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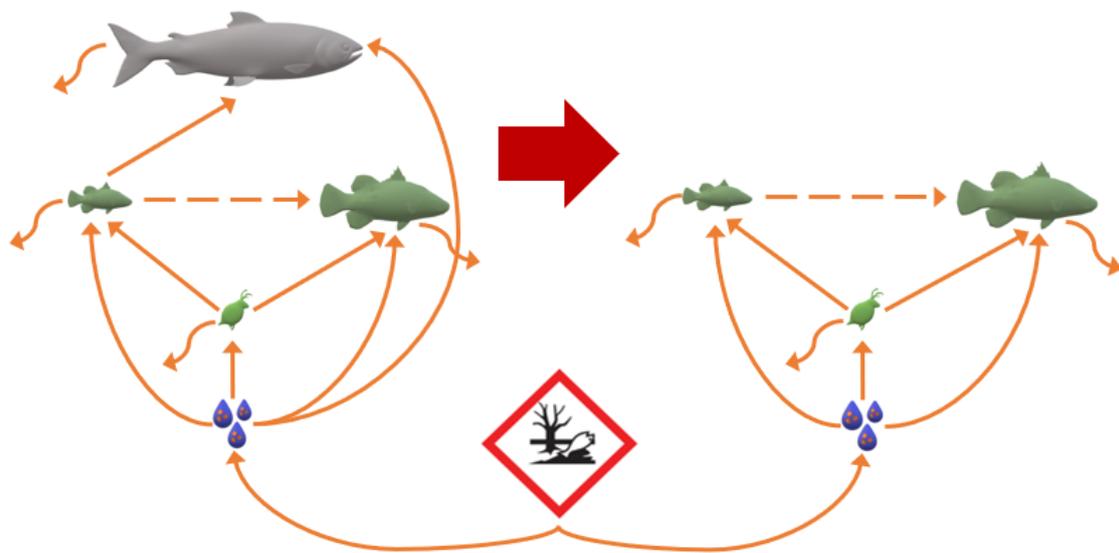
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Change in uptake and transfer of zinc in the food chain when predatory fish disappear from the system

Sara Westerström

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Förändring av upptag och överföring av zink i födokedjan när rovfisk försvinner från systemet



Sara Westerström

Degree Project in Environmental and Water Engineering

Uppsala University and Swedish University of Agricultural Sciences

Supervisor: Anna Gårdmark

Subject Reader: Magnus Huss

Examiner: Fritjof Fagerlund

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Abstract

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Sara Westerström

There is a widespread distribution of possibly toxic heavy metals, such as zinc, in aquatic ecosystems. Simultaneously aquatic food webs are changing due to declining predatory fish stocks. In this study, I examine how such an alteration of the food chain, the disappearance of a top trophic level, can affect the uptake and transfer of pollutants in lower trophic levels. I investigate a tri-trophic food chain containing resources (zooplankton), consumer fish, and predatory fish and use zinc as an example pollutant. This is done by constructing and adding a pollutant module to a stage-structured biomass model. The combined model is based on a system of eight ordinary differential equations to study the zinc concentrations in the consumer fish population in two scenarios: in the presence or absence of predatory fish, i.e., the food chain consists of either three or two trophic levels. The results show that the removal of the predator affects the concentration of the pollutant in the consumer population. In the absence of predators, the uptake of zinc from food is smaller and the zinc concentration is lower in the consumer fish population. The results remain the same for different values of the pollutant-specific parameters, i.e., uptake rate from water, assimilation efficiency, and efflux rate. This could indicate that food chain dynamics have a strong influence on the uptake and transfer of pollutants. Furthermore, this means that even if the model is parametrized to zinc in this study, the modeling tool can also be used for other pollutants with similar biokinetics as zinc. The results from this study highlight the importance to include food chain structure and dynamics when studying the uptake and transfer of pollutants. The novel knowledge and the developed tool from this study could advantageously be included to a higher degree when discussing the impact of pollution on aquatic ecosystems and mitigation measures.

Keywords: Aquatic food web, Food chain structure, Trophic transfer, Decline of top predators, Stage-structured biomass model, Pollutants, Heavy metals, Zinc.

Department of Aquatic Resources (SLU Aqua). Kustlaboratoriet, Almas allé 5, 750 07 Uppsala

Referat

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Det finns en utbredd spridning av potentiellt giftiga tungmetaller, som t.ex. zink, i akvatiska ekosystem. Samtidigt förändras akvatiska födovävar på grund av minskande rovfiskbestånd. I denna studie undersöker jag hur en sådan förändring av födoväven, ett försvinnande av en trofisk toppnivå, kan påverka upptaget och överföringen av föroreningar i lägre trofnivåer. Jag undersöker en tritrofisk födokedja som innehåller resurser (zooplankton), konsumentfisk och rovfisk och använder zink som ett exempel på förorening. Detta görs genom att konstruera och addera en föroreningsmodul till en stegstrukturerad biomassamodell. Den kombinerade modellen bygger på ett system med åtta ordinarie differentialekvationer för att studera zinkhalterna i konsumentfiskpopulationen i två scenarier: i närvaro eller frånvaro av predatorer, dvs. födokedjan innehåller antingen tre eller två trofiska nivåer. Resultaten visar att koncentrationen av föroreningen i konsumentpopulationen förändras när födokedjan ändras. När rovfisk saknas i systemet är upptaget av zink från föda mindre och zinkkoncentrationen lägre i konsumentfiskpopulationen. Resultaten förblir detsamma för olika värden på de föroreningsspecifika parametrarna, d.v.s. upptagshastighet från vatten, assimileringseffektivitet och utflödeshastighet, vilket skulle kunna indikera att födokedjans dynamik har ett starkt inflytande på upptag och överföring av föroreningar. Vidare innebär detta att även om modellen har parametriserats till zink i denna studie, så kan modelleringsverktyget även användas för andra föroreningar som har en liknande biokinetik som zink. Resultaten från denna studie understryker vikten av att inkludera födokedjans struktur och dynamik när man studerar upptag och överföring av föroreningar. Den nya kunskapen och det utvecklade verktyget från denna studie skulle med fördel i högre grad inkluderas när man diskuterar föroreningars påverkan på akvatiska ekosystem och vilka åtgärder som bör sättas in för att minska problemen.

Nyckelord: Akvatisk födoväv, Födovävsstruktur, Trofisk överföring, Minskning av toppredatorer, Stegstrukturerad biomassamodell, Föroreningar, Tungmetaller, Zink.

Institutionen för akvatiska resurser (SLU Aqua). Kustlaboratoriet, Almas allé 5, 750 07 Uppsala

Preface

This 30 credits Degree Project marks the final course in the Environmental and Water Engineering program at Uppsala University and the Swedish University of Agricultural Sciences. My supervisor for this Degree Project was Anna Gårdmark, Department of Aquatic Resources (SLU Aqua), Swedish University of Agricultural Sciences. The subject reviewer was Magnus Huss, Department of Aquatic Resources (SLU Aqua), Swedish University of Agricultural Sciences.

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Jag vill uttrycka ett stort tack till min handledare Anna Gårdmark som både utmanat mig och hjälpt mig att lära mig så mycket som möjligt under examensarbetet. Även tack till hela forskarteamet som breddade mina kunskaper och var en inspirationskälla till vidare studier och forskning.

Jag vill även uttrycka min tacksamhet till mina föräldrar som alltid stöttat och peppat mig under mina universitetsstudier, till min syster som alltid varit tillgänglig för råd och frågor rörande allt som hör studier till, till min partner som varit min bundsförvant och stöttepelare under hela examensarbetet samt till mina studiekamrater som fick min studietid att bli så himla rolig.

Sara Westerström
Uppsala, juli 2023

Populärvetenskaplig sammanfattning

När havens toppredatorer fiskas ut påverkar det upptaget av miljögifter i fiskarna som är kvar

För hög koncentration av miljögifter i kroppen kan vara dödligt för fiskar. Hur mycket det får i sig påverkas av interaktioner mellan organismer i födokedjan. Denna studie visar att när toppredatorer försvinner och födokedjan förändras så ändras även koncentrationen av miljögifter i fiskar längre ner i födokedjan. Förvånande nog så verkar miljögiftshalten minska i fiskarna som är kvar.

Det pågående ohållbara globala fisket har resulterat i att havens toppredatorer har minskat och fortsätter att minska kraftigt. Därav måste många födokedjor ritas om där den översta nivån av kedjan suddas ut. Samtidigt finns utbredda problem med höga halter av miljögifter, som till exempel tungmetaller i många hav och vattendrag. Fiskar och andra vattenlevande organismer är ofta känsliga för miljögifter och kan påverkas negativt av dem. Fiskar kan få i sig miljögifter genom upptag från vatten eller genom upptag från sin föda. Eftersom överföring kan ske via födan så skapas det överföringsvägar via födokedjan och på så sätt kan miljögifterna spridas till samtliga organismer i födokedjan.

Fisk är en viktig del av vattenbaserade ekosystem. Om fiskar mår dåligt eller dör på grund av för höga halter av miljögifter så påverkar det även hela ekosystemets välmående. Fisk är dessutom en livsviktig födokälla för miljoner människor runt om i världen. Djupare kunskap om vad som påverkar koncentrationer av miljögifter i fisk är därför betydelsefullt för att kunna sätta in rätt åtgärder och minimera risken att fiskpopulationer har halter som gör det giftigt för människor att äta fisken.

Resultaten från denna studie visar att toppnivån av en födokedja påverkar koncentrationen av miljögifter i fiskarter längre ner i födokedjan. Det verkar som att när det saknas rovfiskar som äter djurplanktonätande fiskar, så ökar konkurrensen om djurplankton eftersom det är fler djurplanktonätande fiskar kvar. De kvarvarande fiskarna kan inte äta lika mycket och får därför inte i sig lika mycket miljögifter via födan. Detta leder till en möjlig förklaring till varför man kan se variationer av miljögiftshalter i samma fiskart över olika områden, det kan bero på om de har rovfiskar närvarande eller inte.

Det är viktigt att komma ihåg att utfiskning av rovfiskar har en negativ inverkan på många andra funktioner i ekosystemen och processer i födokedjan. Det är sannolikt så att denna ”positiva” effekt av att miljögifterna i fiskarna som är kvar minskar, överskuggas av andra negativa effekter i ekosystemen. Denna studie undersöker inte sådana återkopplingsmekanismer och det går därför inte att veta vad effekten över lång tid skulle bli. Däremot, visar resultaten från denna studie vikten av att inkludera födokedjans struktur och dynamik när man studerar upptag och överföring av miljögifter. Resultat ger en djupare förståelse för konsekvenserna av miljögifter i akvatiska ekosystem, samt konsekvenserna av förändrade födokedjor.

En modell togs fram för att ge prediktioner om hur en förändring i födokedjan kan påverka fiskarnas upptag av miljögifter. Modellen är ett relativt unikt verktyg eftersom den kopplar samman en miljögifts- och en födokedjamodell samt att den tar hänsyn till fiskars olika storlekar och hur det kan påverka upptaget och överföringen.

Den nya kunskapen och det utvecklade verktyget skulle med fördel i högre grad kunna inkluderas när man diskuterar miljögifters effekt och påverkan. Det skapar bättre förutsättningar för att sätta in de mest lämpliga åtgärderna för att minska de negativa effekterna av föroreningar och undvika farliga miljögiftshalter i fisk.

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GLOSSARY

Term	Definition
Bioaccumulation	The accumulation and enrichment of pollutants in organisms, relative to that in the environment (Borgå 2008; Blowes et al. 2014).
Bioavailability	The potential for uptake of a substance by a living organism. Expressed as the fraction that can be taken up by the organism in relation to the total amount of the substance available (Nikinmaa 2014).
Biomagnification	The tendency of pollutants to concentrate as they move from one trophic level to the next (Blowes et al. 2003)
Biomass	Mass of fish (Li et al. 2020) or the total mass of a fish population (Palomares et al. 2020).
Ecosystem regime shift	A sudden shift in the structure and function of an ecosystem, affecting several living components and resulting in an alternate stable state (Scheffer et al. 2001; Cury & Shannon 2004).
Essential metals	Vital metals to live. Includes macronutrients (Na, K, Ca, Mg) and micronutrients (Cu, Zn, Fe, Mn, Ni, Co, Se, Cr, V) (Wood et al. 2012).
Food chain	A description of the transfer of energy from one trophic level to another in an ecosystem (Rai et al. 2017).
Food web	A description of which species in a community interact in feeding and describing which kinds of organisms in a community eat which other kind, often visualized in diagrams (Lévêque 2001). Can be seen both as an idealized representation of ecosystem complexity and as an information source for the patterns we observe in natural systems (Belgrano et al. 2009).
Heavy metals	Metals and metalloids that are potentially harmful to organisms due to their high toxicity, prevalence, and persistence (Brügmann 1981; Santos et al. 2018)
Intraspecific competition	Competition between individuals of the same species for the same limited resources (Gilad 2008).
Interspecific competition	Competition between different species for the same limited resources (Gilad 2008).

Trophic cascade	The effects of predators that propagate downward through food webs across multiple trophic levels (Ripple et al. 2016).
Trophic levels	Trophic levels are a hierarchical way of classifying organisms according to their feeding relationships within an ecosystem and thus their position in the food chain (Trites 2001; Pavluk & bij de Vaate 2017).
Trophic transfer	Elements or contaminants are transferred from one trophic level to another (Hare 2013).

1. INTRODUCTION

Marine pollution, overexploited fish stocks, and climate change are global threats to the aquatic ecosystems functioning and to fish as a food source (United Nations Development Programme n.d.). By negatively impacting the functioning of aquatic ecosystems, humans reduce their ability to help us offset the effects of climate change (United Nations Development Programme n.d.). Therefore, it is not surprising that “Life below water” regarding the world’s oceans, is the fourteenth Sustainable Development Goal adopted by the United Nations (United Nations Development Programme n.d.). One threat to achieving this goal is the widespread distribution of contaminants, for example, heavy metals (Santos et al. 2018; Abu Shmeis 2022), that through tropic transfers in the food web negatively affect the whole aquatic ecosystem (Alp & Cucherousset 2022).

1.1 HEAVY METALS IN AQUATIC ECOSYSTEMS

Heavy metals are naturally occurring elements that include essential metals for living organisms (e.g., copper (Cu), iron (Fe), nickel, and zinc (Zn)) and nonessential metals (cadmium (Cd), mercury (Hg), and lead (Pb)) (Santos et al. 2018). In marine environmental chemistry, “heavy metals” are often defined as metals and metalloids that are potentially harmful to organisms, owing to their high toxicity, prevalence, and persistence in the environment and bioaccumulative potential along the food chain (Brügmann 1981; Santos et al. 2018).

Due to discharge from human activities like industrial-, mining-, and agricultural processes, there is a widespread distribution of heavy metals in aquatic ecosystems (Santos et al. 2018; Abu Shmeis 2022). When crossing tolerance limits, heavy metals are proven to be a potential threat to aquatic organisms due to high toxicity and can even have a lethal outcome (Shahjahan et al. 2022). Because of heavy metals' persistent qualities, aquatic organisms can be continuously exposed to the metals even a long time after the emission occurred (Shahjahan et al. 2022).

Fish are commonly exposed to heavy metals (Shahjahan et al. 2022) and the concentrations of these metals in fish depend on the processes of uptake, internal distribution, storage duration, and excretion (Andres et al. 2000). The concentration of metals in fish also varies with species, diet, size, age (Andres et al. 2000), sex, reproductive status, and body condition (Nfon et al. 2009), as well as exposure duration and water chemistry (McCoy et al. 1995). Additionally, seasonal climate variations can influence biotic and abiotic factors that alter the bioavailability of metals to fish (McCoy et al. 1995).

1.2 ZINC IN FISH AND POTENTIAL TOXICITY

Zinc is an essential micronutrient (Watanabe et al. 1997; Glover et al. 2003; Niyogi et al. 2007) and is the quantitatively second most (after iron) important essential metal for fish (Watanabe et al. 1997). Fish can take up zinc either from the food via the gut or from water via the gills and the excess zinc is excreted via the bile or the gills (Bury et al. 2003). In the natural environment, the gut is the dominant pathway of absorption (Bury et al. 2003). However, with decreasing dietary zinc levels, the gill may become increasingly important, particularly when waterborne zinc levels are elevated (Bury et al. 2003) due to e.g., discharge from human activities (Ejhed et al. 2010). Studies have also shown that the proportion of zinc absorbed from food decreases when the dietary zinc load increases (Bury et al. 2003) which suggests that aquatic organisms have a mechanism for regulating the uptake of dietary zinc (Andres et al. 2000; Przytarska et al. 2010). Furthermore, the uptake of zinc through the gills also seems to be regulated since studies on fish

exposed to elevated waterborne zinc levels show alterations in zinc uptake mechanisms that limit the amount of zinc accumulating on the gill (Hogstrand et al. 1998)

Despite these regulating mechanisms, elevated zinc concentrations can be lethal to aquatic organisms (Glover et al. 2003; Niyogi et al. 2007). According to a review study, lethal concentrations of zinc for fish (determined by LC50 method i.e., the concentration of zinc that killed 50% of the exposed individuals after 96 hours) have a range between 0.17 mg/L and 212.90 mg/L for different species (Shahjahan et al. 2022). It varies with species, age, size, life history, and acclimatization of the fish which can explain the wide range (Skidmore 1964; Shahjahan et al. 2022). However, the duration of exposure has the strongest influence on mortality (Skidmore 1964).

To varying degrees, organisms can adapt to elevated concentrations of metals (Swedish Agency for Marine and Water Management 2016). Zinc can to some extent be detoxified by the liver (Nfon et al. 2009) and therefore, most of the absorbed zinc is discarded if the fish are returned to water with non-elevated zinc concentrations (Skidmore 1964). However, even if aquatic organisms have detoxification mechanisms, they require energy for such processes. The extra energy demand may impair other vital activities of the fish and result in reduced survival in the long term. On an ecosystem level, elevated zinc levels may therefore lead to the disappearance of sensitive species, the gene pool can be depleted, and the remaining population gets more sensitive to other stressors (Swedish Agency for Marine and Water Management 2016).

1.3 CHANGING FOOD WEBS

Food webs form the core of ecosystems (Alp & Cucherousset 2022) and describe the interactions and thus the pathway of transfer between different organisms. They are therefore crucial to include when studying the distribution and toxic effects of pollutants (Mathews & Fisher 2008; Gao et al. 2022). Studies show that the concentration of heavy metals often differs between organisms on different trophic levels and the trophic position of the organism may, for instance, affect the conditions for bioaccumulation (Mathews & Fisher 2008; Ruelas-Inzunza & Páez-Osuna 2008). Furthermore, it is often assumed that a contaminant either shows a trophic dilution (lower concentration in organisms at higher trophic level) or biomagnification between the species in a food chain (Xu & Wang 2002; Zhang & Wang 2007; Ruelas-Inzunza & Páez-Osuna 2008). However, in this context, it seems often forgotten that food chains can change, and as a result, alter many of the ecological functions and dynamics that matter for the uptake and transfer of pollutants. Furthermore, food web studies generally focus on the interactions and transfers between different species in the ecosystem (Ruelas-Inzunza & Páez-Osuna 2008). However, within-species interactions and dynamics can also influence the food web structure (de Roos & Persson 2013) and are thus likely to affect both the transfer between and within species.

Changes in aquatic food webs have been seen all around the world during the last decades (Heithaus et al. 2008; Britten et al. 2014). For example, there has been a pronounced global decline in predatory fish (Myers & Worm 2003; Heithaus et al. 2008; Eriksson et al. 2009; Britten et al. 2014). Unsustainable commercial fishing and degradation of important habitats have resulted in a situation where humans are fishing down the food webs (Pauly et al. 1998; Turner et al. 1999; Myers & Worm 2003).

The effects of removing large predatory fish may cascade down the food web and impact the whole ecosystem (in ecosystems that have top-down control) (Casini et al. 2009).

Multiple anthropogenic stressors such as overfishing, overexploitation, and climatic change have been the cause for such ecosystem regime shifts occurring worldwide during the last few decades (deYoung et al. 2008; Casini et al. 2009; Möllmann et al. 2009). These regime shifts cause abrupt ecosystem reorganizations, i.e., changing the dominating interactions, species compositions (Möllmann et al. 2009), and even ecosystem services (Rocha et al. 2015). Furthermore, recent predictions have shown that warmer temperatures due to climate change can also cause a shift in interactions in fish communities and ultimately lead to predator extinction, thereby changing the structure of the food web (Lindmark et al. 2019a; Thunell et al. 2021).

1.4 THE BALTIC SEA – ZINC POLLUTION AND CHANGING FOOD WEBS

The Baltic Sea both have profound pollution of heavy metals (HELCOM 2021) and significantly altered food web structures (Casini et al. 2009) and is, therefore, a good system to use to study the effect of food web changes on the uptake and transfer of metals. The Baltic Sea has been under strong anthropogenic pressure for several decades. Overfishing, eutrophication, and climate change have significantly been affecting the Baltic ecosystem's structure and function (Casini et al. 2009; Dietz et al. 2021). For example, several decades of high fishing pressure on cod in combination with unfavorable recruitment conditions resulted in a profound decrease in cod biomass. In turn, the cod's prey fish, the zooplanktivorous fish, sprat, could significantly increase instead. This meant a higher feeding pressure on zooplankton and therefore, their prey phytoplankton could increase. Consequently, the cod collapse triggered a trophic cascade in the central Baltic Sea ecosystem that caused an ecosystem regime shift (Casini et al. 2009).

The Baltic Sea has a large drainage basin with a total population of approximately 85 million people generating large amounts of waste and pollutants (Jansson et al. 1999; *Östersjöns historia | Havet.nu* 2022). Due to the slow turnover time in the Baltic Sea, the pollutants easily accumulate in the water column and the sediments underneath (Undeman et al. 2022a), and the sea remains heavily impacted by hazardous substances such as metals, organic contaminants, and radioactive substances (HELCOM 2021).

According to the Swedish Agency for Marine and Water Management, the Baltic Sea is classified with "Good status" if the annual average value of zinc does not exceed 1.1 µg/L (dissolved concentration through a filter). The status is determined by taking the annual average measurement and subtracting the natural background concentration and compare against the limit. Consideration should also be given to the hardness of the water, pH, dissolved organic carbon, or other water quality parameters that can affect the bioavailability of metals in water (The Swedish Agency for Marine and Water Management 2019). The Swedish Agency for Marine and Water Management does not provide the value for the natural background concentration, however, Herbert & Björkvald (2009) have calculated a proxy for this to be 0.555 µg/L filtered zinc in the Baltic Proper region.

As I could not find an appropriate reference to determine the zinc status in the Baltic, I used reported measurements from the DOME (Marine Environment) data portal (*ICES DataPortal* n.d.) to estimate the status. In the Baltic Sea region, they have registered data from Lithuania, Estonia, and Germany on zinc measurements in seawater (Data set "Contaminants data in seawater") and by taking the mean value of all measurements of zinc in [µg/L] per year during 2019-2021 and subtracting with the Herbert & Björkvald's (2009) background concentration for Baltic Proper, I retrieved three proxy values for zinc concentration in the Baltic. During all three years, the value was approximately 3 µg/L which

is higher than 1,1 µg/L and would therefore not be considered a “good status” according to The Swedish Agency for Marine and Water Management. Other studies have found that the highest metal concentrations in aquatic organisms are generally found in near-shore regions and the lowest in the open parts of the Baltic (Brüggmann 1981) and that temporal trends and spatial variations for the zinc concentration in fish, mussels, and birds during 2009-2018 have been very small (Danielsson et al. 2020).

Zinc is one of the most commonly used metals in the world and has many areas of use (Przytarska et al. 2010; Milton 2018). The widespread use of zinc leads to a lot of potential emission sources. The zinc that is emitted to the Baltic Sea can either come from point sources, such as industries and wastewater treatment plants, or diffuse sources such as stormwater, atmospheric deposition, and run-off from forest and agriculture as well as non-reported emissions from industries (Ejhed et al. 2010). It was difficult to find recent data on emission sources, but according to older data, the largest zinc emissions to the Baltic from Sweden are from forest runoff and industries (Figure 1). In all of Europe, one of the most important point sources is the European industries (European Environment Agency n.d.) (Przytarska et al. 2010).

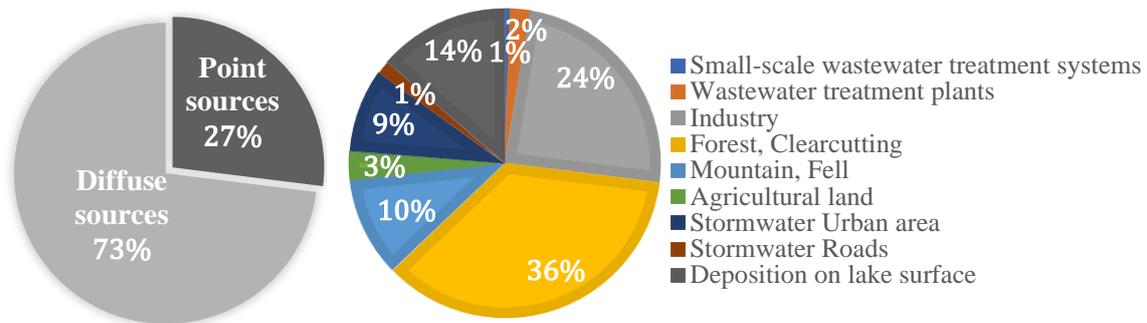


Figure 1. The grey pie chart to the left shows the proportion of Swedish diffuse and point emission sources of zinc. The colorful pie chart to the right shows the distribution of Swedish emission sources of zinc based on gross loads (kg/year) measurements. Both pie charts are based on data from 1985-2008 from Ejhed et al. (2010).

Wastewater treatment plants function as a collection point for pollutants present in our homes, public buildings, workplaces, industries, and stormwater (Luo et al. 2014; Undeman et al. 2022a). Wastewater treatment plants are not a major contributor to zinc emissions in Sweden (Figure 1). However, a recent study shows that metals are the category of micropollutants that wastewater plants have the highest emission of, and zinc has the highest max concentration (790,000 µg/L) and median concentration (27 µg/L) out of 280 substances examined (Undeman et al. 2022b). Therefore, wastewater treatment plants seem to be a potentially important point source for zinc, at least locally. Even though wastewater treatment plants transmit a wide range of micropollutants to both freshwater and marine water bodies, it is only now it has been discussed if it should be added to the European wastewater legislation where it has been missing so far (Directorate-General for Environment 2022; Undeman et al. 2022a).

1.5 AIM OF THE STUDY

There is a widespread distribution of toxic heavy metals, e.g., zinc, in aquatic ecosystems, and at the same time, the aquatic food webs are changing due to declining predatory fish stock. How such an alteration of a food chain, the disappearance of a top trophic level,

can affect the uptake and transfer of pollutants, such as zinc, is to the best of my knowledge, currently not known. This study aims to take steps to fill this knowledge gap and to answer the following research question:

How do the uptake and transfer of zinc in consumer fish populations differ between food chains with or without predatory fish?

I address this question by adding functions for zinc uptake, transfer, and emission to a stage-structured biomass model of interacting organisms in a food chain that in one version includes and, in another version, excludes a predatory fish population at the top of the food chain. With this tool, I will show how within- and between-species interactions affect the dynamics of a tri-trophic food chain and how that in turn can affect the concentration and distribution of zinc in the consumer population. The study aims to develop a tool that can be used in future studies when examining the uptake and transfer of other pollutants as well, in combination with structural changes in the food web.

I predict that the presence or absence of predatory fish will affect the biomass of the consumer population in such a way that processes that control the uptake and transfer of zinc will differ in the two cases and thus change the zinc concentration in the consumer population, depending on if predatory fish is present or not.

2. METHODS

I start by using a stage-structured biomass model developed by (De Roos et al. 2008) to describe a predator-consumer-resource-system with zooplankton and two species of fish; one consumer species that eat zooplankton, and one predatory species on top feeding on the consumer species (Figure 2). In the model, the resource (R) has an intrinsic resource turnover. The consumer species eats the resource to gain energy. The consumer species also show size variation, they are born as small, juvenile fish (J) and use some of their energy production to mature to become larger adult fish (A). The adult fish use all their energy production to reproduce and create new juvenile consumer fish in the system. The predator fish (P) is set to only prey on the juvenile consumer fish since predators usually prefer smaller size prey (e.g. cod, Gårdmark et al. 2015). Each group has a background mortality to which death due to predation is added for the juveniles. Together this generates an efflux from each group. The biomass dynamic model is simplistic and mechanistic and is therefore appropriate to use when you do not have empirical data for a specific system and want to study non-specific food chain dynamics and general mechanisms.

By having the consumer species in both juvenile and adult form as two separate groups, the model can account for the within-species size variation and include size-dependent processes. Metabolism, feeding, population growth rate, and mortality are several ecological traits a fish possesses that strongly depend on body size (Brown et al. 2004; Savage et al. 2004). The combination of within-species size variation and food-dependent life history processes generates feedback between size structure and individual performance which affects the dynamics and the structure of the community (Roos & Persson 2013).

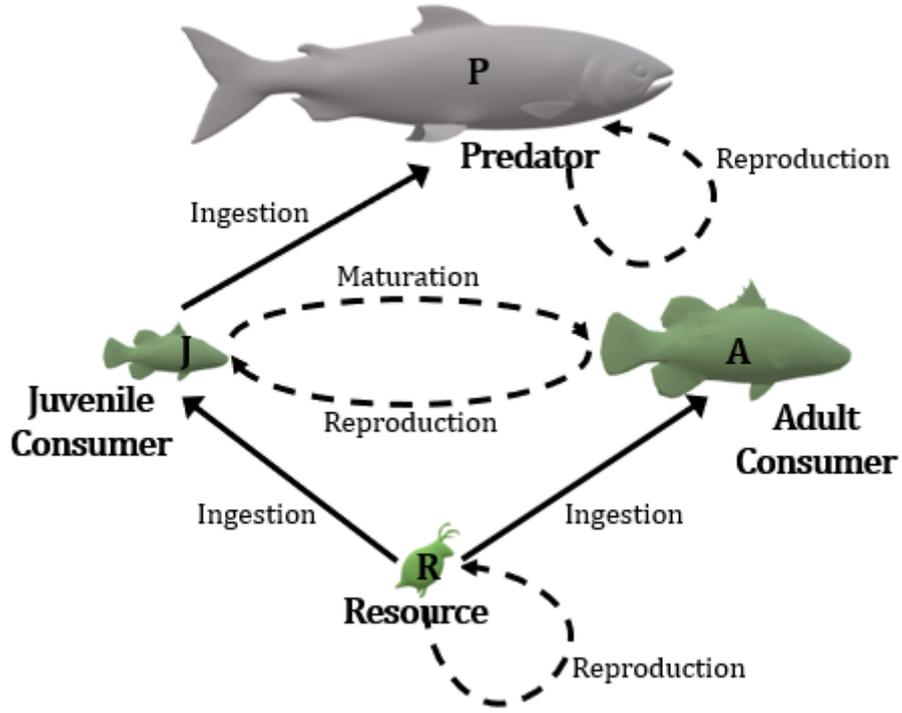


Figure 2. Visualization of the food chain with zooplankton (R), juvenile consumer fish (J), adult consumer fish (A), and predatory fish (P), that the stage-structured biomass model describes with three trophic levels and its simplistic dynamics (arrows).

2.1 MODEL FORMULATION

The stage-structured biomass model (De Roos et al. 2008) is derived from a size-structured population model with a continuous size distribution (as in Metz & Diekmann (1987) and de Roos (1997)) and under equilibrium conditions, the two models give identical predictions (De Roos et al. 2008). The stage-structured biomass model is based on a set of four ordinary differential equations (Equations 1-4) that describe the change in biomass between populations in a food chain with size scaling functions (Table 1) of intrinsic biomass turnover, food intake, energy production, maturation, reproduction, and mortality (De Roos et al. 2008; de Roos & Persson 2013). $\frac{dR}{dt}, \frac{dJ}{dt}, \frac{dA}{dt}, \frac{dP}{dt}$ represents the biomass change per day [g/day] of each group in an arbitrary system volume. I used this model as a baseline to describe the energy interactions and dynamics of the studied food chain and I will hereby call it the “biomass dynamic model” for short.

$$\frac{dR}{dt} = G(R) - \omega_J(R)J - \omega_A(R)A \quad (1)$$

$$\frac{dJ}{dt} = v_A^+(R)A - \gamma(v_J^+, d_J)J + v_J(R)J - d_J(P)J \quad (2)$$

$$\frac{dA}{dt} = \gamma(v_J^+, d_J)J + (v_A(R) - v_A^+(R))A - d_A(P)A \quad (3)$$

$$\frac{dP}{dt} = (v_p(J, A) - \mu_p)P \quad (4)$$

Equations 1-4 consist of functions (Table 1) and parameters (Table 2) which in short can be explained as follows. The biomass dynamics of the resources are dependent on their reproduction which in the model is represented by the intrinsic resource turnover ($G(R)$) and the juveniles' and adults' predation on the resource ($\omega_J(R), \omega_A(R)$). The biomass dynamics of the juveniles are dependent on the reproduction of the adults ($v_A^+(R)$), how fast they mature ($\gamma(v_J^+, d_J)$) their energy production from food ($v_J(R)$) and the predation by predators as well as background mortality ($d_J(P)$). The biomass dynamics of adults are dependent on the juveniles' maturation ($\gamma(v_J^+, d_J)$), their net energy production from food after using some energy for reproduction ($(v_A(R) - v_A^+(R))$), and background mortality ($d_A(P)$). The biomass dynamics of predators depend on their net energy production from their predation on juveniles ($v_p(J, A)$) and background mortality (μ_p). More detailed information about the equations can be found in De Roos et al. (2008) and de Roos & Persson (2013).

Table 1. Functions of the biomass dynamic model. All functions have the unit [g/g/day]. The $v_J^+(R)$ and $v_A^+(R)$ represent the values of $v_J(R)$ and $v_A(R)$ but restricted to non-negative values to imply that growth, maturation, and fecundity are positive as long as juvenile and adult net production respectively are positive and equal to zero otherwise. The reference for all parameters is de Roos & Persson (2013).

Function	Expression	Description	In equation
$G(R)$	$\rho(R_{max} - R)$	Intrinsic resource turnover	(1)
$\omega_J(R)$	$\frac{M_c R}{(H_c + R)}$	Resource intake by juveniles	(1), (2), (6)
$\omega_A(R)$	$\frac{q M_c R}{(H_c + R)}$	Resource intake by adults	(1), (2), (3), (7)
$v_J(R)$	$\sigma_c \omega_J(R) - T_c$	Net energy production by juveniles	(2)
$v_A(R)$	$\sigma_c \omega_A(R) - T_c$	Net energy production by adults	(2), (3)
$v_p(J, A)$	$\sigma_p M_p \frac{\phi J + (1 - \phi)A}{H_p + \phi J + (1 - \phi)A} - T_p$	Net energy production of predators	(4)
$d_J(P)$	$\mu_J + \frac{M_p \phi P}{H_p + \phi J + (1 - \phi)A}$	Mortality rate of juveniles	(2)
$d_A(P)$	$\mu_A + \frac{M_p (1 - \phi)P}{H_p + \phi J + (1 - \phi)A}$	Mortality rate of adults	(3)
$\gamma(v_J^+, d_J)$	$\frac{(v_J^+(R) - d_J(P))}{\left(1 - z \left(1 - \frac{d_J(P)}{v_J^+(R)}\right)\right)}$	Maturation rate of juveniles	(2), (3), (7)

The default parameters in the biomass dynamic model (Table 2) stem from averages from inter-specific relationships based on published experiments on invertebrates. Even though I wanted to represent a system with zooplankton and fish in this study, the default parameters are used because of simplicity and the fact that those parameters have been tested to fit any resource-consumer-predator system with the same size scaling as the default parameters (de Roos & Persson 2013). However, this makes some of the values (e.g., body

weights) unrealistic for an average fish, thus when analyzing the results, it is the dynamics between the different state variables that are of interest, not their particular value.

Table 2. Parameters and their value used for the biomass dynamic model. The reference for all parameters is de Roos & Persson (2013).

Parameter	Size-dependence	Value	Unit	Description
ρ	-	0.1	day ⁻¹	Resource turnover rate
R_{max}	-	30	g/m ³	Resource maximum biomass density
W_A	-	0.0001	g	Average adult consumer body weight
M_c	$0.1W_A^{-0.25}$	1	g/g/day	Consumer mass-specific maximum ingestion rate of resources
H_c	-	3	g/m ³	Consumer ingestion half-saturation resource density
q	-	0.5	-	Adult-juvenile consumer ingestion ratio
T_c	$0.01W_A^{-0.25}$	0.1	g/g/day	Consumer mass-specific maintenance rate
σ_c	-	0.5	-	Consumer conversion efficiency
z	-	0.01	-	Newborn-adult consumer size ratio
μ_j	$0.0015W_A^{-0.25}$	0.015	g/g/day	Juvenile background mortality rate
μ_A	$0.0015W_A^{-0.25}$	0.015	g/g/day	Adult background mortality rate
W_P	-	0.01	g	Average predator body weight
M_P	$0.1W_P^{-0.25}$	0.13162	g/g/day	Predator mass-specific maximum ingestion rate of consumer
H_P	-	3	g/m ³	Predator ingestion half-saturation resource density
T_P	$0.01W_P^{-0.25}$	0.0316	g/g/day	Predator mass-specific maintenance rate
σ_P	-	0.5	-	Predator conversion efficiency
μ_P	$0.0015W_P^{-0.25}$	0.0047	g/g/day	Predator background mortality rate
ϕ	-	1.0	-	Predator foraging preference for juveniles

To this biomass dynamic model, I developed a “pollutant module” to examine how zinc is taken up by the resource and then distributed through the food chain through consumption and trophic transfers. I derived a set of four differential equations (Equations 5-8) to describe the uptake and efflux of zinc in each population group (resources, juveniles, adults, and predators).

$$\frac{dZn_R}{dt} = \left(k_{uWR} C_{wZn} - k_{eR} \frac{Zn_R}{R} \right) R \quad (5)$$

$$\frac{dZn_J}{dt} = \left(k_{uWJ} C_{wZn} + AE_J \omega_J(R) \frac{Zn_R}{R} - k_{eJ} \frac{Zn_J}{J} \right) J \quad (6)$$

$$\frac{dZn_A}{dt} = \left(k_{uWA} C_{wZn} + AE_A \omega_A(R) \frac{Zn_R}{R} - k_{eA} \frac{Zn_A}{A} \right) A + \left(\gamma(v_J^+, d_J) \frac{Zn_J}{J} \right) J \quad (7)$$

$$\frac{dZn_P}{dt} = \left(k_{uWP} C_{wZn} + AE_P \omega_P(J) \frac{Zn_J}{J} - k_{eP} \frac{Zn_P}{P} \right) P \quad (8)$$

The equations (5-8) are derived from functions (Table 1 and 3) and parameters (Table 4) and can be explained as follows. Fish can take up zinc from water and food (Bury et al. 2003). The former depends on the rate of uptake from water (which here is species-specific, k_{uWR} , k_{uWJ} , k_{uWA} , and k_{uWP}) and the concentration of zinc in the water (C_{wZn}). The uptake from food depends on the intake rate of food ($\omega_J(R)$, $\omega_A(R)$ taken from the biomass dynamic model and $\omega_P(J)$ derived from the biomass dynamic model) and the concentration of zinc in food ($\frac{Zn_R}{R}$, $\frac{Zn_J}{J}$, $\frac{Zn_A}{A}$ and $\frac{Zn_P}{P}$) and how fast they assimilate the zinc (AE_J , AE_A , and AE_P). The amount of zinc in adults also depends on zinc accumulated earlier in life, which depends on the concentration of zinc in juveniles ($\frac{Zn_J}{J}$) and the maturation rate of juveniles ($\gamma(v_J^+, d_J)$). The resource is assumed to be filtering their food from the water and is thus simplified to only have one uptake pathway from the water. $\frac{dZn}{dt}$ represents the change in total zinc per day [g/day] in each group and $\frac{Zn_R}{R}$, $\frac{Zn_J}{J}$, $\frac{Zn_A}{A}$ and $\frac{Zn_P}{P}$ the zinc concentration in each group [g_{zinc}/g_{fish}/day]. The dynamics of the pollutant module is visualized in Figure 3.

The median value of wastewater treatment plants' concentrations of zinc emission (27 µg/L) was decided to represent the zinc concentration in the water (C_{wZn}) in the modeled system. For simplicity, it was assumed that all the zinc was bioavailable for the fish. Furthermore, I used the result from Zhang & Wang (2007) experimental study on juvenile Black Sea Bream, and their determined physiological kinetic parameters for uptake rate constant from water, assimilation efficiency, and efflux rate of zinc. They were chosen because their study used similar parameters for metal accumulation and since they found a size dependence for two of these parameters which my study focuses on. They found that the uptake rate constant from water decreased with increased fish size, assimilation efficiency increased with increased fish size and efflux was independent of the fish size (Table 4). In the biomass dynamic model, there was no default value for the weight of the resource which was needed in the pollutant module and therefore I decided to have the same size relation as the other groups have to each other, i.e., 100 times smaller than the next group (in this case juveniles) (Table 4).

Table 3. Model functions of the pollutant module derived from the predator function in the biomass dynamic model from de Roos & Persson (2013).

Function	Expression	Description	In equation
$\omega_p(J)$	$\frac{M_p \phi J}{H_p + \phi J + (1 - \phi)A}$	Juvenile prey intake by predators	(8)

Table 4. Parameters and their value used for the pollutant module specified on zinc.

Parameter	Size-dependence	Value	Unit	Description	Reference
C_{wzn}	-	Varied $27 \cdot 10^{-3}$ $3 \cdot 10^{-3}$ $0.555 \cdot 10^{-3}$	g/m^3	Concentration of bioavailable Zn in water	(Undeman et al. 2022) (<i>ICES DataPortal</i> n.d.) (Herbert & Björkvald 2009)
W_R	$0.0001W_A$	$1 \cdot 10^{-8}$	g	Average resource body weight	Assumption
k_{uwR}	$0.002061W_R^{-0.615}$	0.171	$m^3/g/day$	Resource uptake rate constant of Zn from water	(Zhang & Wang 2007)
k_{eR}	-	0.016	day^{-1}	Resource efflux rate constant of Zn	(Zhang & Wang 2007)
W_J	zW_A	$1 \cdot 10^{-6}$	g	Average juvenile body weight	(de Roos & Persson 2013)
k_{uwJ}	$0.002061W_J^{-0.615}$	0.0101	$m^3/g/day$	Juvenile uptake rate constant of Zn from water	(Zhang & Wang 2007)
AE_J	$0.771W_J^{0.406}$	0.00280	-	Juvenile assimilation efficiency of Zn from food	(Zhang & Wang 2007)
k_{eJ}	-	0.016	day^{-1}	Juvenile efflux rate constant of Zn	(Zhang & Wang 2007)
k_{uwA}	$0.002061W_A^{-0.615}$	0.00594	$m^3/g/day$	Adult uptake rate of Zn from water	(Zhang & Wang 2007)
AE_A	$0.771W_A^{0.406}$	0.0180	-	Adult assimilation efficiency of Zn from food	(Zhang & Wang 2007)
k_{eA}	-	0.016	day^{-1}	Adult efflux rate constant of Zn	(Zhang & Wang 2007)

k_{uwP}	$0.002061W_P^{-0.615}$	$3.50 \cdot 10^{-5}$	$m^3/g/day$	Predator uptake rate of Zn from water	(Zhang & Wang 2007)
AE_P	$0.771W_P^{0.406}$	0.119	-	Predator assimilation efficiency of Zn from food	(Zhang & Wang 2007)
k_{eP}	-	0.016	day^{-1}	Predator efflux rate constant of Zn	(Zhang & Wang 2007)

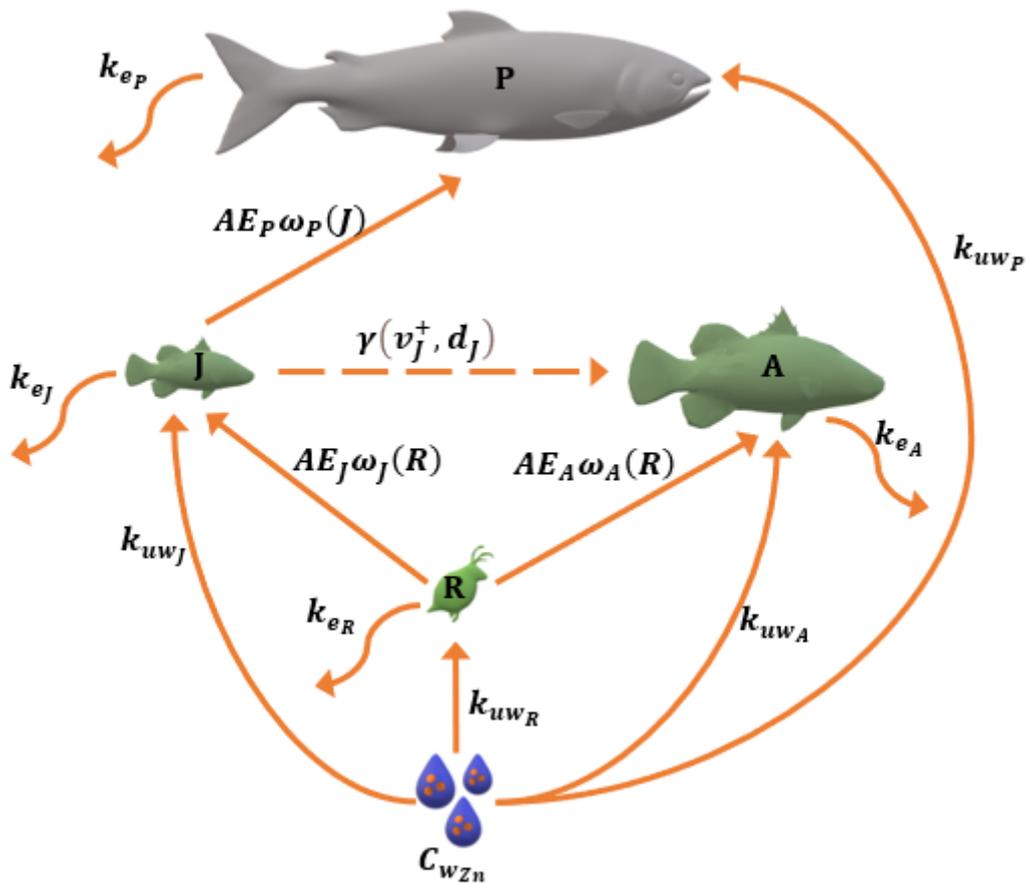


Figure 3. Visualization of the pollutant module with pathways for uptake and efflux of zinc (orange arrows) with corresponding parameters in a food chain of three trophic levels with a predatory species present.

2.2 ANALYSES

The biomass dynamic model together with the pollutant module was implemented in MATLAB (MATLAB R2022b) and the package MatCont GUI (Dhooge et al. 2008). It was implemented in two scripts, one with predators and one without where equations 4 and 8 were excluded. The same analyses were made with both scripts to compare the results. In all the computations, the initial value of the state variables were set to $1 g/m^3$

for R, J, A, and P and to the background concentration of zinc in the Baltic (0.000555 g/m^3) (Herbert & Björkvald 2009) for Zn_R , Zn_J , Zn_A , and Zn_P .

Time simulations were made to examine the equilibrium total zinc amount and biomass densities, and how they differ with or without predators. The length of integration (time steps) was set to 4000. Equilibrium was defined as when the state variables reached a stable state and did not vary on the third significant figure. From the time simulation, the corresponding zinc concentration was calculated by dividing the zinc amount by the biomass for each time step and each population group. Time simulations were also tested for other values for the zinc concentration in the water (C_{wZn} ; Appendix 1). The continuation of equilibrium was studied by doing bifurcations over all the constant zinc parameters, i.e., the uptake rate constants of zinc from water (k_{uwR} , k_{uwJ} , k_{uwA} , k_{uwP}) and assimilation efficiency of zinc from food (AE_J , AE_A , and AE_P). From each run the equations for the linear regression were retrieved by using the MATLAB function “polyfit”.

Additionally, bifurcations were made over the efflux rate constant. For this, the script was rewritten so that the efflux rate constant was the same variable for juvenile and adult consumers (ke_c) (i.e., only species-specific not size-specific). By changing this, the bifurcation over ke_c gave output for both the juvenile and adult zinc concentration. Furthermore, user functions were implemented in MatCont for juvenile and adult intake rates ($\omega_J(R)$, $\omega_A(R)$) and maturation rate ($\gamma(v_J^+, d_J)$) to track their equilibrium value. The aim was to implement user functions for the zinc uptake and efflux expressions, (i.e., $AE_J \omega_J(R) \frac{Zn_R}{R}$, $ke_J \frac{Zn_J}{J}$, and $AE_A \omega_A(R) \frac{Zn_R}{R}$, $ke_A \frac{Zn_A}{A}$, $\gamma(v_J^+, d_J) \frac{Zn_J}{J}$) but due to recurring technical problems with MatCont, bifurcations over these user functions implemented could not be done. Bifurcation over resource maximum biomass density was carried out to examine how the productivity in the system may change the uptake and transfer of zinc. However, due to problems when running the bifurcation, it was only possible to do so for the system with predators. Additionally, zinc uptake from water, food, and maturation in the equilibrium state was calculated by hand using Tables 3-4, Equations 5-8, and the equilibrium values of the biomass and zinc amount state variables.

3. RESULTS

Without predators in the system, the zinc concentrations are lower in juveniles and adults (Figure 4). The greatest difference is in the adult zinc concentration. In the absence of predators, the concentration is only half of what it is when predators are present (0.1 g/g versus 0.2 g/g). In the juveniles, the difference is smaller (0.04 g/g and 0.06 g/g).

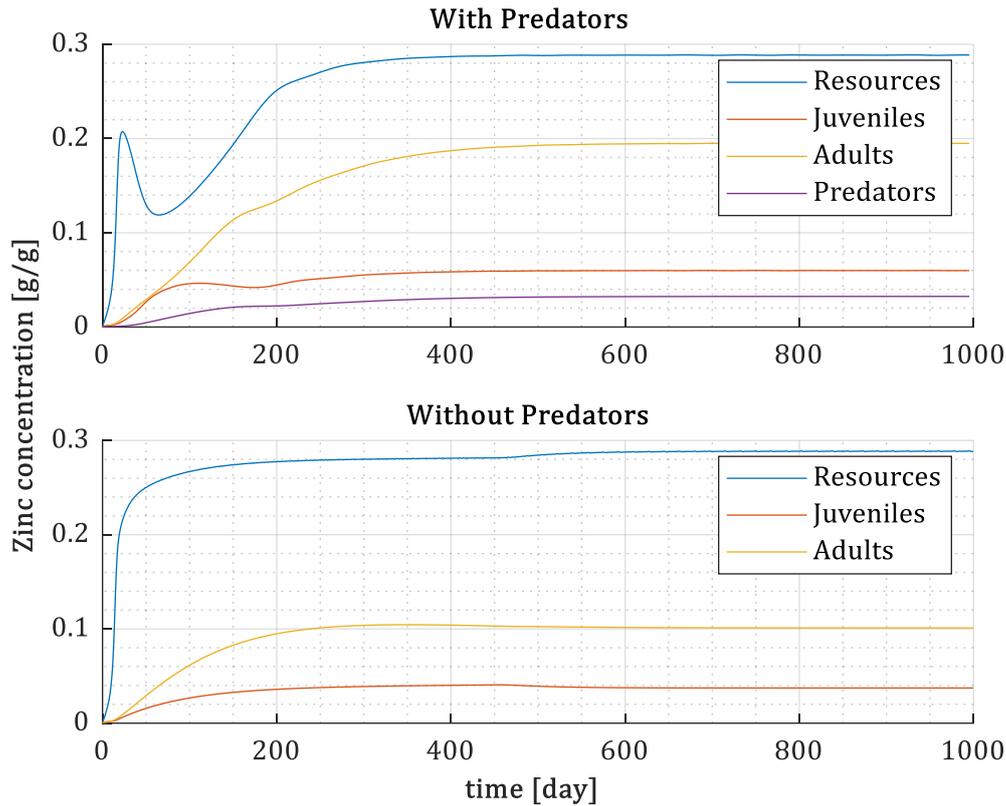


Figure 4. Time simulation of zinc concentration in each population group shows that they differ if predators are present (top) or absent (bottom) in the system.

One explanation for this result could be that without predators, the adult and juvenile biomass are greater (Figure 4), therefore the total zinc amount is divided between more adults and juveniles respectively, and thus the concentration decreases. However, if this was the only explanation, the total zinc amount in adults and juveniles should be the same with or without predators, which they are not (Appendix 1, Figure 1). With predators in the system, the resource has a high amount of zinc in their group (almost 6 g) in comparison to the others (all below 0.5 g) (Appendix 1, Figure 1). Without predators, the amount of zinc in resources is less than one-third of the amount with predators, however, the amount in adults is higher while in juveniles approximately the same (Appendix 1, Figure 1).

Moreover, the difference in zinc concentration between juveniles and adults is greater with predators in the system. Possibly this is because the predators' exclusive predation on juveniles differentiates the dynamics between the two groups more. Furthermore, both with and without predators, the resources are the group with the highest zinc concentration, followed by adults, juveniles, and predators (Figure 4) which indicate some trophic dilution. The uptake rate constants from water are size-dependent and increase with decreasing size (Table 4). Thus, the resource that has the lowest individual weight, has the highest uptake rate constant. The efflux constants are size independent and therefore the difference between water uptake and efflux is the largest in the resource, followed by juvenile, adult, and predator. This could be the explanation for why the resource has the highest zinc concentration in both scenarios (Figure 4). The adults have higher zinc concentration than the juveniles in both cases which is expected since they are accumulating zinc during their juvenile state.

Additionally, it is worth noting that all population groups have a higher zinc concentration than the bioavailable zinc in the water (0.027 g/m^3) by approximately a factor of 10, except for juveniles with a little less, which indicate bioaccumulation of zinc. The curves in Figure 4 are independent of the water concentration of zinc, it is only the explicit values that differ when the zinc concentration in the water change (Appendix 1, Figure 2-3).

The biggest difference in biomass when predators are removed from the system is that the resource biomass decreases and the adult consumer biomass increases. The juvenile biomass increases as well, but not as much as the adults when there are no predators present (Figure 5).

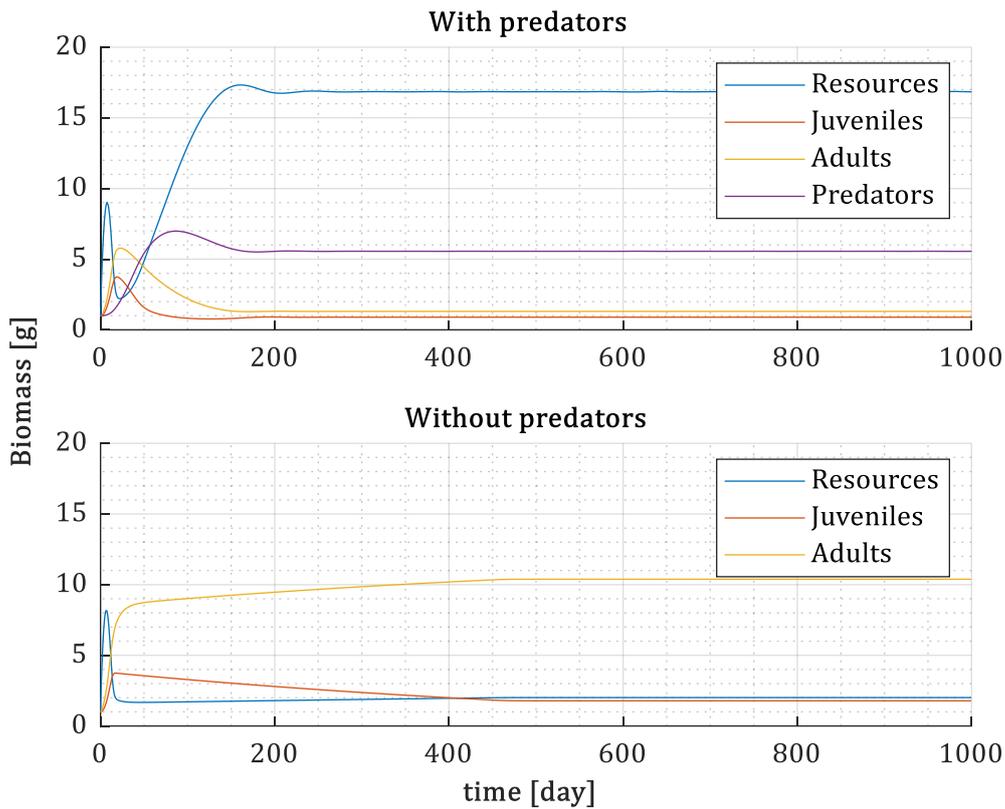


Figure 5. Time simulation of biomass in each population group shows that they differ if predators are present (top) or absent (bottom) in the system.

To explain the main result, that the consumer zinc concentration decreased in the absence of predators, a comparison between the uptake of zinc from water, food, and received through maturation with or without predators was made (Figure 6). The uptake with predators is considerably higher for both juveniles and adults. The uptake from water is independent of predators' presence. Adults have a higher total uptake than juveniles in both scenarios even though they have a smaller uptake from water (Figure 6). Furthermore, there is a larger difference in the uptake from food for adults than juveniles when the predators are removed. The efflux from juveniles is approximately the same as the received zinc through maturation in adults (Figure 6).

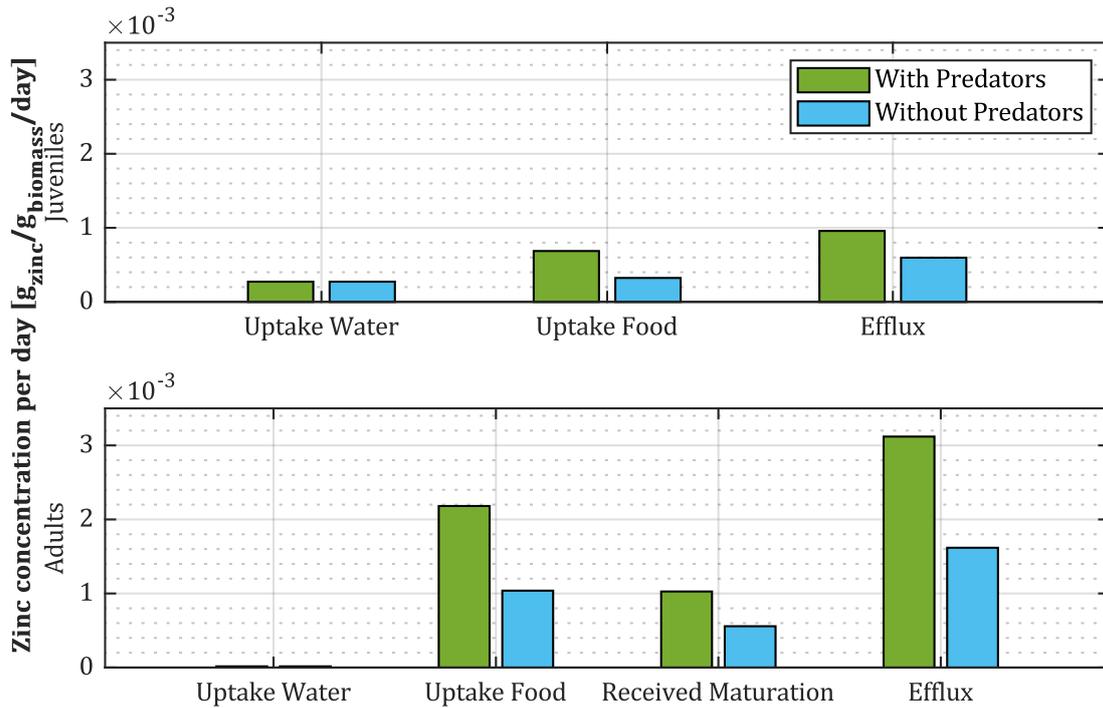


Figure 6. The amount of zinc that the juveniles (top) and adults (bottom) take up from water, food, and maturation (only for adults) per gram of fish per day (i.e., zinc concentration per day) at the equilibrium state. The efflux is equal to the uptake. Note that adults' Uptake Water is too small to be able to view in this figure.

Worth noting is that the consumers' intake rate of resources, and therefore also their uptake of zinc from food, will change if the productivity of the system (the amount of available resources to eat) changes (Appendix 1, Figure 4). The productivity is dependent on the resource maximum biomass density (R_{max}) (Tables 1 and 2). For the system with predators, the intake rates increase when the R_{max} grows larger than the default value ($R_{max}=30$) (Appendix 1, Figure 4). If the R_{max} decreases below 30, the intake rates quickly drop. The R_{max} has to be larger than 10 to be able to sustain all the populations (R, J, A, P). The only difference between the juvenile and adult intake rates is a factor difference due to the consumer ingestion ratio. Furthermore, there are alternative stable states with higher or lower intake rates for the same R_{max} . There are also shifts in equilibrium stability when the productivity of the system changes. The eigenvalues for the red curve were all negative, the following blue curve had one real eigenvalue with positive values close to the branchpoint and the lower blue curve had only negative eigenvalues (Appendix 1, Figure 4). The maturation rate can also be dependent on the productivity of the system (Appendix 1, Figure 5). The bifurcation analysis shows alternative stable states, where one alternative seems to be independent of changes in R_{max} and the other shows a positive linear dependence in the system with predators (Appendix 1, Figure 5).

To examine the zinc parameters' influence on the main result, bifurcations were made for all parameters (Figures 7 and 8). Due to the transfers between different populations in the food chain, a change in a specific zinc parameter for each population group (R, J, A, and P) will have an impact on other population groups as well as their own. The zinc parameters for the resource (kuw_R) affect the zinc concentration in all the other groups (bottom

row in Figure 7). The zinc parameter for the juveniles (ku_{WJ} and AE_J) affects the zinc concentration in the juveniles, adults, and predators (two middle rows in Figure 7). The zinc parameter for the adults and predators (ku_{WA} , AE_A , and ku_{WP} , AE_P) only affects their own zinc concentrations since they are not prey to another group (top two rows in Figure 7).

Regardless of if the zinc parameter values would change, the concentration in the resource, juveniles, and adults will always be higher when predators are present, since their lines (green) all have a steeper slope than the ones without predators (blue lines) (Figure 7). This also indicates that the zinc uptake parameters are more influential to the overall zinc concentrations if predators are present in the system. Moreover, a change in AE_J results in the largest change in zinc concentration for all the population groups in both scenarios with and without predators as their slopes are the steepest (Figure 7). Change in AE_A also results in a large change in the adults' zinc concentration, especially with predators present. For more robust model results, the AE_J parameter (as well as AE_A) should have a low uncertainty in the parameter value since their values have such a large impact on the overall zinc concentration. The equilibrium for each case is stable (the real eigenvalues were all negative) (Figure 7).

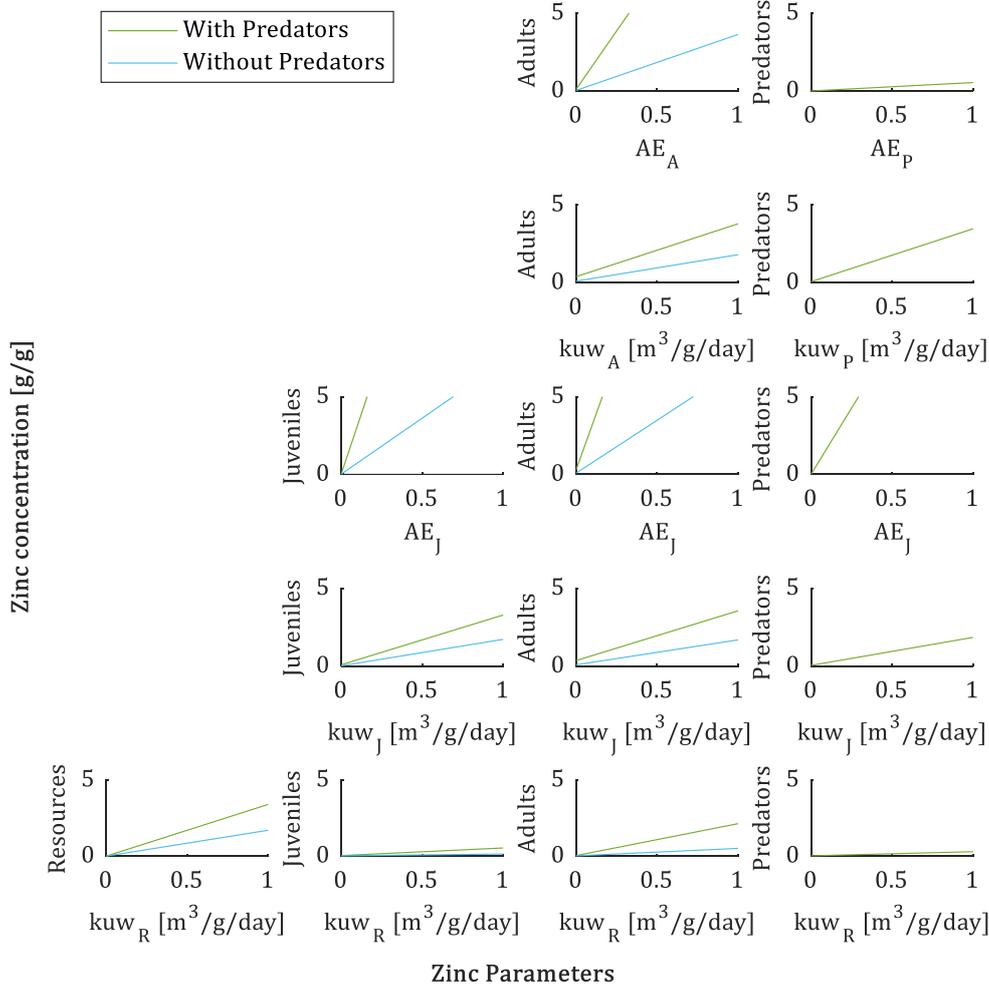


Figure 7. Bifurcation analysis shows how zinc concentrations vary with the uptake rate constants from water (kuw) and assimilation efficiencies (AE) with and without predators in the system. (The slope and intercept coefficients can be viewed in Appendix Tables 1 and 2).

In contrast to the zinc parameters (Figure 7), the efflux rate constant did not have a linear relationship with concentration (Figure 8). Regardless of if the efflux rate would change, the concentration in the juveniles and adults will always be higher when predators are present since they have a higher concentration value for the same efflux rate (the green lines are always above the blue) (Figure 8). As expected, when the efflux rate constant gets closer to zero, the zinc concentration in the juvenile and adult fish increases both with and without predators. Similarly, when the efflux rate constant gets larger, the zinc concentration in the fish decreases and gets closer and closer to zero both with and without predators. (Figure 8). Therefore, the difference between with and without predators (the green and blue lines) decreases the closer you get to an efflux rate equal to zero and equal to something large. Furthermore, adults have a wider span of efflux rate constants that results in a large difference in the zinc concentrations than juveniles (the difference between the green and blue lines are largest in the figure to the right) (Figure 8). The equilibrium for each case is stable (the real eigenvalues were all negative).

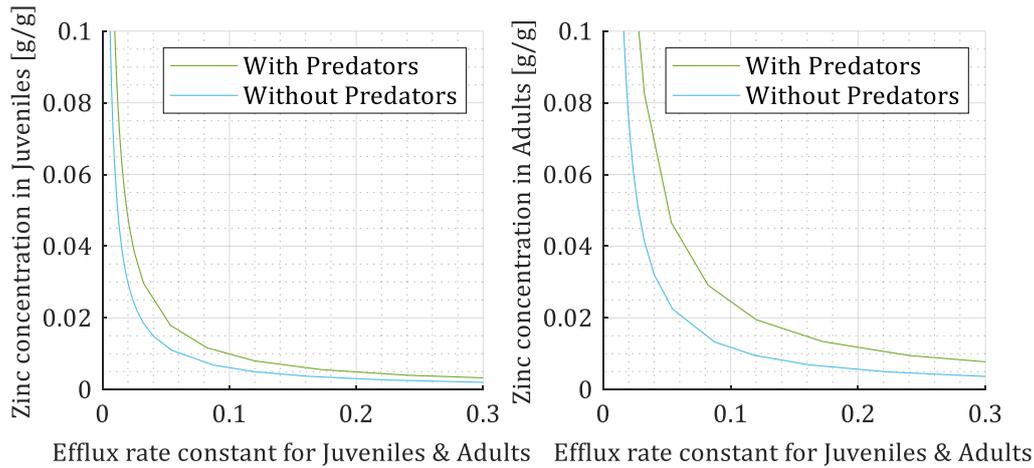


Figure 8. Zinc concentrations in juveniles (left) and adults (right) vary with the efflux rate constant, both with (green) or without (blue) predators in the system.

4. DISCUSSION

Predation releases intraspecific competition in the prey fish (here juveniles), and they can therefore feed faster. When the prey consists of juveniles as in my model, this results in a higher maturation rate due to faster-growing juveniles (e.g., Schröder et al. 2009; Vanni et al. 2009). This can explain why we see a higher zinc uptake from food and higher transfer from maturation and thus the higher zinc concentration when predators are present in the system. The results agree with my prediction that the presence or absence of predatory fish will affect the zinc concentration in the consumer population as predators affect both their biomass and therefore competition and feeding rates. Zotina et al. (2022) state that the trophic position of fish is one of the most important factors controlling the accumulation of contaminants. This study shows that the presence or absence of a predatory fish in the top trophic position can determine the concentration of contaminants in another fish at a lower trophic level.

The main result suggests that changes in food web structure, e.g., removal of large predators, can affect the transfer of pollutants between trophic levels. This provides a possible explanation for variation in pollutant concentration seen between the same species across different areas (Barak & Mason 1990; Noël et al. 2013; Ghosn et al. 2020). It also suggests that the risk for toxic effects on fish is not only species-specific (e.g., Shahjahan et al. 2022) but food-web-specific as well. If the same population gets a new position in the food chain, it could change its pollutant concentration as well. This result gives a deeper understanding of the consequences of pollution on aquatic ecosystems, as well as the importance of altered food chains for the transfer of pollutants. This knowledge can support mitigation measures to reduce the negative impact of pollution and avoid toxic pollution levels to fish.

The result that the concentration in the consumer population decreases without predators, stands even if we change the zinc parameter values. The exception is if the efflux value decreases so much that the concentration gets huge or increases so much that the concentration gets to zero. Consequently, the processes that govern the biomass dynamics of the food chain are more important, or at least as important, as the parameters for the pollutant module to account for when studying pollutant uptake and transfer. Moreover, according

to this study, the parameters in the pollutant module have a stronger influence on the resulting zinc concentration when predators are present. Therefore, the values for the parameters should be chosen with care when used in the model with predators to have the same uncertainty as the model without. This also adds to show the importance of taking food chain structure into account when studying pollutant uptake and transfer.

If the predators are present, the competition between consumer fish decreases and the fish can eat more resources and therefore have a larger zinc uptake from food. However, how much they can eat is also dependent on food availability which is governed by the productivity of the system. Productivity has a strong influence on the community structure and composition (Lindmark et al. 2019b). Hence, if the productivity of the system would change, the main result could potentially change as well. Especially a production decrease could change the result since it would limit the ingestion possible and change the population biomasses (Lindmark et al. 2019b). To better see how this would have affected the results, bifurcations over R_{max} , could be done for the scenario without predators as well and the stability of the equilibriums could be examined more thoroughly.

The decline in top predatory fish (Heithaus et al. 2008; Eriksson et al. 2009; Britten et al. 2014) does not seem to aggravate the potential risk of dangerous zinc pollution according to the results in this study. However, in this study, the biomass of resources decreases significantly without predators, and such a change can impact ecosystem functioning and potentially worsen the problem in other ways (Gorokhova et al. 2016; Lomartire et al. 2021). Such potential feedback mechanisms are not included in this model and the decrease in zinc concentration when predators are absent would potentially not maintain if it was.

According to this study, the decrease in zinc concentration due to predator disappearance is the largest in the adult consumer population. This result is most likely explained by adults' larger difference in uptake from food with and without predators in comparison to juveniles. Furthermore, adults have a higher zinc concentration than juveniles both with and without predators. The reason is probably that adults accumulate zinc as young, i.e., they have an additional pathway of pollutant transfer since adults 'receive' zinc through juveniles maturing. In addition, the adults' larger size results in a higher assimilation efficiency of zinc which makes the zinc uptake from food larger in adults even though their ingestion rate is lower than the juveniles'. This agrees with empirical studies that found a positive correlation between fish size (length and weight) and zinc concentrations (Kamaruzzaman et al. 2008; Tanir 2021). However, other studies have found a negative correlation or no significant correlation (Farkas et al. 2003; Balzani et al. 2022), which may indicate that the adult assimilation efficiency of zinc could be overestimated in this study. Moreover, due to the very small uptake rate constants for water, the uptake of zinc from water is almost insignificant in this model. This agrees with Hogstrand et al.'s (1998) study that shows that the gut appears to have a much greater capacity for zinc uptake compared to the gill.

The resource has the highest concentration of zinc and is therefore most at risk of being negatively affected. Field studies have measured the highest zinc concentration in zooplankton when comparing the concentration in organisms in a pelagic food chain in the Baltic Sea (Nfon et al. 2009). Commonly, commercial fisheries are targeting top predators due to their larger size, and therefore this result could indicate that the risk for toxic transfer of zinc to humans is small. However, if the food chain symbolized a system with Baltic

herring, cod, and seals, humans would mostly eat the Baltic herring which in such a scenario is symbolizing the resource. Thus, general notions of the risks for toxicity for humans are not possible based on this study. Instead, they need to be examined separately in each specific system.

The model predicts that zinc bioaccumulates in fish, as the concentrations in fish are higher than in the surrounding water. Bioaccumulation of zinc has been found in many empirical studies as well (e.g., Handy & Eddy 1990; Köck & Bucher 1997; Zhang & Wang 2007). Consequently, pollutant accumulation over time can result in toxic levels even though the separate emission concentrations do not exceed the limit value. This implies that measures to eliminate the emissions from point sources, e.g., wastewater treatment plants, are important to take regardless of their emission concentrations to avoid toxic levels for fish.

Similar to other studies (Wren et al. 1983; Ward et al. 1986; Barwick & Maher 2003; Mathews et al. 2008; Nfon et al. 2009), the metal concentration decreased with increasing trophic levels, showing that biomagnification of zinc is unlikely. However, other studies (Timmermans et al. 1989; Quinn et al. 2003; Campbell et al. 2005; Ruelas-Inzunza & Páez-Osuna 2008) have shown signs of biomagnification of zinc. Potentially the biomagnification of zinc is ecosystem-specific (Nfon et al. 2009) which could explain the different results. Another explanation shown in this study is that interactions in the food chain matter a great deal for the uptake and transfer of pollutants. Consequently, when examining different food chains we should expect biomagnification occurring in some food chains and not in others.

One of the most important restrictions of this study includes that I simplified the food web into a food chain with only two or three trophic levels. Furthermore, the parameter values for both the biomass model and the pollutant module are general and do not allow for any species- or system-specific predictions. Therefore, the model cannot be seen as a representation of pollutant uptake and transfer in a real food web in a specific ecosystem but should be viewed as a tool to resolve the processes determining the uptake, transfer, and accumulation of a pollutant in a general food chain. However, the aim of this study was not to predict the actual pollutant concentrations but to study the variation of the concentration when the food chain structure changes, thus the model is suitable for this aim.

Nonetheless, there are several assumptions regarding the uptake of zinc in the model worth highlighting. One assumption is that the zinc from food originates from the water via the uptake by zooplankton. Potentially, it would resemble reality more if this zinc in the resources instead originated from another source, e.g., the sediment, instead of originating from the current zinc emission in the water. Metals can accumulate in the sediment and potentially affect benthos (Sharifuzzaman et al. 2015; Holmerin 2022). The benthos is an energy source of benthic and (to some extent) pelagic food webs, thus their intoxication of zinc could likely be seen at higher trophic levels (Holmerin 2022). Consequently, a pathway from sediments to the fish could be added to the model to more accurately describe all potential transfers and all the zinc loads the fish are exposed to. Another way to account for the sediment loading would be to add a background concentration of zinc to the organisms. However, zinc concentrations in the sediments are very spatially variable across the sea bottom (Sharifuzzaman et al. 2015) thus a generalization of such loading was considered to be too uncertain to include in the model.

More assumptions in the model include that the resources (i.e., zooplankton) only have one uptake pathway of zinc from water even though zooplankton eat phytoplankton. Therefore, it would resemble a true food web transfer more if the resources also had a zinc transfer from food. The additional pathway would increase the total zinc load in resources and thus in all trophic levels above. However, it would also require an additional trophic level to the model which perhaps would increase the complexity more than the qualitative result. Moreover, I assume that predators prey exclusively on juveniles because predators usually prefer smaller-sized prey (e.g., cod, Gårdmark et al. 2015). This could have affected the result because the effect on the consumer biomass when removing predators is larger when predators prey exclusively on juvenile fish (de Roos & Persson 2013; Lindmark et al. 2019a). Additionally, I assume a zinc transfer from reproduction is negligible and therefore not included in the model.

Above I discuss several assumptions that could have led to an underestimation of the zinc concentrations in the fish populations. However, there is another assumption that could have contributed to an overestimation. The bioavailability of zinc is assumed to be 100 % throughout the zinc transfers in the model, even though it is known to depend on several abiotic factors. Low oxygen levels in the water seem to increase the assimilation of zinc, potentially because the fish consume less food and have a lower growth rate under hypoxic conditions (McNicholl et al. 2021). Similarly, higher water temperatures seem to increase the toxicity level of zinc (Skidmore 1964; Shahjahan et al. 2022). In contrast, the presence of calcium and sodium ions in the water seems to decrease the toxicity of metals in fish (Skidmore 1964; Hogstrand et al. 1998; Shahjahan et al. 2022). Moreover, throughout the transfers and the fish's digestion of the metal, chemical reactions can occur and change the bioavailability (Bradley et al. 2017). Assuming a 100 % bioavailability is therefore probably a cause for an overestimation of the zinc concentration in this study. Since some of the assumptions probably underestimated the result while others overestimated it, the influence of these assumptions may have been canceled out. Also worth noting is that all mentioned assumptions were done for both scenarios, with and without predators, thus they do not affect my main finding that the presence of top predators affects the zinc concentration in intermediary consumers.

This model is a valuable tool that can give general insights into the uptake and transfer of pollutants. The model can be used to study any pollutant that can be taken up from water and food and has some efflux rate. The same parameters for the pollutant module can be used and their value is the only thing that needs to be updated for the specific pollutant of interest. My model is in many ways very similar to the biokinetic model that Zhang & Wang (2007) applied and found to successfully predict the metal concentration in different sizes of fish. However, they did not account for food chain structure, which I here have shown to be key. Furthermore, they neglected the biomass dependence of ingestion- and growth rate and instead assumed a specific growth rate and growth dilution of metals, which I found to oppose basic ecological principles and potentially has a very large impact on exactly what is studied, the uptake and transfer of pollutants in food webs.

Relatively to other metal accumulation models, there are few published examples of food chain or food web model applications to metals, and the need for such development has been highlighted (Paquin et al. 2011). Several accumulation studies focus on size- and age-specific patterns of heavy metals in fish (e.g., Zhang & Wang 2007; Balzani et al. 2022). Other studies focus on trophic dynamics of heavy metals, but only by studying

trophic magnification- and biomagnification factors (e.g., Mathews & Fisher 2008; Vainio et al. 2022). In contrast to these studies, this study contributes to an understanding of the effect of a change in the food chain structure on pollutant uptake and transfer. My results show that ratios of pollutant concentrations in organisms at different trophic levels, such as biomagnification factors, are not constant, but depend on food web structure. Furthermore, the study's uniqueness is that it accounts for a size variation in the food chain, which both accounts for a fundamental aspect of population and community dynamics and deepens the understanding of food chain dynamics' influence on uptake and transfer of contaminants.

4.1 FUTURE STUDIES & PERSPECTIVES

To deepen the understanding of how abiotic factors (such as temperature, season, salinity, and oxygen) influence the main result, more bifurcation analyses should be made. Maturation depends on the juveniles' net energy production and mortality rate (Table 1). Net energy production of juveniles is, in turn, dependent on resource availability and consumer mass-specific maintenance rate (Table 2), which could vary with for instance temperature and season (Lindmark et al. 2022). The mortality rate of juveniles is dependent on the background mortality (Table 2), which in turn could vary with resource availability and overall fitness of the fish which can be dependent on e.g., temperature, season, salinity, and oxygen supply (Feidantsis et al. 2018; Abdel-Tawwab et al. 2019; Evans & Kultz 2020). By doing bifurcation analyses on these parameters against maturation rate (or most preferably against the full expression for zinc uptake from maturation) you could examine how the pollutant received through juveniles maturing would change and in turn the total concentration of pollutant in adults.

The model in this study can only give general predictions. Therefore, an important next step is an empirical study to validate these predictions. This could be done in a laboratory study, controlling the zinc concentration and creating a food chain by using appropriate species that can represent the three trophic levels. Zinc concentrations are then to be measured in the organisms at all trophic levels and compared between two cases, one with three trophic levels and one excluding the predator on the third trophic level. Laboratory studies have the advantage of controlled conditions, and the possibility to exclude most in situ-specific factors that can influence the result other than the factor of interest (Campbell et al. 2009). However, the disadvantage of such a laboratory study is that they often differ from the results you get in the field and are therefore still like a “prediction” of the real outcome.

If the model should be used to examine contaminant transfers in a food chain in the Baltic Sea, the model would need to be modified to be more Baltic-specific. To achieve this, you would need to specify the species in the food chain and the interactions between them. You could also add bioavailability factors that take into account the increasing low oxygen levels in the Baltic (e.g., Carstensen & Conley 2019) as well as pH, organic matter, and hardness of the water in the Baltic (The Swedish Agency for Marine and Water Management 2019). For example, in hard water, the metal uptake significantly decreases (Shahjahan et al. 2022). Regional climate models predict a possible reduction in the hardness of the water in the Baltic (Sanders et al. 2021), potentially increasing the problem of metal accumulation. Since the bioavailability of zinc in the model is assumed to be 100 %, adding bioavailability factors would have lowered the predicted zinc concentration in the fish. However, adding bioavailability factors would give indications of how much these parameters matter for the result and give more comparable predictions between

different oceans. Nevertheless, it is important to remember that this model is general and far away from the complexity of a real food web. Thus even with such modifications it may still not predict the outcome of a real aquatic ecosystem but give indications that need to be further investigated.

In this study, the predicted outcome is a decrease in pollutant concentration when predatory fish disappear from the system. However, feedback mechanisms of predatory decline should be examined further before stating that a decrease should always be expected. Besides examining feedback mechanisms, future studies should examine if the zinc uptake parameters should be size-dependent or not by studying more empirical studies on the subject. Future studies should also include investigations on what happens if the predatory fish decline gradually (like they do in real ecosystems) instead of being fully present or absent. Moreover, they should examine how other structural changes to the food web, not only predatory disappearance, can affect the uptake and transfer. Additionally, investigate what happens if more trophic levels and more species in each level are included. Lastly, future studies should examine the restrictions for which kind of pollutants this type of model can be used and if it could be incorporated as a tool for the management of general pollution in aquatic systems.

5. CONCLUSION

According to this study's model predictions, the food chain structure has an important effect on the uptake and transfer of pollutants in aquatic ecosystems. In a food chain without a top predator, the uptake of zinc from food is smaller and the zinc concentration is lower in the consumer fish population. These findings provide a possible explanation for variation in pollutant concentration in fish across areas. They also give a wider understanding of the consequences of pollution on aquatic ecosystems, as well as the consequences of changing food webs. Therefore, food chain structure and dynamics and their variability should to a higher degree be included when discussing the impact of pollution and possible mitigation measures. Because there are relatively few previously published examples of food chain model applications to metals, the model I developed and used in this study provides an important addition that moreover accounts for a size variation in the food chain. How changes in food availability and how feedback mechanisms from predatory decline could affect the result would be an important next step to examine this topic further.

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Appendix 1

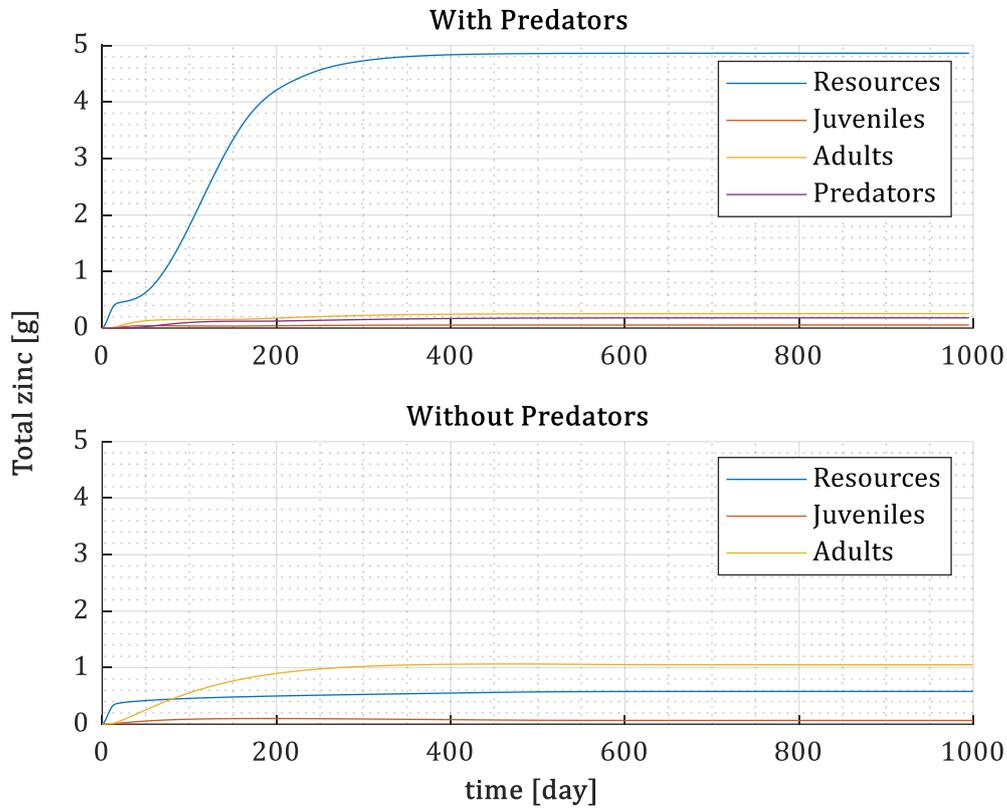


Figure 1. Time simulation to examine the total zinc in each population group and how they differ if predators are present or absent in the system.

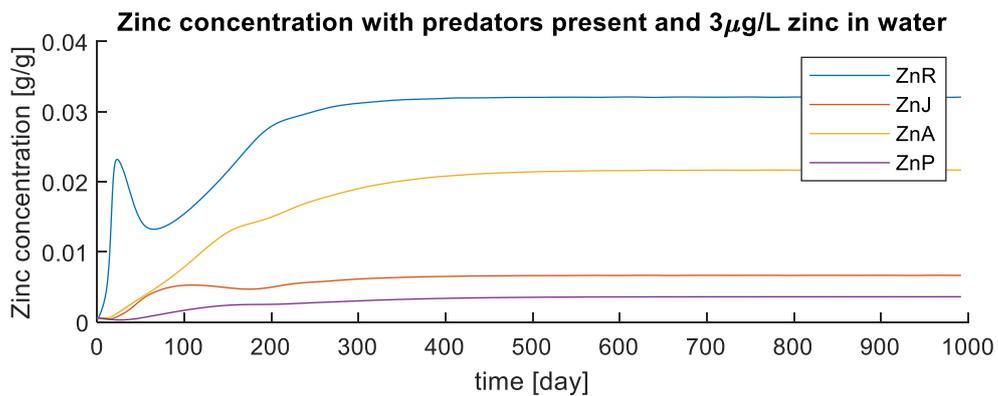


Figure 2. Time simulation to examine the equilibrium zinc concentration in each population group when the zinc concentration in the water is 3 μg/L instead of the default 27 μg/L.

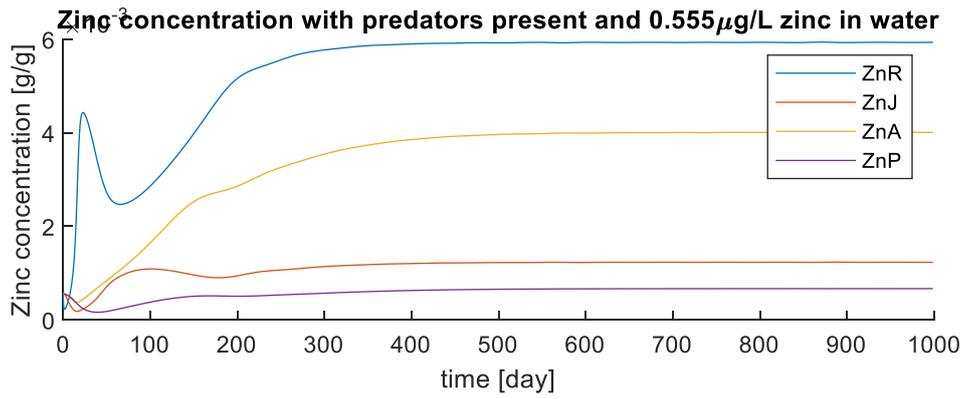


Figure 3. Time simulation to examine the equilibrium zinc concentration in each population group when the zinc concentration in the water is 0.555 $\mu\text{g/L}$ instead of the default 27 $\mu\text{g/L}$.

Table 1. Linear regression ($kx+m$) slope coefficients (k) for the zinc uptake parameters with and without predators in the system.

Zinc parameter	Zinc concentration in Resources		Zinc concentration in Juveniles		Zinc concentration in Adults		Zinc concentration in Predators
	k With Predators	k Without Predators	k With Predators	k Without Predators	k With Predators	k Without Predators	
Resource uptake rate constant from water (k_{uwR}) [$\text{m}^3/\text{g}/\text{day}$]	3.4	1.7	0.50	0.12	2.1	0.49	0.27
Juvenile uptake rate constant from water (k_{uwJ}) [$\text{m}^3/\text{g}/\text{day}$]	0	0	3.2	1.7	3.2	1.6	1.8
Juvenile assimilation efficiency (AE_J)	0	0	31	7.2	29	6.8	17
Adult uptake rate constant from water (k_{uwA}) [$\text{m}^3/\text{g}/\text{day}$]	0	0	0	0	3.4	1.7	0
Adult assimilation efficiency (AE_A)	0	0	0	0	15	3.6	0
Predator uptake rate constant from water (k_{uwP}) [$\text{m}^3/\text{g}/\text{day}$]	0	-	0	-	0	-	3.4
Predator assimilation efficiency (AE_P)	0	-	0	-	0	-	0.54

Table 2. Linear regression ($kx+m$) intercept coefficients (m) for the zinc uptake parameters with and without predators in the system.

Zinc parameter	Zinc concentration in Resources		Zinc concentration in Juveniles		Zinc concentration in Adults		Zinc concentration in Predators
	m With Predators	m Without Predators	m With Predators	m Without Predators	m With Predators	m Without Predators	
k_{uwR} [m ³ /g/day]	0	0	0.034	0.017	0.034	0.017	0.019
k_{uwJ} [m ³ /g/day]	0	0	0.086	0.020	0.36	0.085	0.047
AE_J	0	0	0.034	0.017	0.31	0.082	0.019
k_{uwA} [m ³ /g/day]	0	0	0	0	0.39	0.10	0
AE_A	0	0	0	0	0.11	0.036	0
k_{uwP} [m ³ /g/day]	0	-	0	-	0	-	0.065
AE_P	0	-	0	-	0	-	0.00010

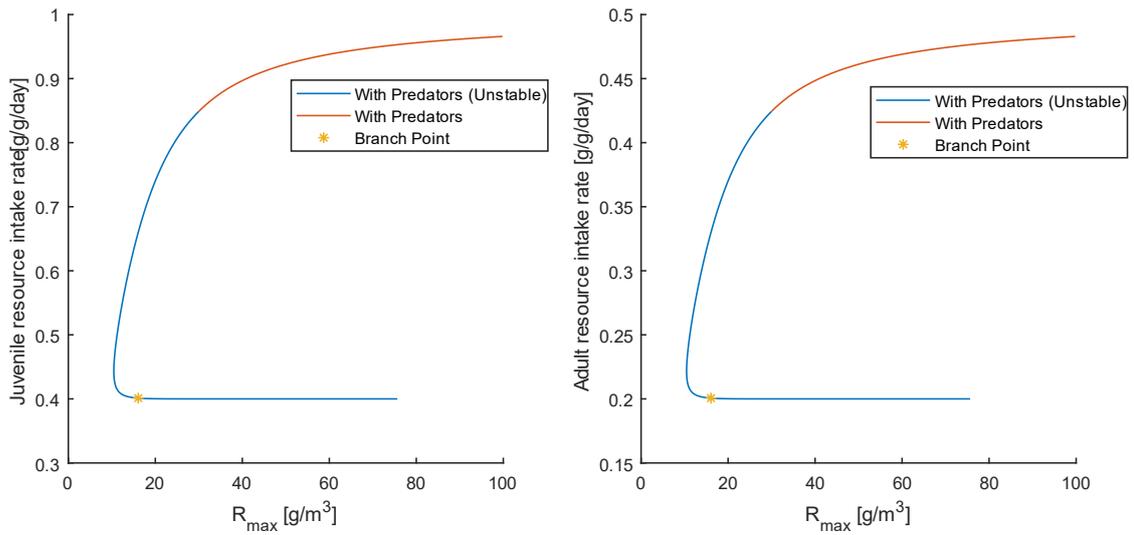


Figure 4. Bifurcation analysis over resource maximum biomass density (R_{max}) against the user function for resource intake rate by juveniles with predators in the system.

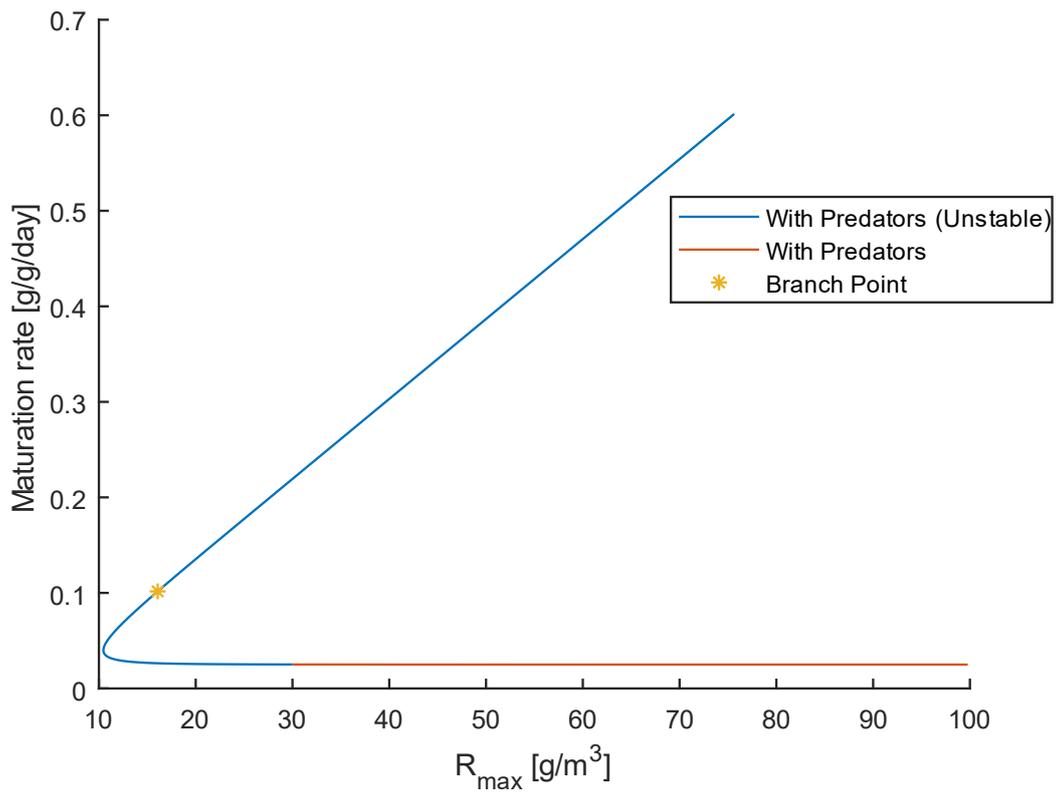


Figure 5. Bifurcation analysis over resource maximum biomass density (R_{max}) against the user function for maturation rate with predators in the system.

Appendix 2

Following script (“P1”) was put in MatCont to create the system when predators are included in the system. Comments in the code should be removed before the script is used in MatCont. The data generated from this script is represented in Figures 4-7 and all Tables and Figures in Appendix 1.

```
%Coordinates
R, J, A, P, ZnR, ZnJ, ZnA, ZnP

%Parameters
rho, Rmax, Wa, Hc, q, Wp, sigc, sigp, phi, Hp, z, Cwzn, kuwr, Wr, ker, kuwj, Wj, kufj, k
ej, kuwa, kufa, kea, kuwp, kufp, kep

G=rho*(Rmax-R) %Intrinsic resource turnover
Mc=0.1*Wa^-0.25 %Consumer mass-specific maximum ingestion rate
wJ=Mc*R/(Hc+R) %Resource intake by juveniles
wA=q*Mc*R/(Hc+R) %Resource intake by adults
Mp=0.1*Wp^-0.25 %Predator mass-specific maximum ingestion rate
Tp=0.01*Wp^-0.25 %Predator mass-specific maintenance rate
Tc=0.01*Wa^-0.25 %Consumer mass-specific maintenance rate
NuJ=sigc*wJ-Tc %Net energy production by juveniles
NuA=sigc*wA-Tc %Net energy production by adults
NuP=(sigp*Mp*((phi*J+(1-phi)*A)/(Hp+phi*J+(1-phi)*A)))-Tp %Net energy
production by predators
uj=0.0015*Wa^-0.25 %Juvenile background mortality rate
ua=0.0015*Wa^-0.25 %Adult background mortality rate
up=0.0015*Wp^-0.25 %Predator background mortality rate
dJ=uj+((Mp*phi*P)/(Hp+phi*J+(1-phi)*A)) %Mortality rate of juveniles
dA=ua+((Mp*(1-phi)*P)/(Hp+phi*J+(1-phi)*A)) %Mortality rate of adults
if(NuA>0), NuAplus=NuA; else ;NuAplus=0; end %Restrict net energy pro-
duction by adults to non-negative values
if(NuJ>0), NuJplus=NuJ; else ;NuJplus=0; end %Restrict net energy pro-
duction by juveniles to non-negative values
mat_rate=(NuJplus-dJ)/(1-z^(1-(dJ/NuJplus))) %Maturation rate of juve-
niles
wP=(Mp*phi*J)/(Hp+phi*J+(1-phi)*A) %Juvenile prey intake by predators
R'=G-wJ*J-wA*A %Derivative of resource biomass with respect to time
J'=NuAplus*A-mat_rate*J+NuJ*J-dJ*J %Derivative of juvenile biomass with
respect to time
A'=mat_rate*J+(NuA-NuAplus)*A-dA*A %Derivative of adult biomass with re-
spect to time
P'=(NuP-up)*P %Derivative of predator biomass with respect to time
ZnR'=(kuwr*Cwzn-ker*ZnR/R)*R %Derivative of zinc amount in resources
with respect to time
ZnJ'=(kuwj*Cwzn+kufj*wJ*ZnR/R-kej*ZnJ/J)*J %Derivative of zinc amount in
juveniles with respect to time
ZnA'=(kuwa*Cwzn+kufa*wA*ZnR/R-kea*ZnA/A)*A+(mat_rate*ZnJ/J)*J %Deriva-
tive of zinc amount in adults with respect to time
ZnP'=(kuwp*Cwzn+kufp*wP*ZnJ/J-kep*ZnP/P)*P %Derivative of zinc amount in
predators with respect to time
```

Following script (“P0”) was put in MatCont to create the system when predators are excluded from the system. The variable names are the same as explained in script (P1) above. The data generated from this script is represented in Figures 4-7 and all Tables and Figures in Appendix 1.

```
%Coordinates
```

```

R, J, A, ZnR, ZnJ, ZnA
%Paramaters

rho, Rmax, Wa, Hc, q, sigc, phi, z, Cwzn, kuwr, Wr, ker, kuwj, Wj, kufj, kej, kuwa, kuf
a, kea

G=rho*(Rmax-R)
Mc=0.1*Wa^-0.25
wJ=Mc*R/(Hc+R)
wA=q*Mc*R/(Hc+R)
Tc=0.01*Wa^-0.25
NuJ=sigc*wJ-Tc
NuA=sigc*wA-Tc
uj=0.0015*Wa^-0.25
ua=0.0015*Wa^-0.25
dJ=uj
dA=ua
if(NuA>0), NuAplus=NuA; else ;NuAplus=0; end
if(NuJ>0), NuJplus=NuJ; else ;NuJplus=0; end
mat_rate=(NuJplus-dJ)/(1-z^(1-(dJ/NuJplus)))
R'=G-wJ*J-wA*A
J'=NuAplus*A-mat_rate*J+NuJ*J-dJ*J
A'=mat_rate*J+(NuA-NuAplus)*A-dA*A
ZnR'=(kuwr*Cwzn-ker*ZnR/R)*R
ZnJ'=(kuwj*Cwzn+kufj*wJ*ZnR/R-kej*ZnJ/J)*J
ZnA'=(kuwa*Cwzn+kufa*wA*ZnR/R-kea*ZnA/A)*A+(mat_rate*ZnJ/J)*J

```

Following script (“P1c”) was put in MatCont to create the system when predators are included in the system and the juveniles and adults have the same efflux rate (kec). Note that the only difference in this script from Script P1 is that parameter “kej” and “kea” is replaced by one variable “kec”. The variable names are the same as explained in script (P1) above. The data generated from this script is represented in Figure 8.

```

%Coordinates
R, J, A, P, ZnR, ZnJ, ZnA, ZnP

%Paramaters
rho, Rmax, Wa, Hc, q, Wp, sigc, sigp, phi, Hp, z, Cwzn, kuwr, Wr, ker, kuwj, Wj, kufj, k
ec, kuwa, kufa, kuwp, kufp, kep

G=rho*(Rmax-R)
Mc=0.1*Wa^-0.25
wJ=Mc*R/(Hc+R)
wA=q*Mc*R/(Hc+R)
Mp=0.1*Wp^-0.25
Tp=0.01*Wp^-0.25
Tc=0.01*Wa^-0.25
NuJ=sigc*wJ-Tc
NuA=sigc*wA-Tc
NuP=(sigp*Mp*((phi*J+(1-phi)*A)/(Hp+phi*J+(1-phi)*A)))-Tp
uj=0.0015*Wa^-0.25
ua=0.0015*Wa^-0.25
up=0.0015*Wp^-0.25
dJ=uj+((Mp*phi*P)/(Hp+phi*J+(1-phi)*A))
dA=ua+((Mp*(1-phi)*P)/(Hp+phi*J+(1-phi)*A))
if(NuA>0), NuAplus=NuA; else ;NuAplus=0; end
if(NuJ>0), NuJplus=NuJ; else ;NuJplus=0; end
mat_rate=(NuJplus-dJ)/(1-z^(1-(dJ/NuJplus)))
wP=(Mp*phi*J)/(Hp+phi*J+(1-phi)*A)
R'=G-wJ*J-wA*A

```

```

J'=NuAplus*A-mat_rate*J+NuJ*J-dJ*J
A'=mat_rate*J+(NuA-NuAplus)*A-dA*A
P'=(NuP-up)*P
ZnR'=(kuwr*Cwzn-ker*ZnR/R)*R
ZnJ'=(kuwj*Cwzn+kufj*wJ*ZnR/R-kec*ZnJ/J)*J
ZnA'=(kuwa*Cwzn+kufa*wA*ZnR/R-kec*ZnA/A)*A+(mat_rate*ZnJ/J)*J
ZnP'=(kuwp*Cwzn+kufp*wP*ZnJ/J-kep*ZnP/P)*P

```

Following script (“P0c”) was put in MatCont to create the system when predators are excluded from the system and the juveniles and adults have the same efflux rate (kec). Note that the only difference in this script from Script P0 is that parameter “kej” and “kea” is replaced by one variable “kec”. The variable names are the same as explained in script (P1) above. The data generated from this script is represented in Figure 8.

```

%Coordinates
R, J, A, ZnR, ZnJ, ZnA

%Paramaters
rho, Rmax, Wa, Hc, q, sigc, phi, z, Cwzn, kuwr, Wr, ker, kuwj, Wj, kufj, kec, kuwa, kuf
a

G=rho*(Rmax-R)
Mc=0.1*Wa^-0.25
wJ=Mc*R/(Hc+R)
wA=q*Mc*R/(Hc+R)
Tc=0.01*Wa^-0.25
NuJ=sigc*wJ-Tc
NuA=sigc*wA-Tc
uj=0.0015*Wa^-0.25
ua=0.0015*Wa^-0.25
dJ=uj
dA=ua
if(NuA>0), NuAplus=NuA; else ;NuAplus=0; end
if(NuJ>0), NuJplus=NuJ; else ;NuJplus=0; end
mat_rate=(NuJplus-dJ)/(1-z^(1-(dJ/NuJplus)))
R'=G-wJ*J-wA*A
J'=NuAplus*A-mat_rate*J+NuJ*J-dJ*J
A'=mat_rate*J+(NuA-NuAplus)*A-dA*A
ZnR'=(kuwr*Cwzn-ker*ZnR/R)*R
ZnJ'=(kuwj*Cwzn+kufj*wJ*ZnR/R-kec*ZnJ/J)*J
ZnA'=(kuwa*Cwzn+kufa*wA*ZnR/R-kec*ZnA/A)*A+(mat_rate*ZnJ/J)*J

```

The following scripts (“User functions P1”) was put in as user functions in MatCont for the system with predators included in the system. “ga” stand for maturation rate, wJ and wA stand for ingestion rate for juveniles and adults respectively. The calculated values was then used in script “Calculations bar figure” and is represented in Figure 6.

```

ga=((sigc*((0.1*Wa^-0.25)*R/(Hc+R))-(0.01*Wa^-0.25))-(((0.1*Wp^-
0.25)*phi*P)/(Hp+phi*J+(1-phi)*A)))/(1-z^(1-(((0.1*Wp^-
0.25)*phi*P)/(Hp+phi*J+(1-phi)*A)))/(sigc*((0.1*Wa^-0.25)*R/(Hc+R))-
(0.01*Wa^-0.25))))

wA=q*(0.1*Wa^-0.25)*R/(Hc+R)

wJ=(0.1*Wa^-0.25)*R/(Hc+R)

```

The following scripts (“User functions P0”) was put in as user functions in MatCont for the system with predators excluded from the system. “ga” stand for maturation rate, wJ

and w_A stand for ingestion rate for juveniles and adults respectively. Note that the equation for w_J and w_A are identical as in User functions P1. The calculated values were then used in script “Calculations bar figure” and is represented in Figure 6.

$$ga = \left(\left(\left(\text{sigc} * \left(\left(0.1 * w_A^{-0.25} \right) * R / (Hc + R) \right) - \left(0.01 * w_A^{-0.25} \right) \right) - \left(0.0015 * w_A^{-0.25} \right) \right) / \left(1 - z^{\left(1 - \left(\left(0.0015 * w_A^{-0.25} \right) / \left(\left(\text{sigc} * \left(\left(0.1 * w_A^{-0.25} \right) * R / (Hc + R) \right) - \left(0.01 * w_A^{-0.25} \right) \right) \right) \right) \right) \right) \right)$$

$$w_A = q * \left(0.1 * w_A^{-0.25} \right) * R / (Hc + R)$$

$$w_J = \left(0.1 * w_A^{-0.25} \right) * R / (Hc + R)$$

Following script (“Calculations bar figure”) was run in MATLAB to calculate the values for uptake and efflux in equilibrium and is represented in Figure 6.

```
clear all
close all

load('C:\Users\User\Documents\MATLAB\MatCont7p3\MatCont7p3\Sys-
tems\MetalModel7_utan_P\diagram\time_P0_27.mat')

%Name all coordinates
R=y(:,1);
J=y(:,2);
A=y(:,3);
t1=t;
ZnR=y(:,4);
ZnJ=y(:,5);
ZnA=y(:,6);

%Calculate Zinc concentration "Zn_conc"
ZnR_conc=ZnR./R;
ZnJ_conc=ZnJ./J;
ZnA_conc=ZnA./A;

load('C:\Users\User\Documents\MATLAB\MatCont7p3\MatCont7p3\Sys-
tems\MetalModel7\diagram\time_P1_m3.mat')

%Name all coordinates
R2=y(:,1);
J2=y(:,2);
A2=y(:,3);
P2=y(:,4);
t2=t;
ZnR2=y(:,5);
ZnJ2=y(:,6);
ZnA2=y(:,7);
ZnP2=y(:,8);

%Calculate Zinc concentration "Zn_conc"
ZnR_conc2=ZnR2./R2;
ZnJ_conc2=ZnJ2./J2;
ZnA_conc2=ZnA2./A2;
ZnP_conc2=ZnP2./P2;

%Retrieving equilibrium values at t=1000

R2(214) %P=1
J2(214) %P=1
A2(214) %P=1
```

```
ZnR2 (214) %P=1
ZnJ2 (214) %P=1
ZnA2 (214) %P=1
ga2=0.025;%P=1
wJ2=0.85;%P=1
wA2=0.42;%P=1
```

```
R (1054) %P=0
J (1054) %P=0
A (1054) %P=0
ZnR (1054) %P=0
ZnJ (1054) %P=0
ZnA (1054) %P=0
ga=0.087;%P=0
wJ=0.40;%P=0
wA=0.20;%P=0
```

```
%Parameters
Cwzn=0.027;
kuwj=0.0101;
kufj=0.00280;
kej=0.016;
kuwa=0.000594;
kufa=0.0180;
kea=0.016;
```

%Below I multiply the equations with J and A to make it to concentrations.

```
%With Predators %%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
BUptake_WaterJ2=kuwj*Cwzn; %P=1
BUptake_FoodJ2=kufj*wJ2*ZnR2 (214) /R2 (214); %P=1
BEffluxJ2=kej*ZnJ2 (214) /J2 (214); %P=1
```

```
BUptake_WaterA2=kuwa*Cwzn; %P=1
BUptake_FoodA2=kufa*wA2*ZnR2 (214) /R2 (214); %P=1
BMaturationA2=ga2*ZnJ2 (214) /J2 (214) *J2 (214) /A2 (214); %P=1
BEffluxA2=kea*ZnA2 (214) /A2 (214); %P=1
```

```
%Without Predators %%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
BUptake_WaterJ=kuwj*Cwzn; %P=0
BUptake_FoodJ=kufj*wJ*ZnR (1054) /R (1054); %P=0
BEffluxJ=kej*ZnJ (1054) /J (1054); %P=0
```

```
BUptake_WaterA=kuwa*Cwzn; %P=0
BUptake_FoodA=kufa*wA*ZnR (1054) /R (1054); %P=0
BMaturationA=ga*ZnJ (1054) /J (1054) *J (1054) /A (1054); %P=0
BEffluxA=kea*ZnA (1054) /A (1054); %P=0
```