttet har også betydning og generelt bliver bytte med højere energi-indhold fordøjet langsommere end bytte med lavere energiindhold (Jobling, 1987).

Swenson & Smith (1973) viste at fordøjelsesraten i walleye (*Stizostedion vitreum vitreum*) steg, hvis et måltid af samme mænge føde bestod af mindre fisk frem for en stor fisk. De postulerede, at det skyldtes den større overflade-volumen ratio i små fisk. Dette resultat står dog i kontrast til en undersøgelse af Nilsson & Brönmark (2000), som ikke fandt nogen effekt af byttedyrsstørrelse på fordøjelsesrate hos gedde og Andersen (1999), som ikke kunne vise nogen effekt på fordøjelsesrate hos hvilling (*Merlangius merlangus*), der blev fodret ens mængde føde baseret på 1, 2 eller 4 byttefisk.

Lysets rolle for geddens fødeindtag

Lys har betydning for geddernes fødesøgning. Generelt menes det, at gedden er en visuel prædator (Raat, 1988), men undersøgelser har vist at voksne gedder er både aktive (Jepsen et al., 2001; Iversen, 2004) og spiser i mørke vha. et veludviklet syn og sidelinie-organ (Volkova, 1973; Dobler, 1977). Der er ikke lavet mange undersøgelser om lysintensitet og sigtdybdens indflydelse på 0+ gedders adfærd og fødesøgning, men Skov et al. (2002a) viste, at 0+ gedder fouragerede lige godt i klart vand som i vand med en sigtdybde på 20 cm.

De danske søer og deres udvikling

Igennem en periode i 1960’erne, 1970’erne og 1980’erne blev der udledt store mængder af fosfor og kvælstof til mange danske åer og søer. Den efterfølgende høje næringsstof-koncentration i vandene medførte mange biologiske ændringer. Mængden af planteplankton steg, hvilket nedsætter sigtdybden. Den lavere sigtdybde forringede lysnedtrængningen og dermed forholdene for undervandsplanterne, som gik kraftigt tilbage eller helt forsvandt. Planter har mange vigtige egenskaber, der hjælper med at opretholde en tilstand med klart vand og hvis planterne først er væk, har de svært ved at etablere sig igen (Jeppesen, 1998). Lav sigtdybde og manglen på planter øger skalle og brasens konkurrenceevne i forhold til aborren, da skallen er bedre tilpasset til at søge føde i frit vand og i mindre afhængig af synet under fødesøgning (Persson, 1991). Det medfører et fiskesamfund domineret af planktivore fisk og med få rovfisk. Mange planktivore fisk betyder øget prædationstryk på zooplankton og derved mindskes græsningstrykket på planteplankton, som derved kan opnå endnu højere koncentration. Det sænker sigtdybden yderligere, og medfører endnu færre planter og sådan fortsætter den dårlige spiral.

Biomanipulation

I de seneste 20-30 år er der brugt mange ressourcer på at nedbringe udledningen af næringsstoffer og på at ændre udviklingen imod klare og rene søer (Søndergaard et al., 1999). En af metoderne man har forsøgt sig med er biomanipulation ved udsætning af geddeyngel.

Udsætning af geddeyngel

Geddeudsætninger har været brugt i mere end 20 store danske søer (Søndergaard et al., 2000). Teorien bag geddeudsætninger er, at geddeynglen vil æde en stor del af det nyklækkede yngel fra planktivore fisk som skalle, brasen, suder, karusse og karpe. Disse små planktivore fisk lever i høj grad af zooplankton, og de præderer ofte selektivt på de store arter af zooplankton. De store arter er mere effektive græssere på planteplankton, og et øget prædationstryk fra fiskeyngelen vil derfor ikke kun nedsætte biomassen af zooplankton, men det vil samtidig ændre zooplankton samfundet fra at bestå af effektive græssere til at bestå af mindre effektive græssere (Jeppesen, 1998; Søndergaard et al., 1999).

Umiddelbart virker geddeyngel som det perfekte redskab i denne forbindelse. De er meget hurtigvoksende, og gedden kan spise fisk fra en størrelse på 20-25 mm (pers. observation). På trods heraf har positive effekter af geddeudsætningerne været sjældne, og kun i et par tilfælde har udsætningerne givet et tydeligt positivt resultat (Prejs et al., 1994; Berg et al., 1997). I Lyngsø ved Silkeborg udsatte Berg et al. (1997) igennem en 4-års periode forskellige densiteter af geddeyngel fra 500-3600 stk/hektar. Resultaterne viste, at der var en negativ korrelation mellem antallet af gedder og antallet af skalleyngel i littoralzonen, og at der var positive kaskadevirkninger i form at højere antal zooplankton/liter og lavere koncentration af klorofyl a (Berg et al., 1997; Søndergaard et al., 1997).

I andre projekter har geddeudsætninger ikke haft den store effekt. I Udbyover sø har Skov et al. (2002b) undersøgt effekten af 7 års geddeudsætninger på antallet af skaller i søen, og de fandt ingen effekt af udsætningerne. Grundene hertil kan være mange, men forfatterne peger selv på manglende piscivori blandt de udsatte gedder eller anti-prædations adfærd hos de planktivore fisk.

Som tidligere nævnt er der stor forskel på hvor lange 0+ gedder er, inden fiskeføde bliver dominerende i fødeindtaget. Hvis det først sker, når gedderne er 120 mm frem for f.eks. 50 mm giver det en forsinkelse på flere uger. Der er klart at i dette tidsrum kunne gedderne have ædt et stort antal fiskeyngel. Samtidig er tætheden af 0+ gedder efter en udsætning så høj, at en del vil dø hver dag pga. prædation eller kannibalisme. Det sænker det potentielle prædationstryk for gedderne yderligere. Samlet set understreger det vigtigheden i at gedderne æder fisk fra udsætningstidspunktet, hvis den ønskede effekt skal opnås.

Andre mulige forklaringer på en manglende effekt af geddeudsætninger er en stor dødelighed efter udsætning, som kan skyldes kannibalisme eller prædation fra andre rovfisk. Kannibalismen kan samtidig forstærkes, hvis gedderne sættes ud på et tidspunkt, hvor der ikke er nok føde til dem (Skov, 2002).

Opfiskning af planktivore fisk

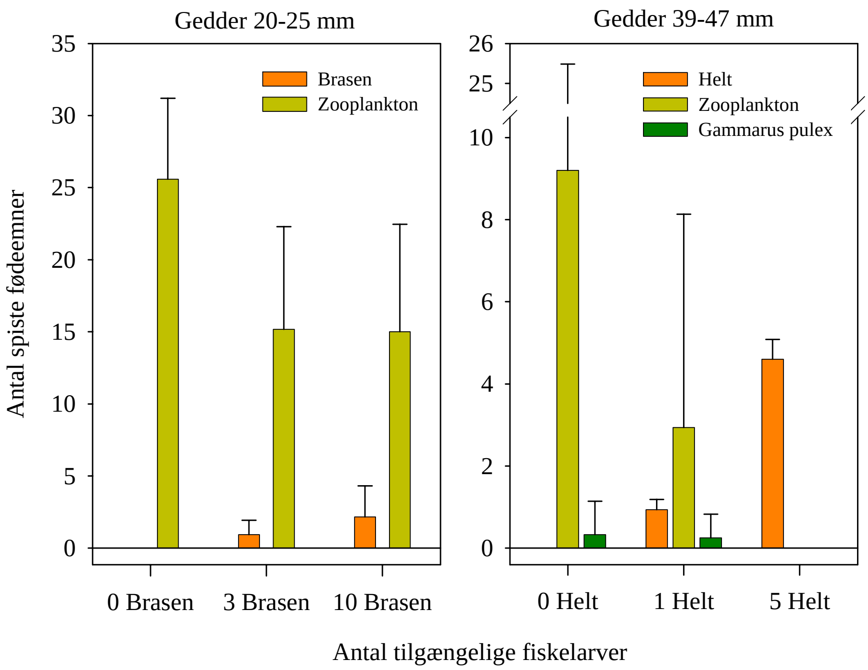
En anden grund til at geddeudsætninger alene ikke har nogen effekt kan skyldes, at der i mange tilfælde findes en høj biomasse af større planktivore fisk, som i forvejen opretholder et højt prædationstryk på zooplankton hele året rundt. I sådanne tilfælde hjælper det ikke meget at fjerne rekrutteringen vha. geddeudsætninger. For at øge effekten af geddeudsætninger har man derfor i mange tilfælde kombineret den med opfiskning af planktivore fisk. For at opfiskningerne skal have en effekt, er det vigtigt, at der opfiskes en stor del – gerne mere end 80% - inden for 1-2 år og at biomassen kommer under 100 kg/hektar. Ved en mindre effektiv opfiskning vil en lavere dødelighed blandt de resterende fisk kompensere for de fjernede fisk og en høj biomasse vil opretholdes (Søndergaard et al., 1999).

Kombinationen af opfiskning og udsætning vil være en dyrere løsning end udsætninger alene, men effekten vil oftest også være større. Et godt eksempel er De Indre Søer i København (Sortedamssøen, Peblingesøen, og Skt. Jørgens Sø), hvor der blev opfisket planktivore fisk og udsat geddeyngel i 2002 og 2003. Efterfølgende steg sigtdybden markant fra typisk under en meter til ofte mere end 2,5 meter og undervandsplanterne er i stort omfang vendt tilbage til søerne (Søren Berg, pers. kommunikation).

Spiser gedder i udsætningsstørrelse overhovedet fiskeyngel?

I forbindelse med mit speciale lavede jeg et mindre observationsforsøg, som havde til formål at undersøge om geddeynglen tager fiskelarver, hvis der var mulighed for at tage andre byttedyr.

Selvom at forsøgene blev udført under kunstige forhold i plastik spande og at omfanget var begrænset, indikerede disse forsøg at geddeyngel gerne tager fiskeyngel, hvis det er tilgængeligt (figur 1). Især var gedderne på 39-47 mm interesseret i fiskelarver. Ud af de 90 heltlarver der var tilgængelige, blev 84 ædt og hvis mængden af fiskelarver var stor nok, tog gedder i denne størrelse ikke andre byttedyr.



Figur 1: Gennemsnitlige antal fødeemner (+ std. afv.), der blev spist af gedder på henholdsvis 20-25 og 39-47 mm. Tætheden af zooplankton og *Gammarus pulex* var altid 300 og 2 individer per liter vand, mens tætheden af fiskelarver blev varieret. Forsøgene blev udført med gedder på 20-25 og 39-47 mm i spande med henholdsvis 1 og 5 liter vand. Fødeindtagelsen blev observeret i 10 minutter. Ved hver fiskelarvetæthed blev der lavet 15 replikater (i alt 90 forsøg).

Selvom de mindste gedder ikke var piscivore i samme omfang som de større, tyder det ikke på, at geddeynglens ”lyst” til at æde fiskeyngel kan være begrænsende for effekten af geddeudsætninger. I stedet kan det være tilgængeligheden af fiskeyngel, der kan forklare den begrænsede piscivori observeret i mange undersøgelser. Gedder er opportunistiske i deres fødevalg og fouragerer på de letteste tilgængelige fødekilder (Holland & Huston, 1984). Da små 0+ gedder i høj grad er tilknyttet tæt vegetation (Grimm & Klinge, 1996), kan det planktivore fiskeyngel udvise anti-prædationsadfærd ved at fouragere/opholde sig på åbent vand. Det betyder få interaktioner mellem 0+ gedderne og deres byttefisk, og gedderne vil i stedet fouragere på de fødeemner, der er tilgængelige i vegetationen.

Formål med specialet

I forbindelse med udsætninger af geddeyngel er det vigtigt at undersøge om geddeudsætningerne har noget effekt, og hvor stor den eventuelle effekt er. Det kan man dels gøre ved at undersøge biomassen af fredfiskeyngel efter udsætningerne, men det kan også gøres ved at undersøge overlevelsen af de udsatte gedder og graden af piscivori. For at undersøge piscivori ses på maveindhold og fordøjelsesrater hos gedderne. Disse aspekter af geddens biologi er grundlaget for dette speciale, som består af to dele:

Første del er en undersøgelse af maveindholdet hos både udsatte og naturligt udklækket geddeyngel i Vallum sø, som samtidig omfatter en undersøgelse af døgnvariationen i fødeindtaget. Der er 3 formål med denne del af specialet:

1. at vise hvilke fødeemner gedderne spiser og i hvilket omfang. I forhold til geddernes rolle som udsætningsfisk er det først og fremmest interessant, hvor mange fisk gedderne spiser.
2. at undersøge om der er forskel i fødeemner og – mængde hos udsatte og naturlige gedder.
3. at undersøge døgnvariation og eventuelle forskelle i fødeindtag hos udsatte og naturlige gedder.

Herved kan man få svar på hvor høj graden af piscivori er, og lige så vigtigt om der er forskel på piscivori hos udsatte og naturlige gedder. Hvis det skulle være tilfældet kan det få betydning for måden af udføre geddeudsætninger på i fremtiden.

Undersøgelserne kan også give svar på om gedderne spiser døgnet rundt eller på bestemte tidspunkter. Langt de fleste fiskeindsamlinger foregår om dagen, og i en situation hvor geddeynglen f.eks. primært spiser fisk om aftenen, og som vil være fordøjet inden morgenen, vil ”normale” fiskeindsamlinger underestimere graden af piscivori.

Anden del er en laboratorie-undersøgelse af geddeyngels fordøjelsesrater af forskellige fødeemner under skiftende temperaturer. I forsøget er der brugt 2 forskellige størrelser gedder, 2-3 forskellige fødeemner og fordøjelsesraten er estimeret ved 2-3 forskellige temperaturer. Sammen med resultaterne fra 1. del kan det give mulighed for at estimere antallet af fisk, som gedderne indtager og fordøjer i løbet af et døgn.

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Diel changes in food intake of stocked and native pike less than 2 month of age

Abstract
Diel changes in stomach contents of stocked and native pike were examined at three 24–hour periods within the first five weeks following stocking. At each sample period, pike were sampled at five different times of the day. Number of food items was lowest at night at the first to sample periods. At the last sampling period, less variation was found. This result was mainly caused by changes in the numbers of zooplankton.

Only small variations were found in stomachs contents of stocked and native pike. The degree of piscivory was generally low, and seemed to be reduced in stocked pike > 60 mm compared to native pike. Low biomass of suitable prey fish most likely caused the low piscivory.

Introduction

Several lakes around Europe and the rest of the world have undergone biomanipulation in recent years (e.g. Meijer et al., 1994; Søndergaard et al., 2000; Skov et al., 2002). The purpose of these projects has been to lower the biomass of planktivore fish such as roach (*Rutilus rutilus*) and bream (*Abramis brama*), which can have a cascading effect through the food web that ultimately decrease phytoplankton biomass and increase water clarity (Carpenter et al., 1985). To maximise impact many attempts has been done as a combination of planktivore fish removal and stocking of 0+ pike (*Esox lucius*) as suggested by Benndorf (1990). A high density of 0+ pike is believed to keep yearly recruitment of planktivore fish at a low level. Repeated yearly pike stockings, in combination with removal of larger planktivores, can consequently bring biomass of planktivore fish to a level where the natural population of predatory fish can control it. Unfortunately, only a few studies have shown an impact on 0+ planktivores following pike stockings (Prejs et al., 1994; Berg et al., 1997), and even fewer have shown a cascading impact on lower trophic levels (Søndergaard et al., 1997). The lack of success can be caused by several different factors such as post-stocking mortality caused by inter- and intracohort cannibalism (e.g. Grimm & Klinge, 1996; Grønkjær et al., 2004), predation by birds (Raat, 1988), insects (Le Louarn & Cloarec, 1997), other fish such as perch (Hunt & Carbine, 1951) or lack of piscivory among stocked pike (Skov et al., 2003b). Several authors have suggested that pike are opportunistic feeders and that availability or abundance of prey is more important than size of prey (e.g. Holland & Huston, 1984; Diana, 1996). In lakes undergoing biomanipulation, abundance of planktivorous fish is normally high, but antipredator behaviour, such as hiding, use of open water or decreased activity in roach in the presence of piscivores, can result in low encounter rate between pike and prey fish and explain the lack of piscivory in many studies (Jacobsen et al., 1997; Jacobsen & Perrow, 1998; Jachner, 2001).

0+ pike follow a typical sequence of food items with increasing size: zooplankton → insects → macro crustaceans → fish (Bry, 1996). However, the size at which fish prey becomes dominant differs greatly from 30-40 mm (Frost, 1954) to > 120 mm (Grimm & Klinge, 1996), and this variation has great implications for pike stocking as a biomanipulation tool. The later pike becomes primarily piscivorous, the less impact pike stocking will have for two reasons. First, the number of pike will decrease due to predation/cannibalism and second, the size and mobility of planktivorous fish will increase, making them harder to catch and increase their impact on the zooplankton biomass. Ideally pike stocking should be timed to match planktivorous fish hatching and size of natural pike population (Prejs et al., 1994; Skov, 2002).

Most lakes undergoing pike stocking also have a natural recruitment of 0+ pike. No previous published studies of 0+ pike diet have differentiated between these and the stocked pike. However, in recent years cost-effective methods of batch markings have made it possible to mark all stocked pike prior to stocking (Skov et al., 2001). This has made it possible to compare the diet and the survival of stocked and native pike, which was one aim of this study. Comparing the diet of stocked and native pike can help to understand the effectiveness of pike stocking. If piscivory is lower in stocked pike than in native pike, methods that improve natural recruitment, i.e. improving spawning grounds and nursery habitats, might yield a better result than pike stocking.

The second aim of this study was to explore diurnal differences in the food intake of small 0+ pike. This was done by examining stomach content of pike sampled at five different times during a 24-hour period. Diurnal differences in diet intake are interesting in relation to fish sampling, which is normally done during daytime. If some prey items are primarily foraged at specific times of the day, exclusive daytime samplings could over- or underemphasize the importance of these. All results are discussed in relation to the use of pike stocking as a biomanipulation tool.

Methods & Materials

Sampling was done in Lake Vallum (10^{o} 32’N, 56^{o} 23’E), a small (11 ha) and shallow (max depth 3,2 m, mean depth 2,1 m) lake with a mean summer Secchi depth of 1,0 m (Skovgaard, 2001). The fish population consisted of roach (*R. rutilus*), bream (*Abramis brama*), rudd (*Scardinius erythrophthalmus*), crucian carp (*Carassius carassius*), tench (*Tinca tinca*), pike (*E. lucius*), ruffe (*Gymnocephalus cernuus*), eel (*Anguilla anguilla*) and perch (*Perca fluviatilis*). The littoral vegetation covered almost the entire lake and was dominated by common reed (*Phragmites australis*) and a mixture of semiaquatic plants. The southwestern part became covered with white water lily (*Nymphaea alba*) during the summer.

Pike fry stocking was initiated in 1998 and have continued until 2003 at a yearly rate of 10-18.000 0+ pike. Fish removal was performed in 2000 and 2001 removing a total of 3,8 tons of mainly bream and roach, but also rudd, small perch and ruffe. This lowered CPUE of cyprinid fish from 3,8 kg/net to 1,9 kg/net and increased the secchi dept from 50 cm to 100 cm (details in Skovgaard, 2002).

In 2003 pike stocking (18.000 pike) took place at May 22. Prior to stocking pike were marked with alizarin, a chemical dye that is incorporated into the otolith (Skov et al., 2001). The dye leaves a mark on the otolith that is visible in a microscope under fluorescent light. The presence or absence of this alizarin mark was used to differentiate between stocked and native pike. Pike sampling was done 3, 16 and 37 days (referred to sampling date 1, 2 & 3 in the following) after stocking by electro fishing in the littoral zone. During sampling date 1, pike were caught in many different habitats, but at later sampling dates only the most densely plant covered parts of the lake held pike. Consequently, sampling was primarily performed in these parts of the lake. If possible, electro fishing was performed by wading, but in deeper areas a boat powered by an electric outboard engine was used. During night-fishing a headlight (Petzl Zoom) was used to spot the fish.

Each sampling date consisted of 5 x 1 hour of sampling during a 24-hour period. These 1-hour periods were set at midday (light), at sunset (dusk), at night (dark), at sunrise (dusk) and the following midday (light) (referred to as sampling time 1, 2, 3, 4 & 5 in the following). Pike were preserved in 96% alcohol every 5 minutes during sampling to stop further digestion of stomach content. In the laboratory each pike was weighed to nearest mg and measured to nearest mm. The stomach (from the end of the oesophagus to the start of the intestine) was removed and the content was emptied into a small petri dish. Each food item was identified grouped into four categories: zooplankton, insects, fish and miscellaneous.

To present ontogenetic diet changes and possible differences between stocked and native pike, results from each of the two groups of pike were grouped with no regard for sampling date or time and divided into 1 cm intervals.

Diurnal intake was shown by plotting average number of each food category against time of day in a cumulative Bar-plot for both native and stocked pike. To compensate for weaknesses in this method (e.g. a high number of food items in a single pike will have great effect on average number) frequency of occurrence of the same results are also presented.

RT Randomisation test (Manly, 1997) was used to test for differences in the diet of stocked and native pike.

Results

During the 3 sampling dates a total of 497 pikes were sampled and analysed for alizarin mark and stomach content (table 1). Stocked pike had a higher growth rate than native pike during the study period. The mean size of stocked pike was significantly smaller than native pike at sampling date 1 (Mann-Whitney U, z=-8.062, p=0.000) and date 2 (Mann-Whitney U, z=-2.733, p<0.01), but no significant length difference was found at sampling date 3 (Mann-Whitney U, z=-1.402, p=0.161) (figure 1). Average daily growth rate of stocked and native pike during the study period were 1.8 mm day^{-1} and 1.5 mm day^{-1}, respectively. At the third

Table 1: Number of stocked and native pike caught at each sampling time. * No fish sampled.

Sampling period	Sampling time	Total # pike	# Stocked pike	# Native pike
25-26. May 2003	Midday	50	46	4
	Sunset	50	41	9
	Night	50	44	6
	Sunrise	50	40	10
	Midday	50	43	7
	Total	250	214	36
07-08. June 2003	Midday	21	17	4
	Sunset	41	34	7
	Night	40	28	12
	Sunrise	22	15	7
	Midday*			
	Total	123	93	30
28-29. June 2003	Midday	10	6	4
	Sunset	26	19	7
	Night	33	20	13
	Sunrise	34	16	18
	Midday	21	14	7
	Total	124	75	49

sampling period both native and stocked pike had an average length close to 90 mm (figure 1). Abundance of stocked pike decreased faster than abundance of native pike. The fraction of native pike increased from 0.15 to 0.40 during the study period (figure 1). The grouping of stocked and native pike into 1 cm intervals showed ontogenetic shifts in food habits for both groups. Zooplankton and insects were the most frequent food categories in pike 2-4 cm. With increasing size zooplankton decreased in frequency and was not found in pike larger than 7 cm (figure 2). Frequency of insects was high throughout the study in both pike groups and only small differences in frequency in relation to size were found (figure 2). In pike larger than 6 cm results indicated a difference in food habits between stocked and native pike. Frequency of fish was always higher and the frequency of miscellaneous always lower in native than in stocked pike (figure 2).

Piscivory or cannibalism was low during the sampling period. A total of 40 fish (38 0+ roach and 2 0+ pike) was found in 19 pike. The two occurrences of cannibalism occurred at sampling date 1 and 2, respectively. At sampling date 2 this was the only occurrence of piscivory. Overall, fish were found in 2.9 % of stocked and 7.0 % of native pike. *Asellus aquaticus*, Hirudinea and

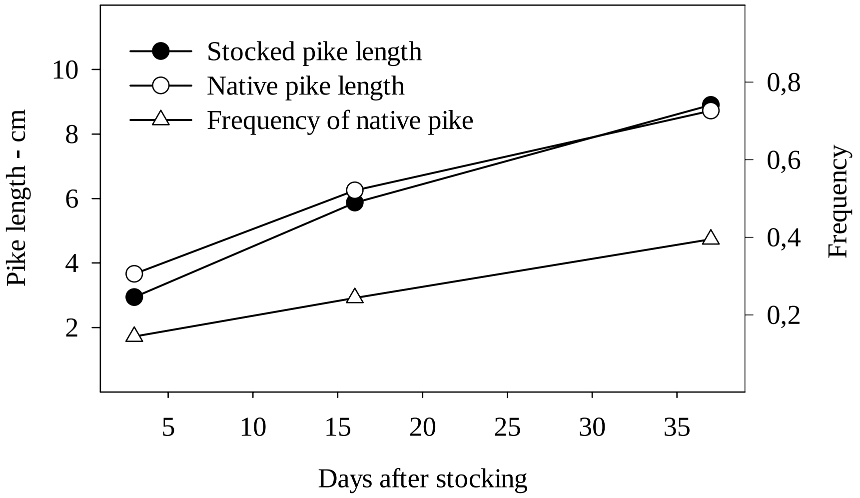

Figure 1: Mean length and frequency of stocked and native pike 3, 16 and 37 days after stocking (sampling date 1, 2 and 3, respectively).

Gastropoda, dominated the miscellaneous category at all sampling dates. Diptera and to a lesser extent Ephemeroptera dominated insects at all sampling dates. *Daphnia sp.* dominated zooplankton at sampling date 1 while *Daphnia sp.* and a range of other cladocera dominated at sampling date 2.

There were only few significant differences in diet between stocked and native pike. At sampling date 1 stocked pike foraged more on zooplankton than native pike at 3 of 5 sampling times (table 2). Although no other significant differences were found, results did indicate other variations in feeding habits. At sampling date 1, native pike appeared to consume more insects than stocked pike as average number of insects was higher in native pike at all sampling times (figure 3). The total average of all sampling times was 7.2 food items/stocked pike and 8.9 food items/native pike. At sampling date 2 an opposite pattern was seen. Apart from the sunrise sampling, stocked pike consumed a higher number of both zooplankton and insects at all sampling times (figure 3). This result could in part be explained by a higher frequency of empty stomachs in native pike at some of the sampling times. The total average of all

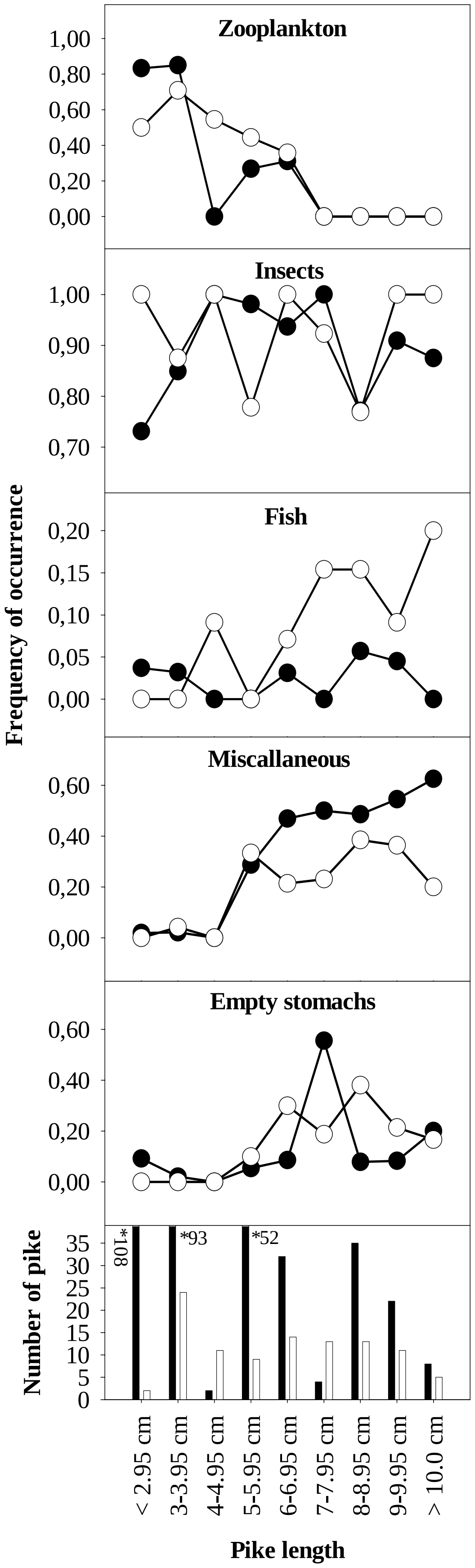

Figure 2 (right): Top: Frequency of occurrence of 4 food categories and empty stomachs. Pike with empty stomachs are not included in frequency of occurrence of the 4 food categories. Bottom: Number of stocked and native pike in each size interval. *The numbers refer to the number of pike in the category.
Closed circles and bars represent stocked pike; open circles and bars represent native pike. Note that in case of complete overlap only the open circle is shown.

Table 2: Statistical results from comparison of stomach contents of stocked and native pike. Number of food items in individual native and stocked pike was compared at each sampling time. Only the two most numerable food categories are shown. No significant results were found in other food categories at any sampling date or time. Test were done using RT Randomization test with 15000 randomisations. Pike with empty stomachs were not included. Significant results (p<0,05) are shown in bold.

	25-26. May 2003		07-08. June 2003		28-29. June 2003	
	Zooplankton	Insects	Zooplankton	Insects	Insects	Miscellaneous
Midday	0.817	0.291	0.196	0.844	0.093	0.055
Sunset	**0.017**	0.062	0.440	0.193	0.458	0.453
Night	**0.037**	0.126	0.487	0.090	0.881	0.631
Sunrise	0.352	0.503	0.298	0.468	0.952	0.054
Midday	**0.006**	0.053	-	-	0.487	0.121

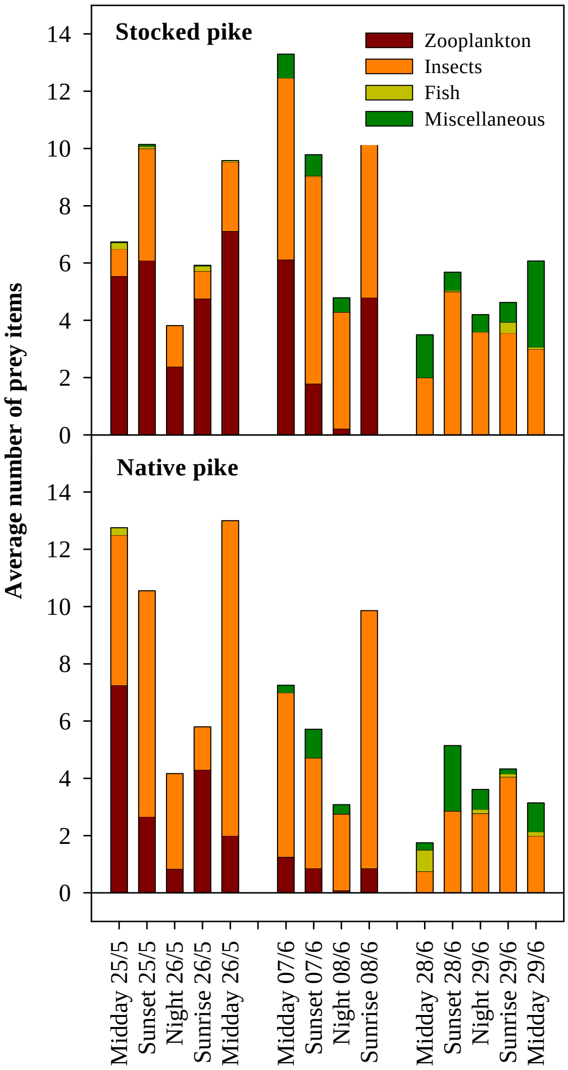

Figure 3: Average number of food items in stocked pike (top) and native pike (bottom) at the different sampling times and periods.

sampling times was 9.2 food items/stocked pike and 5.8 food items/native pike.

A difference in piscivory between stocked and native pike is indicated at sampling date 3. At most sampling times (4 of 5), frequency of fish was higher in the diet of native pike (figure 4). Pooling all sampling times, piscivory occurred in 14.3 % (7 of 49 pike) of native pike compared to 4.0 % (3 of 74 pike) in stocked pike. Instead of fish the stocked pike to a higher extent appeared to feed on miscellaneous (figure 3 and 4). The total number of food items was 5.0 food items/stocked pike and 3.9 items/native pike.

Overall, results indicate that 0+ pike forage during all hours of the day, but peak foraging activity changed with increasing size. On the first two sampling dates number of total food items was always lowest at night (figure 3). This pattern was mainly caused by changes in number of zooplankton in and to a lesser extent for in insects. As size increased, pike stopped foraging on zooplankton and the pattern of daytime foraging changed in to a more evenly distributed foraging activity in both stocked and native pike (figure 3). Based on data from all sampling dates, no statistical significant difference was found in frequency of piscivory between the 5 different sampling times in either stocked pike (Kruskal-Wallis χ^2=4.762, df=4, p=0.313), native pike (Kruskal-Wallis χ^2=7.784, df=4, p=0.100) or all pike (Kruskal-Wallis χ^2=4.310, df=4, p=0.366). However, piscivory appeared to be highest in daylight conditions (figure 5). 33 of 40 fish were found in stomachs sampled at either midday or sunrise.

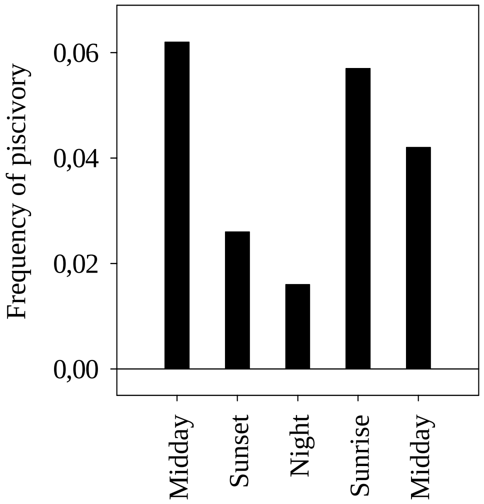

Figure 5: Frequency of piscivory at the five different sampling times of the day. Pikes from all 3 sampling dates are included (Midday (1) = 81, Sunset = 116, Night = 123, Sunrise = 106 and Midday (2) = 71).

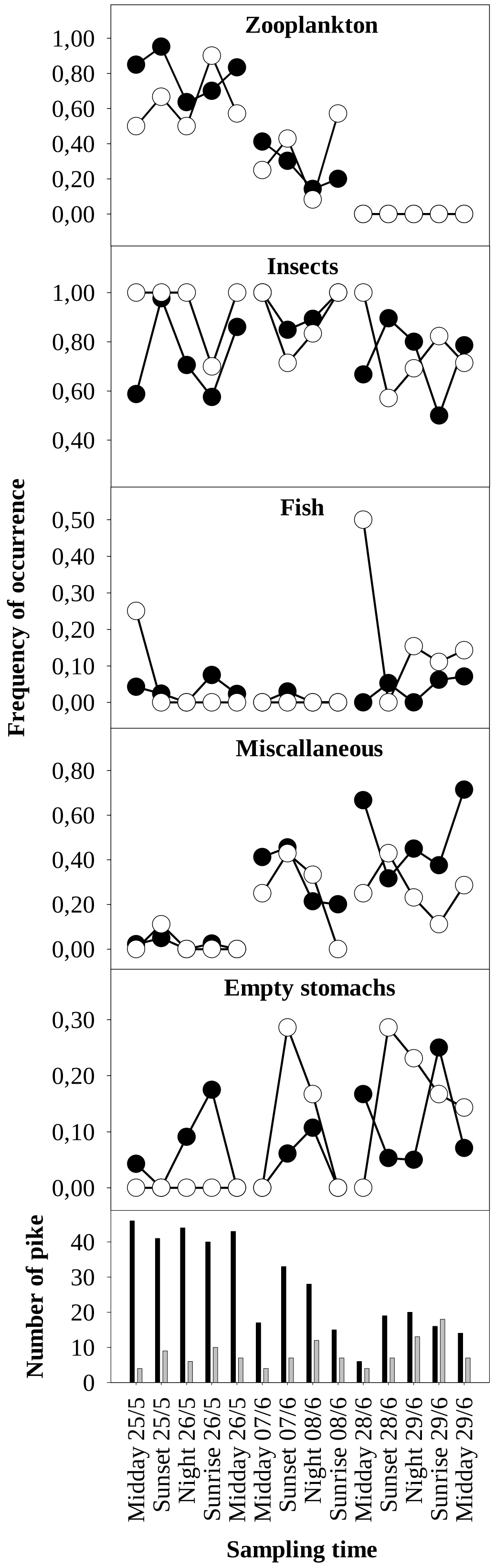

Figure 4 (left) Top: Frequency of occurrence of food categories in stocked and native pike at each sampling date. Bottom: Number of stocked and native pike at each sampling time.
Closed circles and bars represent stocked pike; open circles and bars represent native pike.
Note that in case of complete overlap only the open circle is shown.

Discussion

There was a clear difference in growth and survival of stocked and native pike. Several factors can influence growth and survival, but the initial size difference at stocking probably had great influence. Competition for the best habitats will favor larger (mainly native) pike and push smaller pike into more unsheltered and hazardous areas (Skov & Koed, 2004). Heterogenic size also increases intercohort cannibalism among 0+ pike (Bry & Gillet, 1980; Skov et al., 2003a). Both factors increase mortality of the smallest pike, which was mostly stocked pike. This size-selective mortality could also in part or fully explain the increased growth rate of stocked pike. Another possible explanation was that stocked pike are less aware of predations hazards in the unfamiliar natural conditions and spend more time foraging. This increases food intake, but also susceptibility towards predation.

The results emphasize the importance of stocking time. If stocking was done at an earlier date resulting in stocked pike being larger than native pike, the competition for habitats and risk of intercohort cannibalism would have favored the stocked pike and a different outcome would have been likely. Ideally the stocking time should be attuned to the size of natural recruited 0+ pike and the hatching of planktivore fish (Skov, 2002). That will keep cannibalism at a minimum and ensure abundant food.

Ontogenetic diet shifts and lack of piscivory

Ontogenetic diet shifts was seen in both groups of pike and results were generally in line with the succession of zooplankton, small and large insects, macro crustaceans and fish seen in similar studies (e.g. Hunt & Carbine, 1951; Wright & Giles, 1987; Bry et al., 1995). Piscivory was low throughout the study and fish did not become dominant in the diet during the study period. Other studies have shown a wide range of sizes at which fish has become the most dominant prey item in 0+ pike stomachs; e.g. 30-40 mm (Frost, 1954), 61-80 mm (Hunt & Carbine, 1951), 110 mm (Skov et al., 2003b); > 120 mm (Grimm & Klinge, 1996). The variability in these results indicates an opportunistic feeding strategy in pike, allowing them to adapt their diets to the available prey items. Diana (1996) supports this by arguing that feeding opportunity rather than prey size was crucial to pike predation. Further support comes from Holland & Huston (1984) who found that pike feed on organisms in proportion to their availability. With this in mind, the general lack of piscivory often seen in diet studies of 0+ pike indicate that fish are less available to 0+ pike than other food sources. In the present study low availability could be caused by a low recruitment of cyprinids in 2003. A standard fish survey in autumn of 2003 showed a low biomass of 0+ cyprinids (Morten Carøe, DFU, pers. com.). In line with this, a very low number of potential prey fish (estimated to less than 100 during the total sampling period) was observed during the study period. However, at least two other factors can influence the occurrence of piscivory.

(1) Antipredatory behaviour by prey fish could result in an inversely spatial distribution of pike and prey fish. Various types of antipredatory behaviour have been shown in fish, e.g. fleeing and backing in paradise fish (*Macropundus opercularis*) larvae when subjected to a predator model (Miklosi et al., 1997), response to chemical alarm substances from conspecifics in crucian carp (Petterson et al., 2000) and roach (Jachner, 2001), habitat shift in roach and perch (*Perca fluviatilis*) following stocking of piscivores (Brabrand & Faafeng, 1993; Jacobsen & Perrow, 1998; Jacobsen & Berg, 1998) and decreasing activity level in roach and perch in the presence of piscivores (Jacobsen & Berg, 1998). The sudden increase in 0+ pike biomass in the littoral zone following stocking, combined with chemical alarm cues of conspecifics from pike faeces, could similarly result in an active avoidance of the littoral zone in prey fish in the present study.

(2) Risk of predation or kleptoparasitism could influence feeding opportunity and diet choice in 0+ pike. Nilsson & Brönmark (1999) found that increasing prey size increases handling time and that increasing handling time increases risk of cannibalism or kleptoparasitic interactions. In line with this, several studies have shown that pike select easily handled prey, usually small prey over large or shallow-bodied over deep-bodied, when foraging among conspecifics, (e.g. Beyerle & Williams, 1968; Hambright et al., 1991; Nilsson et al., 1995; Nilsson et al., 2000).

Furthermore, to avoid predation Grimm (1994) suggest that pike less than 14 cm stay in dense vegetation, impermeable to larger predators and consequently forage on a non-fish diet available in these habitats.

Overall, a reluctance of 0+ pike to leave vegetation in combination with antipredator behaviour in prey fish can result in low encounter rate and consequently low piscivory. The dense population of 0+ pike following stocking further enhances the problem by directing prey choice towards small and easily handled non-fish prey.

Diet of stocked and native 0+ pike

Piscivory seemed to be reduced in stocked pike 6-11 cm, which is a problematic result in relation to pike stocking. Stocked pike will greatly outnumber native pike after stocking and reduced piscivory in stocked pike could have great consequence of the outcome of stocking. Unfortunately, no other results have been published on this type of study. Results from a similar study by Skov (in Skov, 2002) also indicated reduced piscivory in stocked pike but no significant results were produced. Future comparative studies can hopefully give more insight into this important part of pike stocking.

Two consequences of rearing conditions of stocked pike can help explain the possible reduction of piscivory in stocked pike. First, pond-reared pike are fed a non-fish and mainly zooplankton diet and this could influence diet preferences after stocking. Studies of two other piscivorous fish, tiger muskellunge and walleye, have shown that time-to-first-capture (of minnows) was longer in naïve (pellet-fed) individuals than experienced (minnows-fed) individuals (Gillen et al., 1981; Wahl et al., 1995). The low number of prey fish observed during sampling could prolong this time period due to low number of encounters. In contrast, Szendrey & Wahl (1995) found no difference in piscivory between naïve and experienced muskellunge and tiger muskellunge. The higher occurrence of zooplankton in stocked pike less than 40 mm also suggest that feeding-history influence diet choice. Stocked pike were reared on zooplankton and might have preferences towards this prey type. Secondly, at the time of lower piscivory in stocked pike (6-11 cm), native and stocked pike were equal or close to equal in size. If size was the most important factor when competing for the best habitats this would make the two pike groups equally successful. Instead decreased foraging skills could account for the possible difference in piscivory. Stocked pike were reared in indoor clear-water ponds without vegetation, which could decrease their post-stocking foraging skills in turbid water and natural conditions, e.g. by making them more visible to prey fish. This could be further improved by altered colour patterns caused by feeding-history (Szendrey & Wahl, 1995) or genetic differences.

A combination of above-mentioned factors is the most likely explanations for the possible lower piscivory in stocked pike compared to native pike.

Diurnal feeding of stocked and native pike

The diurnal feeding of stocked and native pike generally followed the same pattern. At sampling date 1 & 2 stomachs of both pike groups contained fewer food items at night than at other times. At sampling date 3 this changed to a pattern with less variation between sampling times.

Differences in zooplankton intake were the major reason for this variation. Zooplankton has been shown to make horizontal migrations from the vegetation to open water at night, making them less available to the pike at night (Lauridsen & Buenk, 1996). Another possible explanation for the change in diurnal feeding patterns comes from Raat (1988), who states that pike < 60 mm have not fully developed sensory organs. This makes small pike rely entirely on vision when foraging. In line with this, Lindeborgh (2001) found that pike with a mean length of 37 mm did not feed in total darkness.

Other studies of pike feeding related to light intensity have studied larger pike than in the present study; e.g. 9-17 cm (Skov et al., 2002); 21 cm (Volkova, 1973); 23-25 cm (Dobler, 1977). The latter two studies have shown that pike of these sizes are able to forage at low light intensities and that feeding often increased at low light conditions. Prey capture was also observed in darkness (Volkova, 1973), which suggests the use of sensory organs other than vision, most likely the lateral organ.

Pike are normally regarded as visual predators and should therefore be expected to have the highest foraging success during daytime and clear water conditions. Craig & Babaluk (1989) supports this by showing positive correlation between pike condition and water transparency. However, other studies support the view that pike forage most successful during lowlight conditions. Dobler (1977) found that small pike (23-25 cm) foraged most prey in light intensity under 1 lux. At these light conditions schools of preyfish started to disperse and the author suggests that pike are “optically superior to its prey at low illumination” and therefore have the highest forage success at these light intensities. Skov et al. (2002) found equal foraging success in 0+ pike (9-17 cm) in relation to high and low water transparency, which also suggest that forage capabilities are not lowered in low-light conditions. Indirect support for this view also comes from studies of activity in pike. Diana (1980) found the highest activity at low light conditions around sunset and sunrise, which could indicate higher feeding activity. Overall, light conditions may not influence foraging behaviour of pike to a great extent. With a combination of good sight and lateral organ, pike are able to hunt in both bright and dusk conditions and preyfish behaviour rather than illumination could be the deciding factor.

On the contrary to other studies, the present study was done in natural conditions, which made it impossible to note time of capture of food items in the stomach of pikes. With this in mind, is it important to consider the aspects of digestion in 0+ pike when interpreting the results. First, prey species are digested at different speeds, e.g. hard-bodied prey is digested slower than soft-bodied prey (Bromley, 1994). Second, digestion rate of individual food items are influenced by fullness of stomach. A full stomach hindered equal digestion rates of food items, and digestion of food items was limited to the part of the stomach closest to the intestine (personal observation). Consequently food items near the oesophagus could lie undigested for a long period and indicate recent feeding.

Considering the short time interval between sunset and night samplings, one could argue that foraging at night was minimal in 0+ pike and that food items found in night-sampled pike were undigested “leftovers” from foraging activity at sunset. The facts that numbers of food items are always lower at night than at sunset support this hypothesis.

The aspect of digestion rates could also help explain the observed change in feeding pattern. As pike grew bigger, they consumed fewer and most likely larger food items. Larger food items have smaller surface-to-volume ratio, which can decrease digestion rates (Swenson & Smith, 1973). As a result, food items are identifiable in the stomach for a longer time, which even out numerical differences over time.

Concluding comments

The present study cannot support the basic idea of pike stocking. Very few fish was found in stomachs of pike. The reason for this lack of piscivory was not studied, but a general lack of 0+ planktivores probably had great influence.

The indication that piscivory was reduced in stocked pike compared to native pike could have great implications for the way pike stocking are carried out and should be explored further. If similar results are produced in future studies focusing on this issue, better results of pikestocking could be achieved by improving spawning and nursery habitats for the native pike.

The fact that pike stomachs always contained less food at night than at sunset indicated no or very reduced feeding activity in the dark. In line with this only a few fresh food items was found in the stomachs of pike sampled at night, and it is most likely that foraging activity in darkness is very low in small pike.

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The effect of meal type, temperature and body size on gastric evacuation in northern pike fry (*Esox lucius* L.) less than 60 mm in length

Abstract
Evacuation rates of fish larvae, *Gammarus pulex* and zooplankton were estimated at 10, 14 and 18 ^{o}C in 24-29 and 38-53 mm pike (*Esox lucius*). After a starvation period, pike were allowed to eat for a maximum of 60 minutes. Voluntary intake of fish larvae was 2-3 times higher than other prey species. Zooplankton and small fish larvae were evacuated in curvilinear fashion while the evacuation pattern of larger fish larvae and *G. pulex* were less curvilinear and close to linear. Absolute evacuation rates were correlated to pike size. Relative rates were slightly higher in small pike fry. No consistent effect of temperature was found.
The maximum intake of bream larvae in 24-29 mm pike was 32. Based on evacuation rates, it was estimated that 24-29 mm pike potentially could evacuate 20-50 newly hatched planktivore fry on a daily basis.

Introduction

Feeding rate in piscivores is influenced by handling time, which is a combination of manipulation time and gastric evacuation time (Bromley, 1994). Manipulation time is the time elapsing from strike to total swallowing and gastric evacuation time is the time elapsing from swallowing to total evacuation. Manipulation time has been shown to depend on prey size and large prey can take several minutes to manipulate (Nilsson & Brönmark, 1999). However, gastric evacuation time makes up the largest part of handling time. Gastric evacuation time is reliant on gastric evacuation rate, which in turn is primarily influenced by temperature, prey type, meal size and predator size (Bromley, 1994; Andersen, 1999). The effects of these parameters on gastric evacuation rate have been studied in many different fish species, e.g. whiting (*Merlangius merlangus*) (Andersen, 1999), turbot (*Scopthalmus maximus* L.) (Bromley, 1987), pikeperch (*Stizostedion lucioperca* L.) (Koed, 2001), perch (*Perca fluviatilis*) (Persson, 1979, 1981) and burbot (*Lota lota*) (Pääkönen & Marjomaki, 1997).
It is generally accepted that metabolism of ectotherms is partly influenced by temperature. Many studies, including the above-mentioned, have in line with this shown a positive relationship between temperature and gastric evacuation rate, often in an exponential form, i.e. $R = ae^{bT}$ (Dos Santos & Jobling, 1988; Bromley, 1994).
Prey type can effect evacuation in two ways. First, the exoskeleton of hard-bodied prey species can shield against digestive enzymes and prolong digestion time. Several studies have found soft-bodied prey to be evacuated faster than hard-bodied prey (e.g. Singh-Renton & Bromley, 1996; Temming & Herrmann, 2003). Second, the energy content of prey influence evacuation rate and high-energy prey are evacuated slower than low-energy prey (Bromley, 1994). This emphasizes the importance of knowing the nutritional value of prey when comparing gastric evacuation rates of prey species or prey types.
Meal size has shown conflicting effects on gastric evacuation rate. Although some studies found a positive effect of increasing meal size on gastric evacuation rate (Bagge, 1977),

studies have also shown both negative (Ruggerone, 1989; Pääkönen et al., 1999) and no effect (Persson 1981; Bromley, 1987; Koed, 2001). The effect of predator size shows similar disagreements. In general, the absolute rate of evacuation is thought to increase with fish size, while the relative rate (g food g fish^{-1} h^{-1}) decreases with body size (Flowerdew & Grove, 1979). However, Persson (1979) studied evacuation in 2 sizes of perch (*P. fluviatilis*) and found no effect of predator size on absolute digestion rate. Equal evacuation time of similar relative meals in fish of different size has also been shown (Bromley, 1994).

Northern pike (*E. lucius*) is a top predator in many lakes and streams of the northern hemisphere.

Following hatching and yolk sac resorption, ontogeny of feeding in pike typically follows a sequence of microcrustaceans, insects, macrocrustaceans and fish (Bry, 1996). Piscivorous feeding can occur shortly after hatching. Hunt & Carbine (1951) found 25 % of 21-25 mm pike and 32.3 % of 26-30 mm pike to be cannibals. Similarly, a study of stomach content of pike in a small Danish lake revealed 0+ roach (*Rutilus rutilus*) in pike < 30 mm long (Gramkow, unpublished). Due to the piscivorous feeding habits, 0+ pike have been stocked into lakes in several biomanipulation projects in recent years (e.g. Prejs et al., 1994; Berg et al., 1997; Skov et al., 2003). The aim of these projects has been to decimate yearly recruitment of planktivores such as roach and bream *(Abramis brama).* One way of estimating the effect of pike stocking is to combine data from stomach content and evacuation rates in 0+ pike. However, only evacuation rate of zooplankton at a single temperature has previously been estimated in pike fry < 60 mm (Filleul & Le Louarn, 1998). In the present study, evacuation rates of different combinations of temperature, meal type and pike size are estimated. From these evacuation rates, the potential food intake of pike fry can be estimated. In relation to pike fry stocking, evacuation rates of fish larvae are most relevant and the discussion is focused on this area.

Materials and methods

Experiments were performed in May-June 2002. Pike fry were delivered in two sizes from two different pike hatcheries: small of 22-34 mm and large of 37-58 mm.

After delivery pike were acclimatized for a minimum of 3 days in 2 large indoor holding tanks (2 x 2 x 0,6 m). Holding tanks were connected to a water circulating and temperature controlling system, which made it possible to control temperature during the experimental period. Abundant food (zooplankton) was added 4 times a day to lower cannibalism and pike were kept in darkness when no experiments were going on. The light/dark cycle during the study period was generally 12 hours of light and 12 hours of darkness.

The rate of digestion was studied for 2 or 3 different temperatures, 2 or 3 different prey species and 2 sizes of pike (table 1). Due to delivery problems of large pike in the right size, evacuation rates were not estimated at 10 °C.

Table 1: List of combinations of temperatures, pike sizes, prey species and digestion periods, from which gastric evacuation rates have been estimated. Bream and whitefish were larvae.

Experiments	Pike: 24-29 mm	Pike: 38-53 mm	Digestion periods
Temperature 10°C	Bream & zooplankton	-----	0, 2, 4, 8 & 22 hours
Temperature 14°C	Bream & zooplankton	Whitefish, *G. pulex* & zooplankton	0, 1, 2, 4 & 8 hours
Temperature 18°C	Bream	Whitefish, *G. pulex* & zooplankton	0, 1, 2, 4 & 8 hours

Before each experiment 120 pikes were starved for a period of 15-17 hours. To avoid cannibalism starvation was done individually in small (1 L) ventilated buckets placed in 2 large holding tanks (2 x 2 x 0.6 m). These holding tanks were also connected to the water circulating and temperature controlling system.

The experiments were performed in 3 small aquariums, each with 30 liters of water (water-depth 12 cm). Water was taken from the holding tanks in which pikes were starved. At the start of each experiment 20 pikes were gently moved from the starvation buckets to each of the three aquariums where abundant food was pre-added. Feeding period was 60 minutes, however, if a pike was satiated prior to this time limit, it was gently moved back to a bucket for individual digestion. 4-8 pikes were taken out at a time to avoid too much disturbance and randomly divided into one of five digestion periods. Signs that pike had stopped eating were: facing sides of aquarium, a full/round belly, no movement and no interest in food items close to the pike. After 60 minutes the aquariums were emptied and the rest of the pikes were randomly divided into one of five digestion periods (table 1). For each combination of temperature, prey type and pike size, two identical experiments were made - totaling 120 pike. After the digestion period pikes were preserved in 80% alcohol.

In the laboratory, pikes were dissected. Stomach contents (including food items in the esophagus) were dried at 80 °C for 18 hours and weighed to nearest 1/10 mg. Pikes was excluded from the results if no food was found in either stomach or intestine. No exclusions were made at the longest digestion periods (8 or 22 hours), as it was not possible to distinguish between a pike that had not eaten and a pike that had digested and evacuated all the food.

To lower size variation among the pikes, a size selection based on weight was made (table 2). The range was based on a start weight of x and an end weight of 1,5x. This range combined the needs for sufficient numbers of pike and ensured as identical size ranges as possible. Unfortunately, the growth rate of pike made it impossible to have the same size range at all combinations of temperature and prey type. A total of 4-16 pikes were included at each size/temperature/prey type/digestion period combination.

Zooplankton was collected in Lake Ring (UTM32, 6202350N, 537250E) by towing a Hoop-net after a small boat. The population consisted of both copepoda and cladocera. *G. pulex* was collected in a stream using a small sieve mounted on a stick. Bream (delivered as fertilized eggs) and whitefish-larvae were delivered from a fish hatchery. All food items were kept in aerated aquaria and average length and dry weight was measured (table 3).

Table 2: Selected weight and length range and number of pike in each combination. Weight and length of pike are in mg dry weight and mm total length.

Pike size	Temperature	Food item	Pike weight	Length range	Number of pike
Large	14°C	Whitefish larvae	76.0 – 114.0	46 - 54	48
Large	18°C	Whitefish larvae	76.0 – 114.0	45 - 52	57
Large	14°C	*Gammarus pulex*	39.0 – 58.50	38 - 44	64
Large	18°C	*Gammarus pulex*	76.0 – 114.0	45 - 53	47
Large	14°C	Zooplankton	39.0 – 58.50	38 - 45	57
Large	18°C	Zooplankton	76.0 – 114.0	45 - 51	49
Small	10°C	Bream larvae	7.20 – 10.80	25 - 28	49
Small	14°C	Bream larvae	7.20 – 10.80	24 - 28	50
Small	18°C	Bream larvae	9.10 – 13.50	25 - 29	54
Small	10°C	Zooplankton	7.20 – 10.80	24 - 28	47
Small	14°C	Zooplankton	7.20 – 10.80	24 - 27	58

Statistical analysis

Results are shown as mean dried stomach content plotted against digestion time for each food item and temperature. Furthermore the instantaneous gastric evacuation rate was expressed according to the general model (Bromley, 1994):

$$dS/dt = - g\, S^{a} \qquad (1)$$

where S is the weight of the total stomach content, and t is the time. The model was expanded to include temperature, which is generally described as an exponential function in relation to evacuation rates:

$$dS/dt = - g\, e^{bT}\, S^{a} \qquad (2)$$

T is temperature and g, b and a are parameters to be estimated.

Average stomach content at the five different digestion times at each temperature was used to estimate parameters, i.e. parameters in small pike fed bream larvae was estimated from 15 data points. To overcome problems of increasing variation in residual stomach content, S_t, with increasing meal size, S_0, residual stomach contents are expressed relative to initial meal size – see table 5 (Andersen, 1998, 1999).

The parameters of the model were estimated simultaneously by multiple nonlinear regression (Levenberg-Marquardt algorithm - SPSS 10.0) using the integrated expressions of equation 2:

$$S_t = S_0\,(1 - S_0^{(a-1)}\, g\, e^{bT}\,(1-a)\, t)^{(1/(1-a))}$$

Where S_t is the residual stomach content at time t and S_0 is the average meal size at time 0. The other parameters are listed in equations (1) and (2).

Table 3: Mean size and range of prey used in the study. Whitefish was delivered twice during the study period. First batch (whitefish 1) was used in the 14°C experiment and second batch (whitefish 2) as used in the 18°C experiment. Weights are in dry weight. *tail of zooplankton was not included in length measurements.

Food item	Mean size	Range	Average weight
Zooplankton*	1.30 mm	0.75 - 1.97 mm	---
G. pulex	6.02 mm	3.80 - 7.60 mm	---
Bream	---	6.00 - 8.00 mm	0.11 mg
Whitefish 1	15.5 mm	14.0 - 19.0 mm	1.62 mg
Whitefish 2	22.9 mm	19.0 - 30.0 mm	3.45 mg

Results

There were noticeable differences in evacuation patterns of fish larvae in the two sizes of pike. The estimated shape parameter suggested a highly curvilinear evacuation pattern in small pike (table 4) and this pattern was also seen when plotting residual stomach content against time (figure 1a). In large pike the parameter estimate suggested a less curvilinear pattern close to exponential (table 4). However, zero was included in the 95% confidence intervals (C.I.) and an estimate of zero suggests that evacuation pattern is linear.

Table 4: Estimates and 95 % CL of the shape parameter a, the temperature coefficient b and the rate constant g. The estimates are derived using non-linear regression (Levenberg-Marquardt algorithm, SPSS 10.0) using average relative stomach content of initial meal size.

Pike size	Prey	R^2	a	S.E	95% lower	95% upper	b	S.E	95% lower	95% upper	g	S.E	95% lower	95% upper
Small	Bream	0.968	2.036	0.326	1.326	2.745	-0.059	0.033	-0.131	0.013	1.564	0.926	-0.454	3.582
Large	Whitefish	0.721	0.892	1.698	-3.123	4.907	0.237	0.160	-0.142	0.616	0.002	0.004	-0.008	0.012
Small	Zooplankton	0.826	1.540	0.829	-0.419	3.499	0.219	0.132	-0.094	0.532	0.027	0.045	-0.078	1.133
Large	Zooplankton	0.982	1.404	0.248	0.818	1.991	0.190	0.034	0.109	0.271	0.015	0.008	-0.004	0.033
Large	G. pulex	0.860	-1.139	1.084	-3.701	1.423	0.070	0.076	-0.109	0.249	0.017	0.017	-0.023	0.056

In line with this, plots did not indicate a curvilinear pattern in large pike. At 18°C the pattern was close to linear and at 14°C an initial lag phase followed by evacuation was indicated (figure 1b). Overall, relative evacuation was slower in large pike and as a consequence, a large part of the meal was not evacuated at the end of the experiments (figure 1b, table 5).

For both small and large pike fed zooplankton, the estimate of the shape parameter a also indicated a highly curvilinear evacuation pattern (table 4). This was also indicated in the plots, all though less clear in small pike (figure 1a).

The estimate of a in large pike fed *G. pulex* was negative, indicating that gastric evacuation rate increases as the level of stomach content declines (table 4). However, zero was included in the 95% C.I., indicating the possibility of a linear evacuation pattern. Plots also indicated an evacuation pattern close to linear (figure 1b).

There was no consistent effect of temperature. The estimates of the temperature coefficient, b, was mostly positive but the 95% C.I. included zero in most cases (table 4). This indicates that temperature did not have an effect on gastric evacuation rate. Only in large pike fed zooplankton did results indicate an effect of temperature on gastric evacuation rate. Plots did also not indicate an effect of temperature (figure 1a & 1b).

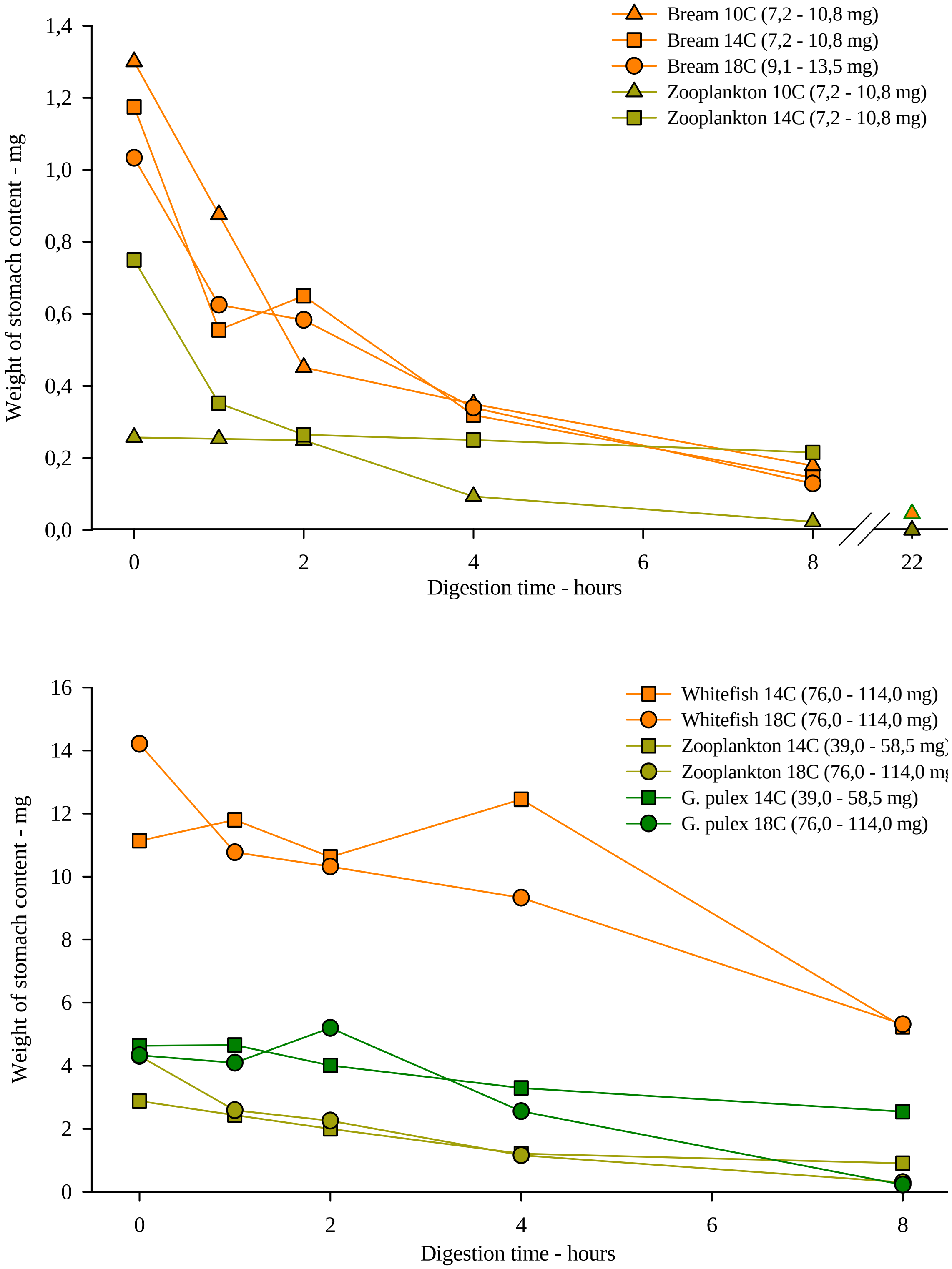

Figure 1: Relationship between average residual stomach contents (dry weight) and time (hours) in small pike (1a - top) and large pike (1b - bottom). Curves for each combination of temperature and prey item are shown.
All weights are measured in mg dry weight. The numbers in parentheses refer to the weight of pike.

Absolute evacuations rates were positively correlated with predator size. In relative terms the differences between small and large pike were small, but higher evacuation rates were seen in small pike (table 5). Absolute evacuations rates of fish larvae were higher than of zooplankton and *G. pulex*, but in relative terms a clear pattern was not seen (table 5). Relative evacuation rates of the different prey species were, however, difficult to compare because initial meal sizes varied greatly.

Table 5: Residual stomach contents in absolute (mg dry weight) and relative terms and evacuation (mg h^{-1}) and relative evacuation rates (mg mg fish^{-1} h^{-1}) at the evacuation times. *Negative evacuation – result not shown.

Stomach content	**Small pike Bream**			**Small pike Zooplankton**		**Large pike Whitefish**		**Large pike *G. pulex***		**Large pike Zooplankton**	
Hours	10^{o}C	14^{o}C	18^{o}C	10^{o}C	14^{o}C	14^{o}C	18^{o}C	14^{o}C	18^{o}C	14^{o}C	18^{o}C
0	1.300	1.175	1.033	0.257	0.750	11.138	14.211	4.633	4.330	2.878	4.310
1		0.556	0.625		0.352	11.800	10.769	4.653	4.091	2.433	2.588
2	0.451	0.650	0.583	0.249	0.265	10.622	10.318	4.008	5.200	2.000	2.260
4	0.350	0.319	0.340	0.093	0.250	12.450	9.327	3.293	2.556	1.210	1.162
8	0.179	0.145	0.129	0.023	0.215	5.236	5.315	2.543	0.225	0.909	0.300
22	0.045			0.000							

Stomach content relative to meal size	**Small pike Bream**			**Small pike Zooplankton**		**Large pike Whitefish**		**Large pike *G. pulex***		**Large pike Zooplankton**	
Hours	10^{o}C	14^{o}C	18^{o}C	10^{o}C	14^{o}C	14^{o}C	18^{o}C	14^{o}C	18^{o}C	14^{o}C	18^{o}C
0	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
1		0.473	0.605		0.469	1.059	0.758	1.004	0.945	0.846	0.600
2	0.347	0.553	0.565	0.969	0.353	0.954	0.726	0.865	1.201	0.695	0.524
4	0.269	0.272	0.329	0.363	0.333	1.118	0.656	0.711	0.590	0.420	0.269
8	0.138	0.124	0.125	0.089	0.287	0.470	0.374	0.549	0.052	0.316	0.070
22	0.035			0.000							

Average evacuation rate mg/hour	**Small pike Bream**			**Small pike Zooplankton**		**Large pike Whitefish**		**Large pike *G. pulex***		**Large pike Zooplankton**	
Hours	10^{o}C	14^{o}C	18^{o}C	10^{o}C	14^{o}C	14^{o}C	18^{o}C	14^{o}C	18^{o}C	14^{o}C	18^{o}C
0 - 1		0.619	0.408		0.398	---*	3.442	---*	0.239	0.444	1.723
0 - 2	0.424	0.263	0.225	0.004	0.243	0.258	1.947	0.313	---*	0.439	1.025
0 – 4	0.238	0.214	0.173	0.041	0.125	---*	1.221	0.335	0.443	0.417	0.787
0 – 8	0.140	0.129	0.113	0.029	0.067	0.738	1.112	0.261	0.513	0.246	0.501
0 - 22	0.057			0.012							

Relative average evacuation rate mg/mg fish/hour	**Small pike Bream**			**Small pike Zooplankton**		**Large pike Whitefish**		**Large pike *G. pulex***		**Large pike Zooplankton**	
Hours	10^{o}C	14^{o}C	18^{o}C	10^{o}C	14^{o}C	14^{o}C	18^{o}C	14^{o}C	18^{o}C	14^{o}C	18^{o}C
0 - 1		0.067	0.038		0.043	---*	0.037	---*	0.003	0.009	0.020
0 - 2	0.047	0.027	0.019	0.001	0.028	0.003	0.020	0.007	---*	0.009	0.012
0 – 4	0.031	0.023	0.016	0.005	0.014	---*	0.013	0.007	0.005	0.009	0.009
0 – 8	0.016	0.014	0.010	0.004	0.008	0.008	0.012	0.006	0.006	0.005	0.006
0 - 22	0.006			0.001							

Results demonstrated that pike have higher satiation levels when feeding on fish larvae than on *G. pulex* or zooplankton. The single-fish maximum intake relative to fish weight was similarly highest for fish larvae, followed by *G. pulex* (in large pike) and zooplankton. The maximum value was 0.22 g fish g pike^{-1} and 0.27 g fish g pike^{-1}, for small and large pike, respectively. In general, the average intake was around half the maximum value (figure 2). In actual numbers, small pike had a maximum intake of 32 bream larva. The average intake was in the range of 10-15 larva pr. pike (figure 2).

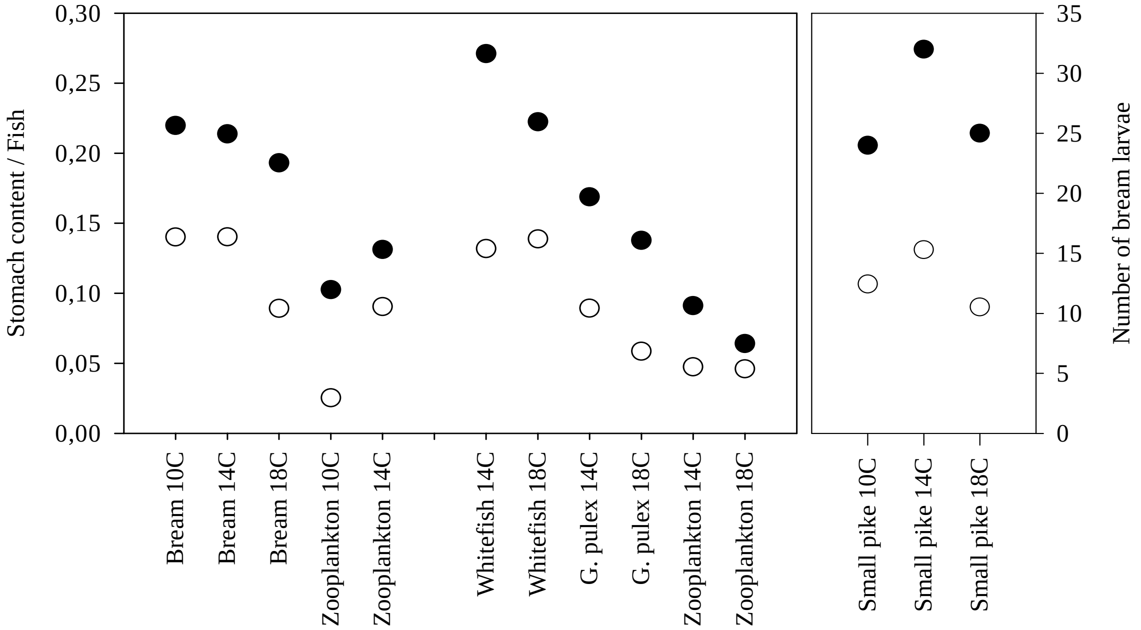

Figure 2: Left: maximum relative food intake and the average food intake at time 0 for all the different combinations of temperature, prey species and pike size. The first five (from left) are small pike and the last six are large pike. Right: maximum and average intake of bream larvae in small pike at 3 temperatures.
Closed circles indicate maximum values and open circles indicate average values.

A weight-length relationship was described from the measurements of dry weight (W) and length (L) of pike (figure 3). The data was best described by a power function of the form W = a L^{β}, where a = 0.000067 ± 0,000003 and β = 3.6345 ± 0.0112 (r^2 = 0.992, n = 883) (figure 3). The relationship between dry weight (DW) and wet weight (WW) was best described by a linear function: DW = 0.2046 WW (r^2 = 0.977, n = 883).

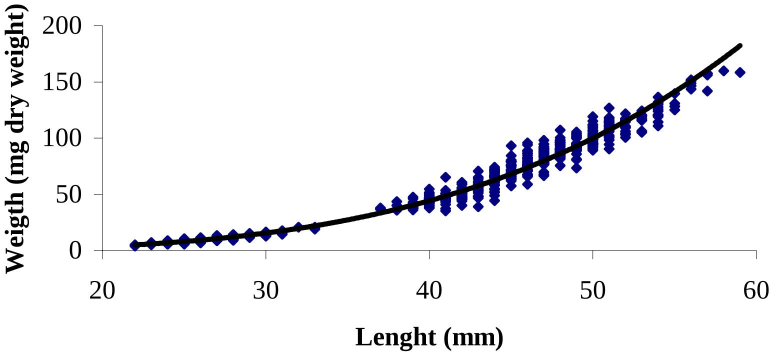

Figure 3: Relationship between length and dry weight of pike.

Discussion

Many recent studies of evacuation rates in fish have either tried to fit evacuation rates to fixed models, i.e. the linear, the square root or the exponential model (Elliott, 1991; Pääkkönen & Marjomäki, 1997; Hayward & Weiland, 1998; Nilsson & Brönmark, 2000) or estimated parameters in the general model described in *Materials & Methods* by non-linear regression (Andersen, 1999; Koed, 2001; Temming & Herrmann, 2003). Overall, the shape parameter a in these studies was estimated in the range of 0.3–1.0, which indicate a curvilinear pattern. However, these studies differ in both predator species and size, and prey size, as they were performed with larger fish and few, but large prey items, and are therefore not directly comparable to results from the present study.

Several factors can influence evacuation and result in the apparent change in evacuation rate from small to large pike fry. Results of the present study are in line with Flowerdew & Grove (1979) who suggested that relative evacuation rate ($g\ g^{-1}\ h^{-1}$) decreases with increasing fish size. This implies that small fish generally have higher evacuation rates of similar relative meal sizes than larger fish as seen in this study.

Fish larvae

Large pike were fed relatively larger and fewer fish larvae than small pike. Lesser surface-to-volume ratio of larger prey can decrease evacuation rate (Swenson & Smith, 1973), but the effect of prey size has shown conflicting results, as some studies found no effect of prey size (Singh-Renton & Bromley, 1996; Nilsson & Brönmark, 2000). The results from these studies were, however, based on the effect of a few prey fish and not a high number of larvae like the present study. It is likely that greatly increased surface area of small fish larvae positively effects evacuation rate. Differences in energy content could also have influenced results. Jobling (1980, 1987) demonstrated that evacuation rates were slower for high-energy prey than low-energy prey. The energy content of bream and whitefish larvae was not known and the effect on evacuation rate was therefore not possible to estimate. Overall, the combination of different prey size/species and larger predator size is a likely cause for the slower evacuation in large pike.

Different prey species could also explain the change in evacuation pattern. Results are in line with Jobling (1987), who proposed that large prey such as fish tends to be evacuated in a linear fashion. The whitefish larvae was not large prey in this context, but larger than the bream larvae and this may have resulted in more linear evacuation pattern.

G. pulex

The negative shape estimate in large pike fed *G. pulex* was mainly caused by elevated stomach content at 2 hours at 18 ^{o}C. If these data were excluded from the estimation calculation, the estimate was –0.283 and the 95% c.i. was similarly smaller, but still included zero. Therefore a linear or slightly increasing evacuation rate seems most likely. In an evacuation study of hard-bodied prey in cod (*Gadus morhua*), Bromley (1991) also found a linear evacuation pattern to give the best fit.

When evacuating small prey, there is normally a positive correlation between stomach content and evacuation rate (concave-shaped evacuation curve). This was not seen in evacuation of *G. pulex*. The evacuation pattern of *G. pulex* is most likely caused by the exoskeleton's shielding effect against digestion juices and generally slow breakdown of the exoskeleton. The shielding effect of exoskeleton was clear in a study of simulated digestion of insects and insect larvae. The study demonstrated that puncturing the chitin exoskeleton of insects increased the breakdown compared to non-punctured insects (Prinz et al., 2003).

Zooplankton

Zooplankton was generally evacuated in a curvilinear fashion in both large and small pike. The estimates of a was close to 1, which indicate an exponential evacuation pattern. The results are in line with Bromley (1987), who suggested that evacuation of small and easily digested food items was best described by an exponential function.

Filleul & Le Louarn (1998) studied the evacuation rate of 29-35 mm northern pike fed a meal consisting of 1.455 mg of zooplankton at 15°C. In relative terms the meal size was close to, but smaller than in the present study. The evacuation rate was high - on average 80% of the meal was digested within 5 hours. This agrees well with results from the present study. Using the parameter estimates for zooplankton, residual stomach content after 5 hours at 15 °C would be 13.5% and 35.3% for 24-29 mm and 38-54 mm pike, respectively.

Effect of temperature

The present data did not indicate a general effect of temperature. In small pike fed bream larvae, the initial meal size was highest at 10 °C and lowest at 18 °C. Moreover, pike were bigger at 18 °C and absolute evacuation rates normally increase with increasing size (Flowerdew & Grove, 1979).

Despite this, residual stomach content after 8 hours was almost the same (0.124-0.138) at the three temperatures, which indicates a negative effect of increasing temperature. In contrast, large pike fed whitefish larvae or zooplankton, initial meal size was highest at 18 °C and residual stomach content after 8 hours lowest, which indicate a positive effect of increasing temperature. However, in the zooplankton experiment, pike were bigger at 18 °C than at 14 °C (table 2) and larger size increase evacuation rate, so temperature may not be responsible for the increase in evacuation rate.

Overall, the variation in initial meal sizes and pike size made it difficult to interpret the effect of temperature and no conclusions could be made. This is in contrast to other studies of temperature effect on gastric evacuation that showed a clear positive effect of increasing temperature. (Persson, 1979, 1981; Bromley, 1994; Pääkkönen & Marjomäki, 1997; Andersen 1999; Koed 2001).

It seems unlikely that temperature does not influence evacuation rate in small pike, when the similarity in results of other studies is considered (e.g. Persson, 1979, 1981; Andersen, 1999; Koed, 2001). However, these authors studied larger fish of different species from pike and it is possible that temperature influence gastric evacuation rate of small pike to a lesser extent. The metabolism of small pike could be less sensitive to temperature and small temperature effects would easily be concealed by variation in food intake. Short acclimatization periods to the different temperatures might also have influenced the results. Due to the aggressive cannibalistic behaviour and the high growth rate of small pike, an acclimatization period of several days or weeks was not possible. The short period of 1-3 days used could have been too short to influence the metabolism of the pikes.

Satiation levels

Appetite (voluntary intake) relative to fish weight was clearly highest when fish larvae were used as prey. Observations during the experiments also showed that pike filled their stomach to a higher degree when fish larvae were used as prey. The pike had great difficulties in handling *G. pulex* and mainly small individuals were eaten. This could account for the large difference in satiation levels of whitefish larvae and *G. pulex*.

The smaller pike was expected to have higher relative satiation levels than the larger pike as seen is other studies (Brett, 1971; Elliott, 1975; Rösch, 1986). Relative satiation levels of fish larvae were, however, in the same range in small and large pike. This indicates initially that large pike filled their stomachs to a higher degree but this result could also be caused by differences in dry-weight-to-volume of bream and whitefish larvae.

Dunbrack (1988) studied satiation levels in 0.5-8.0 g Coho salmon *(Oncorhynchus kisutch).* The salmons were fed live Tubifix at 12°C, which resulted in a relationship between meal size (dry weight - mg) and fish weight (wet weight - g) in the form:

$$\log(\text{meal size}) = 1{,}03 + 0{,}88 \times \log(\text{fish weight})$$

Using this formula to calculate satiation levels in coho salmon at similar weight as the large pike (0.189-0.677 g) and converting the results into dry weights, the corresponding satiation levels were 0.064-0.055 g g fish^{-1}.

This is close to the satiation levels found in large pike when *G. pulex* and zooplankton were used as prey, but less than when whitefish larvae were used. Satiation levels of 10% dry body weight have been shown in 1g Whitefish (*Coregenus laveratus* L.) fed on *Daphnia* (Rösch, 1986) and 11% dry body weight in 5 g Sockeye salmon (*Oncorhynchus nerka*) fed on pellets (Brett, 1971). The average satiation level of fish larvae found in pike fry were higher than in these earlier studies, but when important factors like predator size and prey items are not comparable, these results are not directly comparable.

Impact of pike on planktivore fry

The main purpose of pike stocking is to reduce the biomass of newly recruited planktivores. To estimate the actual effect of pike stocking, data on daily consumption of pike and number of pike and planktivores are needed. Daily consumption was not part of the present study, but a rough estimation of the potential effect of pikestocking can be made from the estimated evacuation rates of fish larvae. Small pike had average satiation levels of 1.0-1.3 mg fish larvae. Results indicate that around 70% (0.7-0.9 mg) of a meal consisting of bream larvae are evacuated in 4 hours. Within this 4-hour period, the average evacuation rate was 0.17-0.24 mg/hour (table 5).

Under assumption that fish larvae are readily available and that an average evacuation rate of 0.2 mg/hour is a maintainable daily rate in small pike, and assuming a feeding period of 16 hours, approximately 3.2 mg food could be evacuated in a day. This equals approximately 32 % body weight or 29 bream larvae in a day. In large pike relative evacuation rates of whitefish larvae was much slower, but absolute evacuation much higher. A similar estimation (based on 8-hour average evacuation rate) gave an approximate daily evacuation of 14.4 mg, which was equal to 15 % body weight.

These are very simplified estimations and many factors can influence the result. The average daily evacuation rate could be higher, especially in small pike where it was highly dependent on satiation level. In contrast, starvation prior to the study might have elevated consumption in the pike, and resulted in evacuation rates that were higher than under normal feeding regimes. The feeding period under natural conditions is also unknown. Considering daylight hours at stocking time, 16 hours seems a valid estimate. However, evacuation continues after intake has stopped and pike might also continue to feed at night, and both these factors will increase the estimate of daily consumption.

Overall, a potential daily intake of 20-50 bream larvae in 24-29 mm pike seems likely, if bream larvae are readily available.

Concluding comments

There is no reason to believe that the potential evacuation rate of fish larvae or the potential appetite for fish larvae are limiting factors in relation to the lack of success in many pike stocking experiments. Satiation levels were 2-3 times higher when fish was used for prey and evacuation rates of fish larvae were also higher than for other prey items. Different factors influencing availability of fish larvae to predators appear more likely for the low success rate. A temperature range of 10-18 ^{o}C seemed to have little or no affect on gastric evacuation rate in pike less than 55 mm. This result was not expected and was in contrast to other studies. However, in aforementioned experiments larger fish were used, and the high metabolism of small fish might be less influenced by temperature. Future exploration of this area will hopefully increase understanding of how temperature affect metabolism in small fish.

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Opsamling og perspektivering

I dette speciale har jeg undersøgt fødeindtag hos naturlige og udsatte 0+ gedder og fordøjelseshastigheder og fødevalg hos to forskellige størrelsesklasser af 0+ gedder. Der er blevet udført 3 separate forsøg, som gav følgende resultater:

- Der var kun få signifikante forskelle i fødeindtaget hos udsatte og naturlige geddeyngel. Disse forskelle skyldes sandsynligvis forskelle i geddestørrelse på prøvetagningstidspunkter eller prægning til forskellige fødeemner pga. forskellige opvækstvilkår.
- Gedderne spiste meget få fisk, men der var indikation på, at naturlige gedder spiste flere fisk end de udsatte gedder.
- Det var døgnvariation i fødeindtaget. Gedderne spiste mindst om natten i tiden efter udsætning, men denne døgnvariation blev mindre efterhånden som gedderne voksede. Der var ikke forskel på døgnvariation i fødeindtag hos udsatte og naturlige gedder.
- Gedderne spiser fisk, hvis de er tilgængelige og hvis tilgængeligheden er stor, foretrækker gedder på 40-50 mm fisk frem for zooplankton eller *Gammarus pulex*.
- Fordøjelsesraterne var meget høje hos små gedder. Resultaterne tydede på at det kunne skyldes stor overflade-volumen ratio hos de små byttedyr.
- 0+ gedder var i stand til at indtage et måltid på mere end 25% af deres egen vægt, når fiskelarver blev brugt som føde. Det svarer til mere end 30 nyklækkede brasen-larver hos gedder på 24-29 mm.
- Der var tilsyneladende ingen effekt af temperatur på fordøjelseshastigheden. Der kan dog have været en mindre effekt af temperatur, som ikke kunne påvises pga. stor variation i individuel fødeindtag. Det manglende effekt at kan skyldes at den generel højere metabolisme hos små fisk er mindre påvirket af temperatur.

Et af formålene med dette speciale var at undersøge effekten af geddeudsætning på biomassen af planktivore fisk i Vallum sø. Samlet set blev der fundet 40 fisk i de 497 gedder som blev indsamlet. 2 af de spiste fisk var gedder, så reelt handler det om 38 planktivore fiskeyngel. Ud af de 497 gedder var kun 19 piscivore (< 4%), og det er sandsynligvis for lidt til at geddeudsætninger kan have en effekt. Resultaterne fra observationsforsøget tyder på at gedderne gerne tager fiskeyngel, så manglende tilgængelighed af planktivore fiskeyngel må være skyld i den lave piscivori. Der blev da også observeret meget få fiskeyngel i løbet af prøvetagningsperioden. Samtidig viste en fiskeundersøgelse foretaget i sensommeren 2003 også meget få 0+ skaller. Til gengæld var der mange 1+ skaller. Det kunne tyde på at skallernes gydning måske var slået fejl i 2003. Under alle omstændigheder var der få fiskeyngel imens undersøgelsen blev foretaget, hvilket selvfølgelig er en uheldig

kombination. Det er derfor ikke muligt at konkludere om gedderne kunne have haft en effekt, hvis det havde været et ”normalt” år mht. til fiskeyngel.
Et af de interessante resultater var den mulige forskel i piscivori mellem udsatte og naturlige gedder. En lignende undersøgelse i Udbyover sø har vist samme, men heller ikke signifikante resultat, og det er et område der bør undersøges nærmere. Hvis naturlige gedder er mere piscivore, kan det give bedre resultater at bruge pengene fra udsætninger - helt eller delvist - til at forbedre gyde- og opvækstområder for søernes naturlige geddepopulation. En anden mulighed er at ændre opvækstbetingelser hos geddeopdrætterne, så de i større grad ligner naturlige forhold, og gedderne derved er bedre ”forberedt” til fouragering i naturlige omgivelser.
En undersøgelse af piscivori hos naturlige og udsatte gedder kunne foretages med samme metode som blev brugt i dette speciale. Dog vil det være fornuftigt at sørge for at størrelsen og antallet af udsatte gedder matcher de naturlige. Dette kan være svært og det ville nok være lettere at indfange naturlige fisk og sammenligne piscivori under kontrollerede forhold.

Et andet formål var at undersøge om den normale prøvetagningsmetode, som foregår om dagen, giver et reelt billede af geddeynglens fødeindtag. Her må konklusionen være at det afhænger af hvor detaljeret en beskrivelse man ønsker. Der var ingen fødegrupper, der var helt fraværende på visse tidspunkter af døgnet, men der var forskelle i fordelingen. Specielt hos de mindste gedder var der tydelig døgnvariation i zooplankton, som hovedsageligt var repræsenteret i de lyse timer. Generelt havde gedderne også størst maveindhold i de lyse timer, og man risikerer derfor at overestimere fødeindtaget, hvis der ikke tages hensyn til dette ved beregninger af fødeindtag. Her skal man samtidig være opmærksom på, at disse resultater ikke nødvendigvis gælder for andre søer. Ved en fødeundersøgelse bør man derfor inkludere natlige prøvetagninger, så man får et billede af eventuelle døgnvariationer i fødeindtag.

Metoden der blev brugt til at bestemme fordøjelsesrater viste sig desværre at give stor individuel variation i fødeindtag. Det gav store konfidensintervaller på de estimerede fordøjelsesrater, som derfor gjorde det svært at give præcise beskrivelser at fordøjelsesmønstret og – rater. Det tyder dog på, at specielt gedder på 24-29 mm kan have meget høje fordøjelsesrater, især hvis tilgængeligheden af fiskeyngel er stor. Ved forsøg med fiskeyngel fordøjede gedderne omkring 70 % af maveindholdet, som i gennemsnit bestod af 12-15 fiskelarver, på 4 timer. Potentialet for at geddeudsætninger kan have en effekt på biomassen af fiskeyngel, er derfor helt klart til tilstede. Gedder på 38-54 mm fordøjer tilsvarende relative fødemængder noget langsommere. Det illustrerer vigtigheden af, at gedderne dels udsættes på tidspunkter der falder sammen med klækningen af planktivore fisk,

og dels bliver piscivore så tidlig som muligt. Nyklækket yngel er ikke særligt mobilt og samtidig så småt, at gedderne kan konsumere et stort antal om dagen.
Det ville sandsynligvis have været muligt at opnå mere præcise resultater med en metode, hvor hver enkelt fisk blev fodret med en bestemt mængde føde. Derved ville udgangspunktet være det samme hos alle fisk, hvilket bl.a. ville fjerne muligheden for stigende maveindhold med tid, som blev observeret. Samtidig ville ens udgangsvægte have givet bedre mulighed for at sammenligne fordøjelsesrater for de forskellige typer af føde.
Grunden til at sådan en metode ikke blev valgt i første omgang, var det begrænsede antal fisk, som kunne indgå indenfor det samme tidsforbrug. Samtidig var det forventet, at gedder der blev sultet i tiden op til forsøget, ville spise sig mætte.

Det var overraskende at temperatur ikke havde en effekt på fordøjelseshastighed. Dette resultat står i modsætning til mange andre forsøg og kan ikke umiddelbart forklares. Det er muligt, at korte akklimatiseringsperioder eller for små forskelle i temperatur har påvirket resultaterne. Lange akklimatiseringsperioder var ikke mulige pga. høje vækstrater og kannibalisme hos gedderne. De voksede over en millimeter i gennemsnit om dagen, så hvis der skulle ventes 1-2 uger mellem hvert forsøg (11 i alt) ville der bliver alt for stor forskel i størrelsen. Samtidig ville kannibalisme betyde, at der efter et par måneder ikke ville være flere fisk tilbage. På trods af rigeligt føde (zooplankton), var det under halvdelen af de leverede gedder, der nåede at indgå i forsøgene. Resten blev enten kanniballister eller udsat for kannibalisme. Der er også muligt at metabolismen i små gedder er mindre påvirket af temperatur end hos større fisk. Det er et aspekt af fødebiologi hos gedder, der bør undersøges nærmere, f.eks. ved at gentage forsøget, men med fokus på et enkelt fødeemne (fiskelarver) og så i stedet bruge flere ressourcer på at opnå ens størrelser på gedder og måltider.