



Aqua Introductory Research Essay 2016:2

Effects of size dependent predator-prey interactions and fisheries on population dynamics and bioaccumulation of dioxins and PCBs in Baltic salmon, *Salmo salar* L., and its fish prey

Philip Jacobson



Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Department of Aquatic Resources

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Philip Jacobson

Swedish University of Agricultural Sciences, Department of Aquatic Resources,
Institute of Coastal Research, Skolgatan 6, 742 42 Öregrund

May 2016

Aqua Introductory Research Essay 2016:2
ISBN: 978-91-576-9415-7 (electronic version)

E-mail:
philip.jacobson@slu.se

Principal supervisor:
Magnus Huss, Associate Senior Lecturer, Department of Aquatic Resources, Swedish University of
Agricultural Sciences

Deputy supervisors:
Prof. Anna Gårdmark, Department of Aquatic Resources, Swedish University of Agricultural Sciences
Johan Östergren, PhD, Department of Aquatic Resources, Swedish University of Agricultural Sciences

Reviewers:
Prof. Erik Petersson, Director of postgraduate studies, Department of Aquatic Resources,
Swedish University of Agricultural Sciences

To be cited as follows:
Jacobson, P. (2016). Effects of size dependent predator-prey interactions and fisheries on population dynamics and bioaccumulation of dioxins and PCBs in Baltic salmon, *Salmo salar* L., and its fish prey. Aqua Introductory Research Essay 2016:2. Department of Aquatic Resources, Swedish University of Agricultural Sciences, Drottningholm Lysekil Öregrund. 47 p.

Keywords:
Baltic Sea, community dynamics, hazardous substances, herring, population dynamics, salmon, size-specific predator-prey interactions, size-structured populations, sprat

The essay can be downloaded at:
<http://pub.epsilon.slu.se/>

Series editor:
Magnus Appelberg, Head of Department, Department of Aquatic Resources, Öregrund

Front cover: The gape of a Baltic salmon smolt caught in the river Rickleån in May 2016.
Photo: Johanna Hägglund, SLU.

Back cover: Baltic Sea herring, sprat and three-spined stickleback caught during the Baltic International Acoustic Survey (BIAS) in 2012. Photo: Yvette Heimbrand, SLU.

Abstract

Animal populations have historically often been viewed as groups consisting of identical individuals. However, as almost all animal taxa grow during ontogeny, populations do consist of differently sized individuals which affect their environment in different ways. As growth, survival and reproduction all scale differently with body size, individual performance and ecology is not constant over life history. This has proven to be crucial for understanding size-structured population- and community dynamics. Consequently, accounting for size- and food-dependent processes is also important for understanding how fish populations, which are highly size-structured, respond to changes in major drivers such as productivity and mortality. Still, despite recent insights about the importance of food- and size-dependent processes few studies take them into account. Knowledge of how food- and size-dependent individual processes affect population- and community dynamics in taxa with complex life cycles, e.g. ontogenetic habitat shifts, is lacking. One example is research and management regarding diadromous fish species, such as the Atlantic salmon. The population of Atlantic salmon roaming in the Baltic Sea, i.e. Baltic salmon, are exploited by both commercial and recreational fisheries and contains elevated concentrations of hazardous substances which they accumulate by feeding on prey fish. One potential management method to reduce the dioxin and PCB in Baltic salmon is increased fishing on the two main prey species of Baltic salmon, herring and sprat. This management method have been suggested without accounting for food- and size dependent individual processes and size-specific predator-prey interactions. This essay clarifies why size- and food dependent individual-level processes and size-specific predator-prey interactions should be accounted for to improve our understanding of the ecology and management of Baltic salmon. Furthermore, this essay specifically highlights the importance of accounting for these processes when designing management measures to decrease the dioxin and PCB content in Baltic salmon and its prey species.

Keywords: Baltic Sea, community dynamics, hazardous substances, herring, population dynamics, salmon, size-specific predator-prey interactions, size-structured populations, sprat.

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Abbreviations

BSAP	The Baltic Sea Action Plan
CRD	Critical Resource Density
DDT	Dichloro-diphenyl-trichloroethane
EC	European Commission
HELCOM	The Helsinki Commission
ICES	The International Council for the Exploration of the Sea
IGP	Intra Guild Predation
OSPAR	A commission formed at the Oslo and Paris environmental convention in 1992
PCB	Polychlorinated biphenyls
PCDD	Polychlorinated-dibenzodioxins
PCDF	Polychlorinated-dibenzofurans
SC	The Stockholm Convention

1 Introduction

Animal populations have historically often been viewed as groups of identical individuals, a view which is still common in population and community ecology (Lindeman, 1942; Pimm et al., 1991; Berryman, 1992; Brose et al., 2006; Edwards et al., 2007; Bolnick et al., 2011). Still, ecologists have since long observed trait variation between individuals, both within and between populations (van Valen, 1965; Roughgarden, 1972; Wilbur, 1980; Werner and Gilliam, 1984; Bolnick et al., 2003). One reason for trait variation within populations is variation in body size. The latter results from that almost all animal taxa grow to maturation, i.e. undergo ontogenetic development, and many also continue to grow after maturation (e.g. fish and reptiles) (Wilbur, 1980; Werner and Gilliam, 1984; Sebens, 1987). Individual body growth requires energy and is thus always dependent on food. As food intake and metabolism vary with body size in different ways, individuals will gain different amounts of energy from a shared prey depending on their body size. To sustain positive growth rates, individuals often change their diet as they grow, i.e. undergo ontogenetic diet shifts. Such diet shifts can also be associated with habitat shifts as different prey organisms occupy different habitats. Therefore, individuals interact differently with their environment over life history, e.g. feed on different organisms and are exposed to different predators (Werner and Gilliam, 1984). Thus, populations consist of differently sized individuals which interact with their surroundings in different ways. Consequently, accounting for individual ontogenetic development has proved important for our understanding of population- and community dynamics in general, and size-dependent competition and predator-prey interactions specifically (Polis and Strong, 1996; Rudolf and Lafferty, 2011; Huss et al., 2012; van Leeuwen et al., 2013; de Roos and Persson, 2013; Gårdmark et al., 2015). Still, a majority of studies about population dynamics ignore variation within populations (e.g. Krivan, 1996; Brose et al., 2006; Edwards et al., 2007; Bolnick et al., 2011).

Accounting for individual size-dependent processes, e.g. growth, mortality and reproduction, are important to gain a mechanistic understanding of size-structured population dynamics. This has been experimentally demonstrated using *Daphnia* (Slobodkin, 1954), soil-mites (Cameron and Benton, 2004), *Holopedium* (Huss and Nilsson, 2011), dragonfly larvae (Rudolf and Armstrong, 2008) and fish (Schröder et al., 2009). For fish, individual size-dependent processes have shown to be important for explaining how fish populations and communities are affected by external drivers such as mortality, e.g. from fisheries and pathogens (van Kooten et al., 2007; Ohlberger et al., 2011; Huss et al., 2014; Persson et al., 2014; Gårdmark et al., 2015) and productivity (Rudolf and Armstrong, 2008; Huss et al., 2012). As been pointed out by Persson et al. (2014), fisheries management still often treats fish

populations as groups of homogenous individuals despite their size-structured nature with few exceptions (e.g. Möllmann et al., 2013). Furthermore, theoretical studies have exemplified the importance of accounting for ontogenetic niche shifts for fisheries management (e.g. van de Wolfshaar et al., 2011; van Leeuwen et al., 2013; 2014). Recent studies have addressed the lack of knowledge regarding food- and size-dependent individual processes and its effects on population and community dynamics in taxa with complex life cycles (Polis and Strong, 1996; Schreiber and Rudolf, 2008; Rudolf and Lafferty, 2011; Reichstein et al., 2015). For example, food- and size-dependent individual-level processes are still overlooked in research and management of anadromous fish species, e.g. the Atlantic salmon, *Salmo salar* L. The Atlantic salmon in the Baltic Sea, hereafter Baltic salmon or salmon, consists of several populations which all undergo ontogenetic diet and habitat shifts (Ståhl, 1987; Karlsson and Karlström, 1994; Hansson et al., 2001; Salminen et al., 2001; Ikonen, 2006; Palmé et al., 2012b; Östergren et al., 2014a). Also, they are exploited by size-selective fisheries (ICES, 2013). Furthermore, Baltic salmon contain elevated levels of hazardous substances, i.e. substances which are persistent, toxic and bioaccumulate (the concentration of these substances increases within each trophic level of the food-web compared to the concentrations in the surrounding environment) (Mackay and Fraser, 2000; Vuorinen et al., 2002; HELCOM, 2010; Livsmedelsverket, 2012). These hazardous substances are present in the Baltic sea food web and enters the salmon as it eats other fish (Strandberg et al., 1998; Vuorinen et al., 2002; 2012). Therefore, given a strong size-dependency in predator-prey interactions, the biomaccumulation of hazardous substances is most likely food- and size-dependent.

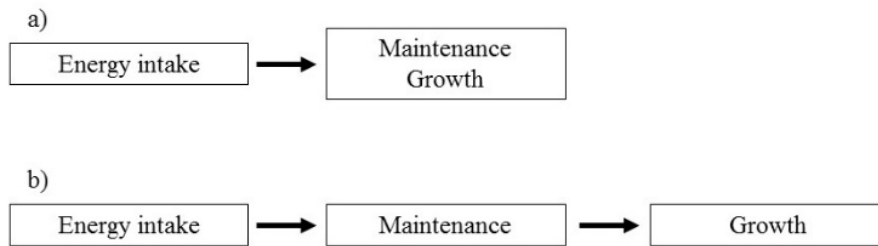
In this essay, I review major implications of food-dependent ontogenetic development for fish population and community dynamics. I specifically clarify why size-specific scaling of individual vital rates, food-dependent body growth, size-selective fisheries and size-specific predator-prey interactions need to be accounted for in research regarding (1) the dynamics and management of anadromous fish populations and (2) bioaccumulation of contaminants in food webs, especially with respect to dioxins and PCBs in Baltic Sea salmon and its prey species.

1.1 Individual size- and food-dependencies

All heterotrophic organisms need energy gained from feeding to sustain vital metabolic processes, enable growth and to develop gonads for reproduction. Energy intake from feeding can be allocated according to the net-assimilation model (Fig. 1a, c) (Kojiman and Metz, 1984) or the net-production model (Fig. 1b, d) (Persson et

al., 1998). For juveniles, the net-assimilation model does not separate between energy allocation for maintenance, i.e. sustaining vital metabolic processes, and growth. Thus, maintenance costs do not have to be covered before energy can be allocated to growth (Fig. 1a). In contrast, in the net-production model, maintenance costs are covered before energy can be allocated to growth (Fig. 1b). For adults, the net-assimilation model does not separate between energy allocation for maintenance and growth. Instead, a threshold of energy allocated into maintenance and growth must be covered before energy can be allocated into reproduction (Fig. 1c). The net-production model separates between energy allocation to maintenance, growth and

Juveniles



Adults

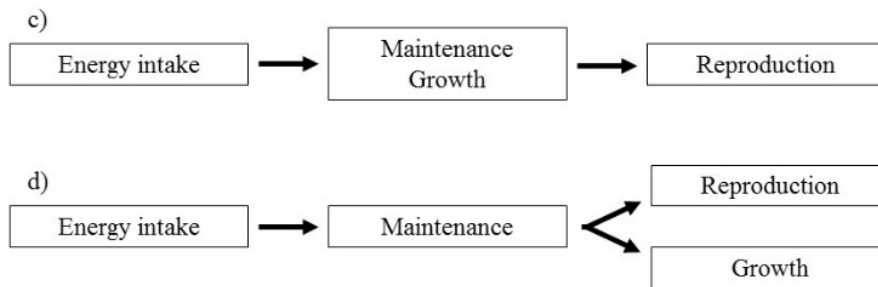


Figure 1. A schematic illustration of two energy allocation models for juvenile (non-mature) and adult (mature) fish. a) and c) show energy allocation according to the net-assimilation model for juveniles and adults (Kojiman and Metz, 1984). b) and d) show energy allocation according to the net-production model for juveniles and adults (Persson et al., 1998). Energy intake = energy gained via consumption. Maintenance = energy needed to sustain vital metabolic processes. Growth = energy invested into somatic (i.e. non-gonadal) growth. Reproduction = energy invested in gonad development.

reproduction. The maintenance cost has to be covered before energy can be allocated into growth and/or reproduction (Fig. 1d). In theoretical studies regarding size-structured fish populations, the net-production model is commonly favored as fish can survive and reproduce without growing and can grow without reproducing (e.g. Persson and de Roos, 2006). Despite the differences between the two models,

energy allocated for maintenance, growth and reproduction are always dependent on energy intake, i.e. the success in capturing and eating prey.

Maintenance costs generally increase with body size (Brown et al., 2004; Glazier, 2005), following equation 1:

$$I(w) = I_0 w^b \quad (1)$$

in which $I(w)$ is the maintenance cost, I_0 is a size-independent metabolic constant, w is body mass and b is the size scaling exponent of the maintenance cost. The mass-specific increase in maintenance cost is derived as:

$$w^b/w^1 = w^{b-1} = w^c \quad (2)$$

The exponent b generally take a value close to $\frac{3}{4}$ for animal taxa (Brown et al., 2004). Thus, the mass-specific metabolism decreases with increased body mass (Fig. 3a). As both maintenance costs and energy intake govern growth and reproduction, the amount of surplus energy gained depends on the size-scaling of maintenance costs and foraging success.

1.1.1 Foraging, maintenance and body growth

For fish (and many other organisms), individual foraging is governed by two processes, attack rate and handling time (Persson and de Roos, 2006). Individual attack rate, i.e. the number of attempts to capture prey during a given time, depends on the predators' ability to detect and capture the prey. Both prey detection and capture are affected by the predators' size, the prey size and the prey density, usually following a Holling type II functional response (Mittelbach, 1981; Mittelbach and Persson, 1998; Byström and Garcia-Berthou, 1999; Hjelm and Persson, 2001). A predator's attack rate on a prey of a fixed size generally follows a hump shaped relationship with predator body size, following equation 3:

$$a(w) = A \left(\frac{w}{w_0} \exp\left(1 - \frac{w}{w_0}\right) \right)^\alpha \quad (3)$$

in which A is the maximum attack rate, w is the body mass, w_0 is the body mass at which A is achieved and α is the size scaling exponent of the attack rate. First, the attack rate increases with increased predator size and then, after reaching a maximum, decreases with increased predator size (Fig. 3b) (Persson et al., 1998; Wahlström et al., 2000; Hjelm and Persson, 2001). The initial increase in attack rate with predator size is due to increased locomotive skills and the increased possibility to distinguish prey (for visual predators) (Webb, 1976; Miller et al., 1993). The

decrease at large predator size is due to decreased fine-scale maneuverability and decreased possibility to distinguish small prey (Schoener, 1969; Webb, 1976; Breck and Gitter, 1983; Miller et al., 1993).

Handling time has been defined in many different ways (e.g. Jeschke et al., 2002). One definition used for fish equals handling time with the digestion time per unit ingested prey biomass (e.g. Claessen et al., 2000). An alternative definition is that it equals the time for a predator to capture and completely swallow a prey (e.g. Nilsson and Brönmark, 2000). Following the definition by Claessen et al. (2000), handling time can be described as:

$$H(w) = dw^f \quad (4)$$

in which $H(w)$ is the handling time, d is a digestion constant, w is body mass and f is the size scaling exponent of digestion. As the digestive tract increases with increased body mass, handling time decreases with increased size (i.e. f is negative, Eq. 4, Fig. 3c). Thus, as both attack rate and handling time vary with body mass (Fig. 3b, c), so does energy intake. Energy intake, in turn, determines the amount of surplus energy that is available for growth and/or reproduction (Fig. 1b, d). As maintenance costs, attack rate and handling time scale differently with body size, the surplus energy gained from a shared resource will not be constant over life history. In a scenario with unlimited resource supply, energy intake is not limited by attack rate and only handling time will affect energy intake. As a consequence, the maximum consumption of the resource equals the inversed handling time:

$$C_m = 1/H(w) \quad (5)$$

in which C_m is the maximum consumption and H is handling time. Consequently, at high resource availability, it is the difference between the body-size scaling of maintenance costs and digestion that determines the surplus energy (Fig. 2). In a scenario with limited resources, it is instead mainly attack rate that will affect foraging success. As metabolic costs increases with size (Fig. 3a), individuals need different amount of resources to cover their maintenance costs depending on their body size, referred to as the Critical Resource Density, CRD (Persson et al., 1998). The CRD is calculated as:

$$CRD = I(w)/a(w)(c - I(w) * H(w)) \quad (6)$$

in which $I(w)$ is the maintenance cost (Eq. 1), $a(w)$ is the attack rate (Eq. 3), c is an energy conversion constant and $H(w)$ is the handling time (Eq. 4). For many fish

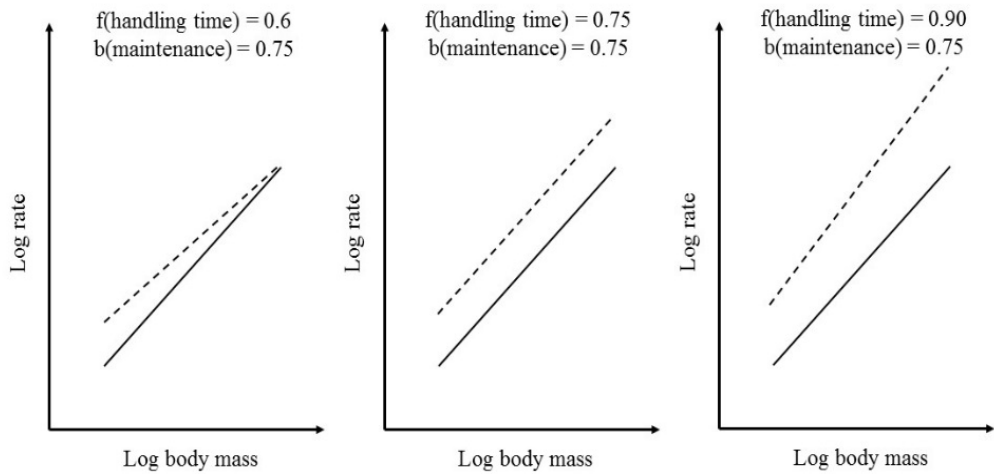


Figure 2. A conceptual figure of the change in surplus energy gained with increased body size at ad lib resource density. Dashed line show the maximum consumption rates (Eq. 5) and solid lines the maintenance costs (Eq. 1). Left panel; consumption max exponent = 0.6, Center panel; consumption max exponent = 0.75 and right panel; consumption max exponent = 0.9. The metabolic scaling exponent = 0.75 in all plots.

species (e.g. roach, *Rutilus rutilus*, L.: Hjelm and Persson, 2001; and Arctic char, *Salvelinus alpinus*, L.: Byström et al., 2006), small individuals can cover their

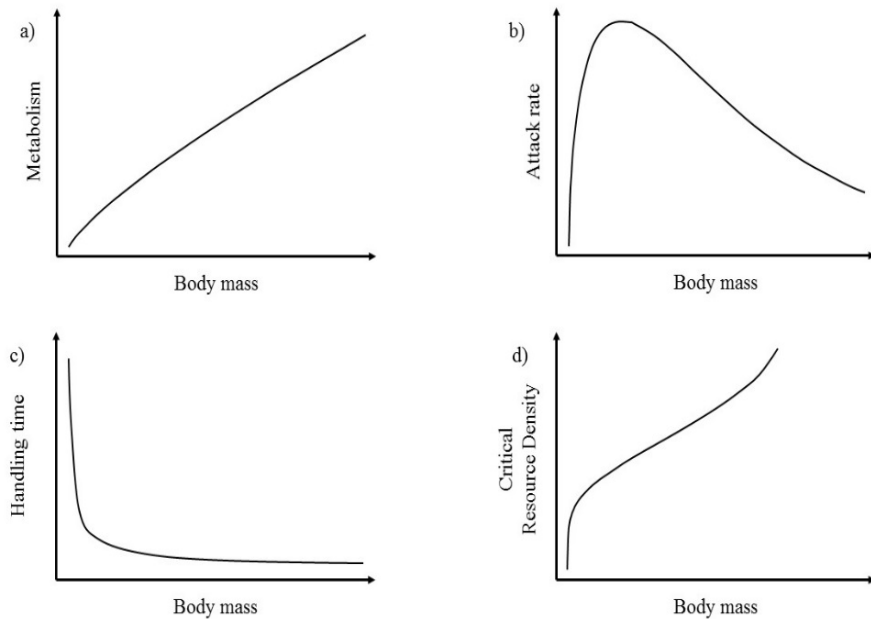


Figure 3. A schematic presentation of a) metabolism, b) attack-rate, c) handling time and d) the critical resource density as a function of body size for a zooplanktivorous sprat, *Sprattus sprattus* L. All parameters are set according to (Huss et al., 2012). For a), equation 1 was used with the following parameters: $I_0 = 0.03$, $b = 0.8$. For b), equation 3 was used with the following parameters: $A = 150$, $w_0 = 50$ and $\alpha = 0.5$. For c), equation 4 was used with the following parameters: $d = 6.7$ and $f = -0.67$. For d), equation 6 was used with the parameters from Eq. 1, 3 & 4.

maintenance costs at a lower resource density than large individuals (Fig. 3d). The latter relates to the difference in size-scaling between maintenance costs and attack rate (Persson and de Roos, 2006). Persson and de Roos (2006) showed that α (Eq. 3) tend to vary between 0.47-0.67 for fishes. As this is generally less than the metabolic scaling exponent, CRD usually increases with increased size, making small individuals superior to large ones in competition for shared resources.

1.1.2 Size-dependent reproduction and mortality

The rates of food intake and of metabolism govern the possibilities for juveniles to grow and reach sexual maturation. Once an individual is mature, surplus energy can be invested in either growth or reproduction (Fig. 1b, d). Reproduction success in fish, i.e. the number of surviving offspring per reproduction effort, has been shown to increase with body size (Hixon et al., 2014). This positive size-dependency can either be the result of an increase in the number of eggs produced, increased egg quality or both (e.g. Duarte and Alcaraz, 1989; Fleming, 1996; Hixon et al., 2014; Vladić and Petersson, 2015). Both strategies are common but there is a trade-off between producing many small or few but large eggs. Generally, pelagic spawning fish tend to produce many, small eggs compared to benthic spawning fish which tend to produce fewer, larger eggs (Duarte and Alcaraz, 1989). Irrespective of strategy, increased body size increases the possibility to invest in larger gonads, increasing either the number or the size of eggs produced (Hixon et al., 2014).

Mortality rates are also commonly size-dependent, generally declining with increased size and age (Werner and Gilliam, 1984; McGurk, 1986; Lorenzen, 1996; Huss et al., 2008). This negative relationship is due to the individual's possibility to survive starvation and to a decreased predation risk. The possibility to store reserves increases with size, showing a linear relationship (Huss et al., 2008). Therefore, the size-specific maintenance cost will determine how fast these reserves are expended and the individual starve to death during periods of low food production, e.g. winter. Because the maintenance cost increases with body size with an exponent that is less than one (Eq. 1), the relative maintenance cost per unit biomass decreases with increased size (Fig. 3a). Therefore, a small individual will expend their reserves faster compared to a large individual. Consequently, a small individual cannot survive starvation to the same extent as a large individual can as it has less reserves on both an absolute and relative scale (Post and Evans, 1989; Huss et al., 2008). Predation risk decreases with size as larger individuals can escape predators better than small. Also, individuals can reach a predation size-refuge, becoming too large to consume for gape-limited predators (Lundvall et al., 1999; Nilsson and Brönmark, 2000; Scharf et al., 2000). Thus, the possibility to invest surplus energy into growth and reserves affects an individual's mortality risk.

1.2 Ontogenetic niche shifts

When maintenance costs increase with size at a faster rate than energy intake (Fig. 2 & 3a), the growth rate will decrease as the individual grows (g_1 in Fig. 4). One way to increase the amount of surplus energy is to shift to feed on a larger, more energy rich prey (g_2 in Fig. 4). In the case that there are no alternative prey types in the

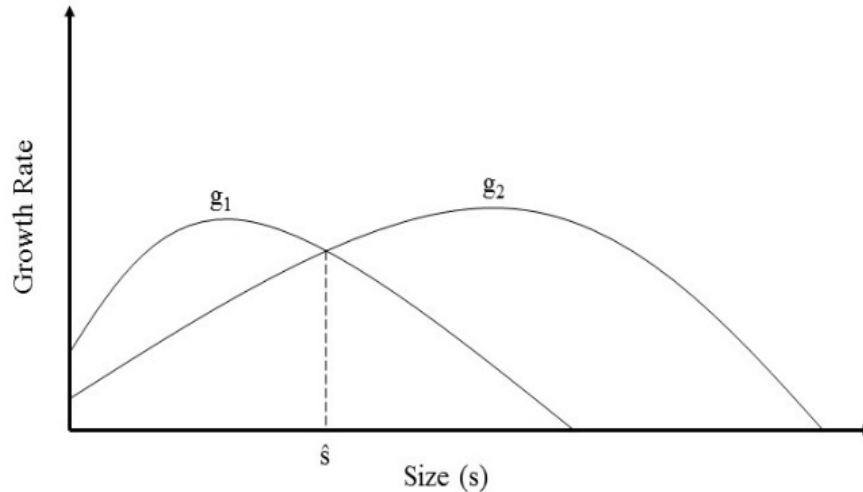


Figure 4. Growth rates when feeding on two different prey-types (g_1) and (g_2) as a function of body size. The dashed line indicates the optimum size for switching prey-type (\hat{s}) for maximizing growth. Reproduced from (Werner and Gilliam, 1984 p. 402).

same habitat, the individual may have to shift habitat to sustain positive growth. Both resource- and/or habitat shifts are common for many fish species. These ontogenetic niche shifts have since long been a topic for both theoretical and empirical studies, mainly focusing on factors affecting the timing of these shifts (Schoener, 1969; 1971; Wilbur, 1980; Mittelbach, 1981; Werner and Gilliam, 1984).

Ontogenetic diet shifts can either be continuous (occur gradually with increased body length) or discrete, occurring at a specific length-threshold or life-stage (i.e. metamorphosis) (Werner and Gilliam, 1984). For fish, ontogenetic diet shifts are very common. Many fish species start feeding on small invertebrates as juveniles, e.g. zooplankton, and with increasing size also feed on larger invertebrates, e.g. amphipods (e.g. Horppila et al., 2000; Hjelm et al., 2003). Some fish species also undergo a second diet shift to feed on prey fish, i.e. piscivory (Mittelbach and Persson, 1998; Scharf et al., 2000). Ontogenetic diet shifts are often associated with habitat shifts, due to a difference of prey composition in different habitats. As an example, the Eurasian perch, *Perca fluviatilis* L., undergoes two diet shifts, from zooplankton to macroinvertebrates to fish, as it increases in length (Horppila et al., 2000; Estlander et al., 2010). Svanbäck and Eklöv (2002) showed that the diet composition

of perch was associated with the habitat in which they were caught. Zooplankton dominated the diet of perch caught in the pelagic habitat compared to perch caught in the littoral zone which mainly fed on macroinvertebrates and fish. Similar diet differences between habitats have been observed for roach. They mainly feed on zooplankton in the pelagic habitat but on plant material in the littoral habitat (Horppila et al., 2000). Thus, diet and habitat shifts can either be two separate shifts or co-occur as a response to a difference in prey composition and abundances between habitats.

1.2.1 Diadromy

One example of ontogenetic diet- and habitat shifts in fish is the movement between marine and freshwater (diadromy), which occurs in several species such as eels, e.g. European eel, *Anguilla anguilla* L., and salmonids, e.g. Atlantic salmon (Gross et al., 1988; Klemetsen et al., 2003; van Ginneken et al., 2005). Studies regarding why diadromy occurs and why some anadromous populations consist of both non-migrating and migrating individuals have focused on the trade-off between energy costs/gain, mortality risk and reproduction success (Nordeng, 1983; Gross, 1987; 1988; Hansen and Quinn, 1998; Kinnison et al., 2001). According to Gross (1987), if the fitness (total reproductive output) is higher for migrating individuals, diadromy should be favored. Accordingly, Gross (1987) argued that migration should be selected for if the increased body growth and reproductive success exceeded the increased mortality risks and increased energy costs of migration. Thus, depending on differences in resource availability, which govern growth, between the two habitats, diadromy will be favored or not. Nordeng (1983) showed that the tendency to migrate in a population of anadromous Arctic charr was dependent both on genetics (if the parents migrated or not) and on the amount of resources in the first habitat. At favorable feeding conditions, fewer individuals with anadromous (migration from freshwater to the ocean and back) parents migrated than at poor feeding conditions. Furthermore, anadromy has been shown to be more common in temperate regions, where oceans tend to be more productive than freshwaters and vice versa in tropical regions, in which catadromy (migration from the ocean to freshwater and back) is more common (Gross et al., 1988). Thus, the feeding migration characterizing diadromous species seems to be based on a trade-off between the costs of migration, i.e. the increased energy demand for the migration and increased mortality risk, and increased reproduction success due to increased body size (Gross, 1987; Fleming, 1996; Hansen and Quinn, 1998; Kinnison et al., 2001; Klemetsen et al., 2003). In Atlantic salmon, anadromy is more common for females than for males. Males can reach sexual maturation without migrating out from their natal river, maturing as parr, while females cannot (Gjerde, 1984; Taggart et al., 2001). Also, the

early matured males have shown to have high fertilization success, despite competing with larger anadromous males for females during spawning (Taggart et al., 2001). Similar patterns between males and females have been observed in different sea trout, *Salmo trutta* L., populations. Jonsson et al. (2001) examined the occurrence of non-migratory sea trout in 17 populations during their spawning period. They showed that ~50% of the examined trout was non-migratory mature males while ~4% was non-migratory mature females. That diadromy is more common for females may be explained by a stronger positive relationship between fecundity and body size for females than males, as the migration enables increased growth, which does not seem as important for males.

1.2.2 Effects of competition and predation risk on ontogenetic niche shifts

Exploitative competition can change prey abundances, affecting both the timing and size at diet and/or habitat shifts of the focal species when a competitor is present (Fig. 5) (Werner and Gilliam, 1984). As an example, Persson and Greenberg (1990)

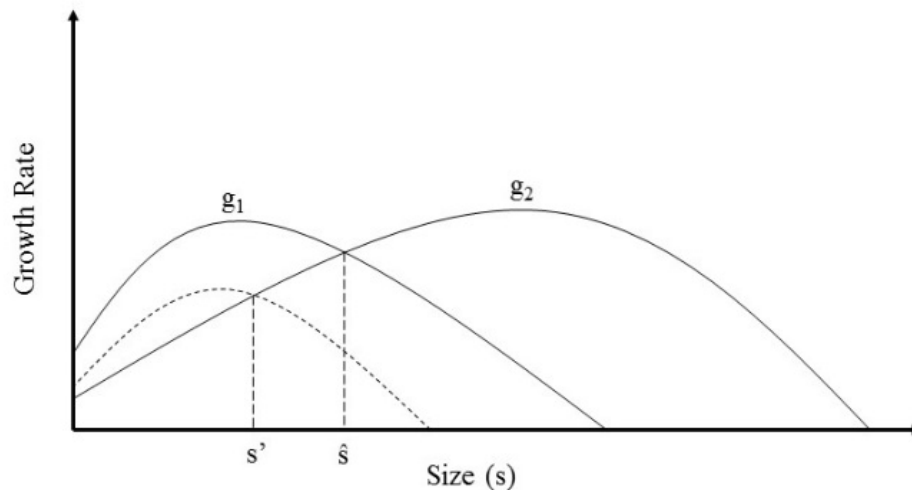


Figure 5. Growth rates when feeding on two different prey-types (g_1) and (g_2) as a function of body size. The dashed vertical lines indicate the optimum size for diet shift (\hat{s}) for maximizing growth. When including interspecific competition the growth rate is lowered due to a decrease in resource availability (dashed curved line) and the optimum switching size is shifted to a smaller size (s'). Reproduced from (Werner and Gilliam, 1984 p. 410).

manipulated the densities of roach co-occurring with 0+ and 1+ year old perch in experimental enclosures. They showed that increased densities of roach decreased the proportion of zooplankton in the perch diet. They further showed that perch switched to benthic prey at smaller sizes at high compared to low roach density. Thus, exploitative competition altered both the diet and the timing of the diet shift for the focal species in their experiment. Also predation risk can change individual

diet and habitat use (Fig. 6) (Mittelbach, 1981; Werner et al., 1983; Werner and Hall, 1988; Lima, 1998). Werner and Hall (1988) tested if the size at which the bluegill sunfish, *Lepomis macrochirus* R., shifted diet and habitat was dependent on densities of largemouth bass, *Micropterus salmoides* L., which, at large body sizes, prey on bluegills. The time bluegill spent in the more protective, littoral habitat in-

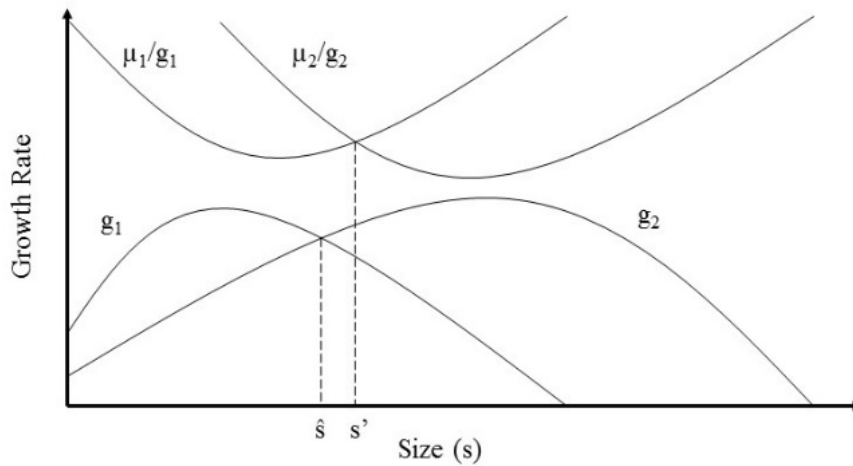


Figure 6. Growth rates in two habitats (g_1) and (g_2) as a function of increased size. The dashed vertical lines indicate optimum size for habitat shift (\hat{s}) for maximizing growth. When including size-specific mortality (μ/g) in both habitats, which is greater in habitat 2 (g_2), the habitat shift will be most profitable at a larger size (s'). Reproduced from (Werner and Gilliam, 1984 p. 409).

creased and their diet shift from littoral prey to pelagic zooplankton occurred at a larger body size at high predator densities. The increased size at diet shift was argued to be due to the increased mortality risk for small bluegill. Thus, as the protective, littoral, habitat was not as profitable as the more risky, pelagic, habitat their experiment indicates a trade-off between growth and predation risk. Therefore, predation risk can alter both the size at which diet shifts occur and habitat choice. This alteration in niche use can, in turn, affect energy intake which governs the amount of surplus energy available for growth and reproduction, affecting the individual's fitness.

1.3 Implications of food-dependent development and size-structure for population and community dynamics

As described in previous sections, individual survival, growth and reproduction vary depending on food availability and body size/life stage. In a scenario in which size-specific processes (metabolism, energy intake, growth, mortality and reproduction) scale with size in the same way (i.e. with the same exponent, Fig. 2 central panel), body size does not have any effect on the rate of biomass production. In this scenario, all individuals will, independent of their body size, be affected in the same way by resource limitation. This scenario is referred to as “ontogenetic symmetry in energetics” (Fig. 7a) (Persson and de Roos, 2013). In the contrasting scenario, in which these processes scale differently with body size, variation in body size distributions does affect population biomass production (Fig. 2 left and right panel) and growth, maturation, reproduction and mortality rates will vary over the course of life. Consequently, maturation and reproduction rates will not be constant among individuals in the population. The latter scenario is referred to as “ontogenetic asymmetry in energetics” (Fig. 7b, c) (Persson and de Roos, 2013). The latter implies that either juveniles or adults are more effective in mass-specific production of new biomass (Fig. 2 left and right panel & Box 1). If juveniles are more efficient in producing new biomass than adults, the population will be under reproduction control (i.e. low reproduction rate, Fig. 2 right panel & 7c). If the adults are more efficient in producing new biomass than juveniles, the population will instead be under development control, i.e. exhibit slow juvenile growth rates (Fig. 2 left panel & 7b) (de Roos and Persson, 2013). When juveniles and adults feed on different resources with different productivity, ontogenetic asymmetry can also result when adults and juveniles have equal energetic efficiency (Persson and de Roos, 2013). In summary,

Box 1. Development versus reproduction control

When a population is limited by *slow development* it consists of many slow growing juveniles and few large adults with high reproduction rate (Fig. 7b). This state occurs when large individuals (adults) are more efficient in mass-specific biomass production than small individuals (juveniles) (Fig. 2 right panel). Accordingly, as juveniles grow (slowly) and mature into the adult stage they increase their energy efficiency and produce more biomass, either via growth or reproduction. This keeps the population in a development controlled stable state.

When a population is limited by *low reproduction rates* it consists of few fast growing juveniles and many small, slow growing adults (Fig. 7c). This state occurs when juveniles have a higher mass-specific biomass production rate than adults. Accordingly, the newborn individuals grow fast, but at large size exhibit a growth-rate decline. This keeps the population in a reproduction controlled stable state characterized by low reproductive output.

depending on the size-scaling of energy efficiency, populations are regulated by either reproduction or development, and will be dominated by adults and juveniles, respectively (Fig. 7, Box 1). Importantly, depending on the type of population regulation, populations respond differently to mortality, with consequences for population and community biomass distributions and stability.

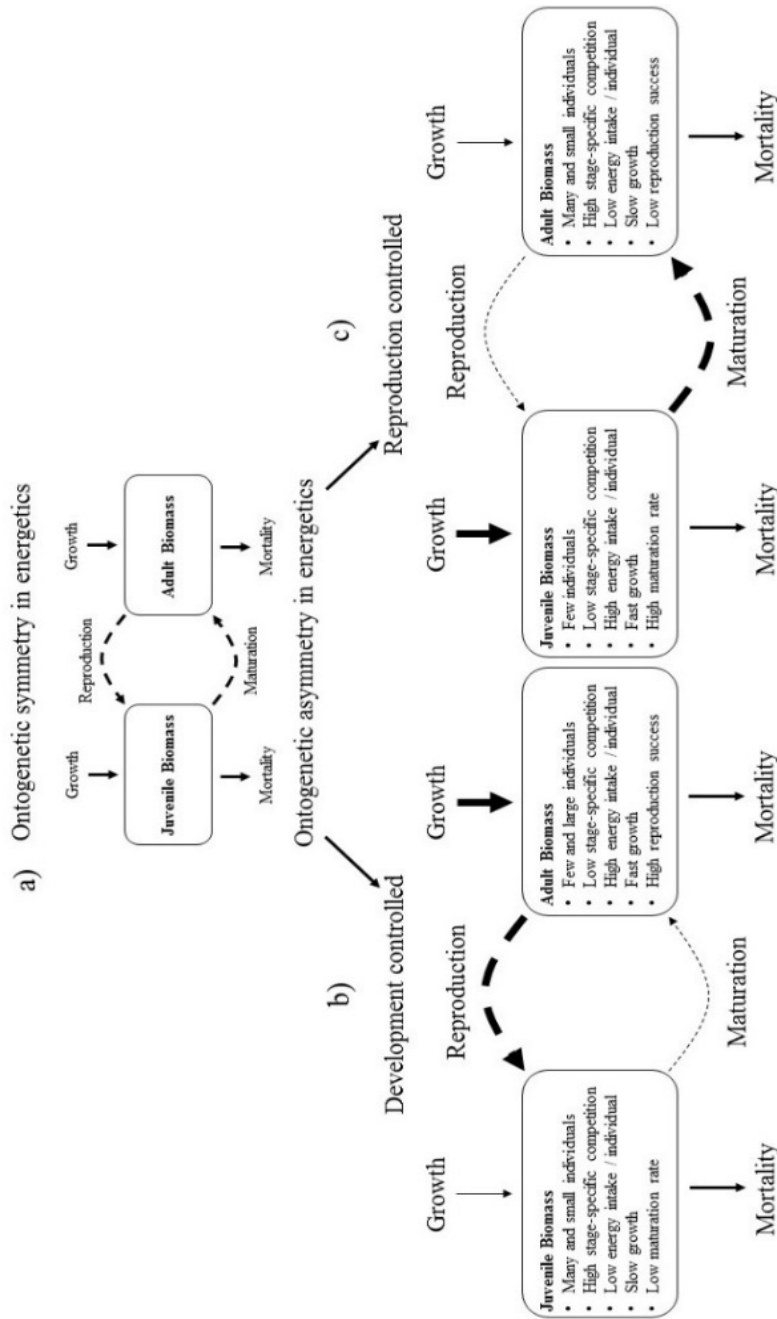


Figure 7. Schematic figure of three different size-structured population energetic states during: a) ontogenetic symmetry in energetics and b, c) ontogenetic asymmetry in energetics. Dashed arrows indicate the linkage between the juvenile and adult stage. Thick dashed arrows indicate a high process rate, thin arrows indicate a low process rate.

1.3.1 Cultivation and depensation

In many fish communities, the predator both competes and feeds on its prey, known as intra-guild predation, IGP (Polis et al., 1989). Thus, depending on the predator's body size, it either feeds on its prey (adult predator) or competes with the prey for shared resources (juvenile predator). At high adult predator densities, the predation pressure is high on the prey. As the prey abundance decreases, competition relaxes and the juvenile predator energy intake increases, enabling high growth and maturation rates. Therefore, the adult predators cultivate a resource rich environment for their juveniles (Walters and Kitchell, 2001). At low adult predator densities, e.g. due to harvesting of adult fish, the predation pressure is low. Therefore, as the prey abundance is high, the competition for shared resources between the prey and the juvenile predator is high. This results in low energy intake for the juvenile predator, which leads to slow growth. Thus, the juvenile predators experience stunted growth, creating a juvenile bottleneck in the predator population, a mechanism referred to as depensation (Walters and Kitchell, 2001). In summary, high predator densities induce the cultivation mechanism while few predators lead to depensation. The latter scenario decreases the possibilities for a predator population to recover from low abundances due to stunted growth.

1.3.2 Biomass overcompensation

Generally, increased mortality on a population is assumed to decrease the population biomass. However, biomass overcompensation, i.e. increased population biomass with increased mortality, can occur in populations with ontogenetic asymmetry in energetics. If mortality increases on a development controlled population, the adult biomass will first increase (i.e. overcompensation) followed by a decrease in biomass while the juvenile biomass will decrease monotonically with increased mortality (Fig. 8a). This increase in adult biomass is due to relaxed intraspecific competition and increased food availability in the juvenile stage. As the energy intake increases in this stage, the surviving juveniles grow and mature faster, increasing the adult biomass (de Roos et al., 2007; 2013). If mortality increases on a reproduction controlled population, the juvenile biomass will first increase (i.e. overcompensation) followed by a decrease in biomass while the adult biomass will decrease monotonically with mortality (Fig. 8b). This increase in juvenile biomass is due to relaxed intraspecific competition and increased food availability in the adult stage (Fig. 7c, 8b) (de Roos et al., 2007; 2013). Thus, theoretical studies suggest that depending on the level of mortality, the population biomass loss can be compensated or overcompensated for (Fig. 8) (de Roos et al., 2007; 2013; de Roos and Persson, 2013). Accordingly, a positive mortality-biomass relationship has been found in experimental studies (Schröder et al., 2009; 2014; Huss and Nilsson, 2011; Ohlberger et al., 2011). Schröder et al. (2009) tested how size (stage)-specific mortality

changed the stage-specific biomass distribution in experimental populations of the least killifish, *Heterandria formosa* G. By selectively removing fish from different stages (juveniles, nonrecruits and adults) they showed that biomass in the juvenile stage increased with juvenile mortality. In another experimental study, Ohlberger et al. (2011) investigated the long-term effects from a pathogen outbreak which increased the adult mortality with 98% in a fish population in lake Windemere, UK.

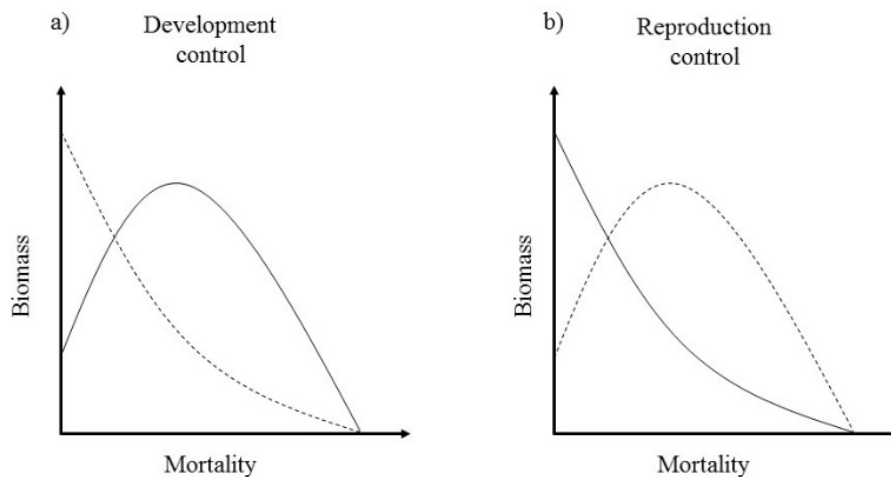


Figure 8. A conceptual illustration on the effects of increased mortality at ontogenetic asymmetry in energetics at a) a development- and b) a reproduction controlled population. Dashed line = juvenile biomass, solid lines = adult biomass. Figures based on (de Roos et al., 2007).

Despite the high increase in adult mortality, the population did not go extinct. Instead, the population shifted from being dominated by adults prior to the outbreak to become juvenile dominated. The few large surviving adults compensated for the increased mortality with increased reproduction rates. These observations are in line with the predicted response of a reproduction controlled population to increased mortality derived from theoretical studies (Fig. 7c, 8b & Box 1).

Also in a scenario in which the increased mortality is due to a predator feeding selectively on the regulating stage (either juvenile or adult) of the prey population, biomass overcompensation in the prey population may result. In a scenario with a predator selectively feeding on juveniles of a prey population limited by reproduction and dominated by adults, predation will decrease competition within the adult stage. This eventually leads to an increase in the juvenile biomass production and density (Fig. 8b). Thus, the predators can increase their own resource as they feed due to biomass overcompensation in the prey population. The latter also implies reduced potential for population growth at too low predator densities (when they have little effect on their prey). Therefore, the predator population may exist and

thrive at a high density, while, at low densities, it cannot invade the system despite high prey biomass, a phenomena referred to as an emergent Allee effect (de Roos and Persson, 2002). Both biomass overcompensation and cultivation/depensation are two possible mechanisms causing shifts between alternative stable states, i.e. a long-term system change characterized by different species and/or stage composition under identical environmental conditions. Also, these mechanisms have been linked to the non-recovery of collapsed fish stocks due to overexploitation (de Roos and Persson, 2002; van Leeuwen et al., 2008; 2013; Gårdmark et al., 2015). In summary, understanding how food- and size-dependent individual processes and species interactions govern individual growth and development is important for our understanding of population- and community dynamics, especially with regards to highly size-structured populations such as fish (Persson et al., 2014).

2. The management of size-structured fish populations

The management of exploited fish populations often ignores food- and size-dependent processes, e.g. growth and reproduction. Fisheries management, for example, mainly focuses on the total population biomass production. This is done without accounting for its dependence on food availability and the role of individual food- and size-dependent processes, e.g. survival, growth and reproduction (section 1) (Persson et al., 2014). Consequently, current management that does not account for food- and size-dependent processes is not able to identify the mechanisms governing size-structured population- and community dynamics, including phenomena such as biomass overcompensation and cultivation/depensation (de Roos and Persson, 2002; Huss et al., 2014; van Leeuwen et al., 2014; Gårdmark et al., 2015). Below, this is exemplified using two studies which identified these mechanisms in natural fish communities which had undergone shifts between alternative stable states (Persson et al., 2007; Gårdmark et al., 2015).

Persson et al. (2007) studied the effects of a large harvesting effort in lake Takvatn, Norway. The lake contained two fish species, Arctic char (prey species) and trout (predator species). Before harvesting, the lake consisted of many small-bodied adult Arctic char, characteristic of a population regulated by reproduction, and an almost absent trout population (Box 1, Fig. 7c). After the large harvesting effort, which targeted Arctic char, the characteristics of both the Arctic char and the trout population changed. The Arctic char population now consisted of fewer individuals with high growth rates and the size-distribution became wider. This was a consequence of relaxed intraspecific competition following the removal of slow growing adults. The result was increased growth and reproduction rate of the adults, which, in turn, increased the juvenile biomass. This response is in line with predictions

regarding the response of a reproduction controlled population to increased mortality (Fig. 8b). Also, the adult trout population density increased after harvesting, as a response to higher prey availability, i.e. an increase in the biomass of juvenile char which they selectively prey on. The system has been stable after the harvesting effort for more than 15 years, suggesting that the system has shifted to an alternative stable state. Before harvesting, the density of trout was too low for predation to thin out the char population, relax competition and increase the juvenile char biomass (Fig. 8b). After harvesting, the trout could persist in the system at a higher density and cultivate its prey, keeping the system in a new stable state characterized by a more abundant trout population and an Arctic char population with a broader size-distribution (section 1.3). This study exemplifies how thinning of a prey population can benefit its predators, something that can only be understood if accounting for food- and size-dependent body growth (Persson et al., 2007; 2014).

Gårdmark et al. (2015) investigated the causes of the non-recovery of the Baltic Sea cod, *Gadus morhua* L., after the population collapsed in the beginning of the 1990s due to overfishing. By taking size-specific predator-prey interactions between cod and sprat into account, the non-recovery could be explained by the overcompensation mechanism (section 1.3.2). Comparisons of stage-specific growth patterns of cod before and after the cod stock collapse showed that the growth rate of piscivorous, but not of the non-piscivorous cod stages, was lower after the collapse. This was explained by a decrease in availability of suitable sized sprat for cod, despite an increase in overall sprat population biomass. Following the cod stock collapse, sprat density increased due to decreased predation from cod. As a consequence, competition increased, leading to a decreased reproduction rate in the sprat population (Fig. 7c). This, in turn, decreased the abundance of small sprat, which is the preferred prey for cod when they turn piscivorous, hampering cod population recovery. The system consequently changed from being cod dominated to sprat dominated. Today, the cod population has still not recovered from the collapse in the early 1990s and mainly consists of small individuals (<40 cm) (ICES, 2015a).

Both these studies suggest that biomass overcompensation in the prey population, i.e. Arctic char and sprat, is a likely mechanism causing alternative stable states with high or low predator abundances. Also, both these studies exemplify the importance of accounting for size-specific predator-prey interactions to understand the mechanisms behind predator recoveries. Therefore, accounting for food- and size-dependent individual processes and size-specific predator-prey interactions should be acknowledged in the management of exploited fish populations (de Roos and Persson, 2002; Claessen et al., 2002; Persson et al., 2007; 2014; van Kooten et al., 2007; van Leeuwen et al., 2008; 2013; 2014; Schröder et al., 2009; Ohlberger et al., 2011; Persson and de Roos, 2013; Huss et al., 2014; Gårdmark et al., 2015). One area where implication for management has not been as well studied, with regards

to food- and size-dependent processes, is the management of fish species with ontogenetic habitat shifts.

2.1 The management of fish species with ontogenetic habitat shifts

Fish species which migrate between habitats during their ontogeny, e.g. utilizing different habitats as juveniles and adults, depend on both habitats to fulfill their life-cycle. Thus, management of such species can be rather complex as these habitats can be located far from each other and differ substantially in terms of productivity, size and mortality risks (Beck et al., 2001). Also, the connectivity between the habitats is important to enable migration (Beck et al., 2001; Able, 2005; Unsworth et al., 2008). There are few studies which have focused on the consequences of habitat differences, i.e. productivity and mortality, on population dynamics while also accounting for food- and size-dependent processes (e.g. Schreiber and Rudolf, 2008; van de Wolfshaar et al., 2011; Reichstein et al., 2015). However, it is clear that changes in productivity and/or mortality in one of the habitats can have large effects on the life stage occupying the other habitat (van de Wolfshaar et al., 2011; Reichstein et al., 2015). van de Wolfshaar et al. (2011) showed that when the productivity in the juvenile habitat was higher than in the adult habitat, the population was under reproduction control with fast growing juveniles and high resource competition in the adult stage (Fig. 7c). When the productivity of the adult habitat was higher than the juvenile habitat, the population was instead under development control with high reproduction rate and high resource competition in the juvenile stage (Fig. 7b). They further showed that increased productivity and/or mortality in one stage have large effects on the biomass in the other stage and concluded that management actions to increase yields should target the stage which regulates population growth (either juvenile or adult). Similarly, Rudolf and Armstrong (2008) showed that an increased productivity and mortality in either the juvenile or adult habitat can shift population regulation (from development to reproduction control or vice-versa, depending on the initial state). As a consequence, they also concluded that productivity and mortality changes in one habitat can have unexpected effects on the population and the community in the other habitat, e.g. due to eutrophication and/or size-selective fishing. Similar results were attained in an experiment altering both resource allocation and mortality on a reproduction controlled least killifish population in which the juveniles and adults utilized different habitats (Reichstein et al., 2015). In their experiment, Reichstein et al. (2015), changed the resource allocation between juveniles and adults from being equal, to increase resource allocation to the adult stage. As the least killifish population was under reproduction control, the increased resource availability in the adult stage increased the total population biomass, mainly adult biomass. Thus, the population biomass increased without increasing the total resource supply. Instead, the response was due to the difference

in resource allocation between the two habitats. Furthermore, in line with theoretical predictions (Fig. 7c) the increased resource allocation to the adult stage, increased the reproduction rate but did not affect the juvenile maturation rate. They further tested how the different resource allocations affected the population response to increased mortality. When the population was under reproduction control (equal resource allocation), as predicted the juvenile biomass increased and the adult biomass decreased with increased mortality (Fig. 8b). When more resources were allocated to adults, both the juvenile and the adult biomass decreased with increased mortality. Thus, the difference in resource allocation between the juvenile and the adult habitat altered both the stage-specific and total population biomass and its response to increased mortality. Thus, accounting for the combination of food- and size-dependent individual-level processes and habitat differences (e.g. productivity and mortality), should be key for management of species undergoing ontogenetic habitat shifts. Still, such processes are not accounted for in the management of diadromous species, such as the Atlantic salmon, which do undergo ontogenetic habitat shifts between freshwater and the ocean, which differ in both productivity and mortality (section 1.2.1).

3. The life-history of the Baltic salmon

The Baltic salmon consist of 39 genetically different populations, spawning in ~100 different rivers located in 7 of the 9 Baltic countries (Fig. 9) (Ståhl, 1987; HELCOM, 2011; Palmé et al., 2012a; Östergren et al., 2014a). The juvenile salmon migrate out from their natal rivers after 1-4 years as smolts, at lengths between 100-300 mm, to the Baltic Sea to feed. However, not all individuals migrate out to sea. Males can reach sexual maturation and spawn successfully without migrating, which is not the case for females (section 1.2.1) (Gjerde, 1984; Taggart et al., 2001). In the north, the salmon on average migrate out from their birth river at an older age than salmon from more southern rivers due to a shorter growth season (Alm, 1934; Lindroth, 1965; Karlsson and Karlström, 1994; Salminen, 1997). During the 1-5 year long feeding period out in the Baltic Sea, the salmon show a rapid increase in growth relative to the growth in the river. Individuals increase in weight by ~2-10 kg/year and in length by ~20-30 cm/year (Alm, 1934; Lindroth, 1965; Larsson et al., 1995; Salminen, 1997; Siira et al., 2009; Mikkonen et al., 2011; Keinänen et al., 2012). After 1-5 years at sea, the adults migrate back to their natal river to spawn

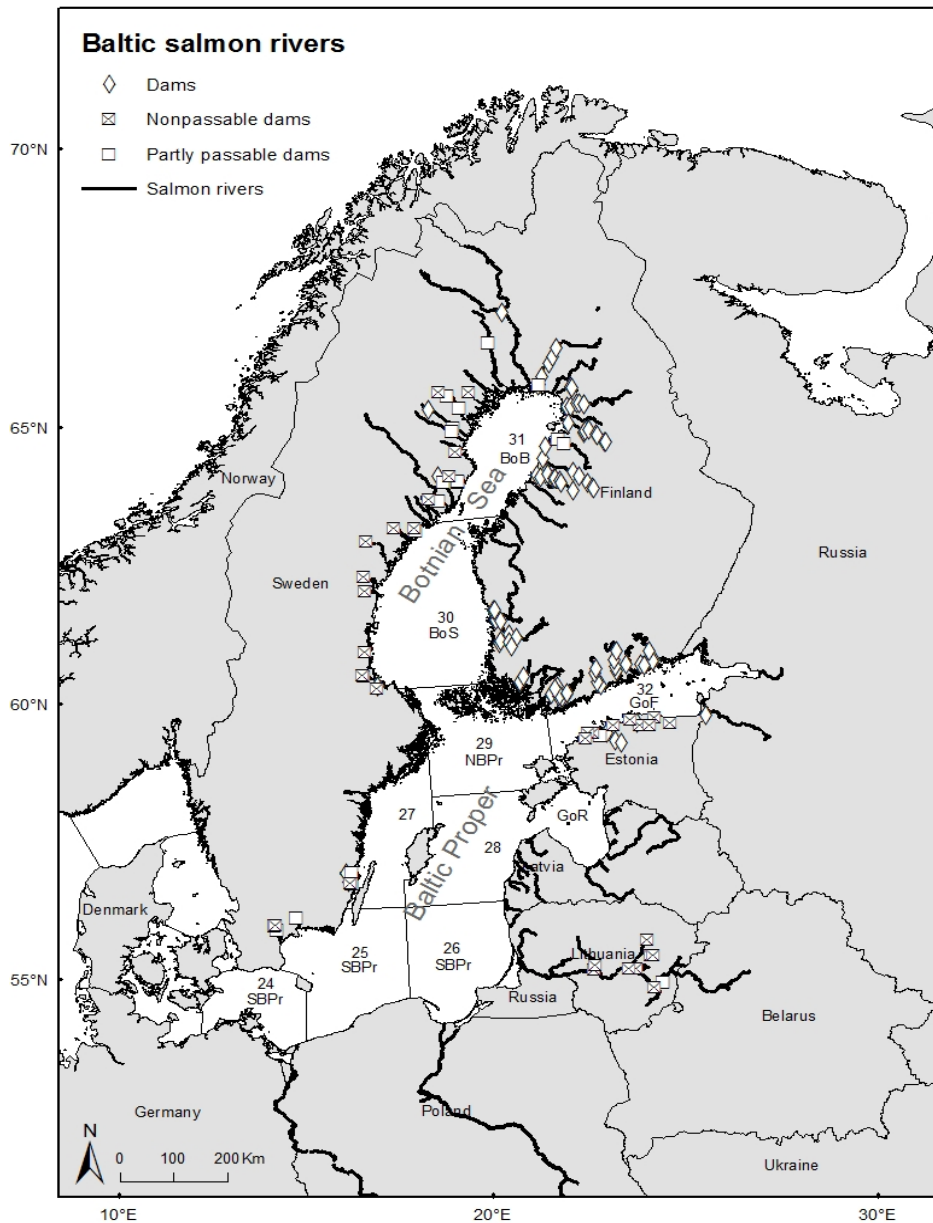


Figure 9. The location of past and present Baltic salmon, *Salmo salar* L. spawning rivers and associated river dams in the Baltic Sea (HELCOM, 2011). The length of each river equals the river area which is accessible for the Baltic salmon. The divisions of the Baltic Sea with associated number (24-32) are the ICES subdivisions. Abbreviations: BoB = Bothnian bay, BoS = Bothnian Sea, NBPr = Northern Baltic Proper, SBPr = Southern Baltic Proper, GoF = Gulf of Finland, GoR = Gulf of Riga. Data and maps retrieved downloaded from the HELCOM Baltic Sea data and map service (HELCOM, EAA).

(Larsson, 1984; Karlsson and Karlström, 1994). Not all individuals return to their natal river as salmon can return to other rivers, i.e. straying, but few studies have

investigated to what extent this occurs within Baltic salmon populations (Vasemägi et al., 2005; Palmé et al., 2012b). During the spawning migration, the salmon cease

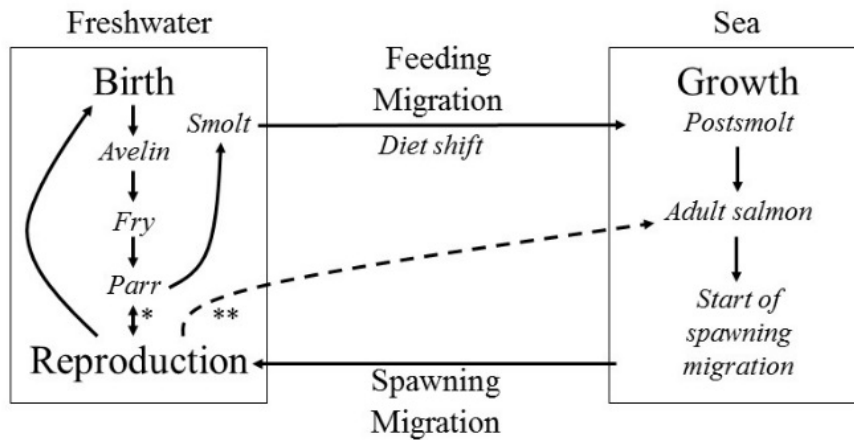


Figure 10. Schematic life-cycle of the diadromous Baltic Sea Atlantic salmon *Salmo salar* L. The diet shift during feeding migration is from terrestrial insects to fish. * Observed for males which can mature as parr, spawn and later undergo smoltification. ** Multiple spawning occurs in Baltic salmon populations.

feeding, undergo both morphological and physiological changes and develop gonads. As the feeding ceases, salmon rely on their built-up fat reserves for the spawning migration out at sea, the up-river migration and the spawning event (Vuorinen et al., 2014). Some individuals survive spawning, migrate back to the sea and return to spawn for a second time, i.e. kelts, but little is known regarding the kelts life-history (Fig. 10) (Jokikokko and Jutila, 2005; Lundqvist et al., 2015). According to Lundqvist et al. (2015), kelts could be very valuable for the production of Baltic salmon populations as kelts have successfully spawned once, survived both periods out at sea and the up- and down-stream migration to the spawning grounds and have high fecundity due to their large size (Lundqvist et al., 2015).

During the last decade, ~8 million smolts have migrated out from their natal rivers to the Baltic Sea annually, of which 4-5 million are of reared origin and 2-3 million are wild (ICES, 2015b). The release of reared salmon smolts is conducted to compensate for the loss of natural salmon production due to hydropower plants. Hydropower plants both directly kill salmon as they migrate out from the river in the turbines and the associated spillways and due to damming of rivers, making upstream migration impossible without the construction of fish-ways (Fig. 9). The rearing of salmon started in the late 19th century and became a large-scale operation in the 1950s as a consequence of the increased number of large hydropower plants (Lindroth, 1965; Larsson, 1984; Karlsson and Karlström, 1994; Palmé et al., 2012b).

The released salmon are often hatched and reared in facilities connected to the river. Mature salmon are caught as they migrate upstream and are used as brood stock to artificially fertilize eggs which are hatched and reared in the facilities. Some rivers do not have their own hatcheries and release salmon originating from other rivers (Laikre et al., 2006; Palmé et al., 2012b; ICES, 2015b). Today, nearly 30 of the ~100 Baltic salmon producing rivers have a wild, self-producing salmon population not relying on compensatory releases to be sustained (EC, 2011b; HELCOM, 2011; ICES, 2015b). To enable comparisons between wild and reared Baltic salmon the adipose fin is commonly removed from the reared salmon prior to their release. Since 2005, all Swedish reared salmon has been fin-clipped but this has not been the case in other Baltic Sea countries. In 2014, all Estonian reared salmon were fin-clipped while only 25% of the Finnish reared salmon were. The majority of the released reared salmon in Russia, Lithuania, Latvia, but none in Poland, had their adipose fin removed prior to their release (ICES, 2015b). Also, additional tagging with either external or internal tags is conducted, but not to the same extent as fin-clipping, to enable comparisons between wild and reared salmon, e.g. concerning survival, growth rates, years at sea and spatial distribution out in the Baltic Sea. Studies based on such tagging have shown that there are differences between wild and reared Baltic salmon. Reared salmon are usually larger compared to wild when released as smolts, have lower survival rates out in the open sea (reared; 2-7%, wild; 10-15%), show different spatial distributions out at sea, return to spawn at younger ages and reach the natal river later in the spawning season (Kallio-Nyberg et al., 1999; 2015; Jutila et al., 2003; Saloniemi et al., 2004; Jokikokko et al., 2006; Siira et al., 2009; ICES, 2015b).

3.1 The diet of post-smolt and adult Baltic salmon at sea

During the first period at sea, Baltic salmon mainly feed on terrestrial insects and to some extent on aquatic invertebrates. At lengths of 240-280 mm, fish starts to appear in the diet and, after reaching sizes >280 mm, the diet consists almost exclusively of fish (Hansson et al., 2001; Salminen et al., 2001). The fish diet composition differs between the main feeding areas. Herring, *Clupea harengus* L., is the main prey in the Bothnian Sea and Bothnian Bay while sprat is the main prey in the Baltic Proper (Fig. 9). Also, the three-spined stickleback, *Gasterosteus aculeatus* L., is a common prey in both areas (Karlsson et al., 1999; Hansson et al., 2001; Salminen et al., 2001; Ikonen, 2006; Vuorinen et al., 2014). The difference in prey species composition between areas has been explained by the different spatial distributions of herring and sprat in the Baltic Sea (Mikkonen et al., 2011). Sprat is common in the Baltic proper but not in the Bothnian Sea as the temperature and salinity is too low for sprat to successfully reproduce (Cardinale et al., 2002; Mackenzie and Köster, 2004; Ojaveer and Kalejs, 2010). Herring is common in both regions but is

less abundant relative to sprat in the Baltic proper. Still, it is not known to what extent these diet differences between areas are due to size- or species specific prey-preferences of the Baltic salmon. There are studies on juvenile salmon indicating that salmon do have size-dependent prey-preferences, actively feeding on a specific size-range of the available prey to optimize growth (Wankowski, 1979; Wankowski and Thorpe, 1979). Kallio-Nyberg et al. (1999) showed that a high abundance of juvenile herring in the Bothnian Sea increased the amount of reared salmon within the area but not wild. This was argued to be a consequence of the larger smolt size of reared salmon, compared to wild, which therefore could start feeding on the juvenile herring at an earlier age. Furthermore, Mäntyniemi et al. (2012) investigated which factors affected post-smolt survival out at sea. According to their model, the abundance of juvenile herring in the Bothnian Sea and Bothnian Bay was, together with seal densities, the most important explanatory factor for post-smolt survival. They also showed that the abundance of adult sprat in the Baltic proper had no effect on post-smolt survival. Thus, both species- and size-specific prey preferences could affect the spatial distribution and post-smolt survival of different Baltic salmon populations.

3.2 The management of Baltic salmon

The Baltic salmon is a culturally, socially and economically valuable fish species in the Baltic Sea region (Kulmala et al., 2013). The Baltic salmon are fished out on the open sea, along the coast and in the rivers. During the last decade, reported catches (commercial and non-commercial) have varied between 900-2103 tons/year (ICES, 2015b). The total reported catch in 2014 was 1020 tones, including non-commercial catches, of which ~20% was caught out on the open sea, ~50% along the coast and ~30% in rivers (ICES, 2015b). Long-lines and trap nets were the two most common methods used in the commercial salmon fisheries in 2014. In all fisheries, the minimum landing size of salmon is 60 cm, except for the Gulf of Bothnia, in which 50 cm is the minimum size. Also, recreational salmon fishing is popular in the Baltic Sea, both along the coast (boat trolling) and in the rivers (rod fishing). In 2014, the non-commercial salmon catch was estimated to be 404 tons (ICES, 2015b).

The future management goals for the Baltic salmon are to achieve healthy wild salmon stocks, focusing on the existing ~30 wild salmon populations and those which are close to becoming self-producing, which should be self-producing and sustainably exploited on a long-term perspective (EC, 2011b). This will most likely increase the need for a more population specific management of the Baltic salmon. The off-shore fisheries are not population specific, which the coastal-fisheries can be and the river fisheries are, as different salmon populations mix out in the open Baltic Sea (Palm et al., 2008; Östergren et al., 2014b; 2014a; ICES, 2015b). However, there are studies regarding the spatial distributions of salmon populations in

the Baltic Sea, based on reported recaptures of tagged reared and wild salmon (Alanära, 1988; Ikonen, 2006; Kallio-Nyberg et al., 2015). According to Ikonen (2006), post-smolts originating from the Finnish rivers located in the north of the Bothnian Bay migrate mainly to the Baltic proper while some tend to stay in the Bothnian Sea (Fig. 9). Post-smolts from the rivers in the Gulf of Finland migrate the shortest distances, mostly staying in the Gulf of Finland while some migrate to the Bothnian Sea and the Baltic proper (Fig. 9). Post-smolts from the rivers in the Baltic proper seem to migrate northwards but mainly stay in the Baltic proper, while some migrate further north to the Gulf of Finland and into the Bothnian Sea (Fig. 9). Kallio-Nyberg et al. (2015) studied the migration pattern of two salmon populations originating from the rivers Tornionjoki and Simojoki, located in the north Bothnian Bay. All of the recaptured wild Simojoki salmon and 96% of the wild Tornionjoki salmon was caught in the Baltic proper. Of the reared salmon, 85% of the salmon from the Simojoki river and 89% of the Tornionjoki salmon was caught in the Baltic proper (Fig. 9). Alanära (1988) investigated the distribution of three salmon populations originating from three rivers along the Swedish coast of the Bothnian Sea and Bothnian Bay. The study showed that the distributions differed between populations but all post-smolts was caught in both the Bothnian Bay and in the Bothnian Sea (Fig. 9). The distribution can have changed over time, as a more recent study have shown that salmon originating from the same rivers have been caught in the Baltic proper (Fig. 9) (Östergren et al., 2014a).

In summary, the Baltic salmon is a highly valuable fish species, originating from rivers located in 7 of the 9 countries in the Baltic region and are of both reared and wild origin. The Baltic salmon dwell in different feeding areas in the Baltic Sea and feed on different fish species in these areas. One of the concerns for the management of the Baltic salmon population is the high levels of hazardous substances which they accumulate as they eat fish prey, often exceeding the limits for human consumption set by the European Commission (Vuorinen et al., 2002; 2012; 2014; HELCOM, 2004; 2007; 2010; Mikkonen et al., 2011; Keinänen et al., 2012; Livsmedelsverket, 2012; ICES, 2015b).

4. Dioxin and PCBs in Baltic Sea fish

The Baltic Sea is often referred to as one of the most polluted large water bodies in the world. This is due to a combination of both anthropogenic activities and hydrological processes, e.g. heavy industrial activities, a large catchment area and slow water exchange (HELCOM, 2010). Dioxins and PCBs have been of great concern in the Baltic Sea region since the 1960s, when elevated levels of dioxin and PCBs was measured in bottom sediments and in Baltic Sea biota (HELCOM, 2004). Di-

oxins (PCDDs, PCDFs and dl-PCBs), and PCBs are classified as hazardous substances, i.e. substances which are toxic, persistent, and bioaccumulate (Box 2) (Mackay and Fraser, 2000; OSPAR, 2007; HELCOM, 2010). Dioxins are unintentionally produced via the combustion of organic compounds as byproducts. Dioxins are produced both naturally, e.g. via volcanic eruptions and forest fires, and from

Box 2. Dioxin and PCB compounds and their health effects on humans.

Dioxins refers to two different polychlorinated compounds, dibenzo-p-dioxin (PCDD) and dibenzofuran (PCDF), consisting of 210 possible configurations of which 17 are known to be toxic. Dioxin exposure to humans increases the risk of cancer and has negative effects on the immune system and motoric and cognitive development. Also, diabetes and heart-diseases have been linked to dioxin exposure. Exposure during early development is considered to be most critical (HELCOM, 2010; WHO, 2010; Livsmedelsverket, 2012).

Dioxin like PCBs (dl-PCBs) refers to polychlorinated biphenyls (PCBs) with similar molecular structure and toxic effects as dioxins (HELCOM, 2010; WHO, 2010).

PCBs refers to polychlorinated biphenyls, consisting of 209 possible configurations. PCB exposure to humans affects organ systems and may increase the risk of e.g. cancer, infections, infertility, liver diseases, asthma, arthritis and heart diseases (HELCOM, 2010), although these effects from PCBs on humans are still debated (Livsmedelsverket, 2012).

anthropogenic processes e.g. waste incineration, chemical-, metal-, and paper industries, small-scale burning and via combustion of fuels (HELCOM, 2004; Quaß et al., 2004; OSPAR, 2007). Dioxins are mainly transported via air but some transportation occurs via run-off water and waste deposits (OSPAR, 2007; Semenna et al., 2014). PCBs are, compared to dioxins, only intentionally produced. PCBs were widely used between the 1920s-1970s by different industries, e.g. as flame retardants, hydraulic fluids, in heat transfer systems and in electronic appliances (Baars et al., 2004; HELCOM, 2010). PCBs enter nature via leakage of products containing PCBs, disposal of waste-products containing PCBs and spills and losses from industries manufacturing PCBs (Nisbet and Sarofim, 1972; HELCOM, 2010). The production of PCBs was banned in the late 1970s in many countries globally and the production of PCBs around the Baltic Sea region stopped around the early 1990s (HELCOM, 2001; Baars et al., 2004; Bignert et al., 2012). As dioxins are not intentionally produced, banning dioxin production is not possible. Instead, legislations and conventions aiming to reduce the amount of dioxins produced as by-product

have been implemented in the Baltic Sea area. The European commission implemented legislation in 2000-2001 regarding incineration of waste which has been followed by several others e.g. the HELCOM Baltic Sea Action Plan, BSAP, and the Stockholm Convention (EC, 2000; 2010; HELCOM, 2007; SC, 2009). Since

Box 3. EU-limits for Dioxin and PCB concentrations in fish for human consumption and fish fodder

Human consumption (EC, 2011a):

Dioxin (PCDD and PCDF) limits for fish muscle: 3.5 pg/g wet weight

Dioxin and dl-PCB limit for fish muscle = 6.5 pg/g wet weight

PCBs limits for fish muscle = 75 ng/g wet weight

Fish fodder (EC, 2012):

Dioxin (PCDD and PCDF) limits of fish fodder = 1.25 ng/kg wet weight*

Dioxin and dl-PCB limits of fish fodder = 4 ng/kg wet weight*

PCBs limits of fish fodder = 30 µg/kg wet weight*

* Fish fodder with moisture content of 12%

2001, both dioxins and PCBs are listed as hazardous substances in the Stockholm Convention, with the goal to phase out and eliminate the use of the listed hazardous substances. Today, the Stockholm convention include dioxins, PCBs and 27 other toxic substances such as the pesticide DDT (SC, 2009; HELCOM, 2010). In 2007, the Baltic Sea countries agreed and signed the HELCOM BSAP consisting of four main goals for the Baltic Sea environment: I) life undisturbed by hazardous substances, II) the sea unaffected by eutrophication, III) towards favorable conservation status of Baltic Sea biodiversity and IV) environmentally friendly maritime traffic (HELCOM, 2007). The main goal regarding hazardous substances was further formulated into four achievement points: I) concentrations of hazardous substances close to natural levels, II) all fish safe to eat, III) healthy wildlife and IV) radioactivity at pre-Chernobyl levels (Box 3) (HELCOM, 2007; 2010). These four main goals are aimed to be achieved by the year of 2021.

After a period with high mortalities and unsuccessful reproduction observed in Baltic Sea biota caused by increased levels of dioxins and PCBs in the 1950-1970s, an annual monitoring program was initiated (Helle et al., 1976; Helle, 1980; Helander et al., 1982; Olsson et al., 1992). Herring, guillemot eggs, *Uria aalge* P., and northern pike, *Esox lucius* L., are some of the species included in the program and which are analyzed annually for different hazardous substances, including dioxins and PCBs (Olsson and Reuthergård, 1986; Bignert et al., 2012). Since the start of the monitoring program in the 1970s the dioxin levels have generally declined in both herring muscles and in guillemot eggs. This decrease has, however, leveled off

during the last 20 years and been rather stable despite an overall decrease in dioxin emissions. In some cases, the dioxin concentrations have even increased slightly in herring muscles (Miller et al., 2012; Bignert et al., 2013; Semenna et al., 2014). The PCB levels have steadily decreased since the start of the monitoring program and today, the levels are down by 70-90% (Bignert et al., 2013). Thus, the banning of PCBs in many countries in the 1970s was successful in decreasing the PCB levels.

The Baltic Sea herring, sprat and salmon are all fat-rich species, i.e. they have a high lipid concentration/body weight. As both dioxins and PCBs are fat-soluble and persistent, these compounds are stored in fatty-tissue (HELCOM, 2004; 2010). These substances accumulate in fish as they feed on other organisms (Strandberg et al., 1998; Koistinen et al., 2008; Nfon et al., 2008; Vuorinen et al., 2012). The dioxin and PCB concentrations in herring, sprat and salmon are positively correlated with age and lipid-content (Larsson et al., 1995; Vuorinen et al., 2002; 2012; Parmanne et al., 2006; Pandelova et al., 2008; Miller et al., 2012; Bignert et al., 2013). Also, the concentrations of dioxin and PCBs differ between fishes caught in different areas of the Baltic Sea (Bignert et al., 2007; 2013; Koistinen et al., 2008; Karl et al., 2010; Miller et al., 2012; Vuorinen et al., 2012). PCB concentrations in herring are highest in the Bothnian Sea and in the most northern and southern parts of the Baltic proper (Fig. 9) (Vuorinen et al., 2012; Bignert et al., 2013). The dioxin concentrations is higher in herring from the Bothnian Sea compared to the Bothnian Bay, Baltic proper and Gulf of Finland (Fig. 9) (Vuorinen et al., 2012; Bignert et al., 2013). Similar spatial patterns have been shown for sprat (Vuorinen et al., 2002; 2014; Pandelova et al., 2008). These regional differences have been linked to a slower growth rate in northern areas, i.e. a 15 cm herring is older in the Bothnian Sea compared to in the Baltic proper (Vuorinen et al., 2012; Bignert et al., 2013). As the Baltic salmon feed on herring and sprat, spatial differences in dioxin and PCB concentrations in salmon show similar patterns, with the highest concentrations in the Bothnian Sea (Vuorinen et al., 2002; 2012; Livsmedelsverket, 2012). In a report from the Swedish national food agency (Livsmedelsverket, 2012), 42 of 44 investigated salmon samples, from both the Baltic proper, the Bothnian Sea and Bothnian Bay exceeded the limits for dioxin and dl-PCBs for human consumption (Fig. 9 & Box 3). All herring >17 cm in the Bothnian Sea and Bothnian Bay showed dioxin concentrations above the limit set for human consumption. For sprat, samples from the Baltic proper was used. No sprat sample exceeded the dioxin limits for human consumption and no spatial differences were observed.

In summary, dioxin and PCBs are present in Baltic Sea herring, sprat and salmon, and increase with age and lipid-content. Also, the concentrations of dioxin and PCBs differ between areas in the Baltic Sea, with the highest dioxin concentrations in herring and salmon from the Bothnian Sea. Studies regarding the PCB and dioxin content in herring, sprat and salmon often only focus on the age of the fish (e.g.

Vuorinen et al., 2012; but see Livsmedelsverket, 2012). Consequently, no study has yet investigated the effects of size-specific individual processes and size-specific predator-prey interactions on the bioaccumulation of dioxin and PCBs in the Baltic Sea herring, sprat and salmon food-web.

5. An ecological perspective on management to reduce dioxin levels in fish

As agreed on by the Baltic Sea countries in the BSAP, all fish in the Baltic Sea should be safe to eat by the year 2021 (HELCOM, 2007; 2010). To date, this goal has not been fulfilled, despite a decrease in the emissions of dioxins and the banning of PCBs (section 4). Thus, other management methods in combination with further reductions in emissions are needed to fulfill the goal agreed upon in the BSAP. Increased fishing on Baltic herring and sprat has been suggested to be one management method to directly remove dioxin and PCB content in Baltic Sea fish (Mackenzie et al., 2004; TemaNord, 2010). Other studies have discussed the possibilities of increasing fishing to rejuvenate, i.e. to remove old but not young individuals (Parmanne et al., 2006) or to increase herring and sprat growth rates (Vuorinen et al., 2012), decreasing the age-at-length in Baltic Sea herring and sprat populations. Consequently, salmon would prey on younger, faster growing prey, decreasing the dioxin and PCB concentrations in Baltic salmon, as both dioxin and PCB concentrations increase with age (section 4) (Parmanne et al., 2006; Vuorinen et al., 2012). Neither Parmanne et al. (2006) nor Vuorinen et al. (2012) has investigated if increased mortality on Baltic herring and sprat populations affects 1) the growth rates of Baltic Sea herring and sprat, 2) the dioxin and PCB content in Baltic herring, sprat and salmon, 3) the diet of the Baltic salmon, and 4) if increased fishing should be size-selective or not. However, there are studies which have studied the individual- and population-level effects of size-selective fisheries on Baltic herring and sprat (Huss et al., 2012; 2014; Appelberg et al., 2013). Appelberg et al. (2013) investigated the effects of increased fishing, i.e. reduction fishing, on Baltic Sea sprat in Kalmarsund, the area between the island of Öland and the Swedish mainland. The reduction fishing did not have any substantial effect on the fished sprat population as the fishing effort was too low relative the natural variation of the population abundance and spatial distribution (Appelberg et al., 2013). As shown by Persson et al. (2007), fishing mortality needs to be substantial to have an effect on the growth rates of individuals in the targeted population (~80% population removal of the Arctic char population, see section 2). Thus, for reduction fishing to have any effect on the targeted population (e.g. sprat and herring), a large increase in fishing effort over a large area is needed. Also, according to Huss et al. (2014), it is mainly increased size-selective mortality on juvenile Baltic Sea herring that would increase individual

growth rates, leading to an overcompensation response in adult biomass (section 1.3.2). For sprat, the growth rates increased with increased mortality targeting small individuals, but not to the same extent as for herring. Thus, the study by Huss et al. (2014) indicates that increased size-selective mortality, targeting small herring, could decrease the age-at-length as well as increase the biomass of adult Baltic Sea herring. This, in turn, could potentially decrease the amount of dioxins and PCBs in herring as the concentration of these substances increases with age (section 4) (Vuorinen et al., 2012). If so, also the dioxin and PCB content in salmon would likely be affected as they would feed on prey with lower concentrations of these hazardous substances. However, to selectively harvest large amounts of small herring could be difficult as the trawls used in off-shore herring fishing do not target only small herrings. Instead, an increase in the Baltic Sea cod population would increase the natural size-specific mortality on Baltic herring, as cod feed selectively on small herring in the Baltic Sea (Huss et al., 2014). As the total Baltic salmon biomass is much lower compared to the Baltic cod biomass (~10%), a similar predation effect of salmon on herring is unlikely. Also, if increased size-selective mortality on juvenile herring (either from fishing or via cod predation) actually would decrease the dioxin levels in Baltic Sea herring and salmon is not certain. For example, no study has yet investigated if Baltic salmon feed selectively, i.e. on a specific prey species or prey size range, or feed on the most abundant prey species and/or prey size. What we do know is that Baltic salmon have fed on prey fish up to ~30 cm in length, but more commonly feed on prey fish <25 cm (Hansson et al., 2001), but to what extent this reflects the absence of large prey fish or not is not known. Furthermore, as the management of Baltic salmon will most likely become more population specific, knowledge regarding the spatial distribution of different salmon populations feeding in the Baltic Sea are important as their prey composition differ between areas (section 3). Also, as similar sized herring and sprat contain different amounts of dioxin and PCBs in different areas of the Baltic Sea, knowledge of where different salmon populations feed is important (section 4). Therefore, to better understand size-dependencies of salmon–clupeid interactions and the spatial distribution of salmon is important for the management of Baltic salmon in general and to manage dioxin levels specifically. Furthermore, too high mortality on small herring could affect the survival of post-smolts in the Bothnian Sea negatively, as high abundances of juvenile herring have been shown to increase post-smolt survival (Mäntyniemi et al., 2012). Also, increased fishing for small herring could increase the bycatch of salmon in the Baltic Sea.

In conclusion, accounting for size- and food-specific processes and size-specific predator-prey interactions is important for the future management of Baltic salmon. Also, there is a need to evaluate the effects of e.g. increased mortality on small Baltic Sea herring (either via size-selective fishing or predation from cod) as an alternative

management method to decrease dioxins and PCBs in Baltic Sea herring and salmon.

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