Bottom-up and top-down regulation of heterogeneous lake food webs

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Abstract

Food webs are networks of organisms linked by trophic interactions that regulate the responses of ecosystems to environmental change. Such regulation is a result of the effects of resources on the abundance of their consumers (i.e. bottom-up effects) and/or the influence of consumers on the abundance of their resources (i.e. top-down effects). Lake food webs comprise pelagic and benthic production pathways and are largely affected by fluxes of resources from/to adjacent terrestrial ecosystems. These pathways are often coupled by mobile generalist consumers, potentially leading to indirect interactions among prey that arise when sharing a predator. In contrast, consumers can also undergo resource specialization that restricts their ability to couple resources at a given time.

In this thesis, I observed that top-down control of predators on benthic and pelagic prey at increasing productivity was highly dependent on apparent mutualism that was driven by switching behaviour of generalist fish. That, in addition to bottom-up responses of benthic pathways at increasing productivity, had important consequences for the fluxes of energy and high quality polyunsaturated fatty acids (PUFAs) to terrestrial systems via insect emergence. I also found that PUFAs were highly regulated over the ontogeny of Eurasian perch (Perca fluviatilis). Mismatches with PUFA composition in prey may in turn affect resource specialization and the timing of ontogenetic diet shifts, altering the role of perch in the food web. Finally, browning, which is a phenomenon affecting many temperate and boreal lakes, did not affect bottom-up and top-down control in open-water lake food webs. Instead, browning affected prey selectivity, probably changing the pathways of energy transfer within the open-water food web. Overall, this thesis demonstrates that predictions of food web responses in lake ecosystems and their exports to adjacent terrestrial systems depend on the coupling of different pathways and subsequent indirect interactions among prey through shared predation. This could not be explained by classic food chain theory, but rather by a framework including resource coupling and resource specialization over the ontogeny of consumers. These observations must not be overlooked when constructing a comprehensive model of food webs across time and space.

Keywords: food webs, resource coupling, ontogenetic diet shifts, resource specialization, bottom-up, top-down, browning, eutrophication, lake, mesocosms, fatty acids, apparent competition

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“Eventually, all things merge into one, and a river runs through it…
… I am haunted by waters”

— Norman Maclean, \textit{A River Runs Through it and Other Stories}
List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.


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In addition to the papers included in this thesis, the author has contributed to the following papers during the PhD studies:

Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Definition</th>
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<tbody>
<tr>
<td>C; N; P</td>
<td>Carbon; Nitrogen; Phosphorus</td>
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<tr>
<td>Fatty acid formula (A:Bn-C)</td>
<td>A, number of carbons; B, number of double bonds; C, position of the first double bond from methyl group</td>
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<tr>
<td>PUFA</td>
<td>Polyunsaturated fatty acid</td>
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<tr>
<td>MUFA</td>
<td>Monounsaturated fatty acid</td>
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<td>SAFA</td>
<td>Saturated fatty acid</td>
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<td>ALA</td>
<td>alpha-Linolenic acid; 18:3n-3</td>
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<td>SDA</td>
<td>Stearidonic acid; 18:4n-3</td>
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<td>EPA</td>
<td>Eicosapentaenoic acid; 20:5n-3</td>
</tr>
<tr>
<td>ARA</td>
<td>Arachidonic acid; 20:4:n-6</td>
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<tr>
<td>DPA</td>
<td>Docosapentaenoic acid; 22:5n-3</td>
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<tr>
<td>DHA</td>
<td>Docosahexaenoic acid; 22:6n-3</td>
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<tr>
<td>HUFAs</td>
<td>Highly unsaturated fatty acids (DHA+EPA+ARA)</td>
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<tr>
<td>HSS</td>
<td>Hairston-Smith-Slobodkin hypothesis</td>
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<tr>
<td>EEH</td>
<td>Ecosystem exploitation hypothesis</td>
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<tr>
<td>PAR</td>
<td>Photosynthetic active radiation</td>
</tr>
<tr>
<td>tDOC</td>
<td>Terrestrial dissolved organic carbon</td>
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<tr>
<td>ANOVA</td>
<td>Analysis of variance</td>
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<tr>
<td>ANCOVA</td>
<td>Analysis of covariance</td>
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<tr>
<td>PERMANOVA</td>
<td>Permutational multivariate ANOVA</td>
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<td>DistLM</td>
<td>Distance-based linear model</td>
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<tr>
<td>SIMPER</td>
<td>Similarity percentages routine</td>
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<tr>
<td>e.g.</td>
<td>Latin “exempli gratia”, “for example”</td>
</tr>
<tr>
<td>i.e.</td>
<td>Latin “id est”, “in other words”</td>
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<tr>
<td>vs.</td>
<td>Latin “versus”, “against”</td>
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<tr>
<td>et al.</td>
<td>Latin “et alia”, “and others”</td>
</tr>
<tr>
<td>de novo</td>
<td>Latin, “from the beginning”</td>
</tr>
<tr>
<td>ind.</td>
<td>number of individuals</td>
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Introduction

Many organisms need to feed on other organisms to fulfill their biological functions of survival, growth and reproduction. As a consequence, consumers and their food resources become linked by trophic interactions (Moore & de Ruiter 2012), which, when all connected, build up a network of organisms called a food web (Elton 1927; Paine 1980; Moore & de Ruiter 2012). By connecting the ecological features of many individuals, a food web can be viewed as a dynamic and complex structure that regulate multiple aspects of nature, such as the flows of energy, materials and nutrients (e.g. Lindeman 1942; Berglund et al. 2007; Moore & de Ruiter 2012), the stability of communities (May 1972; McCann 2012) or their regulation of ecosystem responses to changes in the environment (e.g. Brooks & Dodson 1965; Carpenter et al. 1985). Therefore, the study of food webs becomes crucial to understand, predict, or manage the state of our ecosystems in response to environmental change.

The stepwise nature of trophic interactions helps classify organisms into different trophic levels starting with primary producers, which build up their biomass from inorganic resources, going through various levels of consumers and ending with the top consumers that are not predated by others (Elton 1927; Lindeman 1942). Food webs can be represented in different ways. Connectedness food webs can identify aspects of food web functioning by just focusing on the presence/absence of trophic interactions in multispecies networks (Fig. 1a) (e.g. May 1972; Dunne 2012). The energy flow through food webs is represented in energetic food webs (Fig. 1a), and reveal important aspects such as ecosystem productivity and energy transfer efficiency, which ultimately restrict the maximum number of trophic levels (Lindeman 1942). Finally, food web functioning is addressed in functional food webs (Fig. 1a) by quantifying the effects of organisms on the abundance and dynamics of other taxa in the food web (Paine 1980; Moore & de Ruiter 2012). This eventually describes community structure (i.e. the abundance of different organisms and their position in the food web), and density changes over time that determine community dynamics and stability (McCann & Yodzis 1998).
Figure 1. Food web theory applied in this thesis: a) Food web definitions (CFW, connectedness food web; EFW, energetic food web; FFW, functional food web) with numbers depicting different trophic levels in the food chain. b) Representation of bottom-up and top-down effects through trophic interactions. c) Different theories regarding bottom-up and top-down regulation in food webs: Lindeman’s hypothesis of bottom-up regulation along the food web. HSS (Hairston, Smith and Slobodkin, Hairston et al. 1960) of top down control in tri-trophic food chains, which led to EEH (Ecosystem Exploitation Hypothesis, Oksanen et al. 1981) and TCH (Trophic Cascade Hypothesis, Carpenter et al. 1985). Dashed lines represent the addition of a third trophic level and solid arrows represent responses to increasing productivity of a given trophic level of bi-trophic (black) and tri-trophic (red) food chains. d) Food web concept with generalist predation in contrast to food chains (a−c). e) Indirect interactions (dashed arrows) through shared predation can lead to apparent competition (−,−) or apparent mutualism (+,+). In e), direct consumer–resource interactions are depicted by solid arrows.

Bottom-up vs. top-down control

Over the past decades, food web theory has greatly developed and changed our view of the functioning of food webs. One of the major aspects of the discussion has been whether trophic levels are controlled by the effects of resources on the abundance of their consumers (i.e. bottom-up control, Fig. 1b), or by the effect of predation by consumers on the abundance of their resources (i.e. top-down control, Fig. 1b). Raymond Lindeman, in his “Trophic-dynamic aspect of ecology” (Lindeman 1942), presented a food web model where food-web structure and function mainly depended on the influence of resources on the abundance of their consumers through a bottom-up control where around 10% of the energy of one trophic level was
transferred to a higher trophic level (Fig. 1c). However, Hairston, Smith and Slobodkin on their “green world” or “HSS” hypotheses (Hairston et al. 1960), compiled multiple evidence of a strong top-down control in terrestrial food webs, in which top predators suppressed the abundances of grazers allowing the establishment of world’s forests (Fig. 1c). Once the existence of bottom-up and top-down control in nature was acknowledged, the discussion moved toward how the bottom-up and top-down control in food webs was regulated along environmental gradients. Oksanen et al. (1981) presented in their Ecosystem Exploitation Hypothesis (EEH), a model where increasing productivity would alternate bottom-up and top-down control of trophic levels by allowing the “step-wise” establishment of new top predators (Fig. 1c). In aquatic food webs, Carpenter et al. (1985), similarly proposed that top-down control by top predators would propagate down the food web causing top-down control of every second subsequent lower trophic level. This process was termed after Paine (1980) trophic cascade (Fig. 1c). In practice, the strength of bottom-up and top-down control in food webs varies a lot across systems (Hairston & Hairston 1993; Shurin et al. 2002, 2006). Further attempts are therefore necessary in order to understand mechanisms of bottom-up and top-down regulation in all types of food webs.

Food chains vs. food webs

In addition to the concept of bottom-up and top-down regulation, the way to structure food-webs has changed since the onset of food web ecology. Traditionally, the structure of food webs was defined as food chains of trophic interactions, starting from primary producers and finishing with top consumers (Lindeman 1942; Hairston et al. 1960; Oksanen et al. 1981; Carpenter et al. 1985) (Fig. 1a-c). The concept of food chain simplification is very useful to understand the functioning of rather simple and isolated food webs, such as highly size structured open water food webs or the ones homogenized by the action of humans by intensive agriculture (Carpenter et al. 1985; Polis & Strong 1996). However, further studies have shown that generalist consumers that couple multiple food-web pathways to be widespread (Fig. 1d) (Polis & Strong 1996; McCann et al. 2005; Rooney et al. 2008). As a result of such food-web coupling, different food web pathways become functionally connected. This mostly occurs by means of indirect prey-prey interactions through sharing a predator which are studied by the apparent competition theory (Holt 1977; Holt & Bonsall 2017) (Fig. 1e). Therefore, understanding food web functioning relies on the knowledge that all food web pathways (e.g. Holt 1977; McCann et al. 2005) are connected globally by large and mobile consumers or by fluxes of matter and energy (Polis et al. 1997, 2004; Bartley et al. 2019). Overall, evidence suggests that the frameworks and the theory developed for isolated food chains should be adapted
to the idea of large food webs connected to each other at local, regional and worldwide scale (Polis et al. 2004; Bartley et al. 2019). Despite many modelling efforts have generated many hypotheses about the functionality of coupled food webs (e.g. Holt 1977; McCann 2012; Wollrab et al. 2012), many of those hypotheses are yet to be tested empirically in different systems including lakes (but see e.g. Marklund et al. 2019a; Vasconcelos et al. 2019).

Introduction to lake food webs

In a conceptual lake food web (Fig. 2), phytoplankton, periphyton and macrophytes are the main primary producers forming the base of the so-called “green” or “grazing” food web (Lindeman 1942; Polis & Strong 1996). These primary resources are consumed by planktonic and benthic invertebrates, which in turn are consumed by fish predators that can couple pelagic and benthic food webs (Lindeman 1942; McCann & Rooney 2009). Organic material from both dead or excretions of organisms represent a detrital pool that fuels a parallel food web called the “detrital” food web (Polis & Strong 1996). One important component of detrital food webs in aquatic ecosystems is the presence of a microbial loop formed by several trophic stages of unicellular heterotrophic organisms (i.e. heterotrophic prokaryotes and protists). These are capable of linking the low size fractions of particulate and also dissolved detritus with the rest of the food web that otherwise would be largely out of reach for bigger multicellular consumers (Azam et al. 1983) (Fig. 2).

Within lakes, there are fundamental differences between benthic and pelagic food webs. Pelagic food webs tend to be highly size-structured and have higher biomass turnover rates than benthic food webs (Peters 1983; Shurin et al. 2006; McCann & Rooney 2009). This is expected to lead to asymmetries in the energy transfer through faster pelagic pathways compared to slower benthic pathways (Shurin et al. 2006; McCann & Rooney 2009), which have important consequences for top-down control (Polis & Strong 1996; Ward et al. 2015) and stability properties of the food web (McCann & Rooney 2009). Thus, the spatial heterogeneity in lake food-web dynamics and its coupling via top consumers, make them an interesting model to study the drivers and the emerging properties of multi-pathway food web processes in natural settings (See “Factors driving food webs in general and lake food webs in particular”).
Factors driving food webs in general and lake food webs in particular

Bottom-up processes

**Food quantity vs. food quality**

The existence of trophic interactions ultimately depends on the transfer of energy and nutrients from resources to consumers that support consumers’ survival, growth and reproduction. Traditionally, food web ecologists thought that such **energy transfer** mostly depended on the amount of re-
sources consumed, hereby called food quantity (Lindeman 1942). However, food quality often referred to as the digestibility and the chemical composition (nutrients or toxic substances) of the assimilated food, can strongly influence energy transfer efficiency and subsequent food web processes (Sterner & Elser 2002; Burian et al. 2019; Ruess & Müller-Navarra 2019).

Nutrients and essential biomolecules have received a great attention due to their strong impacts on the energy transfer through the food webs (Sterner & Elser 2002; Ruess & Müller-Navarra 2019). Among them, fatty acids are particularly important because they are abundant in organisms, carry out key functions, and some of them (the polyunsaturated fatty acids, PUFAs) are essential to a wide majority of consumers (Tocher 2003; Bell & Tocher 2009). PUFAs are known to limit growth in consumers (e.g. Yu & Sinnhuber 1979; Müller-Navarra et al. 2000; Twining et al. 2016a). In addition, PUFA availability varies a lot among prey and across habitats: between terrestrial and aquatic environments (Hixson et al. 2015), between benthic and pelagic habitats (Lau et al. 2012), and along environmental gradients of temperature (Hixson & Arts 2016) and nutrient levels (Müller-Navarra et al. 2000). Therefore, PUFAs are one of the target drivers to understand bottom-up regulation of food webs.

From the consumers’ perspective, ensuring sufficient concentrations of high quality PUFAs as well as any potentially limiting nutrients or biomolecules is likely to be highly adaptive. As a response, consumers have two (non-exclusive) adaptive choices to ensure optimal supply of PUFAs: feeding on resources that have higher amounts of good quality fatty acids, and compensating mismatches in their fatty acid needs by using internal regulatory processes to keep a balance on fatty acid composition usually referred as homeostasis (Fig. 3). This leads to multiple strategies towards fatty acid regulation, laying between strict fatty acid collectors that fully reflect the fatty acid composition of their food and fatty acid integrators that completely regulate dietary fatty acid inputs (Guo et al. 2018). Different limitations and costs of these particular strategies are likely affecting the overall energy transfer in food webs and may feed-back on the effects of consumers in the food web by contributing to life-history trade-offs (see “Life-history trade-offs”).

**Spatial heterogeneity and spatial fluxes**

Lake food webs comprise of several pathways structured over space and time that support the production of higher trophic levels of consumers (Fig. 2). The energy mobilization in lake food webs is spatially separated into benthic and pelagic habitats depending on whether production occurs in open water or is associated to sediment surfaces (Fig. 2). Within each habitat category, energy mobilization can also be based on primary production, or on detritus that fuel parallel detrital food webs (Fig. 2). In addition to those, a particular type of energy mobilization based on methane oxidation seems
to contribute substantially to secondary production in some boreal lakes (e.g. Jones & Grey 2011; Agasild et al. 2014; Lau et al. 2014).

Figure 3. Fatty acid regulation in consumers using fish as model organism (see Tocher 2003; Bell & Tocher 2009 for more information). A fraction of the fatty acid ingested are digested and enter the blood where they are either deposited in tissues without minor alteration. SAFAs and MUFAs can be biosynthesized de-novo from non-fatty-acid precursors. However, PUFAs (at least ALA and LIN) are essential in the diets of vertebrates. Mainly in the liver, but also in brain and intestine, PUFAs can be desaturated and elongated into high quality HUFA. In the tissues, some fatty acids are selectively retained whereas others are selectively mobilized either to obtain energy or to be moved to other tissues with high demand of fatty acids (e.g. gonads, liver for bioconversion). Fish picture credit Katrin Attermeyer.

Lake ecosystems have spatial fluxes of organisms or matter both within benthic and pelagic habitats and to/from adjacent terrestrial systems (Polis et al. 1997; Makino et al. 2001; Bartels et al. 2012). Gravity seems to be the most important driver of energy fluxes from pelagic to benthic systems, as dead matter passively settles and accumulates in the sediment. Similarly, leaf litter that falls from trees can also substantially contribute to the production in recipient lakes (Cottingham & Narayan 2013) and once in aquatic systems, terrestrial organic matter follows gravitational hydrologic flows (Polis et al. 1997). In addition, many benthic organisms overcome gravity and migrate from benthic to pelagic systems where they are highly exposed to predation (Makino et al. 2001; Wagner et al. 2012). Some of those have terrestrial adult stages and may constitute key food item for terrestrial consumers (Dreyer et al. 2016; Twining et al. 2018). Fluxes of animals are also recipro-
cal from terrestrial to aquatic systems (Nakano et al. 1999; Nakano & Mura-kami 2001; Bartels et al. 2012), and may be the most important energy source for fish in lakes (Mehner et al. 2005; Cole et al. 2006).

Changes in environmental conditions can affect the importance of energy mobilization by different production pathways. For instance, increasing productivity in lakes is often related to a shift from benthic dominated energy mobilization to pelagic energy mobilization and an increase in the importance of detrital food webs (Fig. 2) (Vadeboncoeur et al. 2003; Ward et al. 2015). In addition, increasing inputs of terrestrial dissolved organic carbon (tDOC) has a twofold effect on energy mobilization by reducing the importance of benthic compared to pelagic pathways while promoting production of heterotrophic microbes over autotrophic ones (Ask et al. 2009). However, the importance of different pathways and spatial subsidies can also vary over different seasons (Sommer et al. 1986; Makino et al. 2001; Agasild et al. 2014; Berggren et al. 2014).

Top-down processes

**Traits affecting the ecological niche**

The effects of consumers on their resources are directly related to their resource use (i.e. what and how much they eat) and their habitat use (i.e. where they live), which are the main aspects of their ecological niche. In turn, consumers’ niche highly depends on a set of features (i.e. traits) that are of interest when studying trophic interactions. Body size is one of the most important traits, as increases in body size scale positively with many other traits that affect consumers niche such as metabolism, mobility and diet size-range (Wilson 1975; Peters 1983). Differences in body size between predator and prey are also linked to predation rates (i.e. number of prey killed per unit of time) by affecting the chances for a prey to escape and changing the times spent in handling the prey (e.g. Lundvall et al. 1999; Nilsson & Brönmark 2000; Hjelm & Persson 2001). In aquatic food webs, such body size effects on consumption rates are even more pronounced as predators generally have to swallow their prey as a whole, rather than consuming parts of it. Other morphological traits emerging from the consumer’s anatomy, such as body shape, mouth shape, teeth type, gut length, etc. are also related to the use and efficiencies on different resources in different habitats (Skúlason & Smith 1995; Bolnick et al. 2003; Svanbäck & Eklöv 2004; Olsson et al. 2007), whereas behavioral traits can determine short-term decisions on resource use and habitat utilization that cannot be regulated by changes in morphology (Sih 1980; Mittelbach 1981; Bolnick et al. 2003).

Altogether, these traits affect the consumer functional responses that represent the resource consumption rate by the consumer as a function of
resource abundance (Fig. 4), and basically summarize the role of the consumer in the food web under certain conditions.

**Figure 4.** Functional responses of the consumption rate of predators as a function of prey abundances. Type I is typical of some filter-feeders (Jeschke et al. 2004). Type II functional response is typical of many taxa as they tend to saturate at higher resource densities (Jeschke et al. 2004), whereas type III accounts for low attack rates when prey are scarce. Type III is typical of switching predators that focus feeding on the most abundant prey (e.g. Begon et al. 2006).

**Life-history tradeoffs**

The ecological niche of consumers (and therefore of the role of consumers in food webs) is highly influenced by **life-history tradeoffs** which are a consequence of changing selective pressures during the life cycle (Werner & Gilliam 1984; Werner 1986). That is because consumers need to adjust the expression of important traits for food webs (e.g. behavior, morphology) to maximize their **fitness** (i.e. mainly survival, growth and reproduction) (Stearns 1992). A typical example of a tradeoff is the compromise of resource uptake, either via suboptimal habitat selection or reduced foraging behavior, to minimize the high risk of mortality in the presence of predators (e.g. Sih 1980; Mittelbach 1981; Gilliam & Fraser 1987). This example also highlights that, in many cases, responses to changes in selective pressures are highly **plastic** and therefore regulated by consumers depending on environmental conditions (West-Eberhard 1989).

Differences in life-history tradeoffs within populations can affect the **resource specialization** and **habitat use** of different individuals (e.g. Olsson et al. 2007; Svanbäck & Persson 2009; Svanbäck & Eklöv 2011). In addition, changes in traits and selecting pressures often change over the life cycle of organisms as they grow in body size, or as they shift between different stages (e.g. juvenile vs. adult, caterpillar vs. butterfly, tadpole vs. frog). This often results in changes of habitat use and/or dietary preferences named **ontogenetic niche shifts** (Werner & Gilliam 1984). Life-history tradeoffs and their subsequent effects on consumer niche preferences will likely have cascading effects in food webs through top-down regulation (Palkovacs & Post 2009; De Roos & Persson 2013; Matthews et al. 2016), but also by bottom-
up regulation by means of ecosystem engineering (Harmon et al. 2009). Thus, studying what regulates life-history tradeoffs is important in order to understand and predict food web functioning.
Aims of the thesis

The overarching aim of this thesis was to understand bottom-up and top-down regulation of lake food webs in response to environmental drivers, aiming to reconcile food-web theory with actual results from experimental and field studies. More specifically, I aimed to test some of the drivers and processes that emerge when shifting from a traditional food-chain paradigm, where energy flow is streamlined and consumers have a single niche during their life, to one of multiple food web pathways linked by generalist predators that can undergo niche shifts during their ontogeny.

The specific aims of the thesis are to:

- Investigate the effect of ontogeny in fatty acid regulation of fish and its implications on their ecological niche (Paper I & II). The study was performed by using fish caught on a single sampling event, including all possible ontogenetic stages from young-of-the-year to mature individuals and all possible diets based on zooplankton, macroinvertebrates or fish.

- Test the effects of indirect interactions between benthic and pelagic prey of lake food webs under generalist predation (Paper III). The short-term effects of shared predation were tested during a mesocosm experiment in which lake food webs were subjected to a gradient of nutrients and the presence/absence of generalist fish.

- Investigate the effects of bottom-up, top-down and reconfiguration processes on food web responses to increasing productivity (Paper III, IV) and to increasing tDOC (Paper V). The study of different food web drivers was tested in short-term mesocosm experiments where both the environmental drivers and the addition of predatory fish were manipulated.

- Investigate the bottom-up and top-down effects on cross-ecosystem fluxes of fatty acids via the emergence of aquatic insects (Paper IV). Fatty-acid exports were assessed by trapping emerging non-biting midges during a mesocosm experiment in which a gradient of nutrients and the addition of predatory fish were manipulated.
Material and methods

Experimental site and designs
All the studies presented in this thesis were based at Erken, (59°51′N, 18°36′E) a meso-eutrophic lake in Central Sweden that covers an area of 24.2 km², has a maximum depth of 21 m and a mean depth of approximate 9 m (Fig. 5a). The lake has been highly monitored since 1940 by the Erken laboratory, which is part of the Swedish infrastructure for Ecosystem Science (SITES; www.fieldsites.se).

Lake study
For studying FA regulation over the ontogeny of fish (Papers I & II), a field study approach was chosen where different age classes of Eurasian perch (Perca fluviatilis) were sampled simultaneously to draw inferences about the population’s ontogenetic niche shifts. Multi-mesh gill nets were used to catch pelagic and littoral sub-populations of different size and age classes. Two locations were chosen: a bay in the littoral zone (Fig. 5a) and a pelagic area in the middle of the lake (Fig. 5b) that were known to yield high numbers of perch of different niches and ages (Marklund et al. 2019b). The fish were sampled at one occasion in the middle of the growing season, In addition, zooplankton, benthic macroinvertebrates and fish prey were sampled for later calculation of perch diet (see “Measuring trophic interactions”). The fatty acids provided by prey were inferred via direct fatty acid analysis (for fish prey) or from published data of zooplankton and benthic macroinvertebrates of the lake Erken during the same time of the year (Scharnweber et al. 2016b).

Mesocosm experiments
To investigate the food web responses of bottom-up, top-down and reconfiguration processes to different environmental change (Papers III, IV & V), two mesocosm experiments were carried out, both manipulating environmental conditions and the addition of predatory fish. The term mesocosm, has its origin in the Greek meso “medium-sized” and cosmos “world” is basically defined as “a biological system that contains the physical features and organisms of an ecosystem but is restricted in size or scope for use in conducting scientific experiments” (Editors of the American heritage dictionaries 2015). Therefore, mesocosm experiments are useful tools in food
web ecology as they combine the complexity of natural food webs, and at the same time the possibilities of controlled and replicated experimental design needed for hypothesis testing.

The mesocosm experiments in the vicinity of the Erken laboratory consisted of 20 white opaque, open-top cylinders with a flat bottom, made of high-density polyethylene that were 2 m deep and had a diameter of 1 m. Once filled with water, the mesocosm volume ranged approximately between 1000–1400 L. The floating mesocosms were attached to a dock in the way presented in Figure 5c.

Figure 5. Map of the lake Erken, Sweden, and location of sampling sites for Papers I & II (a,b) and Papers III, IV & V (c). a) Pelagic gillnet sampling, b) littoral gillnet sampling, c) mesocosm experiments (picture: deployment of the mesocosms). © Lantmäteriet Gävle (2012). Permission i2012/921. Picture credits: (a,b) Peter Eklöv, (c) Anna Cecilia Nydahl.

Overall, for both experiments, lake water was pumped from the surroundings of the dock and filtered through a mesh (200 µm) into the mesocosms in order to avoid fish and to limit the effects of patchy distribution of large zooplankton. Then large zooplankton was added to the mesocosms from a stock of pooled zooplankton tows (mesh size; 100 µm) over a large area in the littoral zone of the lake Erken, whereas aquatic insects could recruit from the egg deposited in the mesocosms or transported in the water (and sediment in case of Papers III & IV).
After treatment manipulations, the different compartments of the food web were sampled regularly, if possible, or otherwise at the end of the experiment.

**Manipulations**

*Browning experiment (Paper V)*

The aim of *Paper V* was to disentangle the twofold effects of tDOC in pelagic lake food webs as a shading agent and as a potential energy flux fueling the detrital food web pathway. To do that, a 2x2 factorial design was created, in which it was manipulated (1) the availability of PAR light in the water by attaching a black chiffon fabric to the top of the mesocosms and (2) the addition of tDOC concentrated from a headwater source. This led to a control, a shading, a DOC and a DOC+shading treatment (Fig. 6a), which were randomly assigned within each group of four mesocosm in order to reduce spatial biases within the mesocosm structure.

In addition to these manipulations of environmental conditions, the length of the food chain was manipulated by adding three young-of-the-year individuals of Eurasian perch to each mesocosm in order to study the combined responses of environmental conditions and top-down predation in relation to prey selectivity of perch.

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**Figure 6.** Designs of mesocosm experiments. a) Browning experiment *(Paper V)*. b) Productivity gradient experiment *(Papers III & IV)*.
Productivity gradient experiment (Papers III & IV)

In this experiment, an ANCOVA type of design was used (i.e. with one continuous predictor and one factor). The continuous predictor was created by increasing productivity along two series of 10 mesocosms, from ambient, mesotrophic lake conditions to hyper-eutrophic conditions (TP: 20–1000 μg/L, TN: 0.45–11.3 mg/L). Two juvenile fish were added (crucian carp, *Carassius carassius*) to 10 mesocosms across the nutrient gradient, so that fish presence (and fish absence) was fully crossed along the productivity gradient. The nutrient treatments were randomly distributed across each side of the mesocosm structure, whereas fish addition was stratified in each block of four mesocosms (Fig. 6b). Our design implied no replication of the same treatments in more than one mesocosm (Fig. 6b). However, since the effects of the productivity gradient were estimated as slopes of a regression line, any random enclosure effect was taken into consideration by the dispersion of the residuals around the regression estimate.

Measuring trophic interactions

The technique used to measure trophic interactions in food webs depends to a large extent on which aspects of food webs are tested. For instance, to measure energy flow through food webs, trophic interactions should measure the contribution of different prey or food-web pathways to consumers’ growth (Moore & de Ruiter 2012). However, to determine functional links in food webs (e.g. top-down control) trophic interactions need to be measured by quantifying responses of prey to changes in the abundance of their predator (Moore & de Ruiter 2012). During our studies, different techniques were used to measure either energetic or functional aspects of trophic interactions.

Gut content analysis

This technique is used to infer consumers diet based on the relative abundance of different resources in their digestive tract, which often allows a high taxonomic resolution and to track differences in life stages of prey compared to molecular approaches (Nielsen *et al.* 2018). However, it only represents a snapshot of consumers’ diet and may lead to biased diet estimates due to differences in the digestibility of different resources (Jackson *et al.* 1987). In this thesis, gut content analysis was used to infer the short-term diet of predatory fish at the end of the mesocosm experiment in Paper V.

Trophic biomarkers

Trophic biomarkers are elements and biomolecules that are transferred from resource to predator with a minor modification. Following this principle of “you are what you eat”, the diet of a consumer can be reconstructed by cal-
calculating the mixture of food sources that explains the composition of trophic biomarkers found in the consumers’ tissues. An important advantage of using trophic biomarkers is that they provide a longer time frame in consumers diet than gut content analysis (Jackson et al. 1987). In addition, different temporal scales of the estimation can be obtained depending on the rate at which biomarkers are replaced in different tissues (Vander Zanden et al. 2015; Mohan et al. 2016).

Widely used biomarkers are the proportions of stable isotopes of important macronutrients (e.g. C, N, H, O, S). Isotope values are often noted as $\delta^nA$ (where $n$ is the heaviest of the two isotopes compared from the element A), and they are expressed as the difference in units per mil (‰) of the isotope ratio as compared to the isotope ratio of an international standard. For example, the original standard for $\delta^{13}C$ is obtained from a particular sample of fossilized belemnites (Peedee belemnite), which were abundant cone-shaped cephalopods in the Jurassic seas.

Figure 7. Isospace plot based on $\delta^{13}C$ and $\delta^{15}N$ values of perch and their main food resources from Papers I & II. Crossed symbols and error bars represent the mean ± SD values of the main food sources of perch after correction of trophic fractionation (see Paper I). Colors represent the classification of individual perch to a diet (blue, planktivorous; green, benthivorous; black, piscivorous).

In lake ecosystems, benthic food web pathways that are based on periphyton production generally have a higher isotope value $\delta^{13}C$ compared to pelagic pathways fueled by phytoplankton (France 1995). In addition, higher trophic levels tend to have higher $\delta^{15}N$ than prey at lower trophic levels due to trophic fractionation of N (e.g. DeNiro & Epstein 1981; Post 2002). This leads to a separation of C and N isotopic signatures of different prey (Fig. 7),
which was used in Papers I & II to infer the proportion of different prey that contribute to fish growth. Quantitative estimates of different prey in fish diet were achieved by using stable isotope mixing models that calculated the prey mixtures that explain the isotope values of $\delta^{13}C$ and $\delta^{15}N$ found in fish tissue.

In addition to stable isotope ratios, fatty acids have also been used as trophic biomarkers due to dietary fatty acid composition being reflected in the consumer’s tissue (e.g. Tocher 2003; Iverson 2009). This can also provide a qualitative estimate of the dominant diet (as used in Paper I).

Finally, both stable isotope and biomolecule markers can be combined by analyzing compound-specific stable isotope ratios, which, apart from being used to determine diet, they can be used to determine the pathway that takes a particular biomolecule when is transferred through the food web (Paper II).

**Top-down control**

There are multiple ways to estimate the strength of top-down control in trophic interactions (see Moore & de Ruiter 2012). In Papers III & V, log-response ratio was used as

$$\log_{10} \left( \frac{N_f}{N_x} \right),$$

where $N_f$ is the abundance of prey in the presence of fish predators and $N_x$ is the abundance of prey in a fishless control (Shurin et al. 2002). Thus, a strong top-down control corresponds to highly negative values, referring to difference in orders of magnitude between the presence and absence of fish.

**Resource selectivity**

Consumers’ selectivity on a particular resource is defined as their preference of that resource compared to its availability in the surrounding environment. Resource selectivity helps discern the contribution of predators to food web coupling aside from the influence of changes in productivity in the different pathways. Resource selectivity can be calculated using frequencies of predation events, prey composition in the diet, or using the remaining not predated prey after predation trials (Manly 1985). In Paper III, prey selectivity was estimated by inferring the ratio of attack rates $a_2/a_1$ on different prey $i = 1, 2$ immediately after the addition of the predator using a model presented by Holt & Kottler (1987)

$$\frac{a_2}{a_1} = \frac{\log R_2(t) - \log R_2(0)}{\log R_1(t) - \log R_1(0)},$$
where $R_i(0)$ and $R_i(t)$ are the densities of prey right before and after fish addition. A value >1 represents selection on prey 2 over prey 1, whereas a value <1 represents selection on prey 1 over prey 2.

In Paper V, resource availability in the mesocosms was compared with the resource proportions in perch stomachs using Ivlev’s selectivity index (Ivlev 1961):

$$E = \frac{r_i - p_i}{r_i + p_i},$$

where $r_i$ is the proportional abundance of prey $i$ within the diet, and $p_i$ is the proportional abundance of prey $i$ in the environment. $E = 0$ represents the non-selective consumer on prey $i$, $0 < E < 1$ represents high preference on prey $i$, whereas $-1 < E < 0$ represents low preference on prey $i$.

**Fatty acid analysis**

Fatty acid analyses in Papers I, II & IV were performed according to previously published protocols (Scharnweber et al. 2016b). In a first step, fatty acids are extracted from tissues and separated from other molecules. Then a methyl group is added to the fatty acid through a transesterification reaction (creating fatty acid methyl esters, FAMEs) in order for them to be measured using a gas-chromatography coupled with a mass spectrometry (GC-MS) in the following step. The GC output provides a series of peaks each of which represent a single fatty acid which are identified using MS output by matching the resulting composition of ions with the ones found in published libraries of chemical compounds. Fatty acid concentrations are obtained by measuring the area under the peak which is finally calibrated using the areas under the peak of fatty acid standards of known concentrations.

**Statistical analyses**

A variety of statistical approaches were used for the many different analyses carried out in the different studies. For fatty acid composition data, multivariate analysis were performed to test for differences in fatty acid composition associated to continuous predictors (DistLM) or factorial predictors (PERMANOVA), whereas SIMPER analysis was used to find indicator fatty acids that explained most of the dissimilarities between groups (Paper I, II & IV). For stable isotope analysis in Papers I & II, the Bayesian mixing model MixSIAR was used (Stock et al. 2018), which allows diet estimation in underdetermined systems (where there are more diet sources than stable isotope markers) and that can incorporate previous knowledge on how resources and consumer populations are structured (Paper I, II). In Papers III


& V, the effects of the mesocosm treatments over time were tested with repeated-measures ANOVAs, using Greenhouse-Geisser correction in case of departure from sphericity. In Paper IV, general linear models were used to test factors and continuous predictors that affected fatty acid variation in emerging aquatic insects. Otherwise, common parametric tests such as linear regressions, ANOVAs, and t-tests, were used throughout the studies and equivalent non-parametric tests (e.g. Wilcoxon signed rank test, Kruskall-Wallis test) were used if the assumptions of normality and homogeneity of variances for parametric tests were not fulfilled.

Ethical considerations

Since fish were used in all the studies, all the studies had to follow the Swedish legislation that applies to experimentation with fish. According to this, I did the training and passed the course “Laboratory Animal Science for Researchers – Fish and Swedish Legislation, Ethics and Animal Use and 3R. Species: Perch (Perca fluviatilis)”. In addition, the studies were approved by the Uppsala Animal Ethic Committee (permit C59/15 for Papers I, II & V; permit number 5.8.18-03672/2017 for Papers III & IV). The fish were euthanized in the most humane way possible given the technique used for their capture. For Papers I, II & V, quick spinal transection was used, whereas for Paper III & IV, an overdose of the anesthetic benzocaine.
Results and discussion

Fatty acid regulation and its effects on consumers niche

There is increasing evidence that fatty acids are key nutrients for the survival, growth and eventually the fitness of consumers (e.g. Yu & Sinnhuber 1979; Müller-Navarra et al. 2000; Twining et al. 2016a). However the knowledge of fatty acid regulation of fish is often restricted to feeding trials in aquaculture (e.g. Abi-Ayad et al. 2000; Xu & Kestemont 2002; Murray et al. 2014), whereas the extent by which consumers regulate fatty acid composition from dietary inputs in natural environments is still rather unknown. Paper I answers that question for the first time, showing that diet only explained 28% of the fatty acid variation of a perch population consisting of individuals with very different diets. This suggests that perch largely regulate their fatty acid composition and therefore act mostly as fatty acid integrators (Guo et al. 2018), which had been previously suggested but not quantified for many other fish species (e.g. Koussoroplis et al. 2011; Strandberg et al. 2015; Kainz et al. 2017). In addition, changes in body size that indicate physiological changes over ontogeny explained 23% of the remaining fatty acid variation (similar as diet), whereas fish condition explained 1% of such variation. These results contrast with previous studies, where within-species fatty acid variation had been thought to mainly depend on diet (Iverson et al. 2002; Czesny et al. 2011). Hence, the results suggest that internal regulation has stronger effects on fatty acid composition over ontogeny of organisms than previously thought, which has major implications for how to interpret the role of fatty acids in ecological studies.

Changes in fatty acid composition over ontogeny were related to changes in physiologically important HUFAs (i.e. EPA, ARA and DHA) (Fig. 8c-e) which play an important role in ontogenetic processes such as hormonal regulation, early growth, development, and reproduction (Tocher 2003). Similarly Keva et al. (2019) found that internal regulation associated to the reproductive cycle explains the seasonal variation of HUFAs in adult whitefish (Coregonus sp.). These pieces of evidence suggests that HUFAs are likely to be highly regulated in relation to key ontogenetic processes in fish. MUFAs, which are important energy sources for fish (Tocher 2003), increased with body size in large mature perch individuals (Fig. 8a-b). This pattern appears in many species of fish (e.g. Iverson et al. 2002; Maazouzi et al. 2011; Czesny et al. 2011), probably reflecting widespread life-history
shifts in metabolism that favor energy reserves over somatic growth once organisms reach maturity (Stearns 1992).

Figure 8. Changes in proportions of the five most responsive fatty acids over the ontogeny of perch in Paper I indicated by increasing total length a) palmitoleic acid, 16:1n-7; b) oleic acid, 18:1n-9 (both MUFAs); c) arachidonic acid (ARA), 20:4n-6; d) eicosapentaenoic acid (EPA), 20:5n-3, e) docosahexaenoic acid (DHA), 22:6n-3. Different diet and habitat preferences are shown in different colors (see legend).
In Papers I & II, it was also tested whether mismatches in fatty acid in diet compared to consumer fatty acid composition could affect life-history tradeoffs in perch (e.g. by affecting the costs of fatty acid regulation of different food preferences). Additionally, indications were assessed of whether such costs were detrimental for fitness (i.e. somatic growth) and if they could lead to niche shifts in perch that affect the role of perch individuals and populations in the food web. Paper II shows that perch tended to have mismatches between their proportions of the high-quality HUFAs compared to their food, where DHA, which is key for growth, was the HUFA that was the most highly retained from diet. This agrees with a wide evidence of selective retention of HUFAs along food webs (Heissenberger et al. 2010; Koussoroplis et al. 2011; Strandberg et al. 2015). However, the extent of mismatch depended on perch feeding type (e.g. benthivorous, planktivorous or piscivorous). For example, the results show that perch feeding on benthic diets selectively retain more EPA and DHA compared to their conspecifics feeding on plankton or on fish.

In Paper II, it was also investigated which mechanisms were used by perch to compensate for fatty acid mismatches. Two alternative but not mutually exclusive hypotheses were tested based on Scharnweber et al. (2016b): (1) perch selectively retained HUFAs from resources, even if those resources had a minor contribution to their diet (2) perch upgraded the quality fatty acids (via bioconversion) from low quality resources that have a major contribution to their diet. To test this, we analyzed the $\delta^{13}$C of each HUFA to assess the contribution of pelagic and benthic pathways to EPA, ARA and DHA. Overall, differences in $\delta^{13}$C of fatty acids reflected to a large extent differences in their diet $\delta^{13}$C, suggesting that HUFAs tended to be obtained from the main proportion of dietary items (Fig. 9). For ARA and EPA, selective retention from main dietary items was most likely as they both are present in all prey types of perch. However, benthivorous perch faced almost a lack of DHA in benthic invertebrates, which were their most abundant resource. Therefore, in order to obtain DHA that reflected benthic $\delta^{13}$C values, benthivorous perch needed to convert shorter PUFAs such as ALA and EPA from benthic resources into DHA, a process that was assumed to be costly and inefficient in vertebrates (Tocher 2003). Alternatively, benthivorous perch may obtain part of the DHA via selective retention from a minor contribution of pelagic prey which was suggested for a species of mullet (Liza saliens) in a saltwater lagoon (Koussoroplis et al. 2010). DHA signatures were significantly more depleted compared to EPA signatures for all feeding types (Fig. 9). This may be explained by the preferential addition of lighter PUFA-$\delta^{13}$C during PUFA bioconversion (Gladyshiev et al. 2012; Fujibayashi et al. 2016) and thus support the bioconversion hypothesis.

To our knowledge, this is the first empirical evidence for the ecological relevance of DHA bioconversion in freshwater fish, which was previously
suggested in aquaculture studies (Xu & Kestemont 2002; Henrotte et al. 2011), and in modelling approaches using closely related yellow perch (Perca flavescens) as a model organism (Sawyer et al. 2016). Further studies are necessary in order to reveal whether this ability is spread across taxa, and the potential cost associated to it.

Figure 9. Compound-specific δ¹³C of a) ARA, b) EPA and c) DHA in the tissues of perch from different feeding groups from Paper II: littoral benthivorous (LB), littoral planktivorous (LP), pelagic benthivorous (PB), pelagic planktivorous (PP), and littoral piscivorous perch (Pisc). Asterisks depict significant results of Bonferroni-adjusted Dunn’s pairwise comparisons (** = \(P \leq 0.01\); * = \(P \leq 0.05\)). Boxplots depict median, 25th and 75th percentile, and whiskers extend to maximum and minimum values, except for outliers (represented by dots).

Overall, the results from Paper II suggest that feeding on benthic diets may come with a cost in terms of fatty acid internal regulation or restricted resource specialization. This potential cost may have contributed to the lower size-at-age of benthivorous perch compared to planktivorous perch caught in the pelagic zone (Paper I). That cost for benthivorous perch may also explain the earlier shift to piscivory, which is a DHA-rich diet, in littoral compared to pelagic perch observed in Paper I. However, it does not explain why littoral planktivorous perch had similar growth trajectories as benthivorous perch. This may occur since morphological adaptations to living in benthic habitats come with a cost of lower feeding efficiency on zooplankton (Svanbäck & Eklöv 2004; Scharnweber et al. 2016a). Alternatively, these
results may be explained by differences in resource competition in littoral vs. pelagic environments, which may have driven selective pressures in perch populations (Svanbäck & Persson 2009). Unfortunately, the latter process was not assessed in Paper I.

Overall, results from Papers I & II suggest that perch regulate their fatty acid composition to a larger extent than previously known, and that fatty acid mismatches can mediate life-history tradeoffs of perch, potentially affecting their degree of benthic resource use and the timing of their transition to piscivory. Therefore fatty acid nutrition may ultimately affect the niche of perch, and the regulation of food webs where perch is a dominant species. However, further experiments in highly controlled conditions are needed to quantify fatty acid effects on consumers’ niche.

The importance of indirect prey interactions through shared predation

Over the last 20 years there has been increasing recognition of the importance of food-web coupling by generalist predators in various aspects of food-web structure and functioning (e.g. McCann 2000; McCann et al. 2005; Rooney & McCann 2012). Theoretical studies predict that apparent competition interaction (−,−) is likely to regulate top-down control of food webs at increasing productivity in the presence of generalist predators (Holt 1977; Polis & Strong 1996; Wollrab et al. 2012). However, mechanistic empirical evidence of indirect interactions due to shared predation at increasing productivity is still scarce.

In Paper III both productivity and the presence of generalist predators were manipulated to see whether indirect interactions via shared predation influenced short-term responses of benthic and pelagic prey. Indeed, the results demonstrated that benthic and pelagic communities highly depended on short-term apparent mutualism (+,+), where increasing proportions of benthic prey at increasing productivity led to a lower top-down control of alternative pelagic prey (Fig. 10). This contrast with Ward et al.(2015), who suggested that apparent competition (−,−) drove the changes in top-down control across marine food webs of increasing productivity. This difference may stem from the difference in time scale of the experiments, as apparent mutualism seems to affect short-term prey dynamics by “diluting” the predator’s attention among a higher number of prey, whereas apparent competition is expected to affect long-term prey abundances, as predators are able to have demographic responses that instead increase top-down control on alternative prey (e.g. Bety et al. 2002; Thomsen et al. 2018; Piovia-Scott et al. 2019).
Figure 10. Trends of top-down control at increasing productivity (depicted as total phosphorus, TP) in Paper III for a) cladoceran abundance (filled circles) and b) Emergence of chironomids (empty squares), and c) scatterplot of the relationship between top-down control in Cladocera and Chironomidae (n=20); filled circles joined by dashed lines represent the two samplings after fish addition (week 1 and 3) when both prey were simultaneously monitored in each mesocosm. A strong top-down control would correspond to highly negative log response ratios, referring to difference between the presence and absence of fish. We show the fit and adjusted $R^2$ of significant linear models at $\alpha=0.05$ (black solid lines and symbols) and non-significant trends over the productivity gradient (grey dashed lines and symbols). In panel c, Pearson’s correlation coefficient $r$ is based on the average top-down control in each mesocosm during the two samplings (n=10).

Apparent mutualism in Paper III was ultimately determined by the foraging behavior of the predator. Using an empirical selectivity model based on prey depletion trends, it was found that the generalist fish (in this case, crucian carps) acted as switching predators that regulated their prey preference according to prey abundance (Type III functional response; Fig. 4). Switching behavior predicts time lags in top-down controls on different prey that are expected to confer food webs with higher stability (e.g. Murdoch & Oaten 1975; Erlinge et al. 1984), whereas other alternative behaviors should lead to more coupled prey dynamics (e.g. opportunistic; Type I or II functional response) or even to apparent competition at short term scales (e.g. anti-switching; Abrams 1987, 2010). These time-lags became longer in cladoceran zooplankton prey at increasing productivity as benthic chironomid prey
were increasingly abundant, suggesting that apparent mutualism via switching behavior ultimately affected the dynamics of prey. Despite it is well-established that many fish couple of benthic and pelagic pathways of lake food webs (Vander Zanden & Vadeboncoeur 2002; Vander Zanden et al. 2011), little is known about the effects of coupling on the regulation of benthic and pelagic pathways (but see Marklund et al. 2019a). Paper III may therefore confirm the predicted effects of indirect interactions between benthic and pelagic prey through shared predation in a highly controlled and replicated experiment. Despite the assumption that effects of habitat coupling can only be viewed at larger spatial scales (e.g. McCann et al. 2005; Rooney et al. 2008), Paper III shows that this also occurs at small spatial scales where pelagic and benthic habitats are highly connected, such as the littoral zones of lakes (Okun et al. 2005) or during insect emergence, where ascending pupae or nymphs are highly susceptible to pelagic fish predation (Makino et al. 2001; Wagner et al. 2012). However, further studies over larger temporal and spatial scales are important to see if these experimental results can be extrapolated (1) to systems where benthic and pelagic habitats are separated by larger distances, and (2) to see if short-term apparent mutualism shifts into apparent competition as predators are enabled to have demographic responses to changes in prey abundance.

Effects of environmental change on food webs (bottom-up, top-down, and food-web reconfiguration)

Changes in environmental conditions can have strong effects in food webs that likely affect food web structure and functioning in a changing world. Environmental change can affect food webs by altering the transfer of energy (i.e. bottom-up processes), the strength of trophic interactions (i.e. top-down control) and the coupling of different pathways by generalist predators (i.e. food web reconfiguration) (Polis & Strong 1996; Bartley et al. 2019). Papers III, IV, & V test for the effects of bottom-up, top-down and food-web reconfiguration in the responses of tri-trophic lake food webs to different types of environmental change in lake ecosystems: the increase of colored tDOC i.e. browning (Paper V), and the increase of nutrient concentrations i.e. eutrophication (Papers III & IV).

Bottom-up effects

As expected, eutrophication elicited strong bottom-up effects in food webs by increasing the abundance of pelagic and benthic consumers, and by leading to 10x higher growth in fish at hyper-eutrophic compared to basal lake conditions (Paper III). In addition, increasing nutrients had different effects
on different food web pathways. In the absence of fish, nutrient additions resulted in a 40-fold increase in the emergence of chironomids, which are some of the most abundant freshwater benthic consumers (Armitage et al. 1995). This contrast with the 7-fold increase of the abundance of cladocerans along the productivity gradient in the absence of fish, leading to a stronger contribution of benthic pathways at increasing productivity. This could be explained by the high surface to volume ratio of the mesocosms, which may have favored benthic over pelagic primary productivity (e.g. Blumenshine et al. 1997). In natural aquatic systems, similar dominance of benthic pathways over zooplankton is found in highly eutrophic conditions, whereas such a pattern is driven by settling detritus from unconsumed pelagic algae, rather than via benthic primary production (Jeppesen et al. 1997; Vadeboncoeur et al. 2003). The effects of increasing nutrients on benthic pathways were smaller or even negative at the higher end of the productivity gradient as seen in the unimodal response of periphyton to nutrients (reaching a maximum biomass at around 540 ± 11 µg L\(^{-1}\) TP) and a similar pattern found in chironomids (Paper III & IV). This may be an effect of nutrient as a stressor apart from a resource or by resource competition between benthic and pelagic algae for nutrients and light (Hansson 1988).

In contrast to the eutrophication results, neither decreased light availability nor the flux of tDOC, which is a driver of browning, led to significant bottom-up changes over the time frame of the 4-week experiment in the main food web compartments of a community from the same lake (Paper V). These results seemed to be explained by the resilience of phytoplankton communities to lower light availability and by a high baseline concentration of DOC in the lake Erken that may be more available to heterotrophic bacteria compared to the highly aromatic tDOC that was added to the mesocosms. These results agree with others that show little responses in the energy mobilization and the energy flow of pelagic food webs with shallow water columns similar to the ones of the mesocosms (~1.5 m) (Ask et al. 2009; Lefèbure et al. 2013; Faithfull et al. 2015; Vasconcelos et al. 2019). However, negative responses of browning on benthic production pathways seem to be consistent across literature (e.g. Ask et al. 2009; Godwin et al. 2014; Vasconcelos et al. 2019). In addition, tDOC may contribute to anoxic water adjacent to sediments that restricts benthic secondary production and the access of fish to such resources (Craig et al. 2015). Lower benthic resource use is also linked to negative effects of tDOC on fish biomass and productivity (Craig et al. 2015; Vasconcelos et al. 2019). Unfortunately, benthic food web pathways were not included in Paper V, since the shading mesh likely affected the recruitment of aquatic insects by blocking the access of egg-laying females (Table 1).
Table 1. Availability of aquatic insects and other benthic macroinvertebrates in the mesocosms and proportions in diet in fish (based on abundances from gut content analysis) from Paper V (Mean ± SD). These results are not shown in Paper V.

<table>
<thead>
<tr>
<th>Mesocosm (n=6)</th>
<th>Fish diet per mesocosm (n=10)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Aquatic Insects (ind. m⁻²)</td>
</tr>
<tr>
<td>Unshaded</td>
<td>3.5 ± 2.9</td>
</tr>
<tr>
<td>Shaded</td>
<td>0.4 ± 0.2</td>
</tr>
</tbody>
</table>

Top-down effects
Eutrophication affected top-down control of fish on benthic and pelagic pathways based on apparent mutualism between benthic and pelagic prey. A detailed discussion of top-down control mechanisms can be found in Paper III. Unfortunately, fully quantitative estimates of chironomids in the mesocosms could not be obtained, because they were measured via the emergence of adults. Therefore it was impossible to calculate top-down control in all resources combined to test whether the experiment supported EEH (Oksanen et al. 1981), or the trophic cascade hypothesis (Carpenter et al. 1985).

Browning is expected to reduce consumption rates of visual predators, such as perch, by likely hampering prey detection and capture success due to the effects of tDOM on light attenuation (Estlander et al. 2012; Jönsson et al. 2012; Ranåker et al. 2012). However, in Paper V, the strong top-down control of young-of-the-year perch on zooplankton taxa did not differ among the treatments. This may be due to insufficient light attenuation to reduce consumption rates. Additionally, since small food items such as zooplankton are detected by predators at shorter distances than larger food items, zooplanktivory is less affected by light attenuation than feeding on fish (Jönsson et al. 2012).

Food-web reconfiguration
As discussed earlier, changes in food web coupling can have important consequences in food web functioning and stability (e.g. McCann 2000; McCann et al. 2005; Rooney & McCann 2012) making it an important food web feature that needs to be addressed. Food-web coupling can be affected by changes in the dominance of different food web pathways, extinctions or invasions of keystone species, changes in predator behavior and changes in the accessibility to different resources by predators, leading to food web reconfigurations (Bartley et al. 2019). In Paper III, the results suggest changes in food web coupling that consist in higher benthic resource use of generalist fish at increasing productivity. This was mainly driven by changes in the dominance of benthic and pelagic pathways, whereas generalist cru-
Cian carp also influenced coupling via frequency-dependent prey selectivity through switching behavior. However, in Paper V, the use of different zooplankton prey by young-of-the-year perch was not related to changes in prey dominance, but probably directly by shading and tDOC additions that led to lower selectivity on copepods and higher selectivity on small cladocerans (Fig. 11). This results may be attributed to higher contrast of pigmented copepods (via carotenoid pigmentation) in clear water compared to brown dark water, as already found by Jönsson et al. (2011), and/or higher contrast of bright-colored cladocerans in dark and brown water compared to clear light water, making them more visible to visually hunting predators. However, these results in prey selectivity contrast with other observational studies in lakes that suggest a lower selectivity of cladocerans and a higher use of copepods at increasing browning (Estlander et al. 2010; Bartels et al. 2016). Therefore, further studies are necessary in order to see which and how consistent are such changes in prey selectivity are in response to browning.

**Figure 11.** Selectivity of perch (means ± SE) on a) small cladocerans, and b) copepods based on zooplankton abundance at the last sampling date (day 29) and stomach content of perch (day 30) in the control (C), shading (Sh), reverse osmosis concentrated DOC (DOC), and combined DOC and shading (DOC+Sh) treatments. Values close to 1 represent high prey selection, whereas values close to -1 represent high prey avoidance. The zero line represents the null hypothesis of no selectivity on prey. Significant effects of the treatments on a Two-way ANOVA are depicted in the figure, with $P \leq 0.05$ (*), $P \leq 0.01$ (**).

**Bottom-up and top-down regulation across ecosystem boundaries**

Ecosystems are often connected with each other via fluxes of organisms, nutrients or energy, that are very important for food-web functioning in recipient ecosystems (Polis et al. 1997). In the relationship between terrestrial and aquatic systems there is a number of spatial fluxes, among which the emergence of aquatic insects is one of the most important (Bartels et al. 2012). Emerging aquatic insects, in addition to being a source of energy for
terrestrial consumers, also contain high quality PUFAs, such as EPA (Gladyshshev et al. 2013; Borisova et al. 2016; Popova et al. 2017), which is key for survival and growth of terrestrial consumers (Twining et al. 2016b, 2018; Fritz et al. 2017). EPA can be considered as especially important since it can be found only in low quantities in recipient terrestrial systems (Hixson et al. 2015).

Bottom-up and top-down effects of donor aquatic systems on the biomass fluxes of aquatic insects are well-known (Nakano & Murakami 2001; Baxter et al. 2004; Knight et al. 2005). Therefore, Paper IV aimed to test not only how bottom-up and top-down processes shape the quantity of the flux, but also its quality. That was achieved by measuring changes in fatty acid content of emerging chironomids, which are one of the most abundant emerging aquatic insects (Baxter et al. 2005; Martin-Creuzburg et al. 2017). The biomass flux of emerging chironomids followed a unimodal response to increasing productivity, where the height of the peak was strongly reduced in the presence of fish (Paper IV). The flux of fatty acids to land followed a similar pattern, being mainly determined by the quantity of the flux (i.e. the more biomass, the higher fluxes of fatty acids; Fig. 12). However, ALA proportions increased while EPA proportions decreased at increasing eutrophication in the tissues of most dominant chironomid species (Fig. 12). Therefore, increases in the quantity of the emergence seemed to offset decreases in fatty-acid quality at increasing productivity. This contrasts to the findings of Müller-Navarra et al. (2000) where food quality responses offset food quantity responses at the phytoplankton-zooplankton interaction in response to eutrophication (Müller-Navarra et al. 2000).

In conclusion, fluxes of high quality fatty acids via insect emergence strongly depend on the nutrients and the food web structure of the donor ecosystem. These results are important in order to know the consequences of bottom-up and top-down control to adjacent terrestrial ecosystems.
Figure 12. Export via emerging Chironomidae of (a) eicosapentaenoic acid (EPA; 20:5n-3); and (b) total polyunsaturated fatty acids (PUFAs) per mesocosm along the nutrient gradient in Paper IV. Black symbols represent mesocosms with added crucian carp, grey symbols represent mesocosms without fish. Significant quadratic relationships are depicted by curves (including goodness-of-fit; $R^2$).
Conclusions and future perspectives

Overall, this thesis highlights the important role of generalist predators in lake food webs by linking different pathways that lead to different interpretations of bottom-up and top-down regulation. Generalist predators that feed on more than one type of prey dominate ecosystems (Vander Zanden & Vadeboncoeur 2002; Rooney et al. 2008; Bartley et al. 2019). However, generalist predators are often not considered in empirical food-web studies, due to the spatial constraints that entails high replication. Even when those generalist predators are present in experimental enclosures, many studies focus only on a single food-web pathway (even Paper V in this thesis, in which I focused on the pelagic food web), assuming that influences from other food-web pathways (e.g. benthic) are negligible (but see e.g. Harmon et al. 2009; Marklund et al. 2019a; Vasconcelos et al. 2019) (Table 1). As this thesis presents, addressing alternative food-web pathways under shared predation is important to understand key food-web processes that otherwise might be neglected and that strongly affect bottom-up and top-down control of food webs (Fig. 13). I therefore urge to study and empirically test food webs as units that are functionally dependent on generalist predators.

This thesis also tested theoretical predictions of apparent competition theory using lake food webs as a model system in experimental mesocosms. By doing so, this thesis mechanistically confirmed the hypothesis that benthic and pelagic pathways of lake systems show strong indirect interactions through shared predation (Vander Zanden & Vadeboncoeur 2002). In addition, the observed indirect prey-prey interactions through shared predation also provide a mechanistic understanding of broad aquatic community changes at increased productivity (Jeppesen et al. 2003; Ward et al. 2015). Other types of environmental change in freshwaters (e.g. warming and browning) are known to affect food web coupling by predators or the dominance of different production pathways (Craig et al. 2015; Bartels et al. 2016; Bartley et al. 2019). Therefore, indirect interactions through shared predation are likely to play a big role on the responses of lake food webs to different types of environmental change.

The traits affecting resource coupling by generalist predators differed depending on the time-scale of the study. Short-term changes in resource coupling were mainly mediated by predator behavior, via changes of prey selection which depended on relative prey abundances (Paper III) or on visual environments that likely affected detection of different prey (Paper V).
However, over the ontogeny of predators, other factors such as fatty acid nutrition and growth likely affected long-term food web coupling of different pathways in addition to behavioral traits (Papers I & II).

Similarly, the measurable effects of resource coupling on food webs likely lead to contrasting responses depending on time scales. In short-term experiments, indirect interactions through shared predation in lake food webs resulted in apparent mutualism through switching predation (Paper III) that is likely to shift to apparent competition over the long term (e.g. Bety et al. 2002; Piovia-Scott et al. 2019). In addition, while the overall structure of pelagic food webs did not change in response to browning (Paper V), changes in traits and predator selection can have important long-term effects on food web structure and functioning.

Responses of lake food webs will likely highly depend on spatial scales too. Further manipulative studies at larger scales such as pond experiments, whole lake manipulations, etc. would be recommended to upscale the results of the 1.5 m deep, 0.8 m² mesocosms presented in this thesis. Spatial separation of habitats in combination with site fidelity and homing behavior of consumers can restrict the coupling shown in this thesis (Eklöv 1997; Quevedo et al. 2009). Yet, most abundant lake systems are small 100−1000-m² lakes (Verpoorter et al. 2014), which may have the highest resemblance in water-column depth and high surface to volume ratios compared to mesocosms. Over large ecosystems, spatial fluxes of resources, such as the ones between benthic to pelagic areas (e.g. via insect emergence, detritus sedimentation) and between terrestrial and aquatic systems may be key to offset the effects of habitat isolation and promote the coupling of resources that otherwise would not be accessible via predator mobility limitations (Polis et al. 1997).

In this thesis, I present responses of food webs mediated by single populations of predators. Although in some cases predation is monopolized by a single species of fish in specific conditions (e.g. Piironen & Holopainen 1988; Persson et al. 2004), one would expect that changes in environmental drivers are also reflected in changes of species composition in fish communities. Fish communities are known to display large changes across environmental gradients (e.g. Persson et al. 1991). Such changes may correlate with changes in main foraging traits that can feedback on top-down control (Jeppesen et al. 2003; Jönsson et al. 2012; Nurminen et al. 2014). Therefore, I suggest a trait based assessment of fish communities where the degree of coupling of different pathways and overall foraging efficiencies will be key in order to upscale the results of this thesis to full-scale communities. Overall, a bridging of spatial and temporal scales in food web studies are necessary to test the importance of the mechanisms presented in this thesis.

This thesis also presents some of the first results on the potential of fatty acid nutrition for regulating the niche over the ontogeny of consumers likely via life-history tradeoffs. In addition, I present some of the first evidences of
the variance partitioning of fatty acid composition over the ontogeny of consumers, showing that a common fish species has a strong capability of internal regulation of their fatty acid composition (which may be up to 70% compared to the 29% explained by diet), where a large fraction of fatty acid regulation (23%) depended on ontogenetic processes. Yet, roughly 50% of the variation attributed to internal regulation was unexplained by the model, leaving some room for further studies to know how other drivers than ontogeny affect fatty acid regulation and hence mediate niche responses to fatty acid nutrition. One of these processes could be fatty acid bioconversion that helps to upgrade the quality of fatty acids received from food. The results show some of the first evidences of the relevance of bioconversion in the fatty acid regulation in a natural population of a common freshwater fish. However, further experimental studies are necessary in order to measure the actual fitness costs of fatty acid regulation and bioconversion to confirm their importance in life-history tradeoffs and consumers niche suggested in this thesis.

Generally, the studies presented suggest that responses of food webs to environmental change seem complex; different drivers have different effects on the energy flow (bottom-up processes), interaction strength (top-down processes) and the coupling of food webs by generalist predators (food web reconfiguration). Nevertheless, one can see common features in terms of the mechanisms driving those changes in all types of food webs. Many consumers are generalist, many of which exhibit switching behavior. Both aquatic and terrestrial consumers need fatty acids and are likely to face mismatches in fatty acid availability compared to their diet, so that fatty acid regulation is likely affecting their life-history tradeoffs and eventually their fitness. Furthermore, indirect interactions through shared predation are also well known in terrestrial systems (Bety et al. 2002; Holt & Bonsall 2017; Thomsen et al. 2018; Piovia-Scott et al. 2019). Similarly, environmental change is likely affecting ecological features of terrestrial and marine predators as well as different production pathways and habitat accessibility across space (Bartley et al. 2019). Therefore, the results and the experimental designs presented in this thesis are likely to be transferrable to other systems.

In order to follow the path opened by Gary A. Polis (Polis et al. 2004), to study a nature without borders it is important to do food web ecology without borders.
Figure 13. Diagram representing lake food web processes according to the thesis, modified from Fig. 2. Solid arrows show trophic interactions. Dashed arrows show important food-web processes (not trophic interactions) that were studied in this thesis, while dashed squares depict the scope of the different papers. Papers I & II show that fatty acid regulation can influence the niche of consumers during their life by affecting their preferences for different resources and eliciting ontogenetic diet shifts. Paper III shows that the coupling of benthic and pelagic pathways in lake food webs by generalist predators can lead to short-term apparent mutualism among prey. Paper IV shows that generalist predation and nutrient inputs have consequences in the fluxes to terrestrial systems via aquatic insect emergence. Papers III, IV & V suggest that environmental change (i.e. browning and eutrophication) can affect food webs via bottom-up effects, top-down effects and also by affecting food web coupling through a food web reconfiguration. Fish pictures credit Katrin Attermeyer. Invertebrate pictures modified from Brönmark and Hansson (2005).
Comprehensive summary

Many organisms, including humans, need to feed on other organisms to fulfil their biological functions of survival, growth and reproduction. As a consequence, consumers and their food resources become linked by trophic interactions that build up a network of organisms called a food web. Food webs regulate the effects of ongoing environmental changes in the ecosystem. Such regulation is a result of the effects of resources on the abundance of their consumers (i.e. bottom-up effects) and/or in the influence of consumers on the abundance of their resources (i.e. top-down effects). Traditionally, the structure of food webs was simplified to linear food chains of trophic interactions where consumers that belong to higher trophic levels consume the biomass produced by the primary producers successively. However, aquatic food webs are known to diverge from the food chain model due to a number of processes inherent to the system. First, aquatic production pathways are often segregated into pelagic and benthic habitats and are largely affected by fluxes of resources from/to adjacent terrestrial ecosystems. These pathways are often coupled to some degree by mobile generalist consumers, such as fish, which lead to indirect effects among prey described by apparent competition theory. Second, consumers can also undergo resource specialization and changes in their diet during their life cycle (ontogenetic diet shifts) that can restrict their resource coupling.

Thus, my aim in this thesis was to test some of the drivers and processes that emerge when shifting from a traditional food-chain paradigm, where energy flow is streamlined and consumers have a single niche during their life to one of multiple food web pathways linked by generalist predators that can undergo changes in habitat use and diet during their life. First, I focused on the relationship between important nutrients, such as polyunsaturated fatty acids (PUFAs), and fish diet and habitat specialization, which should affect the role of fish in aquatic food webs. Using mesocosm experiments (containers that would allow the manipulation of a relatively complex food web), I tested the importance of bottom-up, top-down and reconfiguration processes for the responses of aquatic food webs to two types of environmental change (e.g. increasing nutrients and browning) and checked the effects on important fluxes of energy and nutrients from aquatic to terrestrial environments through the emergence of aquatic insects.

My first two studies investigated how perch, a well-studied and widespread fish species, regulated its nutritional composition of fatty acids during
their life in open-water and nearshore habitats when feeding on plankton, benthic invertebrate or fish. I found that most of the variation in fatty acid composition was determined by diet (28%) but, surprisingly, fatty acid composition was similarly impacted by ontogenetic changes (23%), while the 48% left remained unexplained and was attributed to internal regulation. Changes in the retention and mobilization of important PUFAs and fatty acids associated with energy storage reflected physiological changes over the lifetime of fish. I also found that perch mainly feeding on benthic invertebrates were not supplied with a key fatty acid for growth and development (Docosahexaenoic acid, DHA), but that they, nonetheless, had high proportions of this fatty acid in muscle tissues. To find out the reason behind this mismatch, I used fatty-acid-specific stable isotopes and found that part of the DHA was probably obtained from the bioconversion of other fatty acids such as eicosapentaenoic acid (EPA) in natural conditions. The cost of such fatty acid regulation in benthic feeders may help explain a lower body size and an earlier shift to fish-based diets in perch living in near-shore areas compared to open waters. In conclusion, fatty acid regulation may play an important role on the diet of fish and therefore affect the role of fish as a generalist predators in lake systems.

In a mesocosm experiment consisting of 20 containers each filled with about 1,000 L lake water and organisms, I found that changes in the top-down control on different prey along a productivity gradient were explained by the indirect positive interactions of benthic and pelagic prey via sharing the same predator. This so-called apparent mutualism was influenced by predator behavior, which switched from pelagic to benthic prey as the latter became more abundant at increasing levels of productivity. This study empirically proves former hypotheses that predicted high importance of indirect prey–prey interactions in responses of lake food webs along environmental gradients. In the same experiment, I investigated the consequences of bottom-up and top-down control on the export of PUFAs as important nutrients for terrestrial systems via the emergence of aquatic insects such as non-biting midges. I found that, though increasing productivity changed the PUFA composition of the species of midges, the flux of fatty acids and PUFAs mainly depended on the amount of midges emerging, which peaked at intermediate nutrient additions and highly decreased in the presence of fish. This suggests that bottom-up and top-down processes, as well as the coupling of the food web pathways affects the amount of nutrients and energy available for terrestrial predators.

In my fifth and last study I used another mesocosm study the effects of browning, which an ongoing process in many temperate and boreal lakes mainly (but not only) caused by the increase in colored terrestrial dissolved organic carbon tDOC. Particularly, I aimed to disentangle the effects of the two main features of browning (as both a shading agent and an energy source for organisms) on open-water food webs in the absence and presence
of top-fish predators (fish). Surprisingly, I did not see overall changes in food web structure in response to shading and/or DOC additions (neither by bottom-up or top-down control), which may suggest that open-water food webs can cope with short-term browning just through plastic traits and species composition shifts. However, we found that perch, the fish used, selected for orange-colored copepod plankton in clearwater conditions, whereas they selected for bright cladoceran plankton in low-light and browner water conditions. This means that browning may cause food web reconfiguration based on predator selectivity that could affect food web functioning beyond the time-scale of the study.

Overall, my results suggest that predictions of food web responses in aquatic systems and their exports to adjacent terrestrial systems are dependent on the coupling of different pathways and indirect interactions among prey through shared predation. Thus, this thesis demonstrates that the effect of certain environmental drivers on lake food webs would not be predicted by classic food chain theory, but rather by a conceptual framework including resource coupling and resource specialization over the ontogeny of consumers. These observations must not be overlooked when constructing a comprehensive model of food webs across time and space.
Sammanfattning på Svenska

Många organismer, inklusive människor, behöver livnära sig på andra organismer för att uppfylla sina biologiska funktioner för överlevnad, tillväxt och reproduktion. Som en konsekvens blir konsumenterna och deras resurser kopplade av trofiska interaktioner som bygger upp ett nätverk av organismer som kallas en födoväv. Födovävar reglerar effekter av miljöförändringar i ekosystemet. Regleringen visar sig i de effekter resurser har på antalet konsumenter (det vill säga botten-upp effekter) och/eller i den påverkan konsumenter har på mängden resurser (det vill säga toppen-ner effekter). Traditionellt sett har strukturen hos födovävar förenklats till näringskedjor av trofiska interaktioner där konsumenter på högre trofiska nivåer successivt konsumerar biomassa som producerats av de primära producenterna. Det är dock känt att akvatiska födovävar inte ingår i näringskedjemodellen på grund av ett antal processer bundna till systemet. För det första är akvatisk produktionsofta uppdelad i pelagiska och bentiska livsmiljöer och den påverkas till stor del av inkommande och utgående resurser från/till närliggande terrestra ekosystem. De här lokala resurserna eller spatialis resursflödena är ofta sammankopplade med rörliga generalistpredatorer, vilket leder till indirekta effekter bland bytesdjur som kan beskrivas av så kallad ”apparent competition”-teori. För det andra kan konsumenter bli resursspecialiserade och ontogeniska dietförändringar kan begränsa deras resurskoppling.

Tidigare forskning har varit inriktad på att testa skillnader i drivkrafter och processer av födovävar där energiflödet i näringskedjor är strömlinjeformat och konsumenter har en konstant nisch. I stället har jag i min avhandling använt mig av ett synsätt där flertalet födovävsvägar är kopplade till generalistrovdjur som kan ändra nisch under sin livstid. Först inriktade jag mig på förhållandet mellan viktiga näringsämnen, som till exempel fleromättrade fettsyror (PUFAs), fiskdiet och livsmiljöspecialisering, vilket bör påverka fiskens roll i akvatiska födovävar. Genom att använda mesokosmexperiment (behållare som möjliggör manipulering av en relativt komplex födoväv), undersökte jag vilken effekt av botten-upp och toppen-ner processer och födovävsrekonfigurationer som respons från akvatiska födovävar under två typer av miljöförändringar (det vill säga ökad mängd näringsämnen och förbrunning) samtligt som jag kontrollerade effekterna på viktiga flöden av energi och näringsämnen från akvatisk till terrestre miljö via utkläckning av akvatiska insekter.
Mina två första studier undersökte hur abborre, en välstudierad och utbredd fiskart, reglerade sin näringssammandragning av fettsyror under sitt liv i öppet vatten och strandnära livsmiljöer när de livnär sig på plankton, bentiska ryggradlösa djur eller fiskar. Jag upptäckte att den största delen av variationen i fettsyramansättningen berodde på deras diet (28%), fast förvånande nog var fettsyrona till nästan lika stor del styrd av ontogeniska förändringar (23%). Samtidigt kunde inte 48% av fettsyramansättningen förklaras, annat än att den skulle kunna vara kopplad till intern reglering. Förändringar i retention och mobilisering av viktiga PUFA:s, samt energilagrande fettsyror svarade mot fysiologiska förändringar under fiskens livstid. En fettsyra (Docosahexaenoic syra, DHA) är särskilt viktig för fiskens tillväxt och utveckling. Här visade jag att abborre som huvudsakligen livnär sig på bentiska ryggradlösa djur, som innehåller låga halter av DHA, hade höga halter av fettsyran i muskelvävnaden. För att ta reda på orsaken till den här felmatchningen använde jag fettsyrspecifika stabila isotoper från fiskar i naturliga förhållanden och såg att en del av mängden DHA troligen kommer från biokonvertering av andra fettsyror som t. ex. eicosapentanoic syra (EPA). Kostnaden för en sådan här fetterareglering kan förklaras av en mindre kroppstorlek och en tidigare förändring till fiskdiet för abborrar som lever i strandnära områden jämfört med öppet vatten. Sammanfattningsvis kan fettsyreglering spela en viktig roll för fiskars diet och kan på det viset påverka fiskens roll som en generalistpredator i sjöar.

I ett mesokosm-experiment med 20 behållare som var fyllda med ungefär 1 000 liter sjövatten och organismer, kunde jag visa att förändringar i toppen-ner kontroller av olika rovdjur långs en produktivitetsgradient kunde förklaras med indirekta positiva interaktioner av bentiska och pelagiska byttesdjur då de utsattes för samma predator. Denna så kallade ”apparent mutualism” påverkades av rovdjurets beteende, vilket ändrades från en preferens för pelagiska till bentiska byttesdjur när det senare ökade i mängd på grund av ökad produktivitet. Den här studien bekräftar tidigare empiriskt baserade hypoteser som förutsåg stora effekter av indirekta byte-byteinteraktioner på födovävsv förändring längs miljögradernter. Jag undersökte konsekvenserna av botten-upp och toppen-ner effekter på exporten av PUFAs. Jag studerade också deras betydelse som viktiga näringsämnen för terrestra system i samma experiment via utkläckning av vattenlevande insekter som till exempel stickfria myggor. Jag visade att flödet av fettsyror och PUFAs till största del berodde på mängden myggor som kläckte fram. Jag visade också att ökande produktivitet ändrade sammansättningen av PUFA i myggen och att mängden PUFAs nådde en topp vid medelhögt tillskott av näringsämnen och minskade kraftigt vid närvaro av fiskar. Det här tyder på att botten-upp och toppen-nerprocesser och kopplingen av födovävsgägar påverkar mängden näringsämnen och det energi som är tillgänglig för terrestra rovdjur.

I min femte och sista studie använde jag en annan mesokosm-uppsättning för att reda ut effekten av förbruning. Detta är en pågående process i
många tempererade och boreala sjöar främst (men inte bara) orsakade en ökad mängd färgat terrestert löst organiskt kol, tDOC. I synnerhet ville jag testa effekterna av de två största egenskaperna av förbruning (förändring av ljusklimatet och som energikälla för organismer) för födovävar i öppet vatten med och utan närvaro av rovfiskar i toppen av födoväven. Förvånande nog såg vi inte några övergripande förändringar i strukturen av födoväven som respons på mörkkläggnings och/eller tillsatser av tDOC (inte heller med botten-upp och toppen-nerkontroller). Detta kan tyda på att födovävar i öppet vatten kan hantera korttidsig förbruning genom att ändra sammansättningen av arter och att arterna kan ha plastiska egenskaper. Vi såg dock att den fisk vi studerade, abborre, valde orangefärgade hoppsköldor i klart vatten, men valde ljus färgade hinnkräfter i svagt ljus och brunare vatten. Det betyder att förbruning kan ge upphov till förändringar i födoväven baserad på selektivitet hos rovdjuret, som kan påverka funktionaliteten hos födoväven som kan sträcka sig bortom studiens tidsskala.

Sammantaget pekar mina resultat på att födovävskopplingar är i akvatiska system beror på indirekta interaktioner mellan bytesdjur och gemensamma rovdjur vilket i sin tur påverkar export av näringsämnen till närliggande terrestra system. Med andra ord visar den här avhandlingen att vissa miljöfaktorers effekter på födovävar i sjöar inte kan beskrivas av klassisk näringskedjeteori, utan snarare av en modell som innehåller resurskoppling och resursspecialisering över konsumenternas ontogeni. Man borde ta hänsyn till detta för att få en övergripande modell av födovävar som är användbara över tid och rum.
Muchos organismos, incluidos los seres humanos, necesitan alimentarse de otros organismos para cumplir sus principales funciones biológicas como supervivencia, crecimiento y reproducción. Como consecuencia, los consumidores y sus recursos alimentarios se unen por interacciones tróficas que crean una red de organismos llamada red alimentaria. Las redes alimentarias regulan en gran manera los efectos de cambios medioambientales en el ecosistema, a través de alterar los efectos de los recursos alimentarios en la abundancia de los consumidores (i.e. efectos “bottom-up”) y/o al afectar la influencia de los consumidores en sus fuentes de comida (i.e. efectos “top-down”). Tradicionalmente, la estructura de las redes alimentarias se ha simplificado en cadenas alimentarias, en donde la biomasa creada por los productores primarios es consumida sucesivamente por consumidores que pertenecen a niveles tróficos superiores. Sin embargo, las redes alimentarias en los lagos se alejan de este modelo de “cadena alimentaria” debido a procesos inherentes a dichos ambientes. Primero, la producción en los lagos está separada espacialmente en hábitats pelágicos de aguas abiertas y hábitats bentónicos asociados al sedimento, y asimismo, éstos están grandemente influenciados por los flujos de recursos desde/hacia ecosistemas terrestres adyacentes. Tanto los recursos locales como los intercambiados con otros ecosistemas son fuente de alimento de consumidores móviles y generalistas, como los peces, y esto hace que las distintas presas estén indirectamente relacionadas entre sí (a través del depredador común) siguiendo la teoría de competencia aparente. Segundo, los consumidores también pueden desarrollar especialización hacia ciertas presas y cambios en la dieta durante su ciclo vital, lo cual restringe su capacidad acopladora de distintas redes alimentarias.

Mi objetivo en esta tesis ha sido el de investigar los efectos de las características emergentes de redes alimentarias en contraposición a las simples cadenas alimentarias en ecosistemas lacustres. Dentro de esta cuestión, primero me he focalizado en la relación entre nutrientes importantes como los ácidos grasos poliinsaturados (AGPs), y la especialización de los peces por diferentes recursos y hábitats, lo cual podría afectar al rol de los peces en las redes alimentarias lacustres. Usando experimentos con mesocosmos (o contenedores que permiten manipular una red alimentaria relativamente compleja), he investigado la influencia de los efectos “bottom-up”, “top-down” y de la configuración de las redes
alimentarias en las respuestas de dichas redes a dos tipos comunes de cambios medioambientales (p. ej. incremento de nutrientes y coloración de las aguas) y los posteriores efectos en los flujos de recursos y nutrientes a ecosistemas terrestres a través de la eclosión de insectos acuáticos.

En mis primeros dos estudios he investigado como las percas, una especie común de pez que es común y ampliamente estudiada, regulan su composición de ácidos grasos durante su ciclo vital en aguas abiertas o en las zonas litorales de los lagos, cuando se alimentan de plancton, invertebrados bentónicos o peces. En ellos, he encontrado que la mayor parte de la variación en la composición de ácidos grasos en las percas dependía de regulación interna, en donde la dieta explica solamente un 28% de la variación. Sorprendentemente, cambios en el ciclo vital explican un 23% de la composición de ácidos grasos, mientras que un 48% de la variación asociada a regulación interna no pudo ser explicada. Cambios en la composición de ácidos grasos relacionados con la dieta se explicaron mayoritariamente por de ácidos grasos que no son fisiológicamente importantes, mientras que cambios en la retención o movilización de los AGPs importantes y cambios en ácidos grasos de reserva de energía explican los cambios de composición relativos al ciclo vital de las percas. Asimismo, se encontró que las percas con dietas bentónicas no tenían acceso a un ácido graso clave en el desarrollo y el crecimiento (el ácido docosaeaxenoioco, o DHA), pero que en cambio tenían en altas proporciones en sus tejidos. Para encontrar el proceso detrás de este desequilibrio he utilizado isótopos estables del carbono de cada ácido graso y he encontrado que las percas con dietas bentónicas conseguían parte del DHA probablemente a través de la bio-conversión de otros AGPs precursores, como el ácido eicosapentaenoico (EPA), en circunstancias naturales. El coste de esta regulación de ácidos grasos en percas con dietas bentónicas se puede explicar el menor tamaño y la transición más temprana a dietas piscívoras en las percas litorales del estudio comparadas con las percas de aguas abiertas. Como conclusión, la regulación de ácidos grasos puede que sea un factor importante en la dieta de los peces y en consecuencia afectar el papel de los peces como consumidores generalistas de las redes tróficas lacustres.

En un experimento consistente en 20 mesocosmos de aproximadamente llenados con aproximadamente 1000 L de agua y organismos de un lago, encontré que los cambios substantiales en el “top-down” control de las diferentes presas en un gradiente de productividad se explicaban por las interacciones indirectas positivas entre presas bentónicas y de aguas abiertas al compartir el mismo depredador. Este efecto, conocido como mutualismo aparente, estuvo influenciado por el comportamiento del depredador, el cual focalizó los esfuerzos en la presa más abundante a medida que la densidad de presas bentónicas aumentó promovida por la subida de la productividad. Este es el primer estudio que presenta evidencias experimentales de anteriores hipótesis que predecían la importancia de las interacciones
indirectas entre presas en las redes alimentarias lacustres y consiguientemente en las respuestas de las redes alimentarias a cambios medioambientales. En el mismo estudio, he estudiado las consecuencias de los efectos “bottom-up” y “top-down” en los flujos de AGPs como nutrientes importantes para animales terrestres a través de la eclosión de insectos acuáticos conocidos como quironómidos. Aunque el incremento de productividad en el sistema cambió la composición de los ácidos grasos en las especies más abundantes de quironómidos, el flujo de ácidos grasos y de AGPs dependió en mayor medida en la cantidad de quironómidos que eclosionaron, la cual alcanzó su nivel más alto en concentraciones intermedias de nutrientes y que decreció considerablemente en presencia de peces. Esto sugiere que tanto los efectos “bottom-up” como los “top-down”, así como la estructura de las redes alimentarias afecta la magnitud de los flujos de nutrientes y energía disponibles para organismos terrestres.

En mi quinto y último estudio he usado un diseño de experimentos con los mismos mesocosmos anteriormente citados para estudiar los efectos de la coloración del agua que está ocurriendo en muchos lagos de regiones templadas y boreales, y que en gran medida (pero no solamente) está ocasionada por el incremento de carbón orgánico disuelto de origen terrestre (CODt). Mi objetivo ha sido el de separar los distintos efectos de CODt (como absorbente de luz y como fuente de energía) en las redes alimentarias de aguas abiertas en presencia o ausencia de peces depredadores. Sorprendentemente, no se detectaron grandes cambios en la estructura general de dichas redes alimentarias en respuesta a tratamientos con malla de sombra y/o a las adiciones de CODt (ni tampoco debido a “bottom-up” y “top-down” control), lo que sugiere que las cadenas alimentarias pelágicas pueden sobrellevar la coloración de los lagos a corto plazo a través de cambios en la composición de las comunidades y de cierta plasticidad funcional. Sin embargo, he encontrado que las percas, que fueron el pez introducido en los mesocosmos, seleccionaron copépodos de color naranja en aguas claras, mientras que cladóceros, de un color claro, fueron seleccionados en aguas oscuras provocadas por la sombra y la adición de CODt. Esto significa que la coloración de los lagos podría causar cambios en la configuración de las redes alimentarias basados en cambios de selectividad de presas, que a su vez puede que afecten el funcionamiento de las redes alimentarias a largo plazo.

En general, mis resultados sugieren que las respuestas de las redes alimentarias acuáticas y sus exportaciones a sistemas terrestres adyacentes dependen de la unión de varios caminos tróficos e interacciones indirectas entre presas a través de un depredador común. Por consiguiente, esta tesis demuestra que el efecto de ciertos agentes medioambientales sobre las redes alimentarias lacustres no se podría haber predicho por la teoría de cadenas alimentarias, sino por modelo que incluya la unión de diversos recursos por consumidores generalistas así como la especialización de aquellos
consumidores generalistas en distintas presas y en distintos estadios de su ciclo vital. Estas observaciones no deben pasarse por alto al construir un modelo integral de redes alimentarias a través del espacio y el tiempo.
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References


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