From individuals to ecosystem services: Using individual based models to predict population level ecological functions in response to chemical induced changes in invertebrate feeding activity.

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“Unless there is wildness around you, something terrible happens to the wildness inside of you”

John Moriarty

Declaration

I, Niamh O'Connor, confirm that the Thesis is my own work. I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means). This work has not previously been presented for an award at this, or any other, university.

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Abstract

The aim of this thesis was to explore how information on chemical impacts on the feeding activity of freshwater invertebrates can be used to predict population level effects on ecosystem functions and considering the implications for associated ecosystem services. The research focuses on the effects of feeding inhibition on ecological functions, examining both individual-level impacts and differences in sensitivity among functional feeding groups (FFGs). Using Dynamic Energy Budget Individual-Based Models, the study examines population-level responses of freshwater shredders *Gammarus pulex* and *Asellus aquaticus*, revealing how chemical stress affects the performance of ecological functions within a recreational fishery.

Of the 1500+ chemicals for which toxicity data were available, differences in sensitivity between FFGs could not be evaluated for lack of data across multiple species. Of the 48 chemicals with sufficient data, differences in sensitivity between FFGs were not detected for 70% of chemicals, likely due to species biases in the data. When modelling single-species population responses to individual effects, populations exhibited resistance to feeding inhibition, but were most affected by reductions in assimilation efficiency (reflecting both resource quality and consumer digestion) and food availability—factors that are often overlooked in traditional risk assessments. When interspecific competition was considered, impact thresholds were significantly lower than those for single-species populations, with the initial ratio and density of competing species influencing population resistance to feeding inhibition. Regarding the performance of ecological functions, leaf processing was most responsive and most greatly impacted compared to impacts on prey provision.

The study emphasises the importance of considering both ecological and environmental contexts in risk assessments. Species diversity and varying sensitivity within the same FFG can alter the effects of chemical stress of service providing units. The thesis emphasises the need to consider interspecific competition in predicting chemical stress impacts, advocating for broader risk assessments that include species interactions.

Contents

Chapter 1 – Introduction

Human society benefits greatly from the goods and services delivered by natural systems. These goods and services, 'the direct and indirect contributions of ecosystems to human well-being', are referred to as ecosystem services (Westman, 1977; The Economics of Ecosystems and Biodiversity (TEEB), 2010). Not only do we rely on natural systems for the provision of essential goods and services such as food, clean water, construction materials, and climate regulation, natural systems offer immense benefits to human health, well-being (Bratman et al., 2019; Stock et al., 2022), and longevity (Takano et al., 2002; Soga and Gaston, 2016; Jimenez et al., 2021). These services can be classified into provisioning services (e.g. tangible goods that humans consume or use), cultural services (e.g. non-material benefits that people obtain from ecosystems, including recreational, spiritual, and aesthetic experiences), and regulating services (e.g. typically ecosystem processes, contributing, for example, to the control of climate, floods, disease, water quality, and pollination) (Haines-Young and Potschin, 2018). In the UK, ecosystem services are valued at £1.5 trillion in total asset value, with an annual worth of £47 billion (Office of National Statistics (ONS), 2023). Among these, cultural services constitute the largest portion of the asset value (61%), with health benefits from recreation contributing £445 billion to the total asset value of UK ecosystem services. Therefore, safeguarding and sustainably managing natural ecosystems is imperative, not only for environmental conservation but also for ensuring economic prosperity and human wellbeing.

The delivery of ecosystem services is primarily underpinned by biodiversity (Millenium Ecosystem Services Assessment (MEA), 2005). Specifically, the delivery of different ecosystem services can rely on several biotic attributes; the abundance of individual species, the number of species (species richness), diversity of species (species richness and evenness), particularly in terms of functional traits and roles exhibited by species within an ecological community, i.e., functional diversity (Kremen et al., 2005; Harrison et al., 2014). The ecological attribute of importance can differ between services. For provisioning services, the delivery may depend on a particular population or community attribute, such as the number of individuals present of a specific size or age class (Harrison et al., 2014; Smith et al., 2017). For example, the availability of fish for commercial harvesting relies on the abundance of larger, older breeding females (Thorpe et al., 1984; Hixon et al., 2014), as they contribute disproportionately more to offspring production compared to younger females. Loss of these attributes risks the sustainability and stability of the provision of these services. For example, the reduction of older females due to overfishing can decrease offspring production (Barnett et al., 2017). For regulating services, however, the delivery of the service often depends on the presence and activity of certain species or functional groups that perform key ecological roles (Harrison et al., 2014; Smith et al., 2017). For example, pollination services are, obviously, reliant on the presence and abundance of pollinator species, while water purification services depend on the activity of wetland plant species and microorganisms but also of whole communities of organisms (Harrison et al., 2014). Nutrient cycling may require species from multiple functional groups, as their interactions complement each other to sustain the service (Harrison et al., 2014). Therefore, it may not just be species diversity which is important for ecosystem services, such as nutrient cycling, but also the functional diversity of those species.

Historically, research has focused on linking biodiversity to the performance of ecological functions, demonstrating that species diversity within a system contributes to functional outcomes (Tilman et al., 2014). This has led to the development of the insurance hypothesis (Yachi and Loreau, 1998), which posits that species richness can buffer against functional losses by providing functional redundancy. This means that when multiple species can perform similar roles, ecosystem functions may persist even as species are lost. However, this relationship is not linear nor consistent across all environments (Laureto et al., 2015). Instead, diversity of functional traits often provides a more robust explanation for ecosystem performance than species diversity alone (Laureto et al., 2015). Consequently, loss of species can have varying impacts on ecosystem functions, ranging from minimal to significant, depending on the specific species that are lost. Nevertheless, the loss of key biotic attributes—whether through declines in species abundance, diversity, or changes in population and community structures—poses significant risks to the delivery of ecosystem services (Hooper, 2011; Cardinale et al., 2012; Oliver et al., 2015; Dasgupta, 2019). The impact of anthropogenic stress on ecosystem services is therefore likely to be highly context-dependent, varying across different environments, and species assemblages.

For thousands of years, humans have been altering the natural environment for their use and benefit. Since the industrial revolution, however, the impact of this alteration has been increasingly destructive to the environment, driven by urbanisation and a growing global population (Grimm et al., 2008; Concepción et al., 2015). This increased demand on natural resources has led to a critical decline in biodiversity (Cardinale et al., 2012). It is estimated that 1 million animal and plant species, globally, are now threatened with extinction (The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 2019). While the global living planet index estimates a decline in the relative abundance of monitored populations by 69% (1970-2018) with freshwater populations particularly affected, declining by 83% since 1970 (World Wildlife Fund (WWF), 2020). In the UK, it is estimated one in six species are experiencing decline with, on average, the abundance of species falling by 19% since 1970. Since 2010, species abundance (i.e. the average change in abundance across species) has declined by 3% (uncertainty interval = -8% to +2%) (Burns et al., 2023). The five main drivers of this decline have been identified as land use change, direct overexploitation of resources, climate change, pollution, and invasive alien species (IPBES, 2019). These drivers often intersect. For example, as human populations increase, there is a greater demand for food. This leads to agricultural intensification which increases the risk of agricultural pollution across landscapes, as field runoff converges in connected streams (Martinuzzi et al., 2014). Meanwhile, a changing climate may exacerbate biodiversity loss from chemical pollution as species undergo combined stress of toxicity and increasing extremes of weather (Baste and Watson, 2022). With biodiversity loss a threat to human wellbeing by potentially altering the attributes underpinning the delivery of ecosystem services (Diaz et al., 2006), it is important to understand how such stressors affect the underpinning attributes that deliver these services.

Chemical pollution is a major driver of biodiversity decline, ranking third out of the five main drivers (Jaureguiberry et al., 2022). This has led to declines in nature including species attrition and extinction, reduction in biomass, and loss of biotic resilience (European Commission (EC), 2020; IPBES, 2019, Jaureguiberry et al., 2022). Modern society now relies heavily on synthetic chemicals across various sectors, including agriculture, industry, and consumer products, from pesticides, pharmaceuticals, plastics, and personal care products (The European Chemical Industry Council (CEFIC), 2021). In the European Union alone, there are over 100,000 registered chemicals (European Inventory of Existing Chemical Substances (EINECS), 2024), with 30,000 to 70,000 in daily use (Loos et al., 2009). While persistent organic pollutants (e.g. Dichlorodiphenyltrichloroethane (DDT), dioxins, Per- and Polyfluorinated Substances (PFAS)) have been of concern for some time (Carson, 1962; The Stockholm Convention on Persistent Organic Pollutants, 2001), and continue to be at the forefront of environmental policy (EC, 2019), less persistent chemicals (e.g. pharmaceuticals and modern pesticides) are also of emerging concern (Loos et al., 2009; Reid et al., 2018). This is due to their widespread and continued use by humans resulting in their continued detection in the environment (Fang et al., 2019; Wilkinson et al., 2022).

Once released into the environment, these chemicals often occur as complex unintended mixtures (Posthuma et al., 2022), altering the chemical and ecological status of soil and water (Posthuma et al., 2020; Lemm et al., 2021). The most recent Red List compiled by the International Union for Conservation of Nature (IUCN) considered 11,500 out of the 83,669 animal species assessed to be impacted by pollution (IUCN, 2022). However, the effects of chemical stress on the ecological status of a system are highly specific to each ecosystem, as they are influenced by both abiotic and biotic factors that can either mitigate or exacerbate the impacts of chemical stress (Clements et al., 2016). Abiotic factors include temperature, which can intensify stress (Camp and Buckwalter, 2016; Huang et al., 2023; Verheyen and Stoks, 2023; Mangold-Döring et al., 2024). While the nutrient status of an environment can also influence the system level response to chemical stress, often high level of nutrients acting as an additional stressor, exacerbating impact of chemical exposures (Schafer et al., 2016; Nõges et al., 2016; Birk et al., 2020). Biotic factors include population structure (Clark and Clements, 2006), community composition (Liess et al., 2008), and trophic interactions such as predation (Brookes et al., 2009; Zhao et al., 2020; Van den Brink et al., 2017). Previous exposure to stressors can also either strengthen species resilience through adaptation (Bundschuh et al., 2023) or weaken population recovery due to the loss of key species (Mohr et al., 2012). With chemical pollution a major driver of biodiversity loss, posing significant threats to both human and ecological health (Hoekstra and Wiedmann, 2014; Bernhardt et al., 2017; Groh et al., 2022), loss of species risks the ecological integrity of natural systems and, consequently, the ecosystem goods and services upon which society depends (Dasgupta et al., 2019; Persson et al., 2022). Therefore, it is crucial to apply a context-dependent approach to assess the risks of chemicals before they are introduced into the environment.

Ecological Risk Assessment (ERA) aims to evaluate the risk of chemical contaminants in the environment, assessing the likelihood of adverse ecological effects (Munns et al., 2006). In Europe, various chemical stressors are regulated by different legislative bodies, with regulations differing across chemical sectors and overseen by distinct European agencies (Brown et al., 2017). For example, general chemicals including those used in industrial activities, are regulated under REACH (Regulation [EC] No 1907/2006) while biocides (Regulation [EU] No 528/2012) fall under the authority of the European Chemicals Agency (ECHA). Meanwhile, the European Food Safety Authority (EFSA) is responsible for regulating plant protection products (Regulation [EC] No 1107/2009) and feed additives (Regulation [EC] No 1831/2003). All legislative bodies use protection goals to guide risk assessments, often focusing on protecting high level entities such as biodiversity, ecological populations, food chains, and communities (Brock et al., 2006; Brown et al., 2017). The protection goals themselves have been criticised for their vagueness (Hommen et al., 2010; EFSA 2016), using general terms such as "no unacceptable effects", and not adequately reflecting or specifying what needs to be protected. In current chemical risk assessments, the risk of a potential chemical is assessed within a tiered approach, designed to be protective and conservative (Hommen et al., 2010; EFSA, 2013).

In lowest tier, predicted environmental concentrations (PECs) are compared to lethal and some sublethal endpoints, derived from toxicity tests using individuals of a few select, standardised species in standard toxicity tests (EFSA, 2013; Schuijt et al., 2021). If the predicted effect concentration (PEC) is lower than the LC50, the chemical is deemed low risk and requires no further regulation of assessment. However, these tests lack ecological complexity and do not account for long term impacts, i.e. beyond a few days. Higher tiers are less conservative but more ecologically realistic, where multispecies mesocosm studies may be used to test the impact of chemical exposure over longer time periods i.e. weeks or months. While these studies are more ecologically realistic and less conservative, they are time-consuming, resource-intensive, and carry a high degree of uncertainty. To address the complexities inherent in ecological systems, such as indirect species effects and interactions, assessment factors (i.e. multiplication factors) are applied to risk quotients calculated at all levels of evaluation to account for these uncertainties (European Chemicals Agency (ECHA), 2008; Rohr et al., 2016; Sherborne et al., 2022). This approach, based on the precautionary principle, is designed to be protective (Chapman et al., 1998; Brown et al., 2016). However, despite these safeguards, it can sometimes lead to outcomes that are either overly conservative or insufficiently protective (Roex et al., 2000; Forbes and Calow, 2002; Stark, 2005). Without clear, ecologically focused protection goals, the process may prevent the approval of many chemicals that do not cause 'unacceptable adverse effects'. This poses a challenge, particularly when assessing the ecological risk of chemicals like pesticides and pharmaceuticals, which are valuable to society but are designed to be biologically active and thus inevitably have some effect. The issue then becomes how to manage chemical risks in the field, balancing the trade-offs between chemical risks, societal benefits, while linking what we measure to what we want to protect.

An ecosystem services approach to chemical risk assessment was proposed to link chemical induced responses of ecological entities that perform ecological functions and processes to changes in ecosystem services delivery (Maltby, 2013; Maltby et al., 2017; Devos et al., 2019). The ecosystem services concept, introduced in the 1990s in the field of nature conservation (Daily, 1997), was designed to provide a link between natural capital and human wellbeing (MEA, 2005; Fisher et al., 2009). Since its inception, frameworks have been employed to improve environmental decision making (Daily et al., 2009; Fisher et al., 2009; Maes et al., 2013, 2016), facilitating a deeper understanding of the link between changes in natural capital and the impact on society (Carpenter et al., 2009). For example, the Natural Capital Protocol helps businesses identify, measure, and value their impacts and dependencies on natural capital, linking environmental changes to business risks and opportunities (Natural Capital Coalition. 2016). While the Integrated Valuation of Ecosystem Services and Trade-offs (InVEST) model maps and quantifies the value of ecosystem services, allowing users to assess trade-offs between different land use or policy scenarios (Tallis et al., 2011). The Ecosystem Services Cascade Model describes the link between changes in natural capital and societal impacts by illustrating how ecosystem structures and processes generate services that provide direct and indirect benefits to human well-being (Potschin and Haynes-Young, 2016). Within this approach, entities that support the performance of functions underpinning ES delivery are defined as service-providing units (SPUs) (Luck et al., 2009). SPUs are primarily populations of species (Luck et al., 2003) but can extend to the presence of the functional traits and functionally important populations, communities, guilds, and interacting networks of organisms that deliver services (Kremen et al., 2005). The ES approach to ERA aims to give attention to variation in both hazard and exposure across spatial and temporal scales, enabling more regional specific chemical risk assessments.

The ecosystem services approach to risk assessment aims to enhance the transparency of the risk assessment process, enabling better communication of policy priorities and risk assessments to relevant stakeholders. Additionally, it can facilitate the quantification of trade-offs between ecosystem services under different management interventions (Maltby et al., 2021). However, a key practical challenge of applying the approach lies in managing competing risks. A single chemical may affect multiple ecosystem services within a landscape, such that a particular chemical or management strategy may enhance one service while simultaneously degrading another. This trade-off presents a significant dilemma for risk managers. Assigning monetary value to ecosystem services can help determine the outcomes associated with these trade-offs (Galic et al., 2019). However, not all benefits and losses are easily expressed in monetary terms. For instance, the concept of resilience remains difficult to integrate into risk assessments, and its valuation is still not well understood (Maltby et al., 2021). Nonetheless, by moving away from a protection strategy that protects "everything, everywhere, all the time" toward a targeted, context-specific approach, risk managers can optimise chemical use while ensuring ecosystem resilience and the sustainable provision of ecosystem services (Devos et al., 2015).

Service providing units are used to systematically identify the key components of an ecological system that provide the services of interest (e.g., population density of key species involved in decomposition, pest control, or cultural heritage) (Luck et al., 2003). These can then be linked with measurable outcomes for human well-being (Kontogianni et al., 2010; Van den Brink 2021) (Figure 1.1). In contrast to conventional ERA, the ecosystem services approach to chemical risk assessment is guided by specific protection goals (Nienstedt et al., 2012), that highlight the services and SPUs of interest within different landscapes. Here, links between SPUs and the delivery of ecosystem services are described quantitatively by ecological production functions, or qualitatively with evidence-based logic chains (Hayes et al., 2018; Maltby et al., 2021). However, with a lack of ecological production functions available to quantifiably assess impacts on ES, evidence-based logic chains are the most tractable approach (Faber et al., 2021). These specific protection goals form the terminus of ecological production functions or evidence-based logic chains (Faber et al., 2021; Van den Brink et al., 2021) (Figure 1). These then require tools to populate the path from what we measure to what we want to protect.

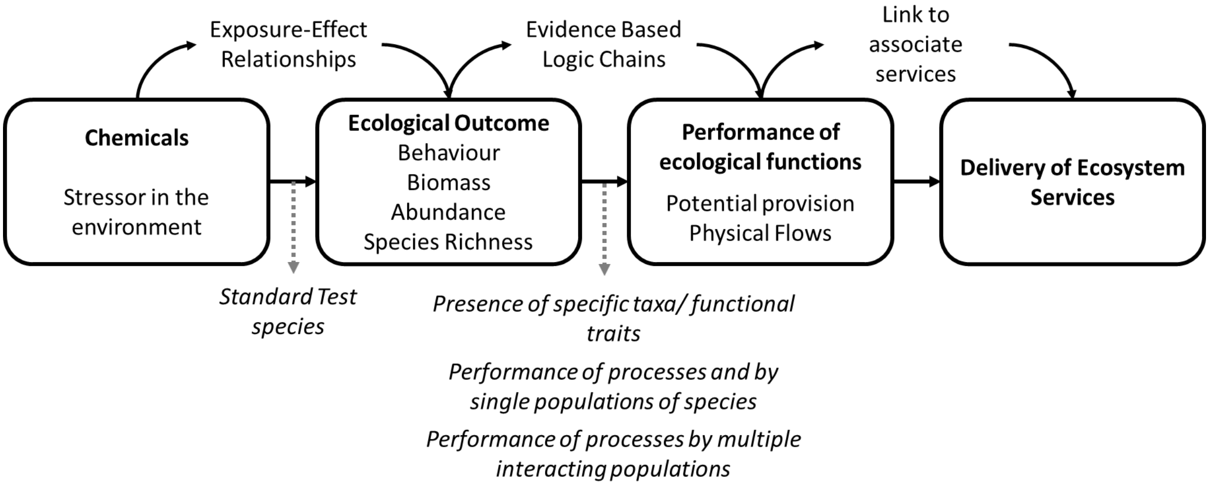

Figure 1.1: Translating effect data from standardised ecotoxicological testing for ES impact assessment using ecotoxicological exposure-effect relationships. Evidence based logic chains qualitatively describe the provision and performance of ecological functions by service providing taxa. The performance of these functions is then linked to the delivery of the associated ecosystem services (adapted from Faber et al., 2021)

Measuring the impacts of chemicals on ecosystem services (ES) is challenging due to the scale and complexity of ES delivery (Maltby et al., 2017). Chemicals may not always have immediate or direct effects on a specific service but can disrupt underlying ecological processes that support multiple services. For instance, while a pesticide may not directly reduce crop yields, it could harm pollinators, indirectly affecting food production (Stanley et al., 2015; Knapp et al., 2022). However, many ecosystem services rely on ecological processes, like nutrient cycling or soil formation, that are driven by the identity and function of species within a system (Hooper et al., 2005; Cadotte et al., 2011; Smith et al., 2017), are difficult to observe or measure in real time. Current tools used in conventional ERA are often inadequate for measuring ecosystem services or generating reliable data that can be linked to ES delivery (Maltby et al., 2017; Faber et al., 2019). Conventional ecological risk assessments (ERAs) tend to focus on structural endpoints, such as population abundance and species richness. These processes can be reflected in both the structure and activity of populations, which are often described as "states" (e.g., species composition) and "rates" (e.g., nutrient cycling rates) (Harrison et al., 2021). To properly employ an ES approach in ERAs, it is essential to measure the impacts of chemicals on entities that are indicative of broader ecological processes.

Acute lethality is one of the most common and well-established toxicological endpoints (Schuijt et al., 2021). While lethal impacts can disrupt the ability of SPUs to deliver ecosystem services through the loss of species (Oginah et al., 2023), the mechanisms underlying ecosystem service delivery are more complex. The performance of ecological functions that support ecosystem services depends not only on the presence of species but also on their activity (Harrison et al., 2021). Behavioural responses, such as changes in feeding activity, can be used to link changes in species activity to ecosystem function. Feeding is a sublethal ecotoxicity endpoint and indicator of general stress as well as an early indicator of changes in individual fitness (Hellou et al., 2010). A general stress response for many species, it can be observed in response to a wide range of stressors (Wong and Candolin, 2015) across a range of chemical modes of action (Melvin and Wilson, 2013) as well as being an ecological relevant endpoint enabling connection between sub-organism and population level processes through energetic links (Barnes et al., 2018; Amiard-Triquet et al., 2009; Ågerstrand, et al., 2020; Ford et al., 2021). Changes in individual feeding behaviour and population consumption have been linked with decomposition (Harrison et al., 2021). Changes in the feeding rate and behaviour often lead to a cascade of effects at the individual level in response to chemical exposure (Ashauer et al., 2011, Agatz et al., 2013) such as decreased growth (Maltby et al., 1990a; Preuss et al., 2009), and reproduction (Ashauer et al., 2011; Maltby and Naylor, 1990), impaired development (Bernot et al., 2005, Agatz et al., 2013), and mortality. Most importantly, feeding has been shown to be affected by chemical exposure (concentrations/doses) much lower than those causing lethal effects (Agatz et al., 2013). However, it is not often included in regulatory evaluation of chemicals, particularly as an endpoint relevant for population level assessments (Ford et al., 2021).

At a population level, individual behaviours, like feeding activity, can influence intra and interspecies interactions which can in turn influence population dynamics (de Villemereuil and Lopez-Sepulcre, 2011; Schoener, 2011). These dynamics are shaped by factors such as population density and competition for resources, which in turn affect individual behaviours and interactions within species. Chemical-induced changes in behaviour, such as feeding activity, can therefore alter key drivers of competition like population density and food consumption, thus influencing population-level responses to chemical exposure (Foit et al., 2012; Knillmann et al., 2012a; Dolciotti et al., 2014). Within populations, changes in feeding activity of individuals can alter population structure by affecting survival, growth, and reproductive rates, leading to shifts in population density (Galic et al., 2017) and age distribution (Hölker and Breckling, 2001). These alterations may cascade through the community, affecting predator-prey relationships and competitive dynamics, potentially disrupting important ecological functions such as nutrient cycling, energy transfer. However, with the majority of ecotoxicity endpoints focussed on measured effects on individuals, for an ecosystem services approach to risk assessment it is essential to develop and incorporate tools that can extrapolate these individual-level effects to population and community level responses.

Furthermore, interspecific interactions, particularly within trophic levels, can be affected significantly by chemical-induced behavioural changes, especially when competing species have different sensitivities to chemical stress (Dawoud et al., 2017; Zhou et al., 2020). For instance, adverse effects on one competitor may inadvertently benefit another, depending on the nature and magnitude of the effect (Knillmann et al., 2012; del Arco et al., 2016; Schnuck and Liess, 2024). The efficiency of tolerant species can also influence the performance of ecological functions following such shifts (Baudy et al., 2021). Meanwhile, direct effects on one species can have indirect consequences for the community or ecosystem, as changes in one species' population can affect others that are dependent on, compete with, or control it. For example, lethal effects on a predator can lead to increased prey populations, while lethal effects on prey can negatively impact predator populations (del Arco et al., 2016). Sublethal effects, such as altered prey behaviour, may increase predator success rates (Brooks et al., 2009), potentially altering predation rates and impacting population control within food webs, which may subsequently affect nutrient cycling. Such changes can subsequently impact the performance of ecological processes and functions, such as changes in population structure and community interactions can disrupt nutrient cycling (Van Dievel et al., 2020), energy flow, and other ecological functions. However, there is limited research addressing this. Understanding these relationships is crucial for assessing the ecological risks associated with chemical exposures.

In an ecosystem services approach to risk assessment, it is therefore essential to consider not just individual-level responses but also the attributes of populations and communities that support broader ecological processes and functions. A key focus in the development of ecological risk assessments (ERA) has been the use of more ecologically relevant endpoints, including those at the population level, which reflect their impact on ecological processes (Cairns et al., 1987; Forbes and Calow, 1999; Barnthouse et al., 2007). Since conducting population-level studies in the laboratory or in the field can be often practically and ethically challenging, modelling approaches that rely on laboratory-measured endpoints are viewed as a necessary and effective alternative (Pastorok et al., 2003; Forbes et al., 2011; Galic et al., 2012).

Models can assist in extrapolating from effects measured in the laboratory to impacts in the field by accounting for population-level or ecological processes, and environmental conditions not captured under controlled laboratory conditions (Galic et al., 2012). The incorporation of modelling approaches in ERA can enable the application of realistic environmental scenarios (Galic et al., 2012; Franco et al., 2016; Larras et al., 2020), such as seasonal variation in temperature and food availability, drivers that can alter population responses to chemical stress (Vlaeminck et al., 2021; Mangold-Doering et al., 2024). Furthermore, toxicokinetic-toxicodynamic (TKTD) modelling, that enables time-resolved predictions of chemical uptake and damage at the individual level (Jager et al., 2006; Jager et al., 2018), allow for the simulation of time-variable exposures (Ashauer et al., 2013), capturing the dynamics of chemical uptake, internal concentrations, damage, and effect on organisms. These models range in complexity and data requirements, with the choice of model depending on its intended use (Accolla et al., 2021; Van den Brink et al., 2021).

Population models generally fall into three categories: unstructured, structured, and individual-based models (Accolla et al., 2021). Unstructured population models typically use endpoints such as growth, reproduction, and survival to estimate population growth rates or survival probabilities

(Forbes and Calow, 1998; Sibly and Hone, 2002; Jager, 2004; Muller et al., 2010; Schmidt et al., 2013; Jager and Ashauer, 2018). For example, the *Lemna* spp. effect model (Schmidt et al., 2013), uses laboratory-measured growth rates of *Lemna* spp. to predict population outcomes in floating macrophyte populations. These endpoints can also be integrated into ecosystem models that assess the effects of chemicals on ecosystem structure, function, and services by incorporating dynamic trophic networks (Traas et al., 2004; Lombardo et al., 2015). While these models can be applied to non-plant species, they fail to account for variations in individual life histories, which are crucial for understanding population dynamics and structure—important factors particularly in provisioning ecosystem services. Populations are not just collections of average individuals—they consist of individuals that vary in size and age. Since certain ecosystem services, such as provisioning, are delivered by specific population attributes (e.g., the number of individuals within a particular size or age class) (Harrison et al., 2014), it is critical that models account for these variations when assessing the impact of chemicals on ecosystem services.

Structured models account for differences in life history and size within populations (Charles et al., 2013). Matrix models, which distinguish between different population classes, offer a mechanistic and data-efficient method for capturing this complexity (Forbes et al., 2008; Salice et al., 2010). They are particularly useful when data is limited, as they can infer population-level effects from minimal input (Wier and Salice, 2021). However, they do not capture the full ecological complexity, such as behavioural changes, local interactions, and, to an extent, individual stochasticity, which also play a role in population dynamics (Accolla et al., 2021). Populations consist of interacting individuals, and these interactions, such as competition for resources, can significantly influence growth and responses to chemical stressors (Schmitt-Jansen et al., 2008; Liess, 2002; Fleeger, 2020). Intraspecific interactions, including competition for space and food, can alter individual responses, leading to population outcomes that differ from those observed in experiments conducted with individuals (Liess, 2004; Knillmann et al., 2012; Gergs et al., 2013; Vougeois et al., 2020; Allen et al., 2021). Oversimplified extrapolations may not capture key population characteristics that are critical for driving ecosystem functions (Galic et al., 2012). To improve the prediction of population-level impacts of chemical stress based on individual-level measurements, models must incorporate ecological complexity and species interactions.

Individual-based models (IBMs), a type of mechanistic effect model, are valuable tools for extrapolating individual-level chemical stressors to population-level responses (Forbes et al., 2008;

Galic et al., 2010). These models capture physiological and behavioural responses of individuals within their environment, making them well-suited for assessing the population and ecosystem-level effects of chemical exposures (Grimm et al., 2017; Accolla et al., 2021). IBMs can simulate population-level responses by accounting for intraspecific interactions such as crowding and resource competition, which are often overlooked in traditional toxicity tests (Gergs et al., 2014b; Vaugeois et al., 2020). This answers the long-standing call to integrate ecological considerations into ecotoxicology (Cairns et al., 1987; Clements & Rohr, 2009; Beketov and Liess, 2012; Grimm et al., 2017). From an ecosystem services perspective, IBMs are particularly valuable as they can be spatially explicit, accounting for landscape heterogeneity (Galic et al., 2012; Forbes et al., 2017). Several models have been adapted to assess the impact of chemicals on ecosystem services. For example, the BEEHAVE model (Becher et al., 2014) has been modified to evaluate chemical effects on pollination services (EFSA SO, 2022), and an earthworm population model has been developed to assess the impact of chemicals on key drivers of soil fertility (Forbes et al., 2021). Van den Brink et al., (2021) demonstrated the application of multiple Individual-Based Models (IBMs) to assess chemical impacts on various focal species (springtails (*Folsomia candida*), ladybirds (*Coccinella septempunctata*), meadow brown butterfly (*Maniola jurtina*), and bees), each linked to multiple ecosystem functions and services within an apple orchard. They concluded that IBMs could be suitable and appropriate for assessing chemical induced effects on focal species linking to crucial ecosystem services.

However, it must be noted that while IBMs offer many advantages in ecological modelling, they are resource-intensive and can require extensive programming, parameterisation, and validation. These models therefore demand significant computational resources and detailed data as they simulate individual organisms with unique traits and behaviours. Van den Brink et al. (2021) used IBMs to assess the impacts of pesticide exposure in an orchard on different focal species and the ecosystem services they provide. However, this study relied on five IBMs that were developed over many years by multiple research groups. While these models provide deeper ecological realism compared to simpler population models, that depth can come at the cost of versatility, making them harder to apply across different systems. In contrast, aquatic ecosystem models such as CASM and AQUATOX rely on aggregate-level data, based on population averages, and simpler bioenergetics model equations to simulate species population dynamics, (Bartell et al., 2020; Park and Clough 2014), making them computationally more efficient and less data hungry than IBMs. Additionally, simpler, well-established equations reduce the time required for their development.

In the context of environmental risk assessment, these models can provide a balance between ecological realism and utility. Furthermore, they are most appropriate for considering indirect effects (Laras et al.,2022). Altogether this makes them perhaps more suitable for higher tier environmental management and decision-making (Galic et al., 2019). However, to address specific research questions concerning population responses to individual mechanisms and behaviours, such as those in this thesis, IBMs and specifically DEB IBMs, provide the most appropriate modelling framework.

When developing individuals-based models, many models do not fully integrate individual energetics in a mechanistic manner, potentially overlooking how chemicals affect metabolic processes that are crucial for population dynamics. One approach to addressing this challenge is through Dynamic Energy Budget (DEB) theory (Kooijman, 2010), which provides a mechanistic framework to study metabolic processes across species and biological levels. DEB models use differential equations to describe changes in an individual's energy reserves—covering food intake, faeces production, maintenance, growth, maturity, and reproduction (Kooijman, 2010). By altering key DEB parameters to simulate chemical stress on metabolic processes like feeding, maintenance, or reproduction, DEB models can predict how chemicals influence life history traits and energy allocation (Jager, 2012; Jager, 2020). While the standard DEB model has been criticised for its lack of adaptivity and plasticity across life stages (Sibley et al., 2013), or in response to chemical stress (Spurgeon et al., 2020), individual allocates energy to maturation and growth and this allocation remains constant throughout the individual's lifetime. However, such elements are rarely modified in current DEB models due to the lack of sufficient species-specific data. DEB theory provides a useful, generic framework, often applying average energy allocation patterns across species, making it a useful but albeit sometimes limited in its realism in ecotoxicological modelling.

For modelling chemical impacts on populations, combining DEB and IBM models (DEB IBMs) offer a bottom-up, mechanistic approach to understanding population-level effects from individual chemical stress responses. DEB models are particularly advantageous because they allow individuals to endure environmental changes, enabling the simulation of population dynamics under varying resource availability (Sousa et al., 2010). These models can be used to extrapolate from changes in individual energy budgets to impacts on population outcomes and subsequent effects on ecological functions, accounting for individual variation and intraspecific interactions like competition for resources (Martin et al., 2013; Galic et al., 2017; Vlaeminck et al., 2019; Mintram et al., 2018). By considering rates of reproduction, resource consumption, and adaptive behaviours, DEB IBMs provide a comprehensive method for predicting changes in total population biomass and dynamics and subsequent impacts on ecological functions underpinning ecosystem service delivery.

The combination of IBMs and DEB models provides a pathway for transitioning from traditional environmental risk assessment to more holistic ecological risk assessments (Forbes and Galic, 2016). By using energy as a currency to link individual effects to ecological functions through population level responses, these models offer a powerful framework for understanding how chemical stressors impact not only population dynamics but also ecosystem functions and services (Goodchild et al., 2018; Murphy et al., 2018). However, further research is needed to explore the effects of sublethal impacts within and between populations, and their broader implications for ecosystem functions.

1.1 Ecosystem services in freshwater systems

Freshwater ecosystems are a significant source of biodiversity, hosting almost 9.5% of the Earth's described animal species yet representing only 0.01% of water on earth (Dudgeon et al., 2006; WWF, 2016). They deliver a number of valuable ecosystem services, from the production of fish for both food and recreation to nutrient cycling, water retention and purification, erosion regulation and regulation of the flow of water (MEA, 2005; Harrison et al., 2010, Haines-Young and Potschin, 2012), as well as contributing directly to human wellbeing providing sites for recreation (e.g. swimming, nature viewing, angling) (Keeler et al., 2012).

Freshwater systems are vulnerable to both point and nonpoint sources of pollution and are therefore particularly exposed to a wide range of chemical stressors (Vorosmarty et al., 2010; Stendera et al., 2012; Malaj et al., 2014; Burns et al., 2018). Point sources include discharges from wastewater treatment plants, which can release various chemical contaminants, such as pharmaceuticals and personal care products, which are frequently detected in river systems (Kasprzyk-Hordern et al., 2008; Burns et al., 2018; Boxall et al., 2024). Whilst, diffuse sources encompass agricultural and urban runoff, contributing pollutants like nitrogen, phosphorus, pesticides, and veterinary pharmaceuticals. These inputs have escalated due to intensified agricultural practices over the past 50 years (Whelan et al., 2022).

The European Union Water Framework Directive (WFD) was established to enhance water quality across Europe, requiring member states to monitor and assess the chemical and ecological status of water bodies, aiming for all to achieve 'good' status by 2015. Despite these efforts, only 40% of Europe's water bodies reached good ecological status by that deadline (European Environmental Agency (EEA), 2018). In England, the situation is worse, with only 16% of all water bodies and 14% of rivers achieving good ecological status, predominantly due to pollution from agriculture, sewage, wastewater, and urban runoff (Environmental Audit Committee (EAC), 2022). These pollutants pose a significant threat to freshwater and wetland species, with one in ten facing extinction in the UK and two-thirds experiencing population declines (EAC, 2021). While there has been an increase in freshwater species overall in the UK, thought to be linked to climate change (Outhwaite et al., 2020; EAC, 2021), the recovery of European freshwater diversity has slowed in recent years with recovery less prominent in communities downstream of dams, urban areas, and cropland (Haase et al., 2023). The latter where pollution is highly likely a driver of this. While biodiversity declines are driven by multiple stressors, poor water quality, linked to chemical pollution, has been specifically associated with decreases in invertebrate diversity (Beketov et al., 2013). Liess et al. (2021) found that, among other stressors such as poor habitat structure, hydromorphology, and oxygen deficiency, pesticides in German lowland streams were a dominant stressor to insects, while Weitere and colleagues (2021) found that micropollutants from water treatment plants negatively affect the diversity invertebrate communities. With the constant introduction of new chemicals into the market and the UK's departure from the EU, there is an increased risk of potentially harmful chemicals entering the environment due to the loss of stringent regulatory oversight (Jones et al., 2024). Therefore, there is an urgent need to develop cost-effective, ecologically relevant methods to protect freshwater systems from chemical pollution targeted at preserving the ecological integrity and the essential services provided by these vital ecosystems.

Utilising an ecosystem services approach to risk assessment, we can employ modelling tools within the framework of ecosystem services to predict the detrimental effects of chemical pollution on the entities responsible for ecological processes and functions within freshwater systems. However, a critical initial step involves identifying the ecological entities that drive and sustain the ecological processes and functions essential for the provision of these services. To assess chemical effects on them, with the majority ecosystem services provided by ecological processes and functions of population species, it is important to identify the entities that drive their delivery.

1.2 Recreational Fisheries

In the UK, angling, also known as recreational fishing, is enjoyed by estimated more than 1 million people annually (UK Environment Agency (EA), 2018). Popular with both residents and visitors to the British Isles, freshwater angling is a billion-pound industry, contributing around £1.4 billion annually to the UK economy annually (gross value added, including cost of bait, transport, as well as licences fees (EA, 2018)). In England and Wales, angling for coarse fish (fish species other than salmon and trout e.g. pike, and perch) is most popular with 19.4 million angling days of a total 22.3 million in 2015 (EA, 2018), with the majority of those days (15.5 million) spent fishing in lakes, reservoirs and ponds, 5.5 million days spent fishing in lakes or streams and 1.4 million in canals. The health of a fishery is dependent on the supply of fish and size of the fish. The satisfaction of anglers correlates strongly with the availability of larger fish and the aesthetic appeal of the fishery environment (Birdsong et al., 2021). The status and sustainability of fisheries are linked to ecological processes that ensure robust fish populations, nutrient cycling, and habitat maintenance. The precise economic and well-being benefits derived from angling are challenging to quantify, but the positive impacts of outdoor recreation on health are well-documented (Public Health England, 2020; Wilson et al., 2023). Often, the value of ES are valued by the cost of remediating and restoring environments that are negatively impacted by drivers of environmental changes (Bullock et al., 2016). Thus, any degradation or loss of the ecological functions supporting these services could incur significant costs on both the economy and the welfare of citizens.

Recreational fisheries have frequently been utilised as a case study system to test ecotoxicological methods for assessing the chemical effects on ecosystem services (Forbes et al., 2017; Galic et al., 2019; Maltby et al., 2021). Their complex species interactions and well-defined services, such as angling opportunities and habitat quality (Fulford et al., 2016), facilitate a focused examination of how environmental changes affect these services. Recreational fisheries are, therefore, an ideal system for exploring the relationship between chemical impacts on key SPUs and the provision of measurable recreational ecosystem services within the context of ecological risk assessment (ERA).

In a recreational fishery, the provision of both game (salmon and trout) and coarse (roach and perch) fish species are of interest to anglers. Such fish, as carnivores, rely on the provision of prey for food, which in turn is reliant on the processing of resources and organic matter in the system (Figure 1.2) (Maltby et al., 2021). Some carnivorous fish prey on macroinvertebrate communities, selecting prey based on the availability of preferred individuals, often of a particular species and above a particular length (Newman and Waters, 1984; Rask and Hiisivuori, 1985; Dodrill et al., 2021). The provision of prey is dependent on the processing organic matter in the system.

As consumers, freshwater invertebrates are a key component of freshwater food webs, performing myriad ecological functions (Cummins and Klug, 1979; Wallace and Webster, 1996; Duffy 2002). They play a vital role in the transformation and consumption of organic material, facilitating the cycling of nutrients, transporting, and mixing of materials, altering the physical structure of ecosystems, and enabling the transfer of energy via secondary production, through the food web as a result of their feeding activity (Gessner et al., 1999; Macadam et al., 2015). For example, benthic invertebrates contribute significantly to nutrient cycling and organic matter processing through their feeding activities, such as processing leaf litter, which supports energy flow in freshwater streams (Gessner et al., 1999; Benke et al., 2018). While the presence of herbivores, for instance, plays a key role in consuming, and thus controlling the presence of primary production and particulate matter, maintaining water clarity (Faber et al., 2021). Such processes support several freshwater ecosystems services and are maintained by a functionally diverse freshwater invertebrate community (Smith et al., 2017).

The range of functions performed by this diverse group of consumers can be categorised by their relationship to their food source (Wallace and Webster, 1996). In 1967, Root introduced the concept of a "functional group" (initially termed "guild") to describe a collection of species that exploit the same class of environmental resources in similar ways, leading to overlapping niche requirements. This resource use generally pertains to food or habitat (Cummins, 1974; Blaum et al., 2011). Functional feeding groups—such as filterers, shredders, predators, gatherers, and herbivores (Tachet et al., 2010)—can include a diverse range of taxa, as species from different taxonomic groups may perform similar functions. Conversely, species within the same taxonomic group can occupy different functional groups. However, some taxa are more prevalent in certain functional feeding groups than others (Schmera et al., 2022). Freshwater invertebrate communities, thus, play a crucial role in maintaining various processes and functions within freshwater ecosystems. Therefore, declines in the diversity and abundance of these invertebrates, or changes in their feeding activities, may adversely affect the provision of ecosystem services in recreational fisheries (Figure 1.2). Such alterations can disrupt both the structure and functioning of the ecosystem, ultimately impacting the overall performance and sustainability of a fishery (Maltby et al., 2021).

In terms of the provision of prey, feeding activity of freshwater invertebrates can link prey population growth and the growth of fish within a recreational fishery. Specifically, prey availability can influence both somatic and population growth in fish populations, which are directly linked to fishery productivity and value (Brown et al., 2019). Both somatic and population growth can be influenced by the individual feeding rates (Kooijman et al., 2010) as well as the quality and quantity of food available to fish. Larger prey often offer greater energy density (Newman and Waters, 1984). Carnivorous fish feeding on fast-growing, energetically rich prey generally have greater somatic growth, leading to larger body sizes (Goodrich and Clarke, 2023). This enhances the appeal of fish to recreational anglers (a cultural ecosystem service) (Birdsong et al., 2021). Equally, high prey population growth can result in greater prey abundance, ensuring more stable supply of food resources for carnivorous fish populations. This supports a steady fish growth, higher biomass, and more reliable fishery yields — key to the economic value of commercial fisheries. These trophic interactions demonstrate that prey characteristics—such as abundance and nutritional quality—are not merely background ecological variables but are fundamental drivers of fish population dynamics and the reliable delivery of ecosystem services in freshwater systems.

The effects of chemicals on freshwater invertebrates and their feeding activities can significantly impact ecological functions and the associated services these ecosystems provide. Given that allochthonous detritus, formed of terrestrial substrates, is a major source of energy in freshwater environments (Marcarelli et al., 2011; Brett et al., 2017), much of the research has concentrated on the breakdown of leaf litter in streams. Studies have shown that exposure to insecticides, fungicides, and antibiotics can reduce leaf litter processing by detritivores (Peters et al., 2013; Harrison et al., 2021; Reiber et al., 2022). Such findings highlight the vulnerability of critical ecosystem processes to chemical stressors. Single-species studies demonstrate that these pollutants can disrupt resource processing, an essential service for nutrient cycling and energy flow (Fernandez et al., 2015; Zubrod et al., 2015). When it comes to community level effects, however, this is influenced by the distribution of sensitivity both between and within functional feeding groups, as well as the resulting chemical effects on intra- and interspecific interactions within these groups or service providing units.

Given that the relationship between invertebrate diversity loss and ecosystem function performance is complex a function of both species and functional diversity and evenness (Laureto et al., 2015). Understanding variations in chemical sensitivity both between and within functional groups can provide valuable insights into how chemicals affect the functions that support ecosystem service delivery. To understand chemical effects on the ecological processes and functions that underpin the delivery of ecosystem services, we must first understand how chemical pollutants affect the activity entities perform those functional and processes, the consumption, production, and translation of energy by individuals, populations, and interacting species.

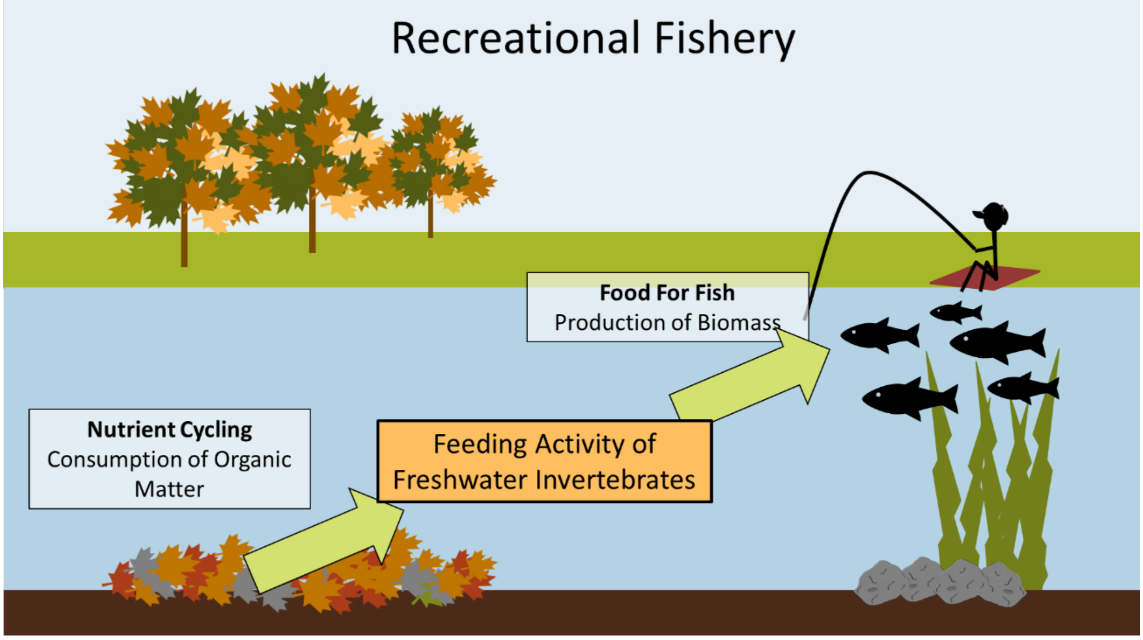

Figure 1.2: The role of the feeding activity of freshwater invertebrates in the performance of ecological functions, i.e. the cycling of nutrients and the provision of prey, that support the provision of fish in a recreational fishery

1.3 Aims and objectives

The aim of this thesis is to explore how information on chemical impacts on the feeding activity of freshwater invertebrates can be used to predict population level effects on ecosystem functions and considering the implications for associated ecosystem services. This is investigated the case study of a recreational fishery where the delivery of ES is supported by the provision of prey and the consumption of organic matter, driving the cycling of nutrients. The thesis addresses the following questions:

- How do chemical stressors impact the feeding activity of freshwater invertebrates, and to functional feeding groups differ in their sensitivity to these stressors?
- How do individual-level impacts on energy uptake translate to population-level responses and the overall performance of ecological functions i.e. the provision of prey for predatory fish and the cycling of nutrients?
    - How do these effects impact single-species populations?
    - How are these population-level responses and ecological functions influenced when interspecific competition and differential sensitivity between species are considered?

Chapter 2 focuses on the individual-level effects of chemical stress, exploring the variation in sensitivity among freshwater invertebrates from different functional feeding groups. It examines how these groups respond to various chemical stressors and Mode of Action. The chapter uses data on lethality from the RIVM ecotoxicity database and data gathered from a systematic review of peer-reviewed literature regarding the impact of chemical stress on feeding activity. This information—lethality and changes in feeding behaviour—serve as proxies for understanding the broader effects on the structure and function of ecological systems.

The objectives of this chapter are:

- To assess the variation in taxonomic composition of functional feeding groups for freshwater invertebrates within each dataset.
- To assess the distribution of sensitivity between functional feeding groups to different chemical stressors with regard to lethality and feeding activity, comparing, where possible, patterns between chemical modes of action
- Assess the relative sensitivity of feeding as an endpoint compared to lethality.

Chapter 3 describes the selection, adaptation, and evaluation of the two individual-based dynamic energy budget models used in the subsequent chapters to study the impact of chemical effects on the feeding activity of individuals on the structure and activity of populations in a service providing unit. Specifically, it focusses on the roles of *Gammarus pulex* and *Asellus aquaticus* in leaf processing and prey provision, two functions critical for maintaining the health and functioning of freshwater ecosystems.

Chapter 4 aims to assess how different pathways of impact on energy uptake by individuals translate to the performance of ecological functions by populations of two freshwater shredder species, *Asellus aquaticus* and *Gammarus pulex*. Specifically, it focuses on their roles in leaf processing and prey provision, which are critical for the delivery of ecosystem services of a recreational fishery. The objectives of this chapter are:

- To utilise Dynamic Energy Budget Individual-Based Models (DEB IBMs) for *Gammarus pulex* and *Asellus aquaticus* to simulate population-level responses to four pathways of impact on the consumer-resource relationship: individual feeding activity, individual assimilation efficiency, resource quality, and resource quantity.
- Compare how these pathways of impact translate to population level responses and the performance of two key ecological functions by these populations of these species, the processing of leaf litter and the provision of food for fish.
- Compare the relative sensitivity of population-level responses between the two shredder species: *Gammarus pulex* and *Asellus aquaticus*.

Chapter 5 couples the two species models and assesses how interspecific competition for food resources affects the impact of chemical induced feeding inhibition in either species and differences in relative sensitivity between the two species populations and performance of ecological functions within the SPU. The chapter addresses the following objectives:

- To investigate how feeding inhibition affects the conditions that allow for coexistence versus exclusion between the species.
- Where coexistence occurs, examine how the relative abundance of species varies with feeding inhibition.
- Where exclusion occurs, examine how feeding inhibition affects the time take for one species to exclude another.

- Finally, this chapter will address how changes in individual feeding rates and relative sensitivity translate into alterations in the ecological functions within the SPU.

Chapter 6 is the general discussion that aims to piece together the results by exploring the implications of findings in the previous chapters assessing how information about feeding behaviour responses to chemical stress, coupled with extrapolatory modelling, be used to make useful predictions about impacts on ecosystem service provision. The main research findings are discussed, exploring implications of assessing effects at different levels of biological organisation affects the prediction of impacts on ecological functions in a recreational fishery, considering the implications for an ecosystem services approach to ecological risk assessment.

Chapter 2 - Invertebrate Sensitivity to Chemical Stress: Implications for Ecosystem Structure and Process

2.1 Introduction

To assess the risks that chemical stressors pose to ecosystem service delivery, it is necessary to understand chemical effects on the ecosystem components that provide the services (i.e. service providing units, SPUs). Many ecosystem services depend on ecological processes (Luck et al., 2009), which are dependent on both the identity of the species present and their contribution to the underpinning functions (Hooper et al., 2005; Cadotte et al., 2011; Smith et al., 2017). This can translate to structure and process or activity within a system, or states and rates (Harrison et al., 2021). Therefore, when assessing chemical effects on the performance of ecological functions, we need information that pertains to the presence and activity of species from particular SPUs.

Invertebrates drive several ecological processes within freshwater food webs (e.g. production and consumption of biomass, transformation of organic matter, nutrient cycling), which are dependent on their food source and feeding behaviour (Wallace and Webster, 1996). The term functional feeding group (originally “feeding guild” has been used to describe “a group of species that exploit the same range of environmental resources in a similar way and thus overlap in the niche needs” (Root, 1967; Cummins, 1979) where the use of resources is typically related to food or habitat (Blaum et al., 2011). Freshwater invertebrates have been ascribed to six functional feeding groups that include filterers, which feed on suspended material through; shredders, that feeding on coarse detritus of both plant or animal material physically breaking down or "shredding" this material into smaller pieces; gatherers, which feed on fine organic particles that settle on the bottom of water bodies; predators, which actively hunt, capture, and consume other animals; and herbivores, which graze on plants or algae (Tachet et al., 2010; Schmera et al., 2015).

Species from different taxonomic groups may occur in the same functional feeding group and, similarly, species within the same taxonomic group may occur in different functional groups. While species diversity can promote functional diversity, the relationship is not always straightforward (Naeem et al., 2002, Cadotte et al., 2011; Loreau et al., 2015). In ecosystems where there is functional redundancy, the loss of a few species might not significantly impact the ecosystem's overall functioning (Biggs et al., 2020). However, if species loss is not random, but systematically affects species that perform a particular function, there can be a significant loss of functional diversity, even if species diversity remains high (Spaak et al., 2016; Baert et al., 2017). With sensitivity to chemical stress partly influenced by taxonomy, differences in the taxonomic composition of functional feeding groups (FFGs) could therefore reveal potential variations in chemical sensitivity. Furthermore, identifying the variation in sensitivity to chemical stress within and between functional feeding groups may shed light on how different chemicals might affect the performance of ecosystem functions and hence the delivery of ecosystem services.

The sensitivity of freshwater invertebrates to chemical stress may vary over 12 orders of magnitude (Oginah et al., 2023) and the relative sensitivity of species is often chemical specific (van den Berg et al., 2019). Chemicals with specific toxicity pathways (e.g. Acetylcholinesterase (AChE) Inhibitors like organophosphates or carbamate insecticides, or polar narcotics, often pharmaceuticals) tend to show greater and systematic variation in sensitivity between taxonomic groups compared to general stressors like non-polar narcotics (Maltby et al., 2005; Maltby et al., 2009; Signore et al., 2016; Van den Berg et al., 2019; Robinson et al., 2021; Oginah et al., 2023). In general, AChE inhibitors disproportionately affect arthropods (Oginah et al., 2023) compared to other taxonomic groups such as molluscs (Van den Berg et al., 2019). Conversely, annelids (Lofts et al., 2005) and molluscs are generally more sensitive to metals (Kraak et al., 1994; Berny, 2002; Van den Berg et al., 2019). Therefore, the taxonomic composition of functional feeding groups may influence their sensitivity to chemical stress. Interspecific variation in chemical sensitivity across ecotoxicological endpoints from single-species toxicity tests can be statistically described using species sensitivity distributions (SSDs). SSDs can then be used to calculate the hazard concentration (HC_5) at which 5% of the species assemblage may be affected (Posthuma et al., 2000; Posthuma et al., 2019). They can be used to compare the sensitivity profile of different groups of species e.g. taxonomic groups (Maltby et al., 2005; van Den Brink et al., 2006; Oginah et al., 2023) or assemblages in particular habitats (Liang et al., 2024; Jupke et al., 2024). The field has moved towards more targeted SSDs for chemical modes of action, grouping or splitting species by broad taxonomic groups (i.e. Microbes, algae, invertebrates, and vertebrates), often yielding regulatory thresholds below those using standard SSDs (Maltby et al., 2005; Van Den Brink et al., 2006; Oginah et al., 2023). Current approaches to SSDs do not explicitly consider how the species contribute to the performance of ecosystem functions (Belanger et al., 2016). If we are to move toward predicting chemical effects on ecological processes and functions, to protect the delivery of ecosystem services, we need to consider not just what a species is, but also what it does i.e. the functions it performs.

The most common ecotoxicity endpoint is mortality, usually reported as the lethal concentration killing 50% of test organisms. The LC_{50} derived from acute (<7 days) toxicity tests. Loss of individuals due to chemical-induced mortality can lead to reduced population sizes and, in extreme cases, local species extinction, which alters community structure and may alter the performance of ecological functions (Rumschlag et al., 2020). Therefore, acute mortality can tell us something about chemical impacts on the structure of assemblages. However, such changes in community structure may not always result in changes in the performance of particular functions, especially in systems with high functional redundancy (De Laender et al., 2011). Moreover, there may be changes in functions which occur as a result of impacts on organisms which do not result in mortality. Sublethal effects, such as decreased feeding, can still have significant ecological consequences. For example, feeding rates in laboratory settings have been shown to correlate with consumption in natural environments (Farrow and Maltby, 2000; Bloor et al., 2005). This is particularly relevant when chemical concentrations are below regulatory thresholds, where subtle behavioural changes may still have significant ecological consequences (Peters et al., 2013).

In terms of an ecosystem services approach to ERA, feeding traits can provide a mechanistic link between organic matter processing, individual growth, and ecosystem function. Assessing feeding behaviour allows for a more comprehensive understanding of impacts on energy transfer, linking to the performance of ecological functions. Feeding traits can be directly associated with prey availability and trophic interactions by influencing body size distributions and i.e. intra and interspecific competition for resources. However, feeding is not a commonly used endpoint and therefore can lack appropriate data.

By contrast, growth is a more commonly measured and data rich endpoint which is also simpler to assess. However, a focus on chemical effects on individual growth or body weight alone may overlook potential effects on ecological processes that drive population-level responses. While changes in body weight can serve as a general indicator of stress (Schuijt et al., 2021), it does not necessarily indicate how an organism is performing its functioning within an ecosystem. Changes in feeding behaviour can directly influence individual growth, but the reverse is not always true (Schuijt et al., 2021). Furthermore, unchanged growth may not always indicate an absence of stress (Mouneyrac et al., 2011), particularly as changes in feeding rate can buffer against environmental disturbances before measurable shifts in body size or reproduction occur. This makes feeding a more sensitive and ecologically relevant metric for assessing chemical effects, as it integrates both individual physiological responses and broader food web interactions.

From an ecotoxicological perspective, feeding activity is both ecologically significant and highly sensitive (Agatz et al., 2014; Ford et al., 2021), often being affected at concentrations lower than those causing lethal effects (Nyman et al., 2013; Agatz et al., 2014; Melvin and Wilson, 2013; Alonso and Romero-Blanco, 2022). Feeding is not frequently measured in standard laboratory studies; it is more commonly assessed in in situ assessments of water quality (Maltby et al., 2001) or in chronic studies as an indicator of ecological function (Van den Brink et al., 2008; Harrison et al., 2021). With only a few standard protocols available for individual-level feeding tests, understanding the chemical impacts on the feeding activity of a range of freshwater invertebrates, and thus the functions they perform, remains limited. Therefore, it is important to understand the relationship between feeding activity and lethality to better infer potential ecological impacts from more commonly measured endpoints.

To gain an understanding of how chemicals influence ecological processes and functions, it is important to study both lethality and changes in feeding rates across species from different functional groups. Lethality provides insights into direct population and community impacts, while changes in feeding rates reveal sublethal effects that can alter ecosystem processes. This study explores how the distribution of sensitivity to chemical stress differs between functional groups with respect to both lethality and feeding activity.

To address this aim, lethality data (acute LC_{50}s) were obtained from the curated and harmonised ecotoxicity dataset of Posthuma et al. (2019) in Oginah et al. (2023). For feeding data, a search of the US Environmental Protection Agency (EPA) ECOTOX database (conducted on 21.12.2022) for behavioural endpoints initially yielded 4,991 of endpoints from 641 of studies. When filtering by strictly feeding behaviour and static exposure, this fell to 606 endpoints from 94 studies. When this was filtered to one endpoint per chemical per species per study, this became 212 endpoints across 41 species (Appendix 2.1). This dataset was therefore considered data poor with regard to feeding endpoints, so, feeding data used in this study was gathered using a systematic review of the peer reviewed literature. Therefore, the first aim of this study was to understand the chemical induced effects on feeding rate and behaviour of freshwater invertebrates.

Using this data, this study addresses the following objectives:

- To assess the distribution of sensitivity across functional feeding groups with a focus on both lethality and feeding activity, in response to different 1) chemical stressors, 2) chemical modes of action.

  - Within which the variation in taxonomic composition of FFGs in the toxicity datasets will be assessed to enable the formulation of hypotheses about the distribution of sensitivity.
- Assess the relative sensitivity of feeding as an endpoint compared to lethality.

2.2 Methods

2.2.1 Data Collection and Preparation

2.2.1.1 Lethality Data

Lethality data was obtained from the curated RIVM (The National Institute for Public Health and Environment, The Netherlands) ecotoxicity database (Posthuma et al., 2019), in Oginah et al., (2023). The database contains 7,102 acute LC_{50}s from 536 taxa (414 species from 298 genera, from 150 families, from 9 phyla), for 1,582 chemical stressors.

2.2.1.2 Systematic Review of Feeding

Feeding data were obtained from a systematic review of the peer reviewed literature, conducted according to the European Food Safety Authority (EFSA) Guidelines for Systematic review (2010). A PECO (or PICO) statement is a device commonly used to guide systematic reviews and formulate clear and specific research questions, identifying the key elements of the review. For questions of the effect of intervention or exposure elements are identified as the population of interest (P), intervention or exposure of interest (I/E), a comparator or control group (C) and the outcomes of interest (O) (EFSA, 2010).

The specific research question setting the scope and goal of the review:

'What are the chemical-induced effects on feeding rate and behaviour of freshwater invertebrates?'

Here, the **(P)**opulation of interest was freshwater macroinvertebrates (across all continents). This excluded marine macroinvertebrates and those studied in estuarine environments, fish of all life stages, crayfish, and studies of decapods conducted in aquacultural conditions. The **(E)**xposures of interest were those of single contaminants of known concentrations, excluding studies with mixtures or field samples. Only studies with a **(C)**ontrol group were included for a fair comparison of effect. With the (**O)**utcomes of interest limited to changes in the feeding, ingestion, filtration, egestion (a proxy for ingestion in oligochaetes), or clearance rate.

The PECO elements of the search were combined to form 4 components of the search string; chemical-induced, changes/effects, feeding activity (rate and behaviour), and freshwater invertebrates (Table 2.1). A list of freshwater taxa was obtained from the Centre for Ecology and Hydrology (CEH) UK freshwater taxa checklist (Gunn et al., 2018) to capture studies for all freshwater taxa. The search was performed in SCOPUS and marker papers, captured during manual preliminary searches, were used to refine the search terms and capture relevant papers. The search terms were finalised when all marker papers were captured in the literature search.

Table 2.1: *Search string for the literature search with the 4 search components separated. The asterisk '*' is used as a wildcard to represent any number of characters that may follow a root word, capturing multiple variations of a term.*

Search component	Search String
Freshwater	freshwater OR fresh-water OR aquatic OR river* OR lotic OR lentic OR fluvia* OR surface-water* OR lake OR pond* OR stream*
Chemical induced change	(toxic* OR effect OR sublethal OR reduce* OR inhibit* OR increase* OR positive* OR enhance*) AND (contaminant* OR chemical* OR metal* OR pesticide* OR insecticide* OR pollut* OR compound* OR exposure OR stress*)
Freshwater invertebrates	macroinvertebrate* OR invertebrate* OR zooplankton OR porifera OR coelenterata OR cnidaria* OR hydra OR tricladida OR turbellari* OR planaria* OR flatworm OR nemato* OR nemerti* OR mollus* OR *gastropod* OR snail OR neriti* OR viviparid* OR valvatid* OR hydrobiid* OR bithynii* OR assimineid OR sorbeoconch* OR heterobranch* OR acochlidi* OR pulmonata OR pupilli* OR bivalv* OR mussel* OR heterodonta OR venerida OR dreissen* OR sphaerii* OR corbicul* OR unionid* OR polychae* OR annelid* OR clitellat* OR oligoch* OR haplotax* OR lumbric* OR tubific* OR moniligast* OR worm* OR hirudin* OR leech* OR branchiobdell* OR araneae OR hydrach* OR arthropod* OR crustac* OR malacostrac* OR bethynell* OR phyllocari* OR hoplocari* OR eumalacostaca OR pericarid* OR amphipod* OR *Gammarus* OR gammarid* OR hyperii* OR ingolfielli* OR hyalella OR isopod* OR *_Asellus_ OR mysid* OR eucarid* OR decapod* OR cephalocar* OR maxillopod* OR branchiura OR hexanaup* OR copepod* OR ostracod* OR branchiopod* OR anostraca OR notostraca OR cyclops OR branchiop* OR cladoc* OR haplopod* OR ctnenopod* OR anomopod* OR onychopod* OR daphni* OR rotifer* OR collemb* OR chilopod* OR insect* OR ephemer* OR odonata OR plecopt* OR heteropt* OR megalopt* OR neuropt* OR coleopt* OR dytiscidae OR hymenopt* OR trichopt* OR lepidopt* OR neopt* OR dipte* OR chironomid* OR brachyo* OR cyclorrhaph* OR bryozoa
Feeding rate and behaviour	(feed* AND (activity OR behaviour OR rate*)) OR (assimilat* OR filtration OR ingestion OR "food intake" OR grazing)

In an initial 'highly sensitive and low specificity' screening, titles and abstracts were screened to exclude citations that were not relevant to the review. All papers were screened by a single reviewer. Following the initial screening of titles and abstracts, relevant papers, i.e. those exclusively reporting laboratory feeding assays, were identified.

The search was performed in SCOPUS on 13.08.21 and returned 3,779 citations. Following the initial screening, 539 papers were deemed relevant. After the full-text screen, 201 studies were found to report laboratory feeding assays. Of these 201 studies, 76 had multiple species/chemical assays resulting in 376 feeding endpoints. Of those endpoints were 99 EC_{50}s, 171 LOECs and 93 NOECs. Thirteen assays reported effects thresholds less than 50% effect. Some assays appeared more than once as the same laboratory assay was reported in multiple papers (Dinh Van et al., 2014, Evens et al., 2014). Here, only one of the two citations was included.

The data from the selected 376 laboratory feeding assays studies were extracted and added to a database with variables: contaminant name, CAS (Chemical Abstracts Service) number, species name, study concentrations, exposure type (food, aqueous or both), study duration, food, feeding endpoint, effect direction, and effect concentration. Effect concentrations for feeding endpoints will hereafter be referred to as $EC_{feeding}$.

2.2.1.3 Assigning Functional Feeding groups

Functional feeding groups were assigned to species in both toxicity databases using a combination of trait databases and information from the literature. The harmonised datasets of Kunz et al. (2021), which gathered traits from four ecological trait databases and converted them to harmonised fuzzy coding tables (EU: Schmidt-Kloiber & Hering, 2015, and Tachet et al., 2010; US: Twardochleb et al., 2021; Australia: Kefford et al., 2020; New Zealand: Philips and Smith, 2018), were utilised.

Functional feeding traits are modal traits. Therefore, the assignment of primary functional feeding groups was conducted using fuzzy coding tables. Information from all trait databases were combined to create one master trait dataset. The primary trait for each species is defined as the trait with the greatest weight. Where possible, the primary FFG was identified for each species in the trait database. Where species appeared in multiple databases, and differed, fuzzy coding was used to determine the primary trait(s) for that species by integrating information from all datasets. If a species had more than one primary functional feeding trait, it was assigned to multiple FFGs. This process was repeated to assign traits at the genus and family levels, creating a master dataset with FFGs for 417 species, 1879 genera, and 442 families (Appendix 2, Figure A2.2) assigned to five FFGs (Table 2.2).

Where traits could not be found in any of the trait databases, additional searches of relevant keys were conducted. Literature was then reviewed, prioritising sources that provided comprehensive reviews of orders, families, or genera. FFGs from the literature were allocated based on the harmonised criteria of Kunz et al. (2021) (Table 2.2). If no evidence for traits could be found, the data was discarded.

Table 2.2: Feeding mode (Here called Functional feeding group) as defined in Kunz et al. (2021)

Functional Feeding group	Combined traits
Filterer	Active/passive filterer, absorber, filter-feeder, collector-filterer, filterer
Gatherer	Deposit-feeder, collector-gatherer, detrivore, gatherer
Herbivore	Grazer, scraper, piercer herbivore, herbivore, algal piercer, piercer (plants)
Predator	Piercer (animals), predator
Shredder	Miner, xylophagus, shredder, shredder detrivore

2.2.1.4 Assigning chemical modes of action

No one chemical database contained chemical modes of action (MoAs) for all chemicals in both datasets. MoAs were therefore assigned based on multiple sources. Categorisation of MoAs used in the Toxicity Estimation Software Tool (TEST), based on the methods of Barron et al., (2015), which categorises chemicals into five broad chemical modes of action was used. The five broad chemical modes of action are; narcosis (non-specific mode of action that affects cellular membranes); reactivity (cause damage by directly interacting with biological molecules); neurotoxicity (affect the nervous system by interfering with nerve signalling processes); AChE inhibition (interfering with the enzyme acetylcholinesterase, which breaks down the neurotransmitter acetylcholine in synapses); electron transport inhibition (disrupting the electron transport chain in mitochondria); iono/osmoregulatory/circulatory regulation. Where possible, narcotics were sub categorised into polar and nonpolar using information on reactivity reported in each associated MOA database. These chemical modes of action were also used in Van den Berg et al., (2019) to study differences in sensitivity between species for difference chemical modes of action.

Where possible, MoAs were first assigned using the TEST categorisation reported in the envirotoxdatabase.org, described in Keinzler et al. (2019). Where MoAs were not available there, MoAs were first assigned from the database of Barron et al. (2015), the database from which the

TEST tool in Keinzler et al. (2019) was based. Where MoAs could not be assigned from either database, mode was considered unknown.

2.2.2 Assessing the variation in the taxonomic composition of FFGs.

To evaluate the taxonomic composition of FFGs in the analysis of sensitivity between different chemical modes of action, the number of families within each FFG were quantified and recorded within both datasets. The distribution of families within FFGs across taxonomic categories (phylum, class, and order) was compared between FFGs, with percentages representing the relative contribution of families to each taxonomic category to the total for each FFG.

To assess the taxonomic composition of FFGs used in the analysis of individual chemicals, differences in the taxonomic composition of functional feeding groups in relation to families were evaluated using a similarity analysis (ANOSIM) based on the Bray–Curtis distance matrices to estimate statistically significant differences between groups. For FFGs found to be significantly different in the ANOSIM analysis, SIMPER (both using the 'vegan' package in R) was used to determine which families contributed to most to the difference between FFGs. By calculating the average similarity between all pairings of each replicate (i.e. chemical) within each functional feeding group to other functional feeding groups, the SIMPER analysis tabulates the average percent contribution of each family to the dissimilarity observed between functional feeding groups. For simplicity only results representing 80% of the cumulative input are shown here.

2.2.3 Analysis of difference in sensitivity between FFGs

2.2.3.1 For individual chemicals

The geometric mean of acute LC_{50} values was calculated for each species for each chemical (as per Oginah et al., 2023). Chemicals with ≥2 functional feeding groups with ≥6 species within each functional feeding group, were regarded as having sufficient data. The differences in the sensitivity to chemical stress between FFGs was determined following the statistical protocol of Oginah et al. (2023). Only the lethality dataset had enough data to be able to assess differences in sensitivity between individual chemicals.

2.2.3.2 For chemical modes of action

To assess differences in sensitivity between FFGs and chemical modes of action within the lethality and feeding datasets, toxicity endpoints were normalised using *Daphnia* LC_{50}s for respective contaminants, gathered from the lethality dataset. Where no lethality data was available for a particular chemical, the assay value was excluded from the analysis. The normalised toxicity endpoint becomes a toxic unit. The toxic unit for each species for each contaminant becomes:

$$TU = \frac{EC_{feeding}}{LC_{50}}$$

The geometric mean of TU values was calculated for each species for each chemical (as per Oginah et al., 2023). Differences in sensitivity between FFGs and chemical modes of action were assessed using a one-way ANOVA. For the feeding dataset, NOECs were excluded from this analysis and subsequent analysis, given NOECS are concentrations where no effects were observed as they say more about the concentrations used in the assay rather than the response of the species. The normality and homogeneity of variances were always tested; when not met, data were log-transformed. If variances were still no homogenous then Kruskal-Wallis tests and Dunn's post hoc test were employed.

2.2.4 Assessing the relative sensitivity of feeding to lethality

Spearman's rank correlation was used to assess the relative sensitivity of feeding endpoints ($EC_{feeding)}$ to lethality (i.e. acute LC_{50}s from the lethality dataset). Rank correlations of the data when grouping by chemical modes of action and functional feeding groups were compared to the whole dataset. Analysis was conducted in R using the "devtools" package.

2.3 Results

2.3.1 Functional Feeding groups

In the lethality dataset, functional feeding groups were assigned to 7,087 of the 7,102 endpoints. Functional feeding groups could not be found for 15 entries; one cnidarian, four decapod families, and one entry where a plecopteran was only described at the level of order. These were removed from the dataset. Furthermore, six taxa were assigned the FFG "Parasite"; parasites were ignored in this analysis. Of the remaining entries, most FFGs within families were assigned from the merged Kunz dataset at the genus level, followed by the genus level and the family level (Appendix 2, Figure A2.2). Thirty-nine families were assigned FFGs using the literature with most assigned at the level of genus (Appendix 2, Figure A2.2). Seven entries were assigned from information at the level of order. Orders of copepods Harpacticoida, Calanoida, and cillates of Euplotida were assigned the FFG "filterer".

Filterer was the most common and diverse FFG in the lethality dataset with 3,487 assays and 180 species followed by gatherer with 2,177 assays ad 139 species. Herbivore, predator and Shredder had similar number of assays but differing number of species with shredder the least diverse FFG.

In the feeding dataset, FFGs were assigned to all 376 datapoints obtained from the literature review, with most FFGs assigned at the species level from the Kunz dataset (Appendix 2, Figure A2.2). When grouped by FFGs, 13 species fell into multiple FFGs, translating to 24 assays assigned to more than one FFG. Across all assays, filterers were the most common with 203 assays, followed by shredders (81) and predators (58), gatherers (47) and herbivores (32). Similar patterns are observed with the number of species per functional group (Table 2.3)

Table 2.3: Number of assays and species within each functional Feeding Group for both lethality and feeding datasets, including 1,995 assays (107 species) and 24 assays (13 species) where multiple FFGs were assigned for lethality and feeding datasets, respectively.

	Lethality Dataset		**Feeding dataset**	
	No. Assays	No. Species	No. Assays	No. Species
Filterer	3,487	180	203	29
Gatherer	2,177	139	47	16
Herbivore	1,514	103	32	12
Predator	1,536	172	58	22
Shredder	1,527	83	81	15

2.3.1.1 Chemical modes of action

Of the 1,582 chemical stressors, chemical modes of action were assigned to 1109 of them. The most common chemical mode of action was nonpolar narcosis, with 742 chemicals, followed by AChE inhibitors (136), neurotoxicity (59) and 56 metals and polar narcotics (48). Uncouplers, reactivity, IOC impairments and electron transport inhibitors totalled 68 chemicals (Figure 2.1).

Among the feeding data, studies were conducted with 163 different chemical stressors across 8 chemical modes of action. The most common were nonpolar narcotics with 62 chemicals, 19 metals and 10 AChE inhibitors (Figure 2.1). Of the 54 chemicals with no chemical modes of action assigned, 34 were nanoparticles.

A few chemical stressors accounted for the majority of the studies; 41 studies with copper, 38 with cadmium, 25 for zinc, 12 for silver, 9 with imidacloprid. Some genus contaminant combinations appeared multiple times, with just 6 genera studied for more than 10 chemicals across 221 assays. There were 60 different chemicals studied with *Daphnia sp.*, 25 for *Gammarus sp.*, 11 with *Dressiena sp.*, 15 with *Brachionus sp.*, 16 for *Hydra sp.,* and 15 for *Corbicular sp.*. However, one third of genera were only studied with one chemical.

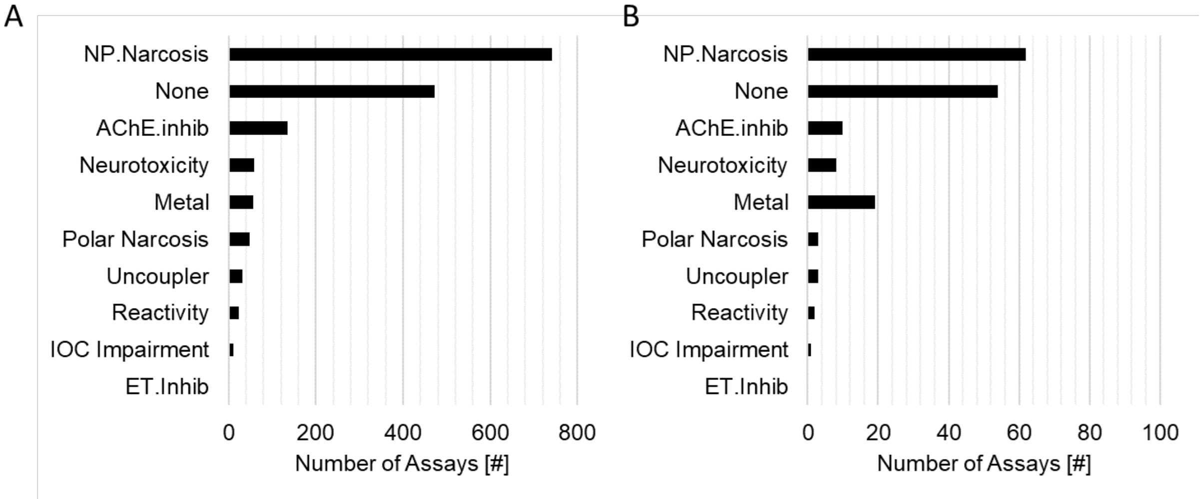

Figure 2.1: Count of entries per chemical mode of action for A) the lethality dataset, and B for the feeding dataset. 'NP. Narcosis' is nonpolar narcosis, 'AChE.inhib' is AChE inhibition, 'IOC impairment' is Iono/osmoregulatory/circulatory impairment, and 'ET inhib' is Electron Transport inhibition

2.3.2 Taxonomic composition of FFGs

2.3.2.1 For chemical modes of action

When grouping the data such that there is one unique endpoint per species per chemical, the taxonomic composition of FFGs differs with FFGs falling into 3, almost 4, distinct clusters (Figure 2.2). All FFGs, apart from the herbivores, were characterised predominantly by arthropods making up at least 80% of all entries (Appendix 2, Table A2.3). Herbivores were characterised largely by gastropod Mollusca (63.2%) and with 37% from Arthropoda (Appendix 2, Table A2.3).

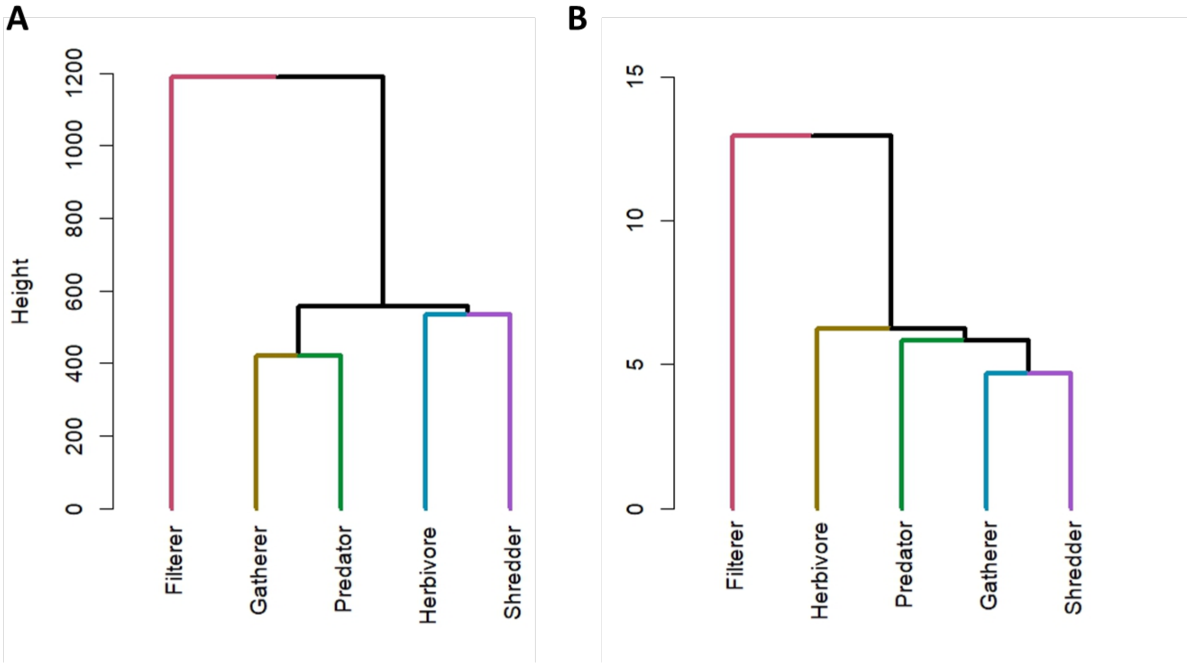

Figure 2.2: Dendrogram describing the taxonomic similarity between FFGs based on UPGMA (unweighted pair-group method with arithmetic averages) analysis of family composition of 5 FFGs for the lethality (A) and feeding (B) datasets. Height refers to the measure of similarity.

In both the lethality (Figure 2.2a) and feeding datasets (Figure 2.2b), filterers were the most taxonomically diverse and distinct FFG, with data from 45 families from 7 Phyla, however they were most data were for Diplostraca with 84% of entries (96% of which was Daphniidae). Other arthropod filterers comprised Malacostraca (21%), including Mysida (77.6%), Decapoda (14.1%), and Gammaridae (8.3%). Other zooplankton filterers included Rotifera (6.2%), Ciliophora (1.1%), and Bryozoa (0.5%). Mollusca (specifically bivalves) constituted 7.5% of the filterers, predominantly represented by Unionoida (44.9%), Mytiloida (33.7%), and Venerida (21.4%).

Predators, gatherers, shredders, and herbivores exhibited greater taxonomic similarity to each other than to filterers (Figure 2.2a). Predators and gatherers formed a distinct cluster, sharing a similar taxonomic composition dominated by arthropods, with malacostracans representing 62.4% and 66.8%, respectively, and insects comprising 25.9% and 21.6% of entries for predators and gatherers respectively (Appendix 2, Table A2.3). Among malacostracans, gatherers were evenly split between amphipods, decapods, and mysids, each accounting for about 30% of the entries, while predators were characterised mainly by decapods and mysids.

Shredders and herbivores clustered closely (Figure 2.2a), indicating distinct but related taxonomic compositions. Shredders were less taxonomically diverse, with only 22 families represented, and were characterised primarily by arthropods, 82.9% of which were malacostracans (Appendix 2, Table A2.3). This group consisted mainly of amphipods (52.8%, with 98.2% from Gammaridae) and decapods (37.6%). Gastropods (only of the family Planorbidae) made up 8.9% of the shredder entries (Appendix 2, Table A2.3). Herbivores, meanwhile, were distinctly dominated by gastropods (Mollusca), accounting for 63.2% of the group. Malacostracan herbivores were almost exclusively decapods (95.7%), with Palaemonidae making up 79.9% and Cambaridae 20.1%, a composition similar to that seen in predators and shredders (Appendix 2, Table A2.3). Insect herbivores were primarily Plecoptera (40.2%, all from the family Pteronarcyidae), Ephemeroptera (23.1%), and Diptera (20.6% - 73% of which were Chironomidae) (Appendix 2, Table A2.3).

Several taxa appear in multiple FFGs, demonstrating their versatile ecological roles. The most functionally diverse families are Chironomidae with covering all five functional feeding groups with most data from *Chironomus* sp. covering gatherers and shredders, forming 50% of all insect entries, and 17% of all arthropod data (Appendix 2, Table A2.3). Furthermore, ephemeropteran families appeared in all FFGs, as did decapods, with both Cambaridae and Palaemonidae present in four FFGs.

For the feeding dataset, with significantly fewer unique species, FFGs were more distinct with less variation in the taxonomic composition. Like in the lethality dataset, filterers were the most distinct FFG, characterised by arthropods (38.4%), molluscs (36.4%), of which all were bivalves, and rotifers (24%).

Herbivores were again a distinct FFG (Figure 2.2b), characterised here solely by Hygrophilla gastropods, Lymnaeidae and Planorbidae. While predators, gatherers and shredders formed another cluster within which gatherers and shredders were more similar (Figure 2.2b). Predators were characterised 58% by arthropods, 33% were cnidarians of the family Hydridae, and 8.3% were Rhabditophora Platyhelminthes of the family Dugesiidae (Appendix 2, Table A2.4).

Gatherers and shredders were more taxonomically similar (Figure 2.2b), showing a strong skew towards arthropods (71.4% and 88.9% for gathers and shredders, respectively), only characterised by malacostracan amphipods and decapods (60% and 40% for gatherers and 75 and 25% for shredders). For the gatherers, unlike shredders, annelids were also present, making up 28% of data (Appendix 2, Table A2.4).

2.3.2.2 For individual chemicals

To analyse the data for distinct chemical modes of action, the dataset was then filtered to have more than 6 species per FFG and more than 2 FFGs per chemical. ANOSIM and SIMPER analysis were conducted on the filtered data to see the percentage contribution of families to the taxonomic composition of the FFGs.

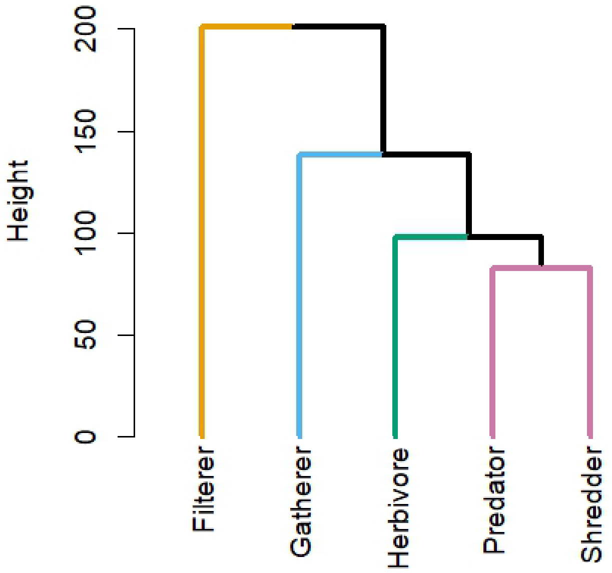

Figure 2.3: Dendrogram based on UPGMA (unweighted pair-group method with arithmetic averages) analysis of family composition of 5 FFGs for the filtered Lethality data for 48 chemicals. Height refers to the measure of similarity.

ANOSIM analysis confirmed significant differences in the taxonomic composition of FFGs (R = 0.821, p< 0.001). SIMPER analysis, which considers the number of data points within each FFG, showed that the differences in the taxonomic composition of the functional feeding groups were driven by a few families (Appendix 2, Figure A2.3, A2.4). Filterers are the most distinct FFG with 94-98.4% dissimilarity to other groups (Table 2.4). Taxonomic differences in the filterers compared to other FFGs are largely driven by the dominance zooplankton species (Crustaceans of Orders Diplostraca, Anocstraca, and Rotifer orders of Ploima) (Appendix 2, Figure A2.3, A2.4). Gatherers, predators, and shredders are largely the same in terms of composition with regard to order but when specifying by family, gatherers and shredders are most similar with 70% dissimilarity, differing from predators with 82.3% and 80.9% dissimilarity due to the presence of Chironomidae and Gammaridae, which are not prominent in predators (Table 2.4). However, the differences in gatherers compared to other FFGs is driven by the presence of chironomids. Herbivores are distinguished from other FFGs by the presence of gastropods and absence of amphipods and decapods, particularly Palaemonidae which is also found in gatherers and shredders and predators.

ANOSIM revealed considerable similarity (R = 1.85, p<0.0001) in the familial composition of the same FFG across chemicals.

Table 2.4: Comparison of family composition of the five functional feeding groups by one-way ANOSIM and SIMPER

Comparator	SIMPER (% Dissimilarity)
Filterer_Gatherer	94.7%
Filterer_Herbivore	98.4%
Filterer_Predator	94.1%
Filterer_Shredder	94.0%
Gatherer_Herbivore	91.0%
Gatherer_Predator	82.3%
Gatherer_Shredder	70.4%
Herbivore_Predator	88.4%
Herbivore_Shredder	83.9%
Predator_Shredder	80.9%

2.3.3 Difference in sensitivity between FFGs

2.3.3.1 For individual chemicals

When applying the criteria of ≥6 species per FFG and ≥2 FFG per chemical, 48 chemicals were available to study. Of the 48 chemicals had more than 6 entries per FFG with more than one FFG, 14 showed differences in functional feeding traits. Of the chemicals where species differed in their sensitivity to chemical stress, 6 (out of 17) were AChE inhibitors, 4 metals (two zinc compounds), 2 neurotoxins, two unclassified compounds (Table 2.5). Post hoc analysis (Tukey Tests) revealed that general trends amongst the chemical modes of action studied (Table 2.5, full results of ANOVA and Tukey post hoc tests can be found in Appendix 2, Table A2.4).

For AChE inhibitors, herbivores were consistently the most tolerant with gatherers consistently most sensitive (Table 2.5). For carbaryl, predator-herbivore ($p < 0.05$, 95% confidence interval (C.I.). = -2.61, 0.242) and shredder-herbivore ($p < 0.05$, 95% C.I. = -2.50, -0.194) comparisons showed significant differences (Appendix 2, Table A2.5). While herbivore-filterer ($p < 0.01$, 95% C.I. = 0.381, 3.14) and herbivore-gatherer ($p < 0.001$, 95% C.I. = 0.636, 3.18) comparisons both indicating that herbivores tend to be less sensitive (Appendix 2, Table A2.5). Similar herbivore-gatherer patterns were observed for diazinon ($p < 0.05$, 95% C.I. = 0.096, 3.23), fenitrothion ($p < 0.05$, 95% C.I. = 0.357, 3.63), and malathion showed similar pattern between gatherer-filterer comparison ($p < 0.05$, 95% C.I. = -2.60, -0.094) (Appendix 2, Table A2.5).

Similar patterns were observed for neurotoxins where lindane showed the greatest differential impact on FFGs (Table 2.5), with all filterers significantly more tolerant gatherers ($p < 0.001$, 95% C.I. = -3.02, -0.816), predators ($p < 0.001$, 95% C.I. = -3.22, -0.77), and shredders ($p < 0.001$, 95% C.I. = -3.17, -0.775). Predator-herbivore ($p < 0.01$, 95% C.I. = -2.60, -0.252) and shredder-herbivore ($p < 0.01$, 95% C.I. = -2.54, -0.257) comparisons also revealed significant differences, but not as strong.

For metals, filterers were consistently the most sensitive group (Table 2.5). For example, for mercury chloride, herbivore-filterer ($p<0.005$, 95% C.I. = 0.244, 1.79), predator-filterer ($p<0.05$, 95% C.I. = 0.024, 1.57), shredder-filterer ($p<0.05$, 95% C.I. = 0.087, 1.81), comparisons were significantly different. Differences were also observed for gatherer-filterer comparison ($p = 0.061$, 95% C.I. = -0.017, 1.17), but not significant. Similar patterns were observed for cadmium chloride in the predator-filterer comparison for ($p<0.005$, 95% C.I. = 0.310, 1.88), and zinc chloride in the gatherer-filterer comparison ($p < 0.001$, 95% C.I. = 0.487, 1.99). Differences between FFGs for phenol and rotenone were not significant (Appendix 2, Table A2.5)

Table 2.5: Post hoc analysis (Tukey test) of differences in sensitivity between functional feeding groups for 14 of 48 chemicals studied.

Mode of action	Chemical Name	No. Species	Most Sensitive Group	Filterer	Herbivore	Gatherer	Shredder	Predator
AChE inhibition	Carbaryl	69	Gatherer	b	a	b	b	b
	Diazinon	38	Gatherer	ab	a	b	ab	NA
	Malathion	102	Gatherer	a	ab	b	ab	ab
	Methomyl	31	Filterer	b	a	b	b	b
	Fenitrothion	55	Gatherer	ab	a	b	b	ab
	Phenthoate	12	Gatherer	NA	a	b	NA	NA
Metals	Cadmium chloride (CdCl2)	117	Filterer	b	ab	ab	ab	a
	Mercury chloride (HgCl2)	66	Filterer	b	a	ab	a	a
	Sulfuric acid, Zinc salt (1:1)	62	Filterer	b	a	a	a	NA
	Zinc chloride (ZnCl2)	31	Filterer	b	NA	a	ab	NA
Neurotoxicity	Lindane	59	Predator	a	a	b	b	b
	Endosulfan	47	Shredder	ab	a	ab	b	ab
Unclassified	Phenol	113	Herbivore	ab	b	b	b	a
	Rotenone	18	Filterer	b	a	NA	NA	NA

2.3.3.2 For chemical modes of action

Feeding Data

Of the 376 endpoints, 186 endpoints were able to be normalised using *Daphnia* lethality. When grouping data to one endpoint per unique species contaminant combination (66 endpoints), following a Levene's test for evenness, no significant differences were found between species, contaminants (one way ANOVA: $F_{(23)}=0.866$, $p=0.636$), FFGs (one way ANOVA: $F_{(4)}=0.435$, $p=0.783$) or chemical modes of action (one way ANOVA: $F_{(4)}=1.403$, $p=0.244$).

Lethality

Of the 7,102 datapoints, there were 4,874 that were normalised using *Daphnia* LC_{50}s. Following a Levene's test for evenness showing the data were not evenly distributed $F_{(4,85)}$, $p<0.001$, A Kruskal-Wallis test revealed that there were significant differences between the functional feeding groups ($H_{(4)} = 157.6$, $p<0.001$) with Dunn's post hoc test showing that herbivores were significantly more tolerant than the other FFGs (Table 2.6). While shredders were more sensitive than predators and gatherers (Z = 3.03, p.adj < 0.02) while filterers more sensitive than gatherers (Z = -3.24, p.adj < 0.01) and predators (Z = -5.03, p.adj < 0.001). No significant differences were found between gatherers and shredders (Z = 1.39, p.adj = 1.00), gatherers and predators (Z = -1.96, p.adj = 0.50).

Table 2.6: Results of Dunn's Test for comparing the *Daphnia* normalised LC50 values between functional feeding groups. The table displays the Z-values, unadjusted p-values, and adjusted p-values for pairwise comparisons among Functional feeding groups. Significant differences are highlighted by adjusted p-values below the threshold of 0.05.

Comparison	*Z*	*adjusted p value*
Herbivore - Shredder	8.94	**0.00**
Herbivore - Predator	6.18	**0.00**
Predator - Shredder	3.03	**0.02**
Gatherer - Shredder	1.39	1.00
Filterer - Shredder	-1.19	1.00
Gatherer - Predator	-1.96	0.50
Filterer - Gatherer	-3.24	**0.01**
Filterer - Predator	-5.03	**0.00**
Gatherer - Herbivore	-8.58	**0.00**
Filterer - Herbivore	-12.17	**0.00**

When grouping by chemical mode of action, there, again, were significant differences between FFGs. Again, variances were unequal ($F_{(9,\ 60)} < 0.001$). Dunn's tests revealed patterns where herbivores were the most tolerant FFG for AChE inhibitors, neurotoxicity, and among those with no

MOA assigned (Appendix 2, Table A2.5). Here, herbivore-shredder comparisons showing great differences for all three chemical modes of action ($Z = 6.81$, $p<0.005$; $Z = 3.25$, $p<0.011$; $Z = 4.38$, $p<0.005$), with gatherers often among the most sensitive (gatherer-herbivore: $Z = -7.51$, $p<0.005$; -2.85, $p<0.05$; $Z = 05.04$, $p<005$). Similar results were found for filterer-herbivore comparisons. In contrast, no significant differences were found between other FFGs. Filterers were the most sensitive group for metals, IOC impairment, and reactivity. No significant differences were found between FFGs for polar narcosis ($H_{(4)}= 5.17$, $p=0.27$), electron transport inhibitors ($H_{(4)}=3.47$, $p=0.48$), and uncouplers ($H_{(4)}=4.10$, $p=0.39$) (Appendix 2, Table 2.5)

2.3.4 Relative sensitivity between Feeding and Lethality

$EC_{feeding}$ values were consistently more sensitive than acute LC_{50} values (Figure 2.4). There is a significant positive correlation between acute lethality data and $EC_{feeding}$ values ($\rho = 0.54$, n = 210, $p < 0.001$) (Table 2.7). When splitting by functional feeding group, rank correlations remained close to that of all data. Shredder had the highest rank correlation with 0.66 (n = 45, $p < 0.001$), while filterer had the lowest with 0.43 (n = 96, $p < 0.01$) (Table 2.7).

When grouping by chemical mode of action, strong rank correlations were found for neurotoxicity ($\rho = 0.81$, n = 19, $p < 0.001$) and polar narcosis ($\rho = 0.54$, n = 16, $p < 0.05$) (Table 2.8). Weak significant rank correlation was found for metals ($\rho = 0.41$, n = 107, $p < 0.001$) and nonpolar narcotics ($\rho = 0.38$, n = 48, $p < 0.01$). Other chemical modes of action, reactivity lacked sufficient data points.

Table 2.7: Spearmans rank correlation for $EC_{feeding}$ values in relation to acute LC_{50} s for all data, splitting by functional feeding groups and by chemical modes of action

	Rank Correlation (ρ)	**p value[1]**	**n**
all Data	0.54	***	210
Functional Feeding Groups			
Filterer	0.43	***	96
Gatherer	0.63	**	22
Herbivore	0.60	*	15
Predator	0.56	***	32
Shredder	0.66	***	45
Chemical Modes of Action			
Neurotoxicity	0.81	***	19
Polar narcosis	0.54	*	16
AChE inhibition	0.51	*	14
Metal	0.41	***	107
Nonpolar narcosis	0.38	**	48
None	-0.11	*	5

[1] If $p < 0.001$ = ***, $p<0.01$ = **, $p<0.05$ = *

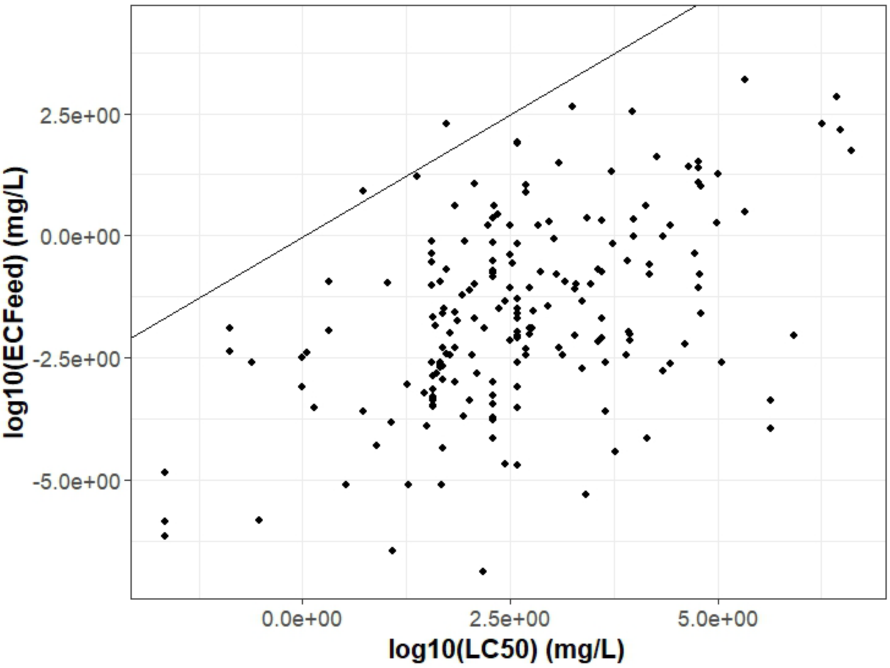

Figure 2.4: Relationship between EC_{50} (feeding inhibition) and LC_{50} (lethality) for freshwater invertebrates. The plot shows the log10-transformed EC_{50} values (mg/L) for feeding inhibition on the y-axis against log10-transformed LC_{50} values (mg/L) on the x-axis for different chemicals. The solid line represents a 1:1 relationship, where the effects on feeding and lethality are equal. Points deviating from this line indicate differences in sensitivity between feeding inhibition and lethality for the tested chemicals.

2.4 Discussion

2.4.1 Summary

The aim of this study was to explore how the distribution of sensitivity to chemical stress differs between freshwater invertebrates from different functional feeding groups. Specifically, it examined this variation across different chemical stressors and groups of stressors (i.e., modes of action), focusing on their effects on lethality and feeding activity in individual freshwater invertebrates. Understanding the differential sensitivity of functional feeding groups to chemical stress, in terms of both lethality and feeding activity, could help predict the effect of chemicals on both the structure and processes in ecological systems. Three objectives were addressed: (1) identify taxonomic composition of functional feeding groups amongst lethality and feeding datasets, (2) assess the difference in sensitivity between functional feeding groups for individual chemicals and broad chemical models of action, (3) whether there is a relationship between lethality and feeding endpoints.

While the taxonomic composition of FFGs varied, arthropods were dominant in the data. For the majority of chemicals studied in the lethality dataset, differences in sensitivity to chemical stress were not found between FFGs. Of the few chemicals for which there were differences in sensitivity to chemical stress, clear patterns emerged for chemical modes of action. No differences in sensitivity to chemical stress were found in the feeding dataset. Strong positive rank correlation was found between feeding and lethality endpoints for neurotoxicants, suggesting that the relative sensitivity of neurotoxicants to feeding could be inferred from lethality data. There was a weaker rank correlation for other chemical modes of action, suggesting that the relationship between feeding and lethality for other contaminants is more complex.

2.4.2 Taxonomic composition of FFGs

Differences in the taxonomic composition of FFGs suggests potential differences in sensitivity to chemical stress. In the lethality dataset, filterers were distinctly characterised by multiple phyla, dominated by zooplankton species and bivalves. These taxa are notably most sensitive to metals (Van den Berg et al., 2019) and are therefore expected to show differential sensitivity to metals than other functional groups. Herbivores were another distinct group, most dissimilar to gatherers due to the absence of chironomids, gammarids, and Palaemonidae decapods and the distinct presence of gastropods, notably family Viviparidae. Gastropods, as with other molluscs, are tolerant to many pesticides and sensitive to metals (Maltby et al., 2005; Van den Berg et al., 2019) and therefore are likely to have distinct difference in sensitivity to metals and tolerance to reactive chemical modes of action such as such as AChE inhibitors, neurotoxicants, and polar narcotics. Gatherers, predators, and shredders are characterised predominantly by arthropods. Previous research has demonstrated that freshwater invertebrates vary in their sensitivity to chemical stress, with arthropods generally being more sensitive, particularly to acetylcholinesterase (AChE) inhibitors (Maltby et al., 2005; Oginah et al., 2023). This suggests that FFGs dominated by arthropods are likely to be the most sensitive to chemical stressors.

In the feeding dataset, with fewer species studied, the distribution of the data among taxonomic groups followed similar patterns to the lethality data with less variation/overlap in taxonomic composition of FFGs. As FFGs are more taxonomically distinct within the feeding dataset, differences in sensitivity between FFGs are expected to follow the same patterns described above but more pronounced.

2.4.3 Difference in sensitivity in between functional feeding groups

Despite taxonomic differences in FFGs at the family level, differences in sensitivity between FFGs, with regard to lethality, varied for only 14 of the 48 chemicals studied. Therefore, for 70% of individual chemicals studied there was no difference in the sensitivity to chemical stress between functional feeding groups, despite an array of chemical modes of action. With regard to feeding, of the 182 chemicals studied, there were no differences in sensitivity to chemical stress. The ubiquity of arthropods, particularly insects and decapods, across all FFGs could mean that the taxonomic composition did not differ enough to affect sensitivity. The assignment of some taxa (34 families out of 155) to multiple FFGs suggests the potential for functional redundancy, which could contribute to ecosystem resilience in species diverse assemblages (Biggs et al., 2020). However, this also implies that chemical stressors affecting one group (e.g., filterers) could have cascading effects across multiple ecological functions due to shared taxonomic vulnerabilities.

Most FFGs were assigned at the species and genus levels using the Kunz harmonised database (Kunz et al., 2021), with some assignments at the family and order levels. However, for certain functionally diverse families, assigning FFGs at the family level can oversimplify the functional diversity within a taxon. In taxonomic groups such as Branchiopoda, Bivalvia, and Rotifera, FFG assignments at the family level remain largely consistent with genus or species-level classifications. In contrast, for more functionally diverse groups, such as insects, assigning FFGs at the family level overlooks intra-family variation. Despite this, the majority of FFGs were assigned at the genus level using the Kunz database, and for orders with minimal FFG variation, literature-based assignments were used. Consequently, there is high confidence in the accuracy of FFG classifications within the lethality and feeding databases.

Of the 14 chemicals that did show differences in sensitivity to chemical stress, most were among the chemicals for which the most data were available (i.e. more than 50 species). The patterns followed were predictable from taxonomic composition of the FFGs. For example, herbivores, comprised largely of gastropods (Mollusca) were most tolerant to AChE inhibitors, agreeing with findings previously reported in the literature (Maltby et al., 2005; Rico and Van den Brink, 2015; Van den Berg et al., 2019). Here, gatherers were consistently the most sensitive species, despite no statistical significance from other FFGs. Gatherers were particularly characterised by insects and malacostracans (crustaceans), with an absence more tolerant taxa like Platyhelminthes, annelids, and gastropods (Maltby et al., 2005; Rico and Van den Brink, 2015). Therefore, gatherer sensitivity is not likely due to the presence of particularly sensitive species but an absence of tolerant ones. Meanwhile, as expected, for metals, filterers, characterised by zooplankton and molluscs were consistently the most sensitive FFG. In contrast, predators were found to be the most tolerant group, which conflicts with the findings of Liess et al. (2017), where metal toxicity in Australian streams was positively correlated with the proportion of predators in the invertebrate community. However, Liess et al. (2017) emphasise that standard laboratory toxicity tests are not reliable predictors of metal effects in the field. This discrepancy arises due to differences in study duration, exposure routes (aqueous vs. dietary), the life stages examined, and the toxicity associated with the internal accumulation of metals over time.

When grouped by chemical modes of action, functional feeding groups exhibited differences that aligned with expectations based on their taxonomic composition (Section 2.4.2). However, contrary to expectations, differences were found between nonpolar narcotics, a general stressor, with gatherers, shredders, and filterers more sensitive than herbivores and predators. This is possibly a limitation of the assignment of chemical modes of action. Kienzler et al., (2019) highlighted that there is low consensus between MoA database when it comes to chemicals with a specific chemical mode of action. They attribute this to a lack of detailed molecular descriptors for these modes of action. Differences in classification systems, particularly if differences relate to specific or non-specific acting stressors, may lead to increasing variation difference potentially leading to different results, increasing the number of datapoints for specific acting chemical modes of action and increasing the robustness analysis of differences between FFGs and MoA.

Furthermore, Oginah et al., (2023) concluded that when looking at differences in sensitivity to chemical stress between taxonomic grouping it is better to split the data by broad taxonomic group (Algae, invertebrates, fish) unless limited by the number and quality of the available test data. A potential limitation of the study was the insufficient number of species within each FFG to adequately capture taxonomic variation. The lack of differences in sensitivity between functional feeding groups could also be a result of too few data points within functional feeding groups to have enough data to capture the variation taxonomic composition of FFGs. Here the criteria for a minimum number of species within FFG was six. This was chosen as a trade-off between increasing number of chemicals to study and decreasing taxonomic variation within FFGs. Maltby et al. (2005) found that hazard concentrations (HC_5 values) calculated from SSDs with only arthropods were significantly lower than when including nonstandard microbial species. The lack of data for nonstandard species is often a limitation for ecosystem services approach to risk assessment (Maltby et al., 2021). It is possible that there were too few data within functional feeding groups to have enough data to capture the variation taxonomic composition of FFGs. While standard test species are useful, there is a growing need for data on the effects of chemicals on a wider range of service providers to better support decision-making.

Overall, it was found that functional feeding groups tend not to differ in their sensitivity to chemical stress due particularly to the ubiquity of arthropod species. However, this is also influenced by the skew towards arthropod species in the toxicity data. Of the differences in sensitivity that were found, only for metals where filterers were the most sensitive did differences in sensitivity result in a FFG more sensitive than the others. For AChE inhibitors, herbivores, were significantly more tolerant than other FFGs.

2.4.4 Chemical effects on the feeding activity of freshwater invertebrates

The systematic review of chemical effects on the feeding activity of freshwater invertebrates yielded 376 toxicity assays collected from 201 citations. Whilst there was feeding data available for 81 unique genera across 7 phyla, with species available in all functional feeding groups, most studies were conducted with only a few genera, with almost 40 percent of assays performed with standard species, *Daphnia spp.* or *Gammarus spp*. Furthermore, of the 161 different chemicals studied, most were studied with only one genus. This suggests that while changes in feeding activity may be an endpoint that can be measured with a wide range of freshwater invertebrates, there is little information about the effects of a single chemical on a range of taxa. This lack of data for chemical effects on the feeding of freshwater invertebrates makes it difficult to make meaningful conclusions about the potential effects of chemicals on the performance of a range of ecosystem functions for any given chemical. However, what we can conclude is that there is some information about chemical effects on feeding activity of several different species across all functional feeding groups studied. The search terms were, however, skewed towards insecticides without explicitly searching for herbicides, fungicides or other specific chemical classes. Investigating chemical impacts of insecticides on invertebrate feeding may be most appropriate as they are designed to target invertebrate physiology and are therefore more likely to elicit sublethal behavioural effects. However, biased search terms towards insecticides may lead to an underrepresentation of effects from other pesticides or chemicals in the results.

Notable functional groups with little feeding data available include gatherers and herbivores. In the lethality dataset, the most studied gatherers were the chironomids. Chironomids were underrepresented in the review, with only two feeding endpoints were available for chironomids. Both these studies observe negative effects on the feeding activity of Chironomids at environmentally relevant concentrations (Heinis et al., 1990; Rodrigues et al., 2018). The feeding of Chironomid larvae have long been used in in situ bioassays to assess sediment contamination and toxicity (Soares et al., 2005; Moreira-Santo et al., 2005; Faria et al., 2006). Furthermore, chironomids serve as a standard model species in ecotoxicology, with OECD guidelines established for chronic water-sediment toxicity testing. These guidelines support the use of chironomids in assessing toxicity under both spiked sediment and aqueous exposure conditions (Weltje et al., 2009; OECD, 2004a, 2004b). However, their feeding activity is not a standard laboratory endpoint, with sediment toxicity tests challenges, post exposure feeding assays have been developed (Soares et al., 2005). For this reason, gatherers, including deposit feeders, were generally underrepresented in the review, potentially due to the literature sampling strategy that excluded ex situ sediment assays and mesocosm studies (Leppänen et al., 1998; Faria et al., 2006; Re et al., 2021), which also excluded worms, some insects, and deposit feeders in general. Given their particular vulnerability to hydrophobic compounds that often accumulate in sediments (Gaskell et al., 2007), the role of gatherers in ecological systems and their vulnerability to persistent, hydrophobic compounds, using the feeding activity of gatherers as a tool for ecological assessment may be valuable.

Herbivores in freshwaters are typically represented by gastropods and some Ephemeropterans. While insects were generally understudied, eighteen assays were performed with gastropods from 6 different families. *Lymnaea stagnalis*, a standard ecotoxicological species, was the most common gastropod reported, with *Physa spp.* (Order hjeterobranchia) and Potamopyrgus (Order:

Littorinimorpha) the next most common. While *Lymnaea stagnalis* is a model Gastropod used in ecotoxicology (Rittschof and McClellan-Green, 2005), it is most commonly used in assays measuring effects in embryo development (Bandow and Weltje, 2012) and reproduction of adults (Zimmer et al., 2013) and therefore both feeding, and lethality data is not available for a range of chemicals. Therefore, while chemical effects on gastropod feeding are important and can be readily studied across various gastropod species, research remains limited in scope for many chemical stressors. There have been calls for more gastropod species to be included in ecotoxicological studies, other gastropods that are known to be more sensitive and more widespread (Alonso and Valle-Torres., 2018). Given that herbivores play an important role in controlling primary production (Wood et al., 2017; Atkinson et al., 2023) it is important that information on their feeding activity be studied with a wide range of chemicals.

Contrary to expectations derived from the analysis of taxonomic composition of FFGs in the feeding dataset, no difference was found in the sensitivity to chemical stress for feeding between functional groups and/or chemical modes of action. While this may suggest that all invertebrates are equally sensitive to feeding inhibition to different chemical modes of action, it is more likely that there were few too data points and too much variation amongst existing datapoints, due to variation in study duration and endpoints studied.

2.4.5 The relative sensitivity of feeding to lethality.

The study found that the relative sensitivity between feeding inhibition and lethality was generally weak. When grouping by chemical mode of action this relationship strengthened for neurotoxicity. These patterns are to be expected given that Neurotoxicants are specific acting chemicals, causing cause adverse functional or structural change in the nervous system (NCR, 1992). This specific mode of action links feeding inhibition to mortality through a chain of effects involving feeding reduction, starvation, and eventually death, as described by Gergs et al. (2021). Many now banned pesticides are neurotoxicants; aldrin, chlordane, endrin (Regulation 9/117/EEC, 1991; Regulation 850/2004). Compounds still in use include pyrethroid pesticides such as deltamethrin, permethrin and antibiotics, oxytetracycline, erythromycin, and corticosteroid dexamethasone. It is therefore likely that we can infer the relative sensitivity of feeding activity of invertebrates from lethality data for these toxicants. Lethality information for these chemicals may be used to hypothesise how such chemicals may affect the performance of ecological processes.

Strong correlations were also expected for polar narcotics (Nyman et al., 2013; Escher, 2002) and AChE inhibitors, as found in Rubach et al. (2011), due to their specific modes of action, but such patterns were not observed. This discrepancy may be due to several factors: a lack of comprehensive data, variations in the duration of the studies, differences in species tested, or inconsistencies in the assignment of chemical modes of action. The review of feeding endpoints yielded 376 endpoints. There is a distinct lack of data on chemical effects on the feeding activity of freshwater invertebrates, particularly compared to lethality with over 7,000 endpoints. Lethality is a standard toxicity endpoint and feeding is a nonstandard endpoint. Lack of data on feeding makes it harder to observe effects and patterns among data points as it is difficult to say that variation is driven by the presence or lack of data. Furthermore, the feeding data is likely to have greater variation than the lethality dataset due to differences in the endpoints reported and the length of the studies included. Acute LC_{50} values in the lethality dataset come from 24-48 hour studies for crustaceans and 2-7 days for molluscs and worms. The duration of studies for insects and other taxa was not reported (Posthuma et al., 2019). In the feeding dataset, study duration ranged from 1 hour to 12 weeks with the median duration of 96 hours (mean of 6 days) (Table 2.8). When grouping by chemical mode of action, studies with metals tended to be longer and therefore are likely to have greater variation due to differences in species detoxification abilities. This variation complicates direct comparisons between the two datasets and may contribute to the lack of concordance observed. Furthermore, individual sensitivity to chemical stress varies across life stages, with juveniles often being more sensitive (Naylor et al., 1999; Alonso et al., 2010; Cadmus et al., 2019; Taddei et al., 2021). Although this is not always the case (Maltby, 1995). Since the toxicity data lacked life stage details, FFGs were assigned based on all invertebrate life stages. As many toxicity tests focus on juveniles or early life stages, the results may represent a worst-case scenario; if individuals are affected early on, their ability to perform functions later in life could be compromised due to reduced recruitment.

Table 2.8: Study duration of Feeding assays found in the review grouped by chemical mode of action.

Chemical Mode of Action	Study Duration [Days]			
	Mean	Max	Min	Count
All data	6.74	84	0.04	376
AChE inhibition	5.9	40.0	0.04	20
Iono/Osmoregulatory/Circulatory impairment	0.1	0.1	0.08	1
Metal	8.6	70.0	0.04	129
Nanoparticles	3.7	24.0	0.04	29
Neurotoxicity	3.7	8.0	0.06	17
Non-Polar Narcosis	6.6	84.0	0.04	106
None	6.7	35.0	0.04	56
Polar Narcosis	4.7	21.0	0.25	10
Reactivity	1.7	4.0	0.08	3
Uncoupler	2.2	4.0	1.00	5

When the data were grouped by functional feeding group, there were also differences in the rank corelation between feeding and lethality. Filterers exhibited the lowest rank correlation while shredders and gatherers showed the highest correlations. These patterns are likely influenced by the types of chemicals tested on these species and the skew in the dataset toward a few standard toxicity models. For example, filterers, typically represented by zooplankton and bivalves, are known to be sensitive to metals (Van der Ohre et al., 2004), and consequently, are frequently tested with these substances. Given the weak rank correlation observed between feeding behaviour and lethality for metals, it is unsurprising that filterers exhibit a lower correlation. In contrast, shredders, which are predominantly arthropods, are more often exposed to neurotoxicants and other specifically acting chemicals, potentially explaining the higher rank correlation observed in this group.

2.4.6 Implications for sensitivity of assemblages in the field

In species-rich and functionally diverse systems, the impact of chemical stress on ecosystem functioning and species diversity may be mitigated due to functional redundancy among species (Baert et al., 2017). This means that in a species rich and functionally diverse system, using results found in this study, it may be that only with exposure to metals would there be a potential loss of both species diversity and functioning. However, the ecological impacts of differing sensitivities among functional groups may be influenced by the distribution of functional traits within an assemblage (Clements and Rohr, 2009; Liess and Beketov, 2011; Baert et al., 2017) and connectivity within the food web (Dunne et al., 2002). If there is high species richness and low connectivity, which is reflected in the results of this study as data is aggregated across species, with all available data across species considered, the system may be highly specialised with species loss having little impact on ecological functions. However, if there is high connectivity and low species richness, for example, as species overlap in their resource use there may be a degree of functional redundancy and therefore little impact on functioning with species loss. However, if there are a few species performing the same or similar functions, species loss may also result in functional decline. A key hypothesis in this context is the principle of competitive exclusion, which suggests that species with overlapping niches—such as those within the same functional feeding group—are less likely to coexist without resource partitiining (Hardin, 1960). The results of this study, which aggregate data across species tested under controlled conditions, may not fully capture characteristics of natural systems. In the field, where niche overlap may occur, there could be more or less functional redundancy within functional feeding groups than suggested by the composite data Results here might reflect a best-case scenario for species assemblages, as they assume a baseline level of species diversity and functional redundancy that may not exist in all natural systems.

The sensitivity species assemblages can differ across spatial scales (Liang et al.,2024). This is influenced by differences in community composition across environments. This can alter risk associate with chemical exposure across landscapes (Holmes et al.,2021). This variation may be partly due to natural assemblages having developed adaptations to prolonged exposure to specific chemical stressors, leading to differing tolerance levels across communities (Biggs et al., 2007; Liang et al., 2024). Standardised single-species toxicity tests, while useful for assessing individual sensitivity to stressors, generally depict a conservative scenario. These tests often overlook local adaptations that could reduce species sensitivity, as well as environmental factors that may alter individual responses to chemical stress, such as temperature (McCauley et al., 2020; Huang et al., 2023), and food availability (Pereira and Gonçalves, 2007; Agatz et al., 2013). Consequently, while toxicity tests may present a worst-case scenario for individual sensitivity, they might represent a best-case scenario regarding the overall composition of species assemblages.

Furthermore, this study does not account for ecological complexities such as the presence of keystone species, which can have disproportionately large impacts on ecosystems, or competition within functional feeding groups. In species-poor, functionally diverse systems with low redundancy, the loss of a keystone species could trigger cascading effects that threaten ecosystem stability and resilience (Fleeger et al., 2020). Understanding these complexities is crucial to assessing chemical impacts on ecological functions and identifying vulnerabilities in ecosystem performance.

2.5 Conclusion

In conclusion, this study highlights the complexities of assessing chemical stress impacts on freshwater invertebrate feeding activity and the varying sensitivities among functional feeding groups (FFGs). While grouping species by functional group and chemicals by mode of action offers a potential simplification for ecological risk assessments (ERAs), the results suggest this approach is limited by the biases in the taxonomic composition of the groups. Arthropod-dominated FFGs, in particular, show significant variability in sensitivity, which may obscure functional differences. However, distinct sensitivities were observed at higher taxonomic levels, particularly between molluscs and arthropods, with filterers showing heightened vulnerability to metal exposure. This poses potential risks to critical ecosystem functions like nutrient regulation and water clarity. The lack of comprehensive feeding activity data for many invertebrates, compounded by the absence of standardised feeding assays across species, continues to hinder efforts to implement an ecosystem services approach to risk assessment. While feeding activity remains a valuable ecotoxicological endpoint, further research is needed to develop cross-species extrapolation methods and to better understand how chemical stressors affect functional processes at the ecosystem level.

Chapter 3 - Using DEB IBMs to extrapolate from individual to population level responses.

3.1 Introduction

To assess chemical effects on ecological functions, we must understand how chemicals impact population-level responses and their associated functions. However, there's a disconnect between the data collected and the ecological attributes we aim to protect. Ecotoxicological endpoints, typically from short-term studies on individual organisms, may not reflect population-level responses or functions due to ecological complexities at higher levels, such as resource competition, predator-prey interactions, and food availability. While mesocosm studies in ecological risk assessments can capture some of these ecological processes, they are often limited in their species selection (Reiber et al., 2022), experimental duration, (Amiard-Triquet, 2015). Hence, there is also a need for tools that extrapolate chemical effects from individual organisms to populations and ecological functions.

Ecological models have been developed to predict changes in ecosystem service delivery by modelling changes in the entities responsible for the ecological processes and functions that underpin these services (Galic et al., 2012). Given the variety of ecological models available, it is crucial to select the appropriate model that accurately captures the ecological attributes associated with the ecosystem function driving the delivery of a specific service. Individual-based models (IBMs) are widely used in ecological risk assessment (ERA) to evaluate the impact of chemical stressors on populations, making up 50% of population models used in ERA for plant protection products (Larras et al., 2022). They can be used to predict changes in population attributes such as abundance and structure, while accounting for local interactions for which other models are less effective. In particular, Dynamic Energy Budget (DEB) IBMs, which apply DEB theory (Kooijman, 2010) to describe individuals and use an individual-based approach for population modelling, offer the further advantage of accounting for individual energetics, which can influence intraspecific interactions such as competition for food, which can influence the consumption and production of biomass within the population. These approaches can provide a framework to move from environmental risk assessment to ecological risk assessments (Forbes and Galic, 2016) using energy as currency to translate effects on individual to population responses (Goodchild et al., 2018; Murphy et al., 2018) and subsequent effects on ecological functions.

DEB IBMs are, however, data- and time-intensive to develop. Since their introduction in 2012, only 10 DEB IBMs have been published across five freshwater invertebrate species (Table 3.1). These include models for *Daphnia magna* (Gergs et al., 2014b; Kim et al., 2019; Pereira et al., 2019; Hansul et al., 2021; Vlaeminck et al., 2021, 2022), *Lymnaea stagnalis* (Vlaeminck et al., 2019), hermaphroditic gastropods (Louati et al., 2020), *Chironomus riparius* (Beaudouin et al., 2012), and *Gammarus pseudolimnaeus* (Galic et al., 2017). However, many lack clear documentation and a focus on assessing effects on ecological functions.

Table 3.1: Published Dynamic energy budget models for freshwater invertebrates as of January 2023

Functional Feeding Group	Taxon	Species	Citation	Implementation
Shredder	Amphipoda	*Gammarus pseudolimnaeus*	Galic et al., 2017	NetLogo
Filterer	Bivalva	*Crassostrea giga*	Bacher et al., 2006	Published equations
	Cladocera	*Daphnia magna*	Gergs et al., 2014	Delphi Xe2
			Hansul et al., 2021	NetLogo
			Kim et al., 2019	NR
			Pereira et al., 2019	NetLogo
			Vlaeminck et al., 2021	NetLogo
			Vlaeminck et al., 2022	NetLogo
Gatherer	Diptera	*Chironomus riparius*	Beaudouin et al., 2012	Published equations
Herbivore	Gastropoda	*Lymnaea stagnalis*	Vlaeminck et al., 2019	NetLogo

3.1.1 Selecting the Service providing unit

The application of ecological models in an ecosystem services (ES) approach to ERA requires first the definition of protection goal, a service of interest (Neinstedt et al., 2016). This thesis focusses on ecological functions that deliver a recreational fishery which is both the processing of organic matter and the provision of prey for carnivorous fish. While invertebrates were identified in general as service providers in a recreational fishery, it is important to identify a specific functional group as the service providing unit.

Allochthonous detritus, formed of terrestrial substrates, is a major source of energy in freshwater environments (Marcarelli et al., 2011; Brett et al., 2017). The rate at which this material is processed significantly influences ecosystem function and biodiversity in aquatic environments by providing energy for secondary production (Gessner et al., 1999; Westlake et al., 2009; Brett et al., 2017). Shredders are an important group of invertebrates in freshwater systems, playing a crucial role in breaking down allochthonous detritus with the abundance and diversity of shredders correlating positively with the rate of leaf litter breakdown (Graça et al., 2001; Jonsson et al., 2001; Dekanova et al., 2023). While leaf litter decomposition is influenced by both abiotic and biotic factors, shredders alone are estimated to contribute to 50-64% of leaf mass loss in streams (Hieber and Gessner, 2002). This activity not only cycles nutrients within the stream, but benthic invertebrates provide a crucial food source for carnivorous fish in both lentic (still water) and lotic (flowing water) environments (Dekanova et al., 2023). By supporting both nutrient cycling and food webs, shredders play a crucial role in maintaining the ecological functions in freshwater systems and their associated ecosystem services.

Gammarus pulex (Amphipoda: Gammaridae) and *Asellus aquaticus* (Isopoda: Asellidae) are both common freshwater shredders that are found across Europe. While both species are capable of processing leaf litter, *G. pulex* is a more efficient shredder (Graça et al., 1994b) ingesting and breaking down entire leaves, while *A. aquaticus* primarily scrapes autochthonous material, such as bacteria and fungi, from the leaf surface, often leaving behind the leaf skeleton resulting in less leaf mass lost (Graça et al., 1994b). Both *Gammarus* and *Asellus* species also serve as important prey for various game and coarse fish species, including trout, perch, bullheads, and stone loach (Rask and Hiisivuori, 1985; Copp et al., 2005) as well as smaller species of fish and invertebrate predators (Har and Gill, 1992). Studies of gut contents of fish have shown that perch tend to prefer asellids, while trout show a preference for gammarids, although these preferences are influenced by the availability of each species in their environments (Newman and Waters, 1984). Fish also tend to prefer to predate upon gammarids and asellids of a certain size, typically individuals larger than 6 mm (Newman and Waters, 1984; Anderson et al., 2016). Primarily, the foraging of fish on invertebrates is influenced by the invertebrate community structure, with larger fish in particular often selecting for size (Newman and Water, 1984; Worischka et al., 2015; Berezina et al., 2021) for maximal energetic gain per unit time (MacArthur, 1966; Werner and Hall, 1974). Therefore, changes in the population age and size structure of the prey could lead to changes in the diet of predators. *Gammarus*, while they feed on leaf litter in the detrital layer, drift downstream at night (Müller, 1963) and therefore are most in the diets of drift feeding fish such as brown trout, rainbow trout and salmonids (Ball, 1961; Newman and Waters, 1984; Dodrill et al., 2021). However, *Gammarus* may also be found in the diets of juvenile (< 1 yr) bottom feeders such as stone loach (Copp et al., 2005). *Asellus* are not often found in the drift but reside in the benthos, therefore while they may play a small role in the diet of drift feeding fish (Dahl, 1998; Enefalk et al., 2019), they contribute mostly to benthos feeders (Rask and Hiisivuori, 1985; Copp et al., 2005). Therefore, changes in *Asellus* and *Gammarus* populations are likely to have effects on different fish species populations.

The two species are known to differ in their sensitivity to water quality and chemical stress, with *Gammarus* often more sensitive than *Asellus* (Oseid and Smith, 1979; Maltby, 1995; Bloor and Banks 2005; Lukančič et al., 2010). *G. pulex* is a standard toxicity species that is sensitive to a wide range of chemical stressors, the second most common species studied in the lethality dataset of Chapter 2. With this sensitivity, laboratory studies have demonstrated a strong correlation between the feeding activity of *G. pulex* and leaf litter processing rates in natural environments (Bloor et al., 2011). Its feeding activity has long been used as an indicator of water quality and chemical stress in natural environments (Farrow and Maltby, 2000). *A. aquaticus*, on the other hand, is known for its tolerance to various chemical stressors, yet it bioaccumulates metals, making it a valuable bioindicator species for metal exposures on the field (O'Callaghan et al., 2019). An assessment of the relative sensitivity of *Gammarus* spp. compared to *Asellus* spp. to chemical stress (Supplementary 3.1) using LC_{50} values from the US EPA Ecotoxicity database, revealed that *Gammarus* was more sensitive than *Asellus* for 42 of the available 67 contaminants, equally tolerant for 14, and less sensitive for 11 (Figure 3.1). Despite these findings, a one-way ANOVA test found no significant relationship between the chemical mode of action and the sensitivity ratio (LC_{50} *Gammarus* spp. / LC_{50} *Asellus* spp.) ($F_{(5)}$= 0.528, p=0.754).

These differences in sensitivity are hypothesised to lead to a shift in the competitive advantage toward *Asellus* populations, in the presence of low-level chemical stress (Oseid and Smith, 1979), due to their high tolerance to many stressors. This difference in sensitivity means that the ratio of *Gammarus* to *Asellus* has long been proposed as an indicator of water quality in freshwater streams (Whitehurst, 2001) and found to correlate highly with species richness in response to organic pollution (McNeil et al., 2002). With many polluted waters not supporting *Gammarus* populations while pristine environments can be devoid of *Asellus* as they are too clean (Holland, 1976).

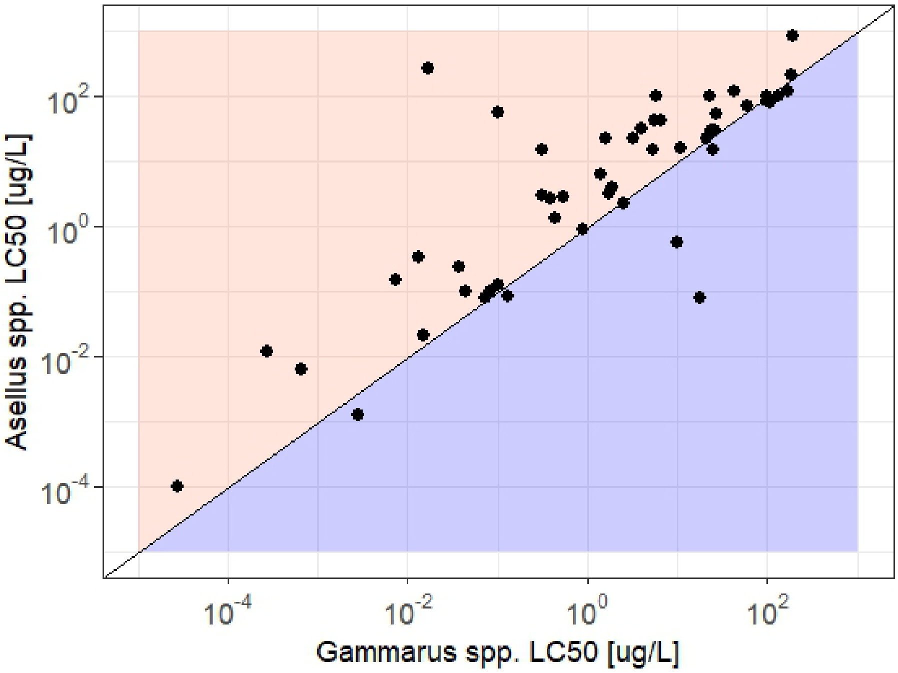

Figure 3.1: Difference in sensitivity of *Asellus* spp. and *Gammarus* spp. to chemical stress. Acute LC_{50}s for each species plotted against each other. Note the log scale of both axes. The black line indicates 1:1 with intercept at 0. The coral shaded area represents the area where *Gammarus* spp. is more sensitive than *Asellus* spp., while the blue area represents the reverse.

Given the ecological importance of *G. pulex* and *A. aquaticus*, their differing sensitivity and vulnerability to a wide range of chemical stressors, and their crucial roles in ecosystem functioning, these species are well-suited for studying the impacts of individual feeding activity on ecological functions within a service-providing unit. Given that DEB IBMs are difficult to develop, the availability of the *Gammarus sp*. model from Galic et al. (2017) further supports their selection as study species for this thesis. By examining how reductions in feeding activity affect these organisms, we can better understand the broader implications for ecosystem services, such as nutrient cycling and energy flow, in freshwater environments.

The chapter outlines the adaptation and evaluation of the individual based DEB models for *G. pulex* and *A. aquaticus* based on the *G. pseudolimnaeus* model of Galic et al., (2017). Given that, *Gammarus* and *Asellus* share similar lifecycles, reproductive mechanisms, and resource, the original *G. pseudolimnaeus* implementation, in NetLogo, is retained while species parameters and fecundity functions are adapted for the respective new species.

The description of the model and follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006). The model is then evaluated at the individual and population levels, comparison to measured values in the published literature. Things common to all models used in this thesis are outlined in this chapter, i.e. parameter values and equations and individual level processes. Where scheduling, processes and design concepts are described in the methods section of subsequent chapters.

This chapter contains:

- Description of adaptations to sub models of Galic et al., 2017
- Model description using ODD approach
    - Purpose
    - Entities, state variables and scales
    - Overview of processes and scheduling
    - Design concepts
- Evaluation of the individual level models
- Description of the scenario for the population model

3.2 Model Description

3.2.1 Purpose

The purpose of the models is to simulate effects of chemical induced changes in feeding activity of on the performance of ecological functions by freshwater shredders *Gammarus pulex* and *Asellus aquaticus* populations, applying DEB theory (Kooijman, 2010) to simulate metabolic processes of individuals.

The *G. pseudolimnaeus* model of Galic et al., (2017) (model code available in supplementary of Galic et al. (2017) while the complete NetLogo file was obtained via personal communication with the author, Nika Galic) was adapted for *Gammarus pulex* and *Asellus aquaticus*. Most modelled processes (i.e. mobilisation, somatic maintenance and growth, maturation and maturity maintenance, reproduction, mortality) are unchanged from those reported in the TRACE documentation of Galic et al., (2017). In summary, changes into the original model are as follows:

- Calibration of the size dependent reproduction buffer for *Asellus aquaticus* and *Gammarus pulex*.
- Update from standard DEB model to abj model (with metabolic acceleration) as the description of *Gammarus* and *Asellus* on the add my pet database has since changed from standard to abj.
- Removal of seasonal temperature and resource dynamics from population level processes.

3.2.2 Entities, state variables, and scales

Entities in the models are individual females of both *Gammarus pulex* and *Asellus aquaticus* and their environment, which, although the spatial aspects are not modelled explicitly due to computational constraints, was defined as 1 metre square patch. The life stages of individuals are distinguished between embryo, juveniles, and adults. Species only differ in their DEB parameters and fecundity functions. All other processes are the same. DEB parameters for *G. pulex* and *A. aquaticus* were obtained from the Add My Pet database (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/species_list.html), an online database of calibrated DEB model parameters for 4,980 species.

Individual females are characterised by the state variables: structure, reserve density, maturity, and a reproduction buffer. The structure, expressed as length, L (cm), determines their size, feeding rate, and maintenance costs. The reserve density, E (J cm^{-3}) serves as an intermediary between the energy consumed and that which is mobilised (Figure 3.1). For juveniles, energy is allocated to a maturity buffer maturity, E_H (in juveniles) (J), until it reaches a species-specific threshold, after which energy is allocated by the now adults to a reproductive buffer, E_R (in adults) (J). Additionally, females are characterised by the number of broods they have carried, calculated by their cumulative fecundity (#), as well as their age (days). The environment is characterised by the amount of available resource (leaf litter; mg). Temperature is kept constant throughout the simulation with temperature set to 20 ◦C - that at which the DEB parameters were calibrated.

Dynamic energy budget theory is expressed mathematically with ordinary differential equations (ODEs) whereby time is continuous. Here, ODEs were solved in discrete timesteps representing 24/20 days[1]. Background mortality for each species was updated daily.

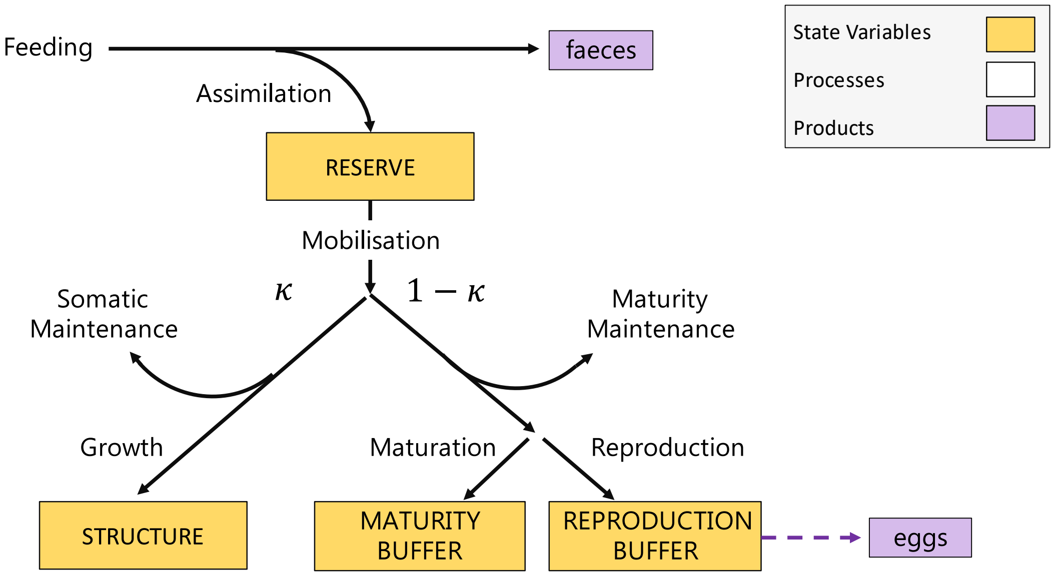

Figure 3.2: Metabolic processes of individual organisms described by Dynamic Energy Budget Theory (Kooijman, 2010)

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[1] This number was chosen as it strikes a balance between enough detail to capture change and not too much to require too much computational power

Table 3.2: DEB Parameters, their interpretation, baseline values, and units. Values are default values found in Kooijman (2010) on the Add My Pet Database (AmP)

Parameter	Interpretation	*Gammarus pulex*	*Asellus aquaticus*	Units	Source
Individuals					
$\{\dot{F}_m\}$	Surface area-specific maximum search rate	6.5	6.5	day^{-1} cm^{-2}	AmP
κ_X	Digestion efficiency	0.8	0.8	–	AmP
$\{\dot{p}_{Xm}\}$	Surface area-specific maximum food intake rate	62.24	62.89	J cm^{-2} day^{-1}	AmP
$\{\dot{p}_{Am}\}$	Surface area-specific maximum assimilation rate	49.79	78.61	J cm^{-2} day^{-1}	AmP
$\dot{v}$	Energy conductance	0.18066	0.01159	cm day^{-1}	AmP
κ	Fraction of utilised energy spent on soma	0.88685	0.9207	–	AmP
$[\dot{p}_M]$	Volume-specific maintenance costs	338.417	362.8	J cm^{-3} day^{-1}	AmP
κ_j	Maturity maintenance rate constant	0.002	0.002	day^{-1}	AmP
$[E_m]$	Maximum reserve density	2756.03	5426.23	J cm^{-3}	AmP
$[E_G]$	Volume-specific costs of growth	4446.22	4400	J cm^{-3}	AmP
κ_R	Reproduction efficiency	0.95	0.95	–	AmP
E_H^b	Maturity at birth	0.06315	0.01813	J	AmP
E_H^p	Maturity at puberty	2.108	0.08808	J	AmP
δ_m	Shape correction factor	0.23453	0.4131	–	AmP
z	Zoom factor – relative volumetric length	0.13048	0.1596	–	AmP
T_A	Arrhenius temperature	10000	6805	K	AmP
T_{ref}	Reference temperature	293.15	293.16	K	AmP
E_0	Reserve density (at embryo formation)	0.770227	0.43525	J	AmP
L_0	Structural length (at embryo formation)	1.0E-5	1.0E-5	cm	AmP
L_b	Structural length (at embryo formation)	0.1892	0.12	cm	AmP

μ_b	Background mortality	0.005	0.005	–	-
x_{G1}	*Gammarus* Reproduction buffer size function	−47.2	-	–	Hynes, 1955
x_{G2}	*Gammarus* Reproduction buffer size function	23.5	-	-	
x_{A2}	*Asellus* Reproduction buffer size function	-	2.15		Steel et al., 1961 in Ridley and Thompson, 1979
x_{A2}	*Asellus* Reproduction buffer size function	-	0.008		
d_v	Specific density of structure	0.17	0.17	g cm^{-3}	AmP
μ_E	Chemical potential of reserve	550 000	550000	J mol^{-1}	AmP
W_E	Molecular weight of reserve	23.9	23.9	g mol^{-1}	AmP
Environment					
Y	Year Length	365		days	-
X_R	Resource (conditioned leaf litter) energetic content	21		J mg^{-1}	Bärlocher & Kendrick (1975)
r	Resource growth rate	0.02		day^{-1}	Gulis et al., 2008
T	Temperature	20		◦C	Parameter Calibration temperature

Table 3.3: Model Equations

Process	Unit	Equation(s)	Number
Temperature correction*	-	$C_T = e^{\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right)}$	3.1
Assimilation	J day^{-1}	$\dot{p}_A = f * \{\dot{p}X_m\}^{C_T} * \kappa_X * L^2$	3.2
Mobilisation	J day^{-1}	$\dot{p}_C = L^3 * [E] * \frac{[E_G]\frac{\dot{v}^{C_T}}{L} + [\dot{p}_M]^{C_T}}{\kappa * [E] + [E_G]}$	3.3
Somatic maintenance	J day^{-1}	$\dot{p}_M = \{\dot{p}_M\}^{C_T} * L^3$	3.4
Growth	J day^{-1}	$\dot{p}_G = \kappa * \dot{p}_C - \dot{p}_M$	3.5
Maturity maintenance	J day^{-1}	$\dot{p}_J = \dot{k}_J^{\,C_T} * E_H$	3.6
Growth dynamics	cm day^{-1}	$\frac{dL}{dt} = \frac{1}{3} * \left(\frac{\kappa * \dot{p}_C}{[E_G] * L^2} - \frac{\dot{p}_M}{[E_G]} * L\right)$	3.7
Maturation/reproduction dynamics	J day^{-1}	$\frac{dE_R}{dt} = (1 - \kappa) * \dot{p}_C - \dot{p}_J$	3.8
Fecundity	# day^{-1}	$F = \frac{\kappa_R * E_R}{E_0}$	3.9
Resource dynamics	mg day^{-1}	$\frac{dR}{dt} = r * (K - R)$	3.10
Physical Length	cm	$L_{Physical} = \frac{L}{\delta_M}$	3.11
Dry Weight of the Structure	mg	$DW_{Structre} = d_V * L^3 * 1000$	3.12a
Dry Weight of the Reserve	mg	$DW_{Reserve} = E_H * \frac{\omega_E}{\mu_E} * 1000$	3.12b
Dry Weight of the Reproduction Buffer	mg	$DW_{Reproduction} = E_R * \frac{\omega_E}{\mu_E} * 1000$	3.12c

[1] Different from Galic et al., 2017 given that only one Arrhenius temperature was available.

3.2.2.1 Process overview and scheduling.

Within each timestep, processes are scheduled for all individuals in a randomised sequence. Individual and resource state variables are then updated at the end of each timestep according to DEB processes (Table 3.2). As individuals are called to the resource randomly within each timestep, competition for food is representative of scramble competition.

Individuals feed on the available resource, X, (mg). Ingestion of the resource scales with the surface area of the organisms, L^2 (cm^2) and is a function of the scaled functional response, surface-area-specific feeding rate (J cm^2) (Table 3.3, Eqn 2). The ingested resource is converted from mg to J using the resource energy content, X_R, used in Galic et al., 2017 and derived from conditioned alder leaves in Bärlocher and Kendrick (1975). The amount of energy assimilated to the reserve compartment is the calculated using the digestion efficiency (-, no units). From the reserve, it is allocated to different metabolic endpoints via a mobilisation flux, $\dot{p}_c$(Table 3.3, Eqn 3). Mobilisation is dependent on the organisms' length and reserve density and not directly dependent on the amount of energy assimilated. A fraction of the reserve (κ) is allocated first to the somatic branch of the energy fluxes which supports maintenance of the organism, $\dot{p}_M$(Table 3.3, Eqn 4), costs of which scales with the structural volume, L^3, and growth of the structural biomass, $\dot{p}_G$, (Table 3.3, Eqns 5 and 7).

Under starvation conditions, reserve density becomes smaller than the scaled length, then the organisms change their reserve allocation rules to only fuel maintenance costs, allocating energy only to survival. If there are insufficient energy fluxes to supply the maintenance costs, individuals 'die' and are removed from the simulation. In a typical DEB abj model, individuals under starvation shrink, taking energy from their structural reserve. However, *Gammarus* and *Asellus* are arthropods, producing an exoskeleton that cannot be digested after creation. Therefore, this starvation rule is not applied here.

The energy that is not allocated to the somatic branch (1-κ) is allocated to maturity and reproduction in the organism. Here, juveniles allocate energy to their process of maturation and while adults to their reproductive potential. The mobilisation flux allocates energy to maturity maintenance, $\dot{p}_J$, (Table 3.3, Eqn 6), which scales with maturity, E_H, via the maturity maintenance constant, $\dot{k}_J$, and to maturation or reproduction, $\dot{p}_R$, (Table 3.3, Eqn 8). The reproductive flux, $\dot{p}_R$, allocates energy to maturation of embryos and juveniles and to reproduction in adults. The maturity state variable, E_H, is monitored throughout the simulation and as, $E_H$reaches the threshold of maturity at birth, E_H^b, embryos become juveniles. They become adults when E_H reaches the threshold of maturity at puberty, E_H^p (Table 3.3).

Once they are adults, modelled individuals are assigned a reproductive buffer, E_R which is dependent on the size of the individual, using a species-specific calibrated fecundity function. Size of the reproductive buffer is updated after each hatching event as individuals continue to grow thereby increasing their reproductive capacity. Once the buffer is full, individuals produce a number of eggs which is dependent on the size of the reproductive buffer, reproductive efficiency, κ_R, and the cost of producing an egg, E_0 (Table 3.3, Eqn 9). In standard DEB models, at the moment that the individual hatches, the embryo is assumed to have the same energy density as the mother at the time of embryo creation (maternal effects rule). However, modelling this requires a further sub model to calculate the reserve dynamics of embryonic development. This approach increases the computational demand of the model, slowing it down. This process is therefore not modelled here. Instead, the energy cost of an egg, defined in the species DEB parameters, is the amount of energy that is then allocated to each egg at the time of hatching. Eggs contain developing embryos that are attached to the mother until they become juveniles. If a mother dies during the simulation and has embryos attached, all embryos also die. Once they are juveniles, individuals detach from their mothers and become independent entities.

Resource dynamics represent leaf litter, following semichemostatic dynamics. Resource growth rate, *r*, and carrying capacity, *K*, are independent of temperature and current resource density.

At the end of every time step, individual state variables are updated. Once a day, death of individuals due to background mortality is calculated. Background mortality is a constant probability of dying due to, for example, predation or age, in the case of both species, while for *Gammarus* this may also be cannibalism. In the original model of Galic et al. (2017), background mortality was 'switched off' when the number of individuals in the population fell below 20 to reduce the risk of extinction. The approach also represents population buffer effects such as drift and that reduce the risk of extinction in the field. However, this was not included here as this study is more of a virtual laboratory than simulated field study.

DEB theory describes the length of individuals in terms of structural length. This is converted to physical length using the shape factor which is species specific (Table 3.2). Individual dry mass is calculated as the sum of the mass of the structural length, the reserve compartment and that of the reproduction buffer (Table 3.2)

3.2.3 Design concepts.

Basic principles: Key processes in the model follow the basic principles of Dynamic Energy Budget theory (Kooijman, 2010), which posits that uptake of resources by individuals' scales with their surface area, and the allocation of energy scales with the volume of the organism. The theory is based on conservation of mass and energy. Space is not modelled explicitly in the model, but species populations are assumed to exist on a patch of one metre square. Individuals do not move on or between patches.

Emergence: Individual life-history traits, such as growth, maturation time, and reproductive effort, emerge from rules of metabolic organisation. Population dynamics emerge from indirect interactions between individuals via competition for the resource.

Interaction: Individuals in the model interact with each other indirectly through resource competition. Population growth is constrained by the amount of resource in the system (carrying capacity); when population densities go beyond available resource, and individual consumption does not meet their maintenance costs, modelled individuals experience starvation mortality. The amount of resource in the model never reaches zero. Density dependence in the model emerges from modelled indirect interactions. Embryos in broods are explicitly linked to females, resulting in embryo mortality when females die due to starvation or background mortality.

Stochasticity: Species specific background mortality is implemented as a stochastic process that occurs daily. Furthermore, as DEB parameters are constants, a scatter multiplier is added to the surface area-specific ingestion rate to implement a measure of variation between individuals. The scatter multiplier is a random number pulled from a log-normal distribution (Kooijman et al., 1989; Martin et al., 2013) with a standard deviation of 0.1.

3.3 Calibration and development of sub-models

Calibration is the process by which model parameters are determined from empirical data (Schmolke et al., 2010). The majority of species DEB model parameters were taken from the AddMyPet database (Kooijman et al.,2010). The only parameters that were 'calibrated' in this study was the size of the reproduction buffer.

The main model code was not altered and therefore not tested. Where the metabolic acceleration module was added, the calculation of the metabolic acceleration factor and how this affected the feeding rate was tested in excel before addition to the model code.

Fecundity

DEB theory does not inherently account for certain life history traits, such as reproductive strategies (e.g. broods or eggs) or how the size of the reproduction buffer should be calculated (Koojman et al., 2010; Jager et al., 2022). To address this, Galic et al. (2017) made specific assumptions regarding the brood size of gammarids, linking it to their body length based on existing literature (Hynes, 1955; Hynes and Harper 1972). These studies demonstrate that brood size is size-dependent, increasing with amphipod length. For the purposes of this study, fecundity function was updated from that of G. *pseudolimnaeus* (Hynes and Harper 1972; Galic et al., 2017) for *G. pulex* using data from Hynes (1955) was used to calculate a new fecundity function for *G. pulex*. The relationship between size and fecundity was updated to better reflect the specific characteristics of *Asellus*.

3.3.1.1 Fecundity Functions

Asellus aquaticus

Ridley and Thompson (1979) summarised the findings of 5 studies into the life history of *Asellus* across Europe, reporting linear regressions to the relationship between asellids length and brood size (logarithmic). Of the 5 regressions reported, Steel (1961) reported the largest sample size over multiple years, also reporting the raw data.

Steel, (1961) fitted the following linear model to measured data of *Asellus* brood size per size of individual:

$$\mathbf{\log 10(y) = 2.1536 * \log 10(x) + 0.0081}$$

Equation 3.13

To implement this in NetLogo and calculate the size of the reproduction buffer, this becomes:

$$y = x^{2.1536} * \ 10^{0.0081}$$

Equation 3.14

So that:

$$Fecund_{Funct} = Length^{2.15} * 10^{0.008}$$

Equation 3.15

Where $Fecund_{Funct}$is the fecundity function and length in the physical brooding length of the individual. This brooding length is calculated for each individual at the point of maturity and is updated immediately after each brood reaches maturity. The fecundity function is then used to determine the size of the reproductive buffer:

$$t_{BroodReserve} = E_0 * Fecund_{Funct}$$

Equation 3.16

Where $t_{BroodReserve}$ is the brood reserve [J] and E_0 is the amount of energy [J] that goes to each egg. The brood reserve then acts as a threshold, signalling females to produce a brood once reproduction buffer crosses this threshold. After which, the number brood size is calculated:

$$Brood\ Size = \frac{t_{E_R} * kap_R}{E_0}$$

Equation 3.17

Where t_{E_R} is the reproduction buffer [J cm-2], kap_R is the reproduction efficiency [-].

Gammarus pulex

Hynes (1955) reported the brood sizes of *G. pulex*, reporting a brood size of individual 11-12mm of 29.1, the shortest brooding females were 6mm with a mean brood size of 5 eggs. This results in the following regression equation:

$$Fecund_{Funct} = 47.7 * Length - 25.6$$

Equation 3.18

Where length is the physical length of gammarids, (cm) as in Eqn 3.15

3.3.2 Metabolic acceleration

The original model code was designed for standard DEB models, where the metabolic rate does not change through an individuals' lifetime. However, since the publication of the Galic et al. (2017) model, the parameters for *Gammarus* sp. have been recalibrated in the Add My Pet database to align with the abj model type. Abj DEB model types account for metabolic acceleration between the juvenile and adult life stages where the metabolic rate of an individual increases with age (Kooijman, 2014). Metabolic acceleration predicts upcurving in the growth of organisms, observed in *Gammarus pulex* (Sutcliffe et al., 1981; McCahon and Pascoe, 1988) and *Asellus aquaticus* (Hoefnagel and Verberk, 2015), but not consistently (Galic and Forbes, 2017; Marcus et al., 1978; Arakelova, 2001). According to Kooijman (2014), the standard DEB model does not accurately describe the growth of crustaceans like *Gammarus* and *Asellus*, including *Gammarus pulex*, which exhibit growth acceleration during their early life stages. To address this, the abj model was developed.

Kooijman (2014) describes various types of metabolic acceleration across organisms. Here, I explore two abj model types: Type A and Type M. In Type A, metabolic acceleration involves an increase in surface area-specific assimilation capacity at a specific developmental stage. In contrast, Type M involves a simultaneous increase in surface area-specific assimilation rate and energy conductance during the period between birth and metabolic metamorphosis. This increase is proportional to structural length, with metabolic metamorphosis occurring once a certain threshold is reached (Kooijman et al., 2011). The application of abj models to *Gammarus* and *Asellus* is contested, as these species do not undergo physical metamorphosis; however, in DEB theory, metamorphosis relates to metabolic changes over an organism's lifetime, not necessarily physical changes.

Additionally, the starvation mechanism for the abj model type involves shrinking, reclaiming energy from the structure when food availability is low (Kooijman, 2014). *Gammarus* and *Asellus*, however, have rigid exoskeletons that do not shrink. This mechanism is therefore not implemented in the model and therefore, under starvation (energy is only taken from the reserve).

The model code was therefore adapted to account for metabolic acceleration between juveniles and adult life stage by applying a metabolic acceleration factor ($M(L)$) to the surface area specific ingestion rate of the individual (Type M, Kooijman 2014). Therefore, the model code was adapted to account for this mechanism with the following equations:

$$\begin{cases} M(L) = \dfrac{L_b}{L_b} = 1 \;\; if\ E_h < E_h^b \\ M(L) = \dfrac{L}{L_b} \;\; if\ E_h^b < \ E_h < E_h^J \\ M(L) = \dfrac{L_J}{L_b} \;\; if\ E_h > E_h^j \end{cases}$$

Where L_J is the length of the individual at puberty, L_b is the length at birth, E_h is the reserve density [J], E_h^b is the maturity at birth [J], E_h^j is the maturity at metamorphosis [J].

3.4 Individual level model validation and evaluation

Model validation is where the model outputs are compared with independent empirical data sets to assess how accurately the model represents ecological processes (Schmolke et al., 2010). However, deviating from conventional methods (Augusiak et al., 2014), due to lack of independent data, not all individual processes were validated against independent empirical data. Instead, as in Galic et al. (2017) model outputs (i.e. growth, in terms of length and dry weight over time) were compared against a combination of both calibration datasets and, where possible, to independent laboratory and field data (Table 3.4). Additionally, dry weight, time to maturation, and brood size, as a function of individual size, were also compared. All model predictions were calculated at the default calibration temperature of 20°C with no restrictions on food consumption ($f = 1$).

The growth of a single individual was simulated from birth, and the resulting changes in length and dry weight over time were compared to published data. Time to maturity and brood sizes were further evaluated by simulating 500 juveniles over a 5-year period, to calculate mean brood sizes for different individual sizes. The mean and standard deviation of time to maturation were compared between models, and the maximum brood size for each individual size was recorded. The average maximum brood sizes within each size category were calculated across the 5-year period.

Model predictions from both the abj A and abj M models were compared against literature data. However, due the specific data requirements of DEB models and their calibration, it was not always possible to validate model predictions with data that were independent of the calibration process. The datasets used in these evaluations are listed in Table 3.4.

Table 3.4: References for datasets used in the individual validation.

Species	endpoint	Literature	Notes	Used in AmP calibration?
Gammarus pulex	Length	Welton and Clarke, 1981	Laboratory study conducted at 20C	Yes
	Dry Weight	Gee et al., 1988	Field samples across seasons	Yes
	Reproduction	Hynes, 1955	Used to calculate the size of reproduction buffer	No
Asellus aquaticus	Length	Hoefnagel and Verberk, 2015	Laboratory study conducted at 20C. No data available beyond 100 days	Yes
	Dry Weight	Arakelova et al., 2001	Wet Weights reported	Yes
		Adcock, 1982	Field samples across seasons	No
	Reproduction	Steel,1961	Used to calculate the size of reproduction buffer	No

3.4.1 Length

Both species follow Bertalanffy growth (Kooijman, 2010) with the abj A model showing lower growth trajectory than the abj M model (Figure 3.3). For *G. pulex*, the individual reaches 1.29 cm (1.16 – 1.41 cm) after 200 days with the abj A model while the abj M shows rapid growth in the first 25 days and reaching 1.53 cm (1.38 – 1.68 cm) after 200 days. Comparing the growth trajectories to Welton and Clark (1981) the abj A model shows better alignment with the independent data than that of the abj M model.

For *A. aquaticus*, the individual reaches 0.83 cm (0.76 – 0.89 cm) after 200 days with the abj A model and 0.90 cm (0.82 – 0.97 cm) with the abj M model. The dataset of Hoefnagel and Verberk (2015) has great variation with both models showing alignment with the data.

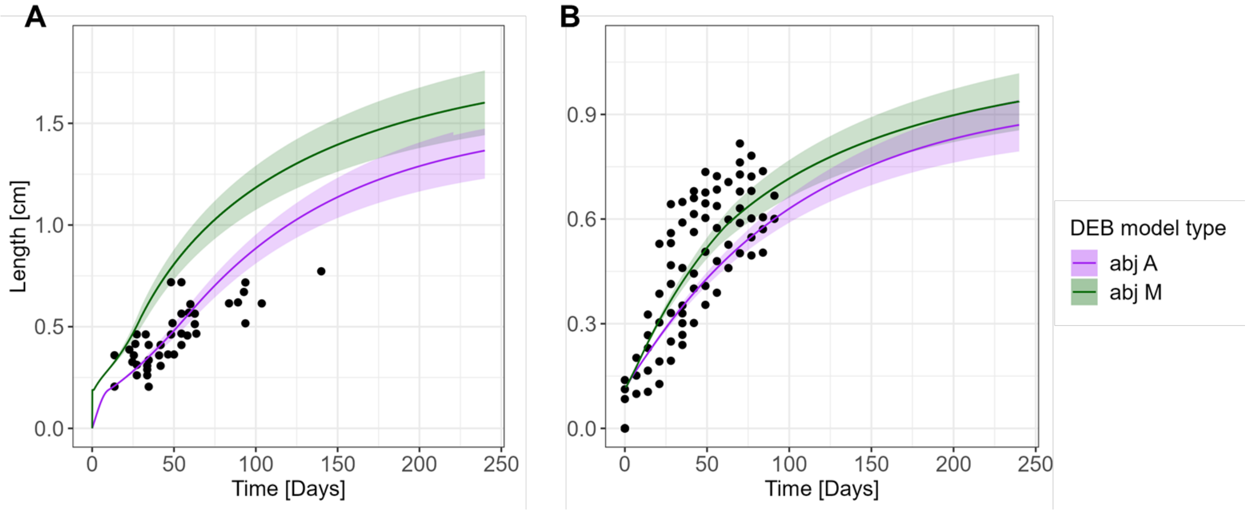


Figure 3.3: Growth trajectory of *Gammarus pulex (A) and Asellus aquaticus (B)* at 20◦C with abj types A (purple) and M (green) showing length [mm] over time. The ribbon represents the range of values predicted with a scatter multiplier pulled from a distribution with standard deviation of 0.1. Data points (black dots) differ between species plot with growth data reported for *G. pulex* in Welton and Clark (1981) and *A. aquaticus* in Hoefnagel and Verberk, 2015.

3.4.2 Dry Weight

Neither model for either species accurately predicts dry weight compared to the observed data (Figure 3.4). In both cases, the abj M model predicted lower dry weights than the abj A model.

When comparing model predictions to the weight of gammarids collected from field data, both type A and M models, over-predict the dry weight of *G. pulex* in relation to the data from Gee et al., (1988) with individuals of 12mm at 7mg of dry weight, while the Type A and Type M models predict 15 and 14.8 mg respectively. Predicted dry weights of smaller size categories (5 – 8 mm) were closer to those of the measured data. Note that while dry weight of individuals measured in Gee et al., (1988) was from field populations where individuals are often food limited.

For *Asellus*, both models produced a similar length to dry weight relationship. Both models underpredicted length weight relationships compared to the calibration dataset of (Arakelova, 2001) but over predicted the dry weight of individuals compared to the independent dataset of Adcock (1975) for size categories above 5 mm.

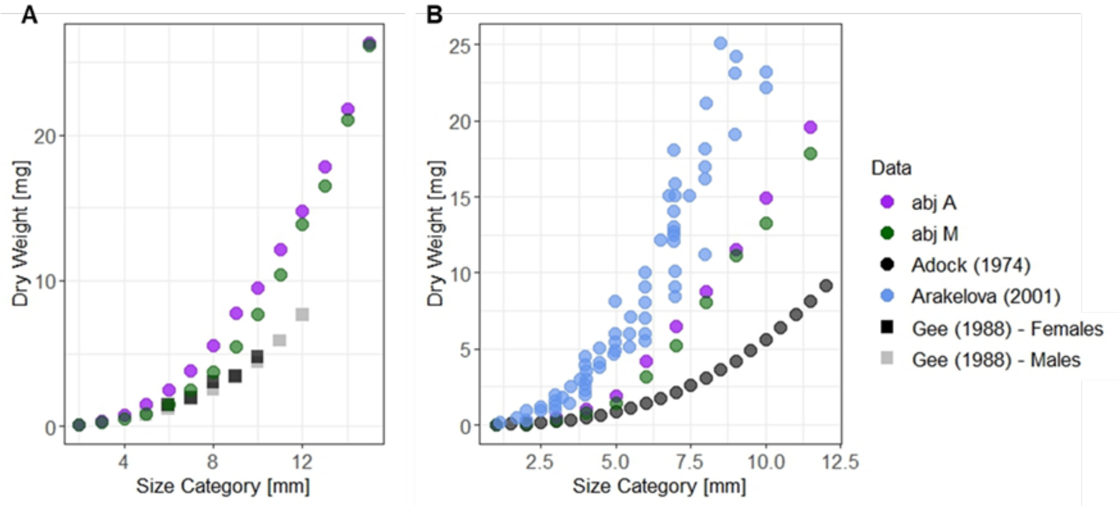


Figure 3.4: Dry weight [mg] as a function of length [mm] of *Gammarus pulex* (A) and *Asellus aquaticus* (B) for both abj A (purple) and abj M (green) models. With data from male and female *G. pulex* reported in Gee (1988) for *G. pulex*, Arakelova et al., (2001) and Adcock (1974) for *A. aquaticus*.

3.4.3 Maturation time and Fecundity

The abj M model predicted shorter maturity times compared to the abj A model for both species, with maturation times lower than those reported in the literature (Figure 3.5). For *Gammarus*, at 20°C, the time to maturation was 35 days (SD ± 3) in the abj M model and 44.5 days (SD ± 3) in the abj A model. However, both models result in the length at maturity of 5.5 cm (SD±0.06) in the field. For *Asellus*, the time to maturation at 20°C was 23 days (SD ± 2) in the abj M model and 29 days (SD ± 2) in the abj A model. The abj A model aligned better with the input data than the abj M model.

For both species, the abj M model predicted lower mean brood sizes per size category, while the abj A model was closer to the fecundity functions used to calibrate the size of the reproduction buffer (Figure 3.5). Asellids do not reach beyond 12 mm in either model type.

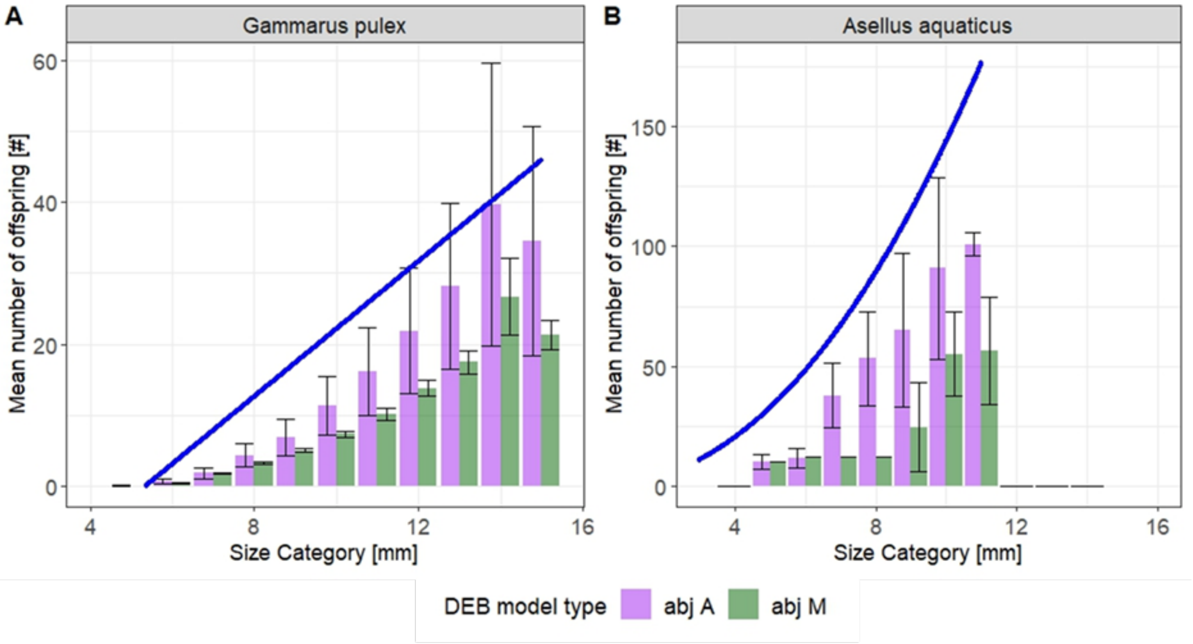


Figure 3.5: Mean Brood size of both *Gammarus* and *Asellus* females from different size categories from simulations run over 5 years with no resource limitation. Error bars represent the standard deviation. The blue line represents the fecundity function used to calibrate the size of the reproduction buffer.

3.5 Population models

This section outlines the definition of the ecological scenario for the *Gammarus* and *Asellus* models within the effects of chemical stress on population responses and ecological functions will be examined.

3.5.1 Scenario definition

The ecological scenario for both shredder species, *Gammarus* and *Asellus*, is defined as a 1 m^2 patch where population density is regulated by competition for a variable food resource. Thus, the population dynamics of each species emerge from individual life histories and intraspecific competition for this resource.

Both *Gammarus* and *Asellus* feed on conditioned leaf litter, a matrix of leaf litter and microbial biomass (Graça et al., 1993a). In the field, fungi and bacteria condition the leaf litter, making it more palatable (Bloor et al., 2011) and nutritious (Bärlocher, 1985). In this model, the resource is defined as a leaf-microbial biomass matrix, expressed in mg m^{-2}. The models are calibrated at a temperature of 20°C, reflecting the ecological conditions of summer when shredders often face resource limitations due to reduced food availability (Gee et al., 1988).

The baseline carrying capacity of the resource is set at 400 mg m^{-2}, representing the typical standing stock during summer. The daily growth rate of microbial biomass is 0.02 mg per mg of leaf litter per m^2 per day, which is consistent with fungal biomass growth on leaf litter in temperate climates (Gessner et al., 1997; Gulis et al., 2008). Although this value is relatively low compared to typical field measurements, it is not uncommon in summer conditions (Iversen et al., 1989; Pretty et al., 2005; Gulis et al., 2008; Little et al., 2020). In the field, detrital matter can range from 0 to 4000 mg C m^2, but summer values are often lower due to a lack of leaf litter input and the cumulative consumption and decomposition by shredders and microbial biomass from autumn, when leaves fall, through to summer.

It is acknowledged that this model definition of the resource as a leaf litter and microbial biomass matrix simplifies reality. In nature, the detrital matter that *Gammarus* and *Asellus* consume is a complex system of allochthonous inputs, including leaf litter, which varies seasonally and is colonised by fungi and bacteria. The biomass of these microorganisms also fluctuates seasonally due to changes in substrate availability and temperature (Gee, 1988). However, in this model, the carrying capacity of the resource remains constant throughout the experiment, and resource growth is primarily influenced by consumption by shredders.

3.5.2 Model Behaviour

This section outlines the population dynamics of both species' models in the absence of stressors, representing the baseline situation, and assess the number of replicates required to get stable predicted outputs.

3.5.2.1 Replicates

The output population sizes were not affected by the simulation variability after 100 replicates (Figure 3.6) therefore all simulations were run with 100 replicates.

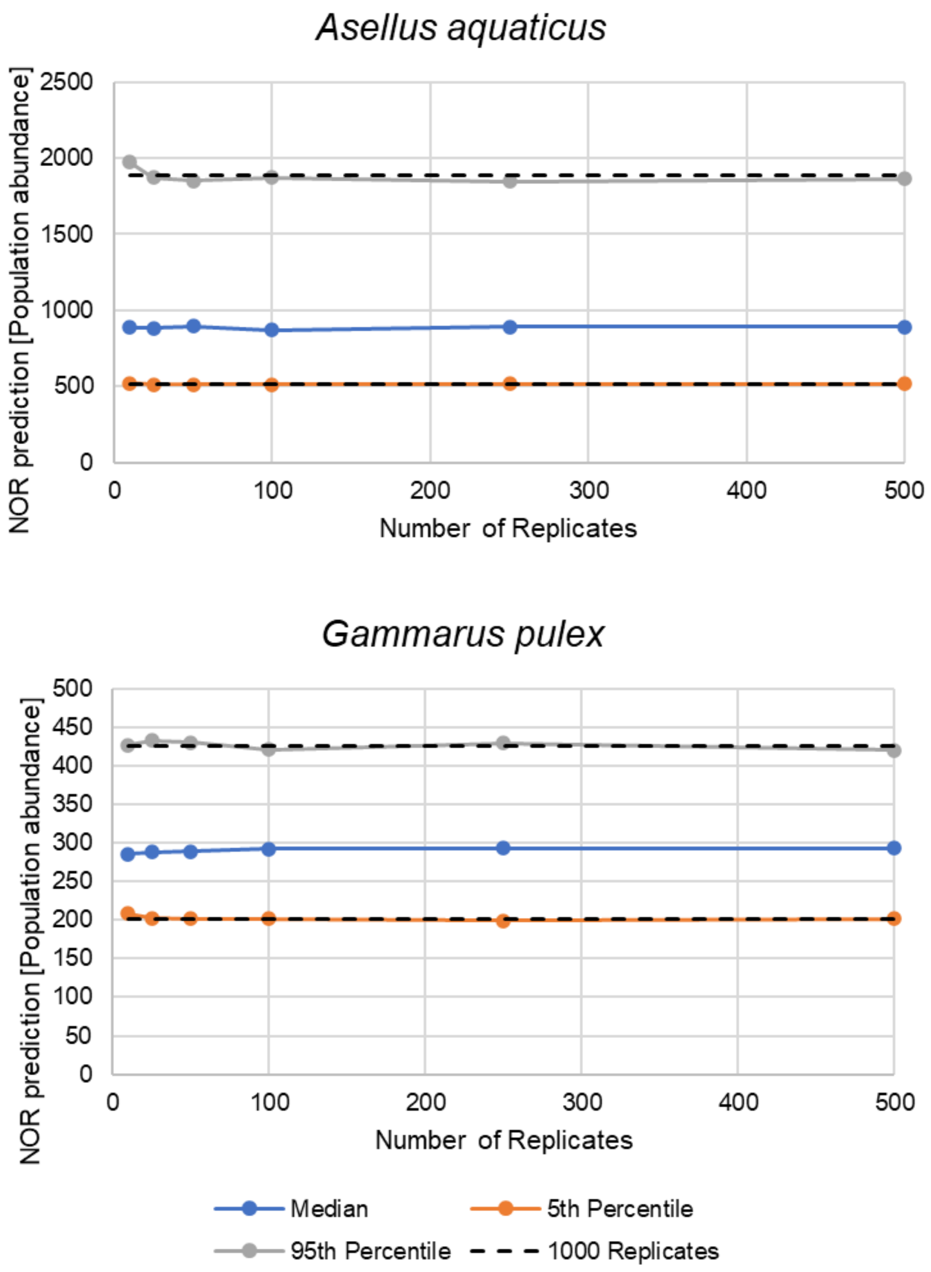


Figure 3.6: Median, 5th and 95th percentile values of population output plotted against the number of simulation replicates for *Asellus* and *Gammarus* models.

3.5.3 Population endpoints

Five hundred individuals were simulated for 20 years at constant temperature and baseline food availability and growth conditions with 100 replicates. The first 10 years were discarded with the aim of removing any remaining impact of the initial conditions and therefore focuses on the model's behaviour after it has stabilised.

Population abundance, biomass, consumption rate and size and age structure were reported every 30 days. The minimum, maximum, mean, and median values and coefficients of variation for a population abundance and biomass were calculated across the reported values across the 10 years across 100 replicates (Table 3.5).

Table 3.5: Descriptive statistics of the baseline model for *Asellus aquaticus* and *Gammarus pulex* adapted from Galic et al., (2017).

		Asellus					***Gammarus***				
		min	**max**	**mean**	**median**	**CV**	**min**	**max**	**mean**	**median**	**CV**
Individual	**Time to Maturity [Days]**	29.7	169.1	73.3	73.4	10.4%	69.3	236	124	122.1	12.1%
	Adult Size [cm]	0.19	0.38	0.31	0.31	24.5%	0.47	0.6	0.51	0.51	3.1%
Population	**Total Abundance [#]**	392	2356	952.5	874	40.2%	199	420	292.7	289	13.3%
	Juvenile Abundance [#]	0	1858	343.1	4	153.8%	14	331	152.9	146	33.9%
	Adult Abundance [#]	0	1337	609.4	601	46.1%	88	211	139.8	138	12.9%
	Population Biomass [mg DW]	37.4	154.8	114.3	118.3	18.8%	79.1	101.5	89.4	89.3	3.0%
	Consumption [mg/day]	0.2	1.5	0.4	0.4	34.8%	0.37	0.64	0.45	0.44	8.5%

3.5.3.1 *Asellus* dynamics

Population abundance ranged from 392 to 2356 individuals m^{-2} across 100 replicates with a mean and median abundance of 952 and 874 individuals, respectively (Figure 3.7). The population biomass ranged from 37.4 to 154.8 mg m^{-2} (dry weight). Across the 10 years simulation and 100 replicates, the population abundance had a coefficient of variation of 40% while the CV of the population biomass was 19%.

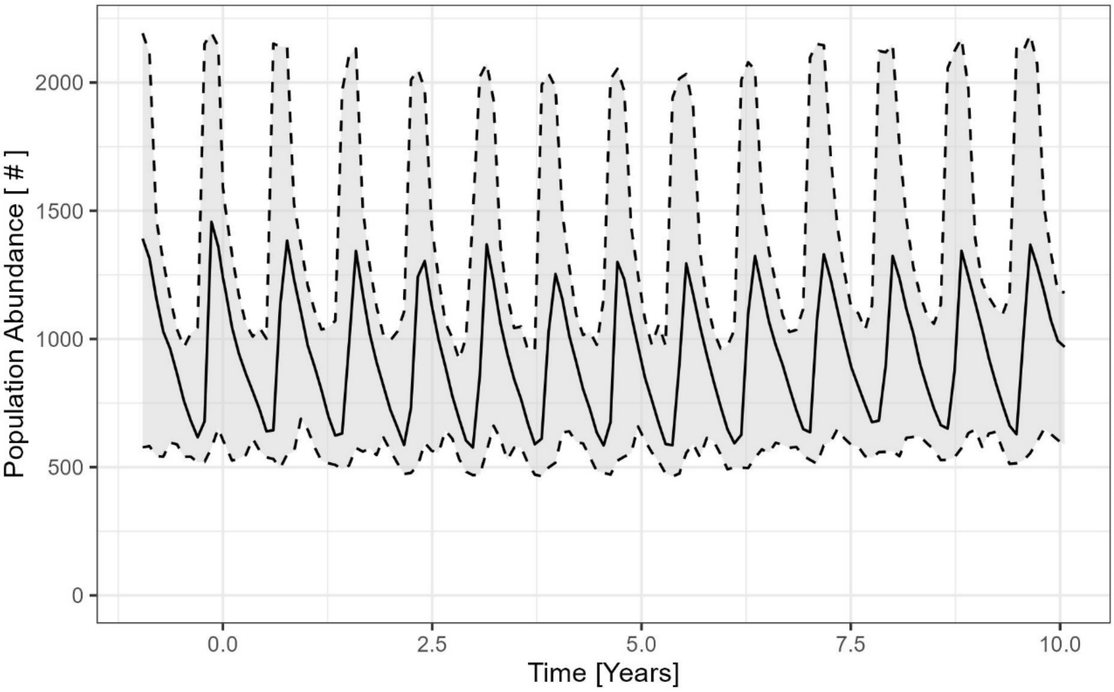


Figure 3.7: Baseline population dynamics for *Asellus aquaticus* at constant Temperature (20C) with dynamic resource 400 mg C m2 over 10 years, after an initial 10 year burn period

Asellus population size was comparable to values from Iversen and Thorup (1988) where the maximum population size in September (at 5000 to 20000 individuals m^{-2}), minimum size in late winter around March (at around 100 individuals m^{-2}).

The maximum size of adult asellids in the baseline scenario was 3.6 cm), which is smaller than the over 10 mm which can be observed in the field (Steel, 1961) The smallest brooding female in August in a British stream measured 3.5 mm (Steel, 1961) so sizes here are not unrealistic but plausibly representative of a resource limited situation, reflecting the summer conditions simulated, where limited resources result in shorter adult asellids.

3.5.3.2 *Gammarus pulex*

Population abundance ranged from 199 to 420 individuals m^{-2} with a mean and median abundance of 292.7 and 289 individuals, respectively (Figure 3.8). The population biomass ranged from 79.1 to 101.50 mg m^{-2} (dry weight). Across the 10 years simulation and 100 replicates, the population abundance had a coefficient of variation of 13.3% while the CV of the population biomass was 3%.

The maximum size of *G. pulex* in this baseline situation was 6 mm with a mean of 5.1 mm. This is below values found in the field smallest brooding females gammarids are about 6 mm long (Hynes, 1955). However, agrees with Gee (1988) where the shorter individuals were found in the summer.

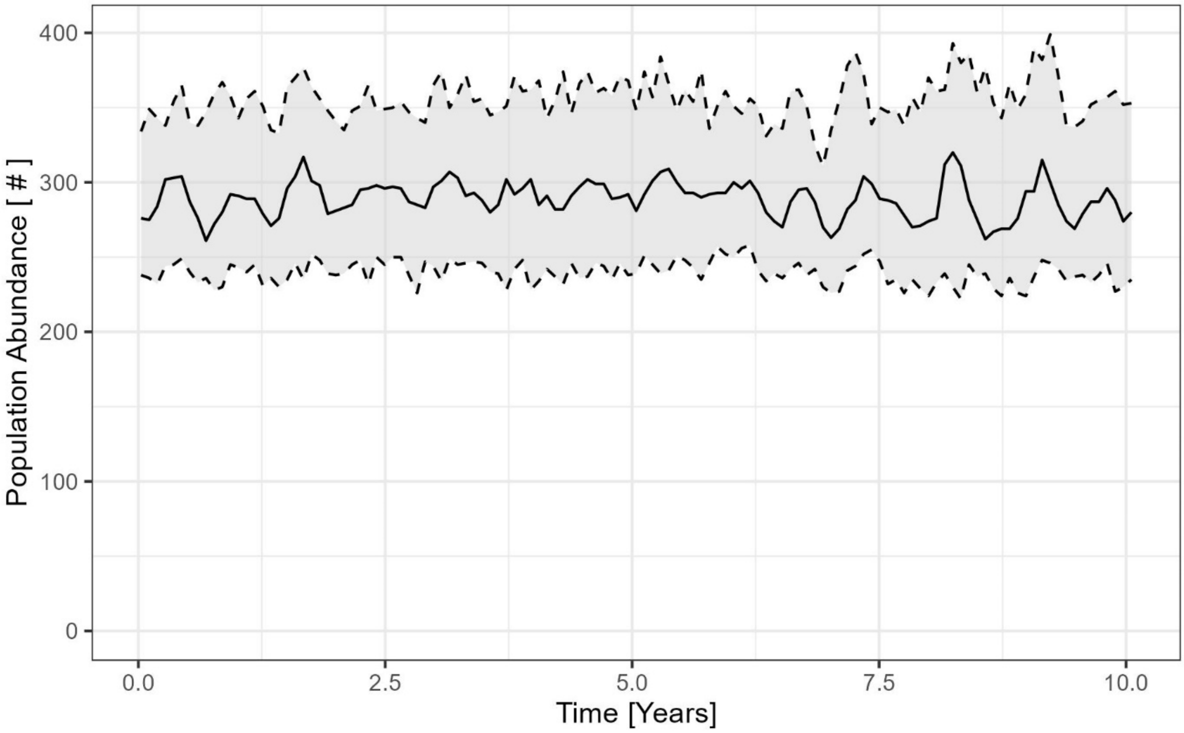


Figure 3.8: Baseline population dynamics for *Gammarus pulex* at constant Temperature (20C) with dynamic resource 400 mg C m2 over 10 years, after an initial 10 year burn period

3.6 Discussion

This chapter implemented an Individual-Based Dynamic Energy Budget Model (DEB IBM) for *Gammarus pulex* and *Asellus aquaticus* based on the framework by Galic et al. (2017). Two variations of the DEB model were considered: the abj M model and the abj A model, each with distinct strengths in representing biological processes. The abj A model, however, better captured individual reproductive output compared to the input data. Since population models rely heavily on vital rates like reproduction, the abj A model was deemed more suitable for this study.

While individual-level parameters align well with calibration data, and to an extent, independent laboratory data, the population model underpredicts population abundance and size compared to field observations, particularly for *Gammarus pulex*. This discrepancy is likely due to two factors. First, both individual species models underestimate reproductive output, which, in a population model, leads to reduced overall abundance. Second, the model lacks seasonal variation in resource availability and temperature, which can influence recruitment (Sibley et al., 2002), altering population growth rates. In the field, seasonal fluctuations in resource availability, temperature can create periodic favourable conditions that support juvenile survival and adult growth (Varpe, 2017), increasing population reproductive rates, increasing recruitment driving higher abundance. *Gammarus* and *Asellus* typically experience high recruitment rates in spring due to both increasing temperatures and resource availability (Hynes, 1955, Iversen and Jessen, 1977; Gee, 1982; Gee, 1988, Iversen and Thorup, 1988). In a non-seasonal, fixed environment, such as the one modelled here, these periods do not occur, limiting individual growth and reproductive output, thereby reducing recruitment rates, and leading to lower population abundance. Differences in abundance between the two population models, despite identical resource conditions, are likely to stem from differences in fecundity between the two species, with *Asellus* producing larger brood sizes than *Gammarus* for females of the same size. Furthermore, *Gammarus*, at the individual level, has a higher consumption rate than *Asellus*. At the population level, this means greater resource demand within the *Gammarus* population, leading to fewer individuals surviving on the same amount of resource.

With regard to density dependence and modelling intraspecific competition, classic intraspecific density dependency works via feeding and starvation. However, crowding mortality also plays a part in density dependence (Gergs et al., 2013), particularly for *Gammarus* which has been observed to exhibit cannibalistic behaviour (Kelly et al., 2003). This however is not modelled explicitly here but assumed to be encapsulated by the background mortality. While density dependence relationships can be calibrated with both field or laboratory data (Strauss et al., 2016; Accolla et al., 2020). However, for IBMs, there is the advantage of allowing density dependence to emerge providing that, for well-studied species, sufficient data can allow the realistic representation of resource availability and behaviour (Stillman and Goss-Custard 2010).

Another limitation of the use of DEB models over other types of energetic models could be the lack of adaptation and plasticity. In DEB theory, the kappa rule describes how an individual allocates energy to maturation and growth and this allocation remains constant throughout the individual's lifetime. This assumption implies that adults are essentially larger versions of juveniles for all species. However, empirical studies suggest that this phenomenon is not observed in all species (Glazier and Carlow, 1992; Nisbet et al., 2004; Johnston et al., 2014). Furthermore, when an individual is exposed to chemical stress, individuals may adapt by altering their energy allocation strategy, reallocating resources between the two processes (Calow, 1985; Perrin and Sibly, 1993; Sokolova et al., 2012). As a result, the standard DEB model which assumes a constant kappa value, may not always be the best model to predict changes individual growth in responses to chemical stress as it fails to account for adaptive behaviours (Sibly et al., 2013).

Nonetheless, the DEB models used in this thesis are considered appropriate for addressing the research questions for several reasons. First, the simplification of the kappa rule is reasonable for the study species, *Gammarus* and *Asellus*, as they undergo minimal changes in shape and energy allocation throughout their life cycle, apart from during moulting (Charron et al., 2014) which is not modelled here. Second, alternative DEB models have not been developed for the study species. Third, this thesis does not look at chemical induced stress explicitly, but the consequences of effects reductions in feeding, assimilation and food availability. In future, alternative effect scenarios could be developed, such as compensatory mechanisms like an increase in feeding rate following a reduction in assimilation efficiency. More broadly, DEB theory serves as a generic framework, often applying average energy allocation patterns across species. The kappa rule is rarely modified due to the lack of sufficient species-specific data, making it a useful but sometimes limiting assumption in ecological modelling.

Despite its limitations, the model provides insights into species dynamics under resource-limited conditions by offering a controlled framework for studying key ecological processes that may influence chemical induced effect on the feeding of *Gammarus* and *Asellus*. The absence of seasonal environmental variation is intentional, as the primary goal is to investigate the mechanisms of species interactions in a stable, resource-constrained environment. Rather than direct analogues to field observations, the results in the following chapters are derived from a virtual laboratory setting. This design allows for a focused examination of how intra- and interspecific interactions influence the effects of feeding inhibition on the ecological performance of two freshwater shredder species.

These models will be used in the following chapters to explore how individual-level impacts on energy uptake translate to population-level responses and the overall performance of ecological functions. Chapter 4 will focus on different in population responses to pathways of impact on the consumer resource system., while Chapter 5 assesses how the duration and magnitude of such pathway of impact influence the recovery of populations. The models will then be coupled in Chapter 6, so that the species compete for resources, to assess how interspecific competition for food affect population responses to reduction in individual feeding rates and the structure of the service providing unit.

Chapter 4 - Modelling different pathways of impact on consumer-resource interactions and consequences for ecological functions in two freshwater shredder populations.

4.1 Introduction

Consumer-resource interactions are central to driving the flow of energy and nutrients through ecosystems (Atkinson et al., 2017). Through activities such as ingestion, nutrient storage, excretion, and egestion, consumers play a vital role in biogeochemical cycles, influencing the cycling, storage, and redistribution of nutrients, altering their availability within ecosystems (Vanni, 2002). These processes regulate key ecological functions, including primary production, providing organic matter and nutrient cycling, and decomposition through the consumption and processing of that organic matter (Atkinson et al., 2017), often essential for the delivery of certain ecosystem services (Harrison et al., 2014; Smith et al., 2017). By studying these relationships, we can better predict how environmental stressors, including chemical stressors, affect not only individual species but also the broader ecological functions that underpin the delivery of ecosystem services.

Chemicals can alter consumer-resource interactions by affecting both the consumers ability to access and utilise resources, as well as the resources themselves (Fleeger et al., 2003; Fleeger, 2020). For consumers, chemicals may impair their foraging ability (Fong and Ford, 2014), ‘prey’ handling, and consumption efficiency by altering their physiology (Zeeshan et al., 2017) and/or behaviour (Nyman et al., 2013). While chemicals can also impact the accessibility, quality, and availability of resource, having both positive and negative impacts on the feeding by consumers. For example, insecticides reducing the mobility of prey can increase the capture rate of predators (Brookes et a 2009), while herbicides impacting the nutritional quality (Konschak et al., 2021) or quantity (Zhao et al., 2023) of a resource may have negative impacts on consumer dynamics (Fleeger, 2020). These changes can cascade through the food web, altering the dynamics between consumers and their resources. For example, endocrine-disrupting chemicals, specifically 17α-ethynyloestradiol, impacting reproduction of a key prey species, fathead minnow in a Canadian lake, resulted in both increased zooplankton populations, due to reduced grazing, and a decreased trout (predator) biomass for lack of available prey (Kidd et al., 2014).

At the population level, chemical exposure can influence consumer-resource interactions by affecting factors related to intraspecific competition for resources, such as population density and food availability. These dynamics can significantly influence population-level responses to chemical stress (Foit et al., 2012; Knillman et al., 2013; Dolciotti et al., 2014). Intraspecific interactions, shaped by consumer-resource dynamics, further influence population dynamics and individual behaviours, including feeding activity (Little et al., 2020), which subsequently affects responses to chemical exposure (de Villemereuil and Lopez-Sepulcre, 2011; Schoener, 2011). Therefore, understanding intraspecific competition for food and related individual behaviours is crucial when assessing the ecological impacts of chemicals on species populations and their functions.

In a recreational fishery, predatory fish rely on macroinvertebrate communities for food, often selecting prey based on size and availability (Newman and Waters, 1984; Rask and Hiisivuori, 1985; Dodrill et al., 2021). The abundance and sustainability of these prey species are, in turn, dependent on the processing of organic matter within the ecosystem. Additionally, detrital processing in particular plays a significant role in energy flows within freshwaters (Benke, 2018). Freshwater invertebrates, particularly shredders, are key players in this process, with their feeding activities contributing between 50% and 64% of leaf mass loss in streams (Hieber and Gessner, 2002). These shredders break down organic matter, facilitating the release of energy that is essential for the growth of secondary producers and the broader food web. Consequently, the ecological functions provided by shredder populations are important to the productivity of freshwater ecosystems.

Gammarus pulex and *Asellus aquaticus* are two key freshwater shredder species commonly found across Europe. As consumers, they play a vital role in transferring energy through trophic levels (Wallace and Webster, 1979). As freshwater shredders, they contribute to the processing of allochthonous material, a major source of energy to freshwater systems (Brett et al., 2017), through their feeding activity (Wallace and Webster, 1979). Furthermore, *Gammarus pulex* and *Asellus aquaticus* serve as prey for predatory fish, important in freshwater fisheries, such as perch, trout, and salmon (Anderson et al., 2016; Dodrill et al., 2021), with fish selecting for larger invertebrates, often mature individuals > 6 mm (Newman and Waters, 1984; Anderson et al., 2016). Therefore, changes in their feeding activity and the availability of larger individuals may impact the performance of ecological functions in a recreational fishery.

Both species are vulnerable to a wide range of chemical stressors. As arthropods, they are susceptible to insecticides, and neurologically acting chemicals in particular, which can have direct effects on their individual fitness and feeding activity (Maltby et al., 1994; Agatz et al., 2014), impacting their reproduction, growth, and survival. Chemicals can also disrupt the assimilation of energy through chemical action (Lebrun and Gismondi, 2020; Campos et al., 2014, Bhavan et al., 2011, Li et al., 2020) or physical blockage (López-Doval et al., 2017), both affecting growth and survival but not necessarily feeding activity (Seyoum et al., 2021). Additionally, due to their reliance on microbial-conditioned leaf litter as a primary food source (Bärlocher et al., 1979), these shredders may also be indirectly impacted by chemical induced alterations in the quantity or quality of conditioned leaf litter (Jumars and Wheatcroft, 1989; Andersen and Cummins, 1979; Andersen et al., 2007). *Gammarus* and *Asellus* are particularly sensitive to changes in the microbial composition of conditioned leaf litter (Graca et al., 1994; Bloor et al., 2011). Certain chemicals, such as fungicides and antibiotics, can impact this interaction by altering the microbial composition of conditioned leaf litter, thereby affecting its nutritional quality and palatability for detritivores (Dimitrov et al., 2014; Zubrod et al., 2011; Zubrod et al., 2014; Bundschuh et al., 2017; Konschak et al., 2020). Such changes in food quality and availability can adversely affect growth, maturity, and reproduction (McCaffery, 1975; Congdon et al., 2009).

Although reductions in feeding activity, assimilation efficiency, food quality, and quantity may manifest similarly at the individual level (e.g., reduced growth and reproduction), differences in food consumption and competition can lead to different population-level outcomes through the consumer-resource relationship. An ecosystem services approach to ecological risk assessment seeks to protect the provision of ecosystem services by safeguarding the ecological functions and processes performed by populations of species (Maltby, 2013). However, current assessments often focus primarily on individual effects (Forbes et al., 2008), neglecting important population-level processes, like intraspecific competition for resources, which can significantly alter individual responses to chemical exposure (Fleeger et al., 2003; Knillman et al., 2012; Vaugeois et al., 2020; Allen et al., 2021). Therefore, focussing on individual level impacts may not provide a clear link to chemical induced changes in the ecological attributes that drive the performance of functions and processes, upon which the delivery for ecosystem services rely.

Therefore, the overarching aim of this chapter is to assess how different impact pathways affect the energy uptake by individuals, through the consumer resource relationship, and how these impacts influence ecological functions performed by populations of two freshwater shredder species, *Asellus aquaticus* and *Gammarus pulex*. Specifically, it focuses on their roles in leaf processing and prey provision, which are critical for the delivery of ecosystem services of a recreational fishery.

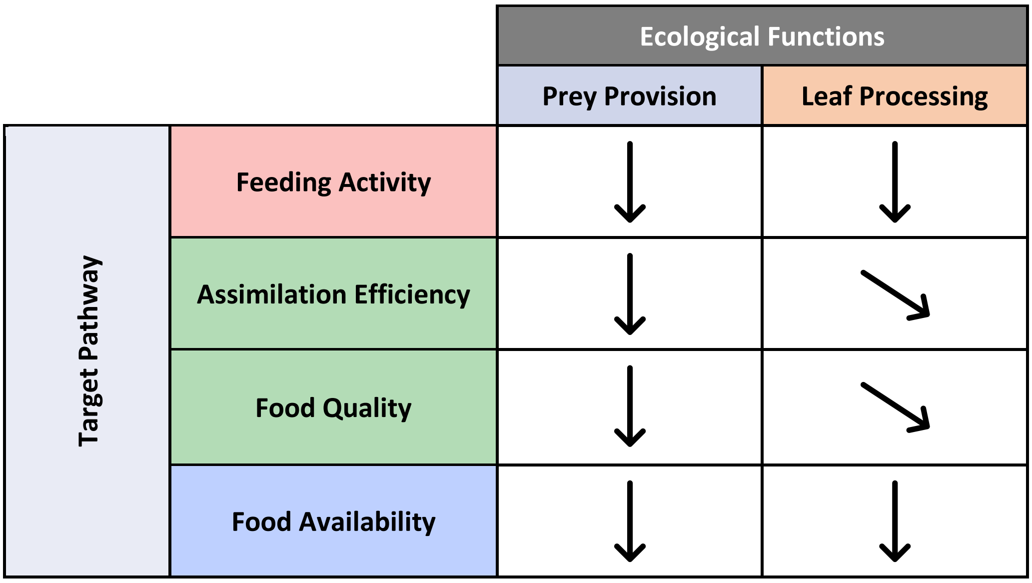
Individual based Dynamic Energy Budget Models (DEB IBMs) for *Gammarus pulex* and *Asellus aquaticus* will be used to simulate population-level responses to different pathways of impact;

direct impacts of chemicals stress on consumers (i.e. reduced feeding rates and assimilation efficiency) and direct impacts on resources, including declines in food quality and availability (Table 4.1). The study will compare how these impacts translate to population abundance, leaf litter processing, and prey provision for fish, assessing the maximum deviation from the baseline, the duration of effect and the cumulative impact of the population level endpoints and ecological functions. Additionally, it will compare the relative sensitivity of population-level responses to direct and indirect effects on energy uptake between the two species.

It is expected that population level responses will differ between pathways of impact (1). It is expected that prey provision, defined as the biomass of the adult portion of the population, will decline across all pathways. This decrease is attributed to reduced growth rates stemming from diminished food assimilation (2). While reductions in feeding activity and food availability will result in the greatest reductions in leaf processing due to the direct effect on individual consumption (3). In contrast, reductions in assimilation efficiency and food quality, assuming there is no feedback between energy assimilation and feeding rate, will have a lesser impact on leaf processing since they do not directly affect consumption (4) (Figure 4.1).

The chapter therefore addresses the following research questions:

- How do different pathways of impact on energy uptake by individuals translate to population level responses by populations of the freshwater shredder species *Asellus aquaticus* and *Gammarus pulex?*
- How do different pathways of impact on energy uptake by individuals translate to performance of ecological functions, specifically leaf processing and prey provision, by the two populations?
- What is the relative sensitivity of population-level responses to these pathways of impact between the two shredder species, *Gammarus pulex* and *Asellus aquaticus*?



		Ecological Functions	
		Prey Provision	Leaf Processing
Target Pathway	Feeding Activity	↓	↓
	Assimilation Efficiency	↓	↘
	Food Quality	↓	↘
	Food Availability	↓	↓

Figure 4.1: Hypothesised impact on the ecological functions, prey provision, and leaf processing, for four pathways of impact studied

4.2 Methods

4.2.1 Overall Approach

In this chapter, DEB IBMs for *Gammarus pulex* and *Asellus aquaticus*, established in Chapter 3, were used to simulate impacts on consumer and resource and subsequent impact on the energy uptake by individuals, and to assess their effects on the performance of ecological functions by populations. The models are described using the ODD protocol (Overview, Design, Concepts, Details; Grimm et al., 2006). State variables & scales, process overview, and scheduling are described in Chapter 3.

4.2.2 Design concepts

Basic principles: The model is based on the basic principles of Dynamic Energy Budget theory (Kooijman, 2010), which posits that resource uptake by individuals scales with their surface area, while energy allocation scales with their volume. The theory is based on conservation of mass and energy. Space is not modelled explicitly, but species populations are assumed to exist on a patch of one square meter with move movement of individuals between or within patches.

Emergence: Individual life-history traits, such as growth, maturation time, and reproductive effort, emerge from rules of metabolic organisation. Population dynamics emerge from indirect interactions between individuals via competition for resources and the presence of a hypothetical toxicant.

Interaction: Individuals in the model interact with each other indirectly through resource competition. Population growth is constrained by the amount of resource in the system (carrying capacity); when population densities exceed the available resource, modelled individuals experience starvation mortality. The amount of resource in the model never reaches zero. Density dependence in the model emerges from modelled indirect interactions. Embryos in broods are explicitly linked to females, resulting in embryo mortality when females die due to starvation or background mortality.

Stochasticity: Species specific background mortality is implemented as a stochastic process that occurs daily. Furthermore, as DEB parameters are constants, a scatter multiplier is added to the surface area-specific ingestion rate to implement a measure of variation between individuals. The scatter multiplier is a random number pulled from a log-normal distribution (Kooijman et al., 1989; Martin et al., 2013) with a standard deviation of 0.1.

Initialisation: DEB parameters for *Asellus aquaticus* and *Gammarus pulex* were obtained from the add my pet database. An initial 500 individuals were simulated for 20 years at constant temperature (20◦C) and baseline food availability (400 mg per m^2) with 100 replicates. The first 10 years were ‘burned’ with the aim of removing any remaining impact of the initial conditions, focussing on the model behaviour after it has stabilised.

Observation: The primary endpoints of interest were population abundance, cumulative population consumption (indicative of leaf processing) over time, and adult biomass. Adult biomass reflects prey provision and is representative—though not directly related to—the selectivity of *Gammarus* and *Asellus* by predatory fish species particularly those important for recreational fisheries, targeting specifically larger individuals. Additionally, cumulative population mortality and reproduction, and the amount of resource in the system were recorded. Simulation outputs were reported every thirty days, beginning on day 10 of the stress period and running for 10 years.

4.2.2.1 Simulation Scenarios

This study investigates four different pathways of impact on the consumer resource system. Since, within this model, reductions in digestion efficiency of the consumer and the nutritional quality of the resource are equivalent to a reduction in the amount of energy gained per unit of resource consumed, they are simulated via the same method and referred to from here as assimilation efficiency. Therefore, the population responses to three effect scenarios were simulations: 1) reductions in consumer feeding rate; 2) reductions in consumer assimilation efficiency; 3) reduction in resource availability. Hypothetical chemical stress is simulated by applying a relative reduction to the respective parameters from 10 to 100%.

For clarity, the term "stress" refers to the period during which the hypothetical stressor affects individual-level consumer-resource interactions, while "response" describes the population-level impacts of stress on either the consumer or the resource. The stress period begins after an initial 10-year period and continues for an additional 10 years. Throughout the simulation, the stress is assumed to be constant across all impact pathways, with no mechanism for damage accumulation at the individual level.

Individual uptake and assimilation of energy

In all models, the amount of energy assimilated by each individual, P_A, in each timestep is calculated using the following equations:

$$P_A = P_x \cdot kap_x$$

Equation 4.1

Where P_x [J], the amount of food ingested, is multiplied by, kap_x, the digestion efficiency. Where P_x is:

$$P_x = P_{Xm} \cdot\ L^2 \cdot f$$

Equation 4.2

Where P_{Xm} is the surface-area-specific ingestion rate in [J/cm^2 ·d]., L is the structural length of the individual in cm, and f (-) is the scaled amount of food ingested based on the scaled functional response (Holling type II):

$$f = \frac{X}{X + K}$$

Equation 4.3

Here, X is food density (J / m^2) and K is the individual half saturation constant:

$$K = \frac{P_{Xm}}{Fm}$$

Equation 4.4

Where Fm is the maximum surface area specific searching rate [J/cm^2 ·d]. This parameter obtained from the DEB parameter calibration and is available for each species from the AddMyPet database (Kooijman, 2010).

4.2.2.2 Direct effects on consumers

Reduction in individual feeding rate

To simulate changes in feeding behaviour, stress was applied to the surface-area-specific ingestion rate of the individual (p_{Xm}):

$$p_{Xm_{stressed}} = p_{Xm}\ \cdot (1 - stress)$$

Equation 4.5

This is then used in Eqns 4.1 and 4.3. Resulting in a reduction in the total amount of food ingested and subsequently assimilated. From here on, changes in the individual feeding behaviour refer to change in the feeding rate of an individual and changes in the total amount of energy consumed by and individual – referring to the fact that the feeding rate of individuals remains the same but the consumption by individuals is length dependent (Eqn 4.2).

Reductions in individual digestion efficiency

Change in both digestion efficiency and nutritional quality of the food can be simulated by changing the assimilation efficiency of individuals (DEB notation: kap_x). Assimilation efficiency represents the proportion of ingested energy that is ultimately assimilated. This can be modelled under stress conditions using the following equation:

$$kap_{x_{stressed}} = kap_x \cdot (1 - stress)$$

Equation 4.6

4.2.2.3 Direct effects on the Resource

Reductions in food availability

The change resource in each timestep is calculated by the following equation:

$$\frac{dResource}{dt} = r \cdot (resourceK - resource)$$

Equation 4.7

For shredders, changes in resource availability are representative of effects on the availability of the preferred resource of shredders. The carrying capacity (resourceK) of the resource was reduced simulated a change in the availability of preferred resource.

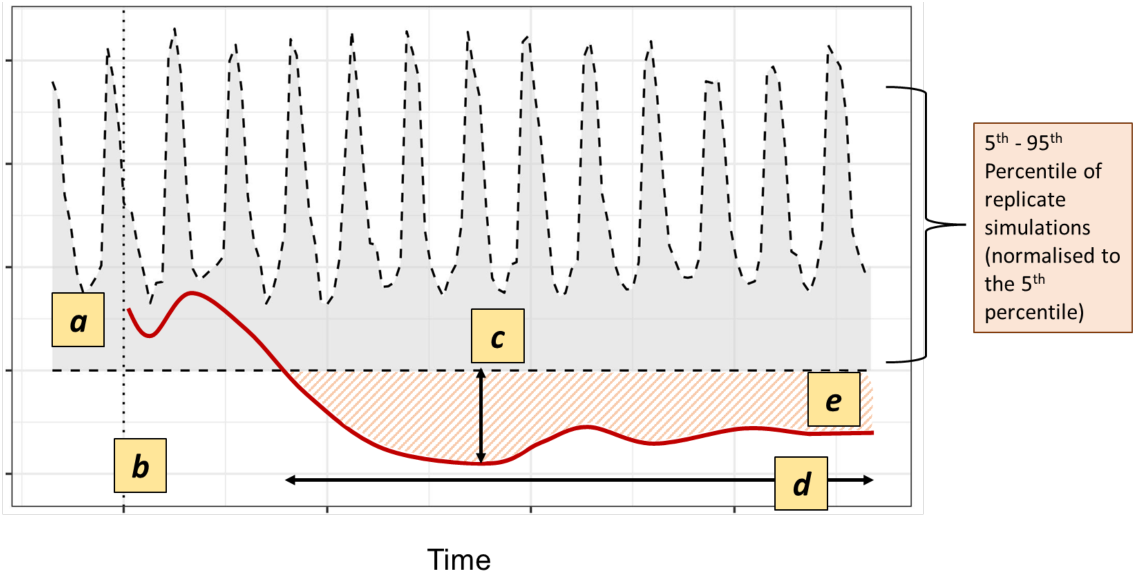
Reduction in the food quality.

Changes in the nutritional quality of food result in a reduced amount of energy assimilation from per unit of food ingested. Therefore, to simulate reduction in food quality, the assimilation efficiency was reduced (Equation 4.6).

4.2.3 Analysis of model outputs

Population outputs (described section 4.2.2) are reported every 30 days for 10 years, with the first reported timestep 10 days after the start of the stress period. To capture the variation across the 100 replicate simulations and establish the baseline situation from which to calculate deviation in the treated population, the median, 5th, and 95th percentile values of population level endpoints across the 100 replicates were reported in each time step (Figure 4.2).

The threshold of population collapse was the percentage of surviving populations of the 100 replicates. For the population abundance, prey biomass and leaf consumption, the magnitude, duration, and the cumulative impact was compared between effect scenarios. For the magnitude of effect for population abundance and leaf processing, the maximum deviation of the median abundance of the stressed population from the 5th percentile of the baseline population was calculated (c in Figure 4.2) and then plotted against each effect level for each effect scenario. Prey biomass exhibited different dynamics compared to population abundance and measurement of effect was affected by temporal asynchrony. Therefore, the magnitude of impact was assessed instead using the change in mean prey biomass across replicates between treatments rather than the maximum deviation from the 5th percentile of the baseline (A more detailed explanation is provided in Appendix 4.1). The duration of impact was defined as the percentage of reported timepoints where the median abundance fell below the 5th percentile of the baseline scenario (d in Figure 4.2). To assess the both the magnitude and duration of impact, the cumulative impact was calculated, summing the difference between the median and the 5th percentile of the baseline for all reported timesteps (e in Figure 4.2). Differences in the median cumulative population mortality and reproduction across replicates, and the median resource across time were also calculated as explanatory variables. The median cumulative population mortality was compared between treatments within the first 70 days. Cumulative reproduction and leaf processing was compared after 1 year of the stress period.



a. Median of the stressed population
b. Beginning of the stress period
c. Maximum deviation of the median from the 5th percentile of the baseline
d. Duration of Response
e. Cumulative Impact

Figure 4.2: Definition of the baseline situation (where the effect level is 0%) using the 5 – 95th percentile values of the 100 replicates of the baseline scenario. The metrics of impact are the maximum deviation of the median of the stressed population from the 5th percentile of the baseline (c), Duration of response (d), and the cumulative impact (e: the shaded area under the 5th percentile of the baseline).

4.3 Results

4.3.1 Population level response

Simulated chemical stress resulted in a reduction in the median population abundance of both *Asellus* and *Gammarus*. However, the magnitude, duration, and cumulative impact of the population response was dependent on the pathway of impact (Figure 4.3). Population abundance was most responsive to reductions in food availability or assimilation efficiency with a 20% effect resulting in deviation from the 5th percentile of the baseline. A 20% reduction in assimilation efficiency resulted in a maximum deviation of population abundance of -17% and -6% for *Asellus* and *Gammarus*, respectively (Figure 4.3A). For the same level of effect, the median population abundance fell below the bounds of the baseline for 16.3% and 4.1% of the duration of the experiment period, for *Asellus* and *Gammarus* respectively (Figure 4.3B). Reductions in food availability had a comparable response (Figure 4.3). At a 20% reduction in food availability, the median population abundance for *Asellus* fell 21% below the 5th percentile of the baseline, while for *Gammarus* population abundance fell below the baseline with a 30% reduction in food availability by 14%. Here, the duration of the response is also comparable to reductions in assimilation efficiency with a 20% reduction in food availability resulting in deviation from the bounds of the baseline for 16.5% of the experiment time for *Asellus* and for 20.3% of the experiment period for *Gammarus* with a 30% reduction in food availability. Reductions in assimilation efficiency and food availability had comparable cumulative impact over the 10-year stress period on population abundance, with assimilation efficiency having a greater cumulative on *Asellus* populations than *Gammarus* up to the 50% effect level, -44% compared to -26%, beyond which impacts on *Gammarus* were greater, with a 60% reduction in assimilation efficiency resulting in -61% cumulative impact compared to -81% for *Gammarus*. At the 50% effect level, however, reductions in assimilation efficiency for both species resulted in around a 50% deviation of the median population abundance from the 5th percentile of the baseline. The median population abundance remained outside the baseline for nearly the entire experiment duration at the 50% effect level for *Asellus* and the 60% effect level for *Gammarus*.

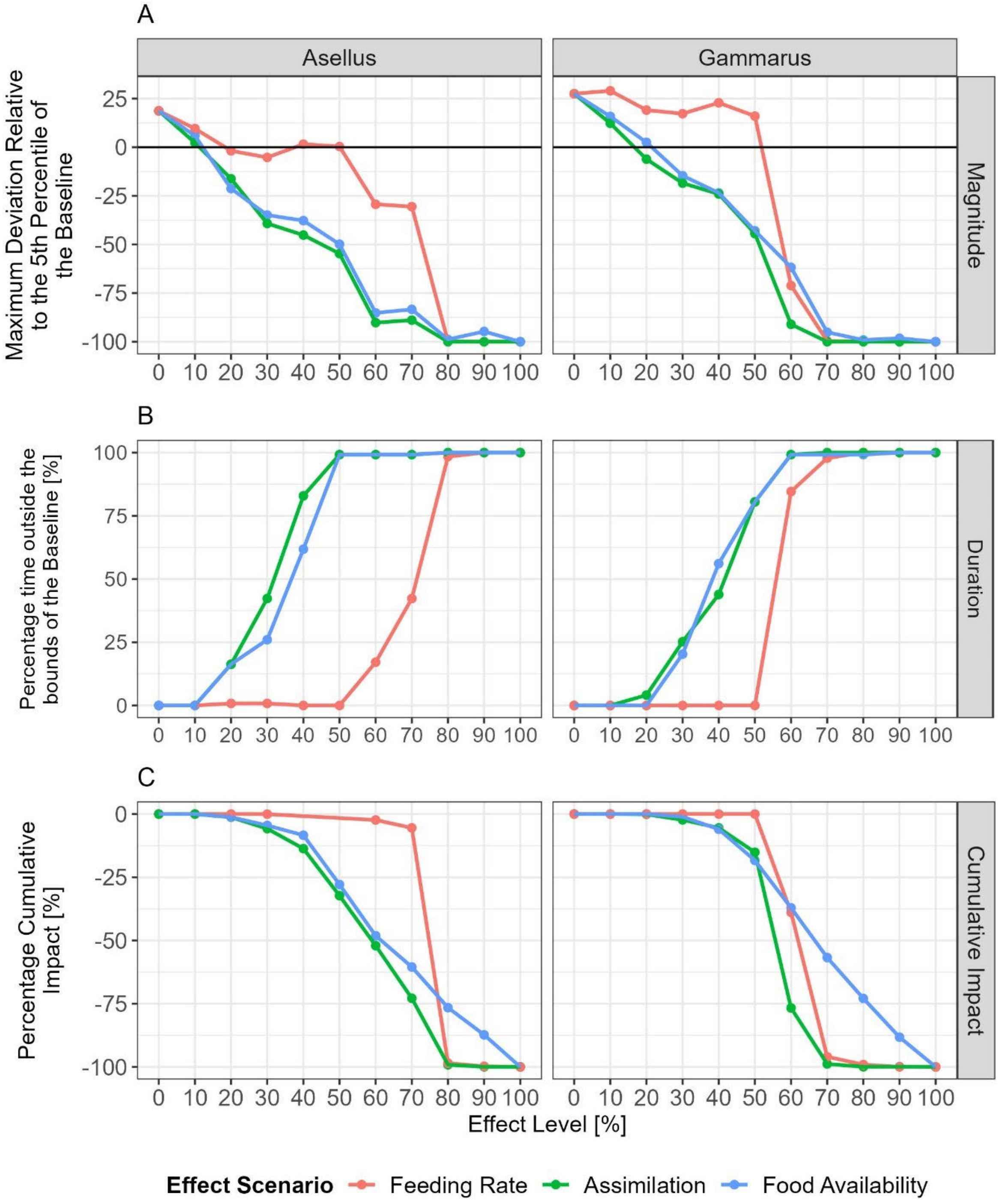


Figure 4.3: The impact of three effect scenarios—Feeding Rate (red), Assimilation (green), and Food Availability (blue)—on *Asellus* and *Gammarus* population abundance, evaluated across three metrics: (A) Magnitude (Maximum Deviation Relative to the Baseline), (B) Duration (percentage time outside the bounds of the Baseline), and (C) Cumulative Impact (percentage cumulative impact). Each subplot shows the relationship between effect level (%) and the respective impact metric for both species.

Median population abundance was more resistant to reductions in individual feeding rates than the other effect scenarios. With the median population abundance, not until a 60% reduction in feeding rate was required to cause the median population abundance of both species to fall below the 5th percentile of the baseline (Figure 4.3.A). When looking at the cumulative impact, results follow similar patterns to the magnitude and time under the curve, however, reductions in feeding rates do not result in deviation from the baseline by more than 10% until the 70% effect level for both species (Figure 4.3.C).

Reductions in food availability were most resistant in terms of total population collapse (Table 4.1). A 70%-80% reduction in assimilation efficiency or feeding rate resulted in all 100 simulated populations becoming extinct for both species. In contrast some populations persisted with a 90% reduction in food availability and total collapse was only observed at the 100% effect level (i.e. no food). Specifically, populations began to collapse at the 60% and 70% effect levels for *Asellus* and *Gammarus* respectively. Even with a 90% reduction in food availability, populations persisted, though their abundances were reduced to just 5% of the 5th percentile of the baseline (i.e. 95% deviation from the baseline).

Table 4.1: The percentage of collapsed populations at the end of the 10-year stress period for *Gammarus* and *Asellus* within each effect scenario (100 replicate simulations)

	Assimilation Efficiency		***Feeding Rate***		***Food Availability***	
Effect Level [%]	***Asellus***	***Gammarus***	***Asellus***	***Gammarus***	***Asellus***	***Gammarus***
0	0	0	0	0	0	0
10	0	0	0	0	0	0
20	0	0	0	0	0	0
30	0	0	0	0	0	0
40	0	0	0	0	0	0
50	0	0	0	0	0	0
60	0	31	0	1	9	0
70	64	100	0	100	55	18
80	100	100	100	100	83	83
90	100	100	100	100	95	91
100	100	100	100	100	100	100

Median cumulative mortality differed between effect scenarios. In the first 40 days of the stress period, median cumulative mortality increased with increasing effect level for reductions in food availability and assimilation efficiency from the 40% effect level, doubling that of that of the baseline increasing by 123% for *Asellus* and 20% for *Gammarus* (Figure 4.4). Reductions in feeding rates had no impact on the median cumulative population mortality for both species until the 70% effect level, increasing by 104% for *Asellus* and over 200% for *Gammarus*.

Cumulative population reproduction followed the same pattern to mortality, decreasing with increase effect level for all effect (Figure 4.5). The reduction in median cumulative population reproduction was greatest for reductions in assimilation efficiency and food availability. For *Gammarus*, median cumulative population reproduction fell almost linearly with increasing effect level up to the 60% effect level, beyond which reduction in assimilation efficiency had a greater impact on reproduction (-78% compared to -65%) (Figure 4.5). In contrast, for *Asellus*, reductions in assimilation efficiency had the greatest impacts on population reproduction up to the 50% effect level, beyond which, impacts on food availability and assimilation efficiency were similar. Reductions in feeding rates had little impact on the cumulative population reproduction, particularly for *Gammarus*, For *Asellus*, cumulative reproduction fell by -23% compared to the baseline at the 50% effect level (Figure 4.5), beyond which populations began to collapse (Table 4.1).

With regard to the resource, the median amount of resource in the system increased with increasing effect level for reductions in feeding rates and assimilation efficiency, most significantly beyond the 50% effect level, reaching the carrying capacity of 400 mg at the collapse thresholds for both species (Figure 4.6). In contrast, the amount of resource in the system remained constant despite reductions in food availability, corresponding with a reduction in consumption rates.

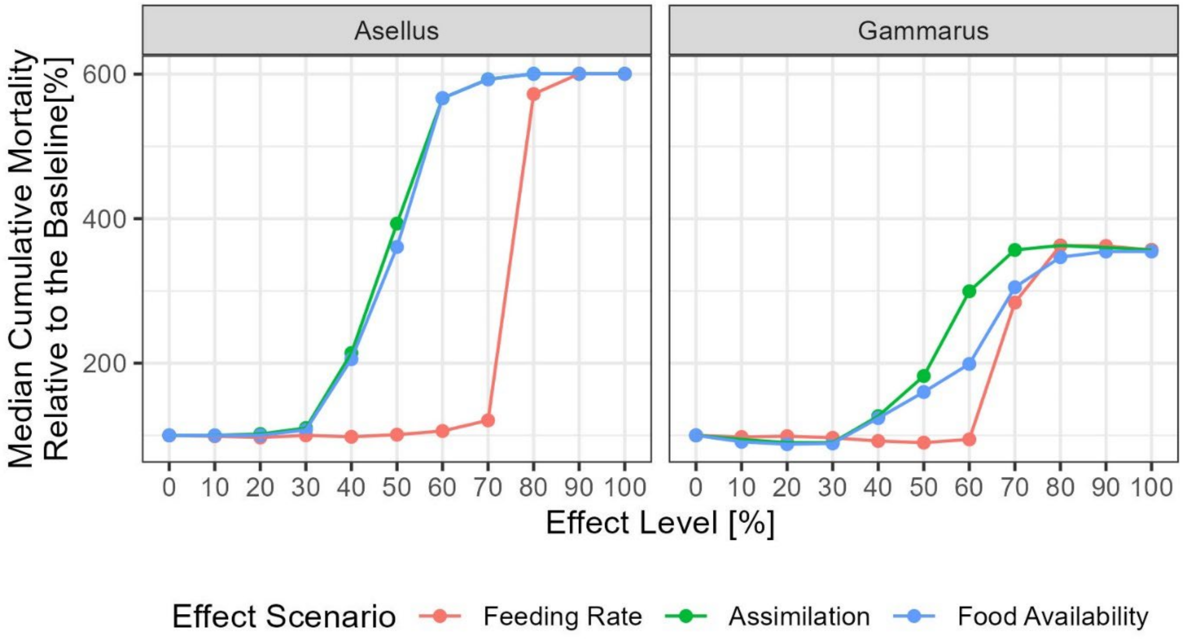


Figure 4.4: Median cumulative mortality relative to the Median of the baseline for populations *G.pulex* and *A.aquaticus* for three effect scenarios—Feeding Rate (red), Assimilation (green), and Food Availability (blue) —within 40 days of the start of the stress period.

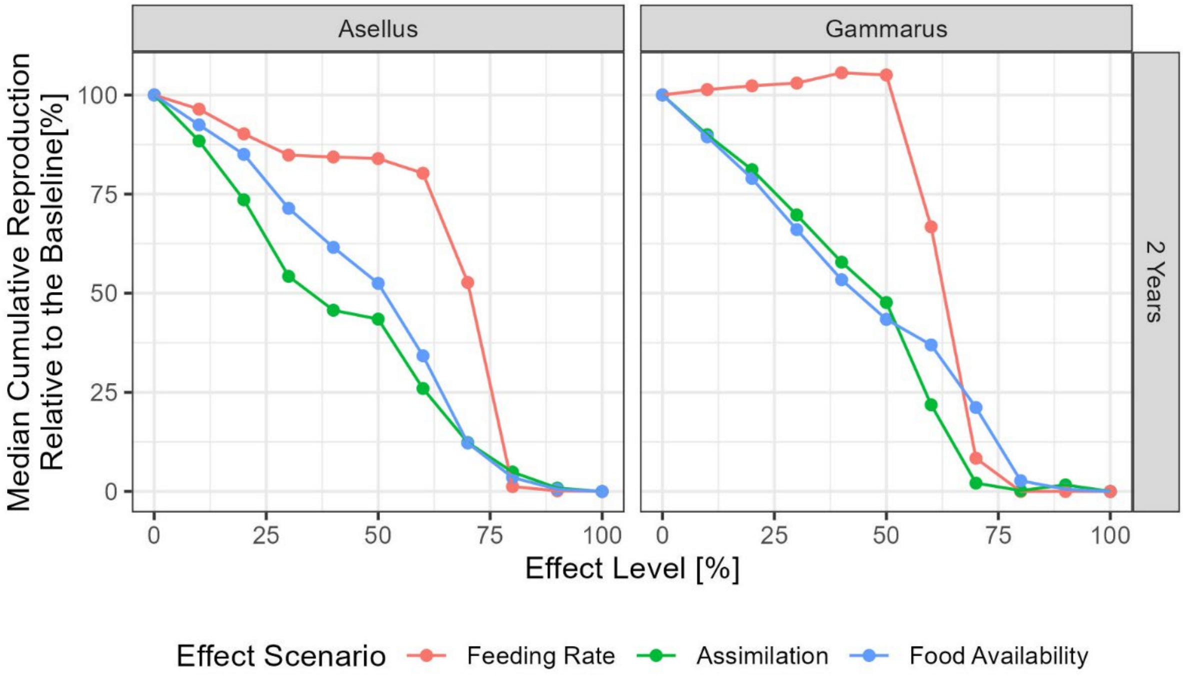


Figure 4.5: Median cumulative reproduction relative to the Median of the baseline for populations *G.pulex* and *A.aquaticus* for three effect scenarios—Feeding Rate (red), Assimilation (green), and Food Availability (blue)

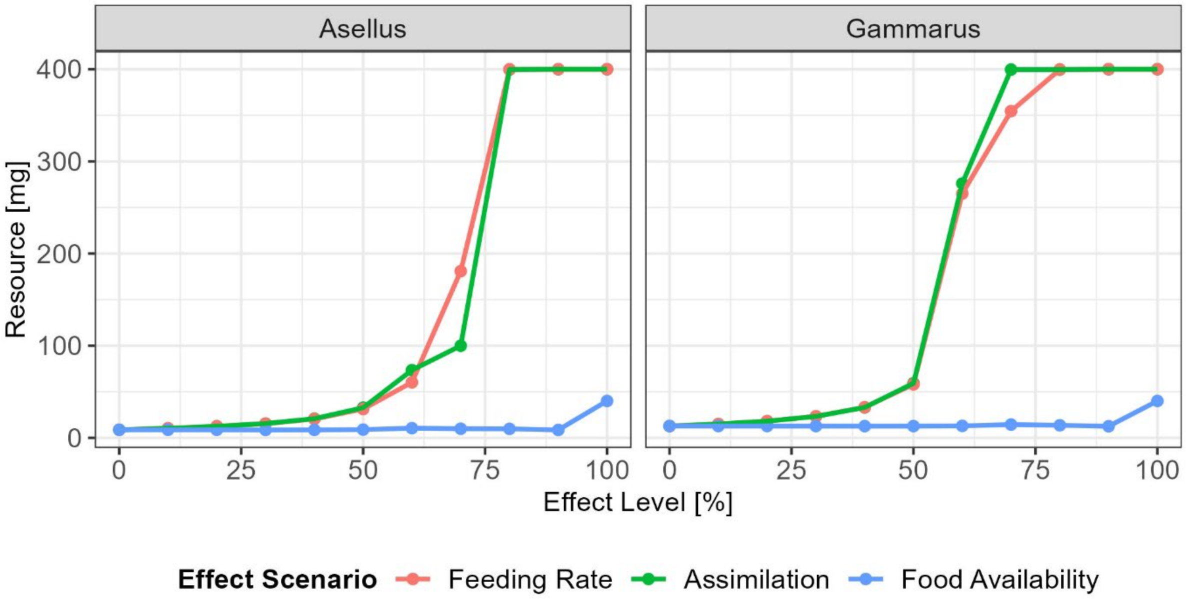


Figure 4.6: Median amount of resource in the experiment system over 10 year simulation period for populations *Gammarus pulex* and *Asellus aquaticus* with increasing effect level for three effect scenarios—Feeding Rate (red), Assimilation (green), and Food Availability (blue).

4.3.2 Ecological functions

4.3.2.1 Prey provision.

Similar to population abundance, prey provision (i.e., adult biomass) was most responsive to reductions in food availability and assimilation efficiency (Figure 4.7) with just a 10% reduction in food availability or assimilation efficiency results in a reduction in the prey biomass by at least 10%. (Figure 4.7A). The time outside the bounds of the baseline followed similar patterns for both food availability and assimilation efficiency until the 60% effect level for *Asellus* and the 50% effect level for *Gammarus*, after which the responses deviated from each other (Figure 4.6B). The duration of response increased with increasing stress for both species with notable declines from the 20% effect level for *Asellus* and the 30% effect level for *Gammarus*. For *Asellus*, both reductions in food availability and assimilation efficiency result in a sharp increase in response duration followed by a plateau at 56 and 61% between the 40 and 60% effect levels. While for *Gammarus* the increase in response duration is steady, falling to 65 and 68% for a 50% reduction in food availability and assimilation efficiency, respectively. The cumulative impacts were similar for food availability and assimilation efficiency for *Asellus* but reductions in assimilation efficiency had a greater cumulative impact on *Gammarus* populations from the 50% effect level where reduction in assimilation efficiency had a greater impact than other effect scenarios. For *Gammarus*, both effects scenarios resulted in very similar responses until the 60% effect level where a reduction in assimilation efficiency both species resulted in a greater magnitude of impact, -95% of the baseline compared to -75% of the baseline for food availability.

Prey provision was less responsive to reduction in feeding rates than the other pathways of impact studied, although differed between the two species (Figure 4.7A). *Asellus* showed a slight increase (up to 5%) at 10–40% reductions, followed by a moderate decline (-15% at 70% effect level). *Gammarus* biomass remained stable until a threshold at 50% reduction, after which it sharply declined (71% decrease at 60% effect level). However, the duration of impact was less than 10% of the experiment duration (i.e. 2 years in total across the 20-year simulation) until the 60% effect level, where the maximum deviation was -26% and the duration was 27% of the experiment time. Prey provision by *Gammarus* did not deviate from the bounds of the baseline until the 60% effect level, where the maximum deviation was -82%, and the response duration was >75% of the experiment time. When looking at the cumulative impact, the impacts were similar for both species up to the 50% effect level beyond which reductions in feeding rates had a greater impact on *Gammarus* populations with the cumulative impact 50% below the baseline at the 60% effect level and -94% at the 70% effect level. Whereas for *Asellus* the cumulative impact was only -7% and the 60% effect level and -35% at the 70% effect level with the population collapsing at beyond the 80% effect level.

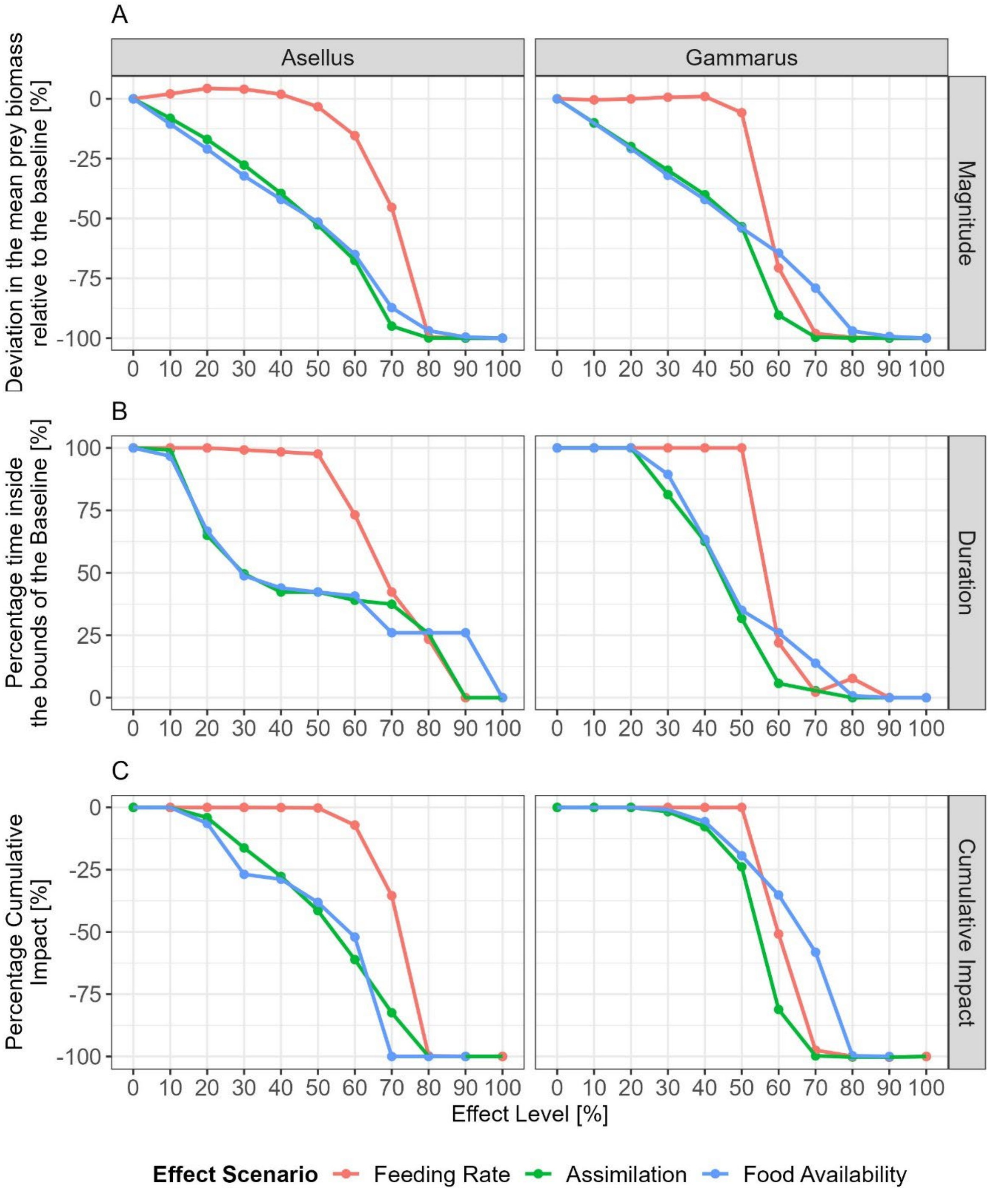


Figure 4.7: The impact of three effect scenarios—Feeding Rate (red), Assimilation (green), and Food Availability (blue)—on *Asellus* and *Gammarus* Prey Provision (Adult Biomass), evaluated across three metrics: (A) Magnitude (Deviation in the mean prey biomass relative to the baseline), (B) Duration (percentage time outside the bounds of the baseline), and (C) Cumulative Impact (percentage cumulative reduction in prey provision). Each subplot shows the relationship between effect level (%) and the respective impact metric for both species.

4.3.2.2 Leaf Processing.

For both species, negative impacts on leaf processing (i.e. total amount of resource consumed) were observed for all effect scenarios from the 10% effect level (Figure 4.7). However, in contrast to the findings for population abundance and prey provision, the effect of reductions in food availability and assimilation efficiency on leaf processing were markedly different. Reductions in food availability had the greatest impact on leaf processing rates with almost a linear decrease in the magnitude of impact on leaf processing with increasing effect level (Figure 4.7.A). Impacts on leaf processing caused by a reduction in food availability were also long lasting, deviating from the baseline close to 100% of the simulation time from the 10% effect level (Figure 4.7.B). Reductions in feeding rates and assimilation efficiency had little impact on leaf processing until the 50% effect level, where leaf processing most greatly impacted by reductions in feeding rates, falling to -18% for *Asellus* and -27% for *Gammarus*, while with reduction in assimilation efficiency leaf processing fell to only -12%. Reductions in both feeding rates and assimilation efficiency had little impact (less than -20%) on the cumulative leaf processing for both species until the 50% effect level for both species (Figure 4.7.C), beyond which, reductions in assimilation efficiency had the greatest impact on leaf processing, particularly for *Asellus*. This corresponds with a reduction in population abundance and increase in mortality (Figure 4.3B).

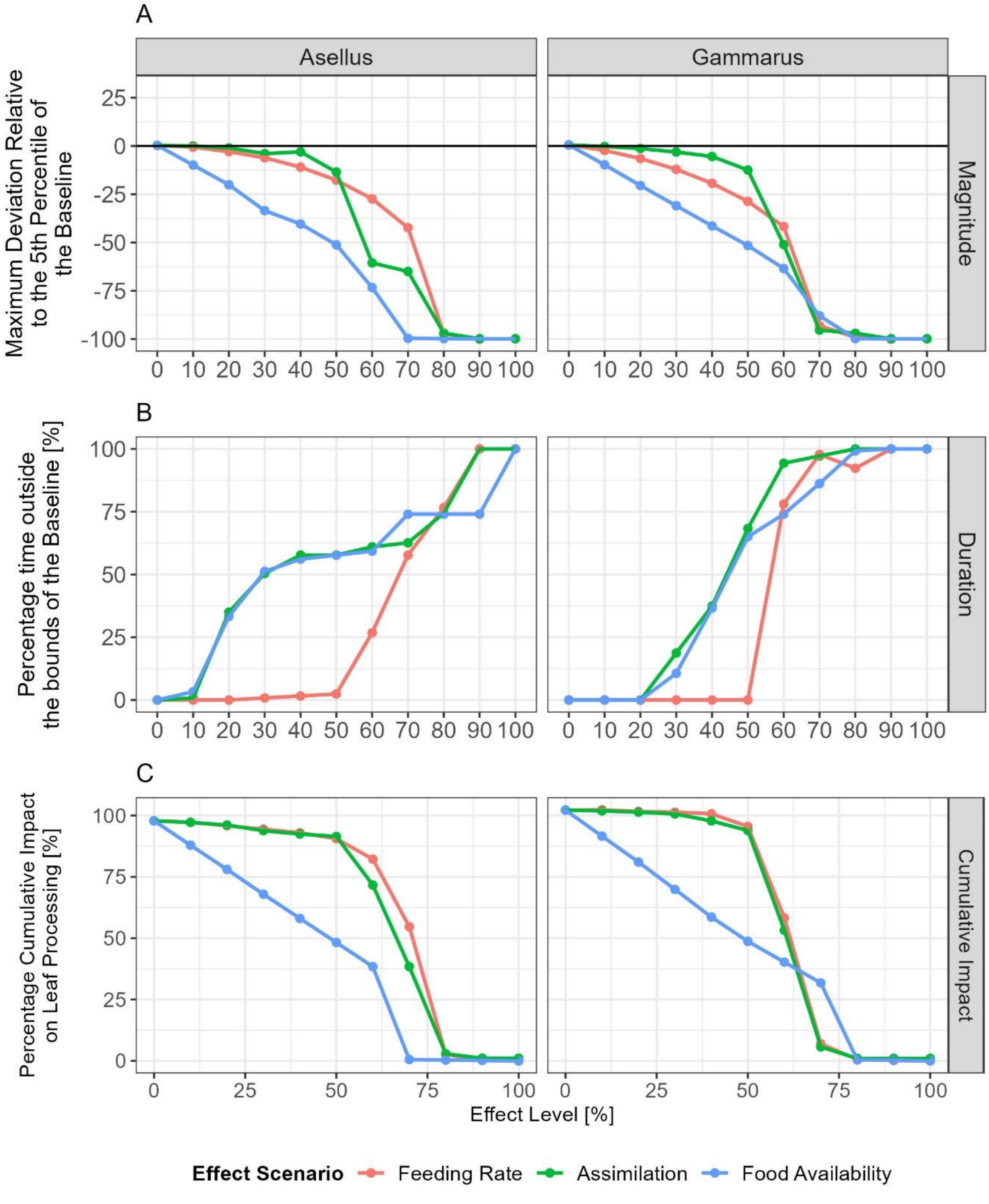


Figure 4.8: The impact of three effect scenarios—Feeding Rate (red), Assimilation (green), and Food Availability (blue)—on *Asellus* and *Gammarus* Leaf Processing (Cumulative Consumption), evaluated across three metrics: (A) Magnitude (maximum deviation relative to the baseline), (B) Duration (percentage time outside the bounds of the baseline), and (C) Cumulative Impact (percentage cumulative impact). Each subplot shows the relationship between effect level (%) and the respective impact metric for both species.

4.4 Discussion

The aim of this chapter was to use single-species, individual-based Dynamic energy budget (DEB) populations models to explore how chemical effects on consumer-resource interactions translate to consumer population level effects and influence key ecological functions of leaf processing and provision of food for fish. The study focussed on two freshwater shredder species, *Gammarus pulex* and *Asellus aquaticus*, and effects of chemical stress on consumers (reduced feeding rates and assimilation efficiency) and resource (food quality and availability) were investigated. Within the DEB models, reductions in food quality and assimilation efficiency were modelled in the same way and therefore it is not possible to distinguish between them. It was predicted that stress effect on the consumer and resource would result in a reduction in prey provision, but leaf processing would be principally affected by a reduction in feeding rate and food availability.

4.4.1 Population level impacts

Population responses varied across the impact pathways studied, as demonstrated by Gabsi et al. (2014) and Galic et al. (2017). Both studies employed individual-based models of differing complexity to evaluate population-level effects of various consumer impact pathways. In this chapter, both species populations were highly responsive to and similarly impacted by effects on the resource (food availability) and the consumer (assimilation efficiency), although the mechanisms differ. When food availability decreases, resources become externally limited, preventing individuals from meeting their energy demands and leading to higher rates of starvation mortality. This pattern aligns with the Lotka-Volterra consumer-resource model (Lotka, 1925; Volterra, 1926; Tilman, 1982), which predicts that as prey (resources) become scarce, predator populations decline due to insufficient food. These concepts are also supported by field observations of animal population densities in relation to primary production (Whittaker, 1975). However, low assimilation efficiency increases energy demands without a corresponding increase in food intake, forcing individuals to consume more to maintain metabolic processes. This leads to starvation when resources are insufficient to meet these heightened demands, particularly in nutrient-limited environments (Hessen et al., 2013). Furthermore, metabolic constraints, such as poor resource quality, which result in reduced assimilation efficiency, are associated with reduced growth and reproduction in individuals (Becker and Boersma, 2003). Here, this further exacerbates population declines beyond that of mortality alone. Consequently, in this context, the cumulative impact on population abundance was more strongly associated with assimilation efficiency than with food availability, particularly at higher effects levels.

Population abundance decreased almost linearly with a reduction in food availability. This agrees with previous field studies showing a positive correlation between shredder density and leaf litter availability (Cummins et al., 1973; Murphy and Giller, 2000). However, reductions in individual assimilation efficiency also had greater negative impacts on population abundance. While invertebrate feeding rates and leaf mass loss of *Gammarus* and *Asellus* have been observed to decrease when offered conditioned leaf litter exposed to antimicrobial compounds (Dimitrov et al., 2014; Feckler et al., 2016), few population studies have been conducted focussing on effects on species abundance with chemical impacts on the resource availability (Zubrod et al., 2019). In the field, long term fungicide exposure in streams is associated with reductions in macroinvertebrate communities (Lin et al., 2012; Fernández et al., 2015), particularly in colder climates where fungal growth rates are lower (van der Linden et al., 2019). While in mesocosm studies, fungicide exposure resulted in declines in gammarid density associated with loss of fungal biomass (Zubrod et al., 2014). There, the abundance of gammarids fell by less than 50% after 56 days, which was less pronounced than the population declines recorded in the current modelling study. However, this discrepancy is likely due to the lack of dose-dependent decreases in resource quality and differences in the level of intraspecific competition in the experimental system (del Arco et al., 2016). However, results from this modelling study are only one fixed scenario whereas, in natural environments, the impact of chemical stress on the availability and quality of leaf litter may vary between sites due to differences in nutrient availability and other environmental factors (Rasmussen et al., 2018).

Similar patterns were observed for reductions in assimilation efficiency, having immediate and severe impacts, with population abundance declining linearly as effect levels increase. Although empirical studies on population-level effects are limited, it is well-documented that such reductions seldom occur in isolation and frequently affect both microbial communities and the digestive enzymes of consumers (Dedourge-Geffard et al., 2009). Chemicals like fungicides and contaminants with fungicidal properties (e.g., copper) can impair both microbial communities and consumer digestion (Dedourge-Geffard et al., 2009; Zubrod et al., 2015). Additionally, decreased nutritional quality or digestion efficiency can lead to increased competition for limited resources, further exacerbating negative impacts on population abundance. Consequently, understanding these impacts is critical for chemical risk assessment.

In contrast, populations exhibited the greatest resistance to reductions in individual feeding rates, as observed in modelling studies by Gabsi et al. (2014) and Galic et al. (2017) using a *Daphnia* IBM and *Gammarus* DEB IBM, respectively. This resilience can likely be attributed to stressor-induced competitive release: whereby, in a population at carrying capacity, exposure to a chemical stressor that impairs population growth can reduce intraspecific competition for resources (Forbes et al., 2001). The reduction in competition can mitigate chemical induced mortality over time, supporting population resistance by offsetting declines in abundance (Postma et al., 1994; Forbes et al., 2001; Liess, 2002; Beketov and Liess, 2005). However, once a critical threshold is surpassed, population decline becomes inevitable. In this study, population abundance remained stable until feeding rates were reduced by 60% for *Gammarus* and 50% for *Asellus*, with population collapse occurring at 80% and 70% reduction levels, respectively. Thresholds of collapse differ between models. Where Gabsi et al. (2014), a *Daphnia* IBM, reported a 90% threshold of collapse for *Daphnia* feeding rates, and Galic et al. (2017), whose model underpins this study, showed that an 80% reduction in *Gammarus pseudolimnaeus* feeding led to population collapse. This is likely due to differences in the description of the individual, i.e. differences in individual energy budget parameters highlighting how modelled processes can influence tolerance to reduced energy intake. Although population-level data on *Asellus* responses to chemical stress or feeding inhibition are limited, similar patterns have been observed in *Gammarus*. Baird et al. (2007), for instance, identified a critical threshold of a 50% reduction in feeding rates as a precursor to population collapse in *Gammarus pulex* using a dynamic energy budget model. With regard to the relevance of the finding to impacts in the field, Baird et al. (2007) reported that a 50% reduction in *Gammarus* feeding during short-term *in situ* assays conducted downstream of pollution discharge sites was linked to a substantial decline in *Gammarus* populations at these sites compared to reference sites located upstream. Suggesting that DEB IBMs may be able to indicate biologically relevant population level impacts of reductions in *Gammarus* sp. feeding. The discrepancies between these results and those of Baird et al. (2007) may stem from system-level factors, such as interspecific competition for resources, which can increase the sensitivity of the more sensitive species (Lüring and Roessink, 2006; del Arco et al., 2016a). This will be explored further in Chapter 5. They may also emerge from differences in model assumptions such as temperature and baseline food availability, given that field organisms are already food limited compared to those grown in the laboratory (Romero-Blanco and Alonso, 2022) (i.e. those often used to calibrate DEB parameters)

Furthermore, it is important to note that the model used in this study is a closed model with only one type of resource available. In natural environments, *Gammarus* and *Asellus* do not rely exclusively on leaf litter; thus, a reduction in the availability of one energy source may be mitigated through "prey switching." When their preferred food source is scarce, they may turn to alternative nutritional sources, which could support population sustainability. For example, *Gammarus* also feed on unconditioned matter (Bloor et al., 2011) and are known to exhibit cannibalistic (Dick, 1995) and predatory behaviour (Kelly et al., 2002), while *Asellus* consume algae and macrophyte matter (Lafuente et al., 2021). Consequently, the results presented here may reflect a worst-case scenario of chemical impact on the food availability for shredder populations, assuming no other food sources are available. Nonetheless these results highlight the significance of this impact pathway as a potential risk factor, where effects on resource availability could influence consumer dynamics (Fleeger, 2020).

4.4.2 Impacts on Ecological functions

4.4.2.1 Prey Provision

It was expected that prey provision, defined as the biomass of the adult portion of the population, would decrease with reductions in all pathways due to reductions in growth from decreased food assimilation. As with changes in population abundance, prey provision was differentially impacted by the pathways of impact, with prey provision most greatly impacted by reductions in food availability and assimilation efficiency, and somewhat resistant to reductions in feeding rates. However, prey provision was more sensitive to all impact scenarios than population abundance, particularly for *Asellus*. This is due to scheduling of the DEB model where energy for growth and maintenance is prioritised over maturity and reproduction (Chapter 3). Reductions in individual energy intake primarily impact reproduction, resulting in a lack of recruitment and thus a reduction in the adult population (Barnett et al., 2017).

The maximum deviation in median prey provision decreased almost linearly with increasing reductions in food availability and assimilation efficiency. Both *Gammarus* and *Asellus* species serve as important prey for various game and coarse fish, including trout, perch, bullheads, and stone loach (Rask and Hiisivuori, 1985; Copp et al., 2005), as well as smaller fish and invertebrate predators (Har and Gill, 1992). Gut content studies reveal perch tend to prefer asellids (Dahl, 1998; Enefalk et al., 2019), while trout favour gammarids (Newman and Waters, 1984; Andersen et al., 2016; Dodrill et al., 2021), though these preferences depend on prey availability in their environments (Newman and Waters, 1984; Keeley and Grant, 1997). Additionally, salmonid biomass is strongly correlated with drifting invertebrate biomass (Wilzbach et al., 1986; Romaniszyn et al., 2007). While the elimination of large-bodied invertebrates from Lake Erie, USA, between 1960 and 1980 due to pollution-induced anoxic events, led to food limitations and subsequent declines in yellow perch growth and abundance (Tyson and Knight, 2001). Therefore, chemical-induced reductions in food availability and assimilation efficiency could directly reduce fish populations that rely on these invertebrates as prey.

Differences between pathways were less pronounced when considering the cumulative impact on populations, particularly for *Gammarus*. This is attributed to an initial sharp increase in mortality due to reductions in food availability and assimilation efficiency, causing a significant deviation from the baseline. However, populations tend to recoverter this event, reaching a new equilibrium. In contrast, reductions in feeding rates result in a gradual decline over time, primarily driven by long-term reductions in reproduction. Assessing cumulative impact (i.e., area under the curve) rather than maximum deviation from the control, provides a more relevant measure of chemical impacts on invertebrate populations and the provision of food for fish. This approach better captures the long-term effects on prey availability, which is critical for understanding sustained impacts on fish growth, survival, and reproduction. Additionally, cumulative impact analysis can detect subtle but persistent reductions in prey availability that may be overlooked when focusing only on the maximum deviation.

Furthermore, for direct impacts on the consumer, the model assumes consistent stress across the population, but sensitivity to stress varies among individuals, often depending on life stage size (Adam et al., 2010; Gergs et al., 2014a). Brooding females, for example, may be more sensitive to chemical stress (Maltby and Naylor, 1990). While size-dependent sensitivity differences can be applied generically, a more accurate approach would involve using a DEB-tox model. This model integrates individual toxicokinetic and toxicodynamic processes, adjusted for size (Gergs et al., 2016), and incorporates starvation stress (Gergs et al., 2021). Such an approach may effectively simulate the population-level consequences of size-related sensitivity differences and may result in greater impacts on population structure for direct impacts on the consumer.

4.4.2.2 Leaf Processing

It was expected that reductions in feeding activity and food availability would result in the greatest reductions in leaf processing due to the direct effect on individual consumption. While in contrast, reductions in assimilation efficiency would have a lesser impact on leaf processing since they do not directly affect consumption. In contrast to the effects of population abundance and prey provision, food availability had the strongest impact on leaf processing rates, with rates declining almost linearly as food availability decreased. Notably, leaf consumption remained relatively resilient to reductions in feeding rates, particularly in *Gammarus* populations. Leaf processing was less affected by reductions in assimilation efficiency, following similar patterns to reductions in feeding rates. While this was not expected, this can be explained by the fact that consumption is not directly impacted by reductions in assimilation efficiency, but growth instead. This indicates that populations could compensate for decreased feeding rates, likely due to competitive release (Beketov and Liess, 2009), which led to a more even distribution of resources among individuals. This contrasts with findings from other studies, which primarily focus on individual responses rather than population-level effects. Population studies generally support the idea that changes in abundance and community structure lead to population and community collapse (Baird et al., 2007; Maltby et al., 2005), with less pronounced effects on abundance.

This study found that leaf processing by both *Gammarus* and *Asellus* was the most responsive and impacted endpoint compared to population abundance and prey provision. Macroinvertebrates play a disproportionate role in the decomposition of leaf litter (Hieber and Gessner, 2002; Carlilse and Clements, 2005), therefore changes in macroinvertebrate populations and communities will disproportionately affect leaf processing rates (Schafer et al., 2012; Flores et al., 2014). These findings support the use of invertebrate-driven leaf loss as an indicator of chemical stress (Gessner and Chauvet, 2002; Young et al., 2008). *Gammarus* feeding rates, a known ecological endpoint, are often used in situ as water quality indicators and are analogous to leaf processing rates (Maltby et al., 2002; Bloor et al., 2006). The study highlights the importance of leaf litter processing rates as indicators of chemical stress, responsive to various toxicity pathways, though population-level effects may vary due to intraspecific interactions.

Species differences in responses may be due to intraspecific competition, life history traits, and individual energy budgets. *Gammarus*, with its higher competition and energy demands, is more affected by reductions in energy assimilation and allocation to growth, leading to more significant impacts on population-level consumption. In addition to their individual sensitivity (Maltby et al., 1994; Chapter 3), *Gammarus* is a more efficient shredder than *Asellus* (Graça et al., 1994b), suggesting that chemical-induced reductions in feeding rates may have a greater impact on leaf processing in *Gammarus*-dominated ecosystems compared to *Asellus*-dominated systems.

It is also important to acknowledge that the resource matrix in this model is a simplification of reality. Microbial biomass, dependent on substrate availability, also contributes to leaf litter decomposition, reducing its availability. Additionally, shredder feeding activity positively impacts leaf litter decomposition. As a result, leaf mass loss per unit time is likely greater than modelled here, leading to a more pronounced negative impact on shredder leaf processing due to a greater reduction in leaf mass availability over time.

4.4.3 Differences between Species

At the individual level, *Gammarus* and *Asellus* differ in their sensitivity to chemical stress, with *Gammarus* often being more sensitive (Chapter 3). Results here indicate generally, both species populations show similar patterns of response to the different effect pathways studied. However, the magnitude of the responses generally differed between the two species. *Asellus* is more responsive to small decreases across all effect pathways, whereas *Gammarus* shows greater resilience, particularly to reductions in feeding rates. This difference is likely due to variations in per capita consumption within these populations, which influences intraspecific competition, and differences in reproductive output between the two species. *Gammarus*, with its higher consumption rates per capita, experiences greater competition for resources and therefore reductions in feeding rates have a greater buffering effect on the remaining gammarids. Additionally, modelled gammarids produce fewer eggs for the same size female than asellids (Chapter 3). For *Asellus*, reductions in reproductive output significantly impact population size due to the production of fewer eggs. In contrast, *Gammarus* is less affected by reduced energy allocation to reproduction until energy intake drops further, making it more susceptible to population declines under stress. This susceptibility is evident in the lower threshold of collapse observed in *Gammarus* compared to *Asellus*. These findings highlight that ecological factors often play a more critical role in determining population-level effects than toxicological factors alone (Dalkvist et al., 2009).

4.5 Conclusion

In conclusion, both direct impacts on the consumer and the resource in simulated shredder-detritus systems result in changes in the performance of ecological functions. However, the relative sensitivity of the pathways of impact studied differed. Reductions in assimilation efficiency and food availability had pronounced impacts on population abundance and the provision of prey, highlighting their crucial role in shaping population dynamics and potential impact on the feeding of fish. However, while leaf processing was the most responsive endpoint, only reductions in the availability of resources led to diminished leaf processing in both species' populations at lower effect levels, while leaf processing was more resistant to reductions in assimilation efficiency and feeding rates.

Additionally, the study highlighted differences in species sensitivity to chemical stress at both individual and population levels. As well as having differing individual sensitivities, both species showed slightly different population consequences under similar stress conditions, attributed to differences in life history traits. These findings underscore the need to consider species-specific responses when assessing chemical impacts on ecosystems. Furthermore, incorporating mechanistic effect models, such as DEB IBMs, enables a more comprehensive evaluation of the intricate relationships between individual responses and ecosystem services, thereby enhancing our ability to make informed decisions for the sustainable management of aquatic ecosystems. However, the study also highlighted limitations in current modelling approaches, particularly in assessing population-level responses and interpreting deviations from baseline conditions. These limitations underscore the need for further research to better understand the long-term effects of chemical stressors on ecosystem dynamics and to refine modelling techniques for more accurate predictions of population responses.

Chapter 5 - Interspecific competition for resources and differences in species sensitivity on the structure and function within a service providing unit

5.1 Introduction

Current ecological risk assessments are centred around extrapolation from individual level responses to population and ecosystem level effects but pay little mechanistic attention to interactions between species (De Laender et al., 2008; Van den Brink, 2013). In the field, populations of species rarely exist in isolation. Instead, they exist in assemblages of interacting species. In some systems, multiple species may perform the same or similar functions via their shared relationship to a food source, as members of the same functional feeding group (Cummins and Klug, 1979). When multiple species perform the same or similar functions, functional redundancy within the system may buffer against functional loss, so that a decline in species diversity does not necessarily result in a loss of ecosystem function (Baert et al., 2017). Functional redundancy positively impacts ecological stability and resilience, especially when measured by species richness within functional groups (Biggs et al., 2020). However, what species remain and how they contribute to functions can influence the impact of chemical stress on the performance of functions (Laureto et al., 2015; Radchuck et a 2016). In the context of an ecosystem services approach to risk assessment, understanding functional redundancy is vital for determining ecosystem resilience to various stressors, including chemical pollutants. It ensures that critical ecosystem services are maintained even if certain species are adversely affected (Oginah et al., 2023).

Gammarus pulex and *Asellus aquaticus* are both common freshwater shredders that are found across Europe and are involved in the breakdown of leaf litter in streams, cycling of nutrients, and producing fine particulate organic matter on which other species can feed (Wallace et al., 1982; Wallace et al., 1997; Gessner et al., 1999; Graca, 2001). The species are both shredders and are part of the same functional group, but they also often co-occur and share a resource and are therefore part of the same feeding guild (Blondel, 2003). *Gammarus* and *Asellus* are known to differ in their sensitivity to water quality and chemical stress, with *Gammarus* often more sensitive than *Asellus* (Oseid and Smith, 1979; Maltby, 1995; Lukančič et al., 2010) (Figure 3.1). This difference in sensitivity means that the ratio of *Gammarus* to *Asellus*, which has been observed to range from 197:1 to 1:100, has long been used as an indicator of water quality in freshwater streams (Whitehurst, 1991, 2001) and found to correlate highly with species richness in response to organic pollution (McNeil et al., 2002). In the presence of low-level chemical stress, these differences in sensitivity are hypothesised to lead to a shift in the competitive advantage toward *Asellus* populations (Oseid and Smith, 1979). In the field, the spatial distribution of *Gammarus* and *Asellus* differs between upland and lowland streams: *Gammarus* primarily inhabits the more pristine upland streams, while *Asellus* predominates in the lower-quality water conditions typical of lowland streams (Holland, 1976; MacNeil et al., 2002).

Shifts from *Gammarus* to *Asellus* dominated systems are thought to result in decreased leaf processing. This is because *Gammarus* is the more efficient shredder of the two species (Graca et al., 1994). In situ *Gammarus* feeding inhibition is associated with decreased invertebrate diversity and leaf decomposition in the field (Maltby et al., 2002) and reduced *Gammarus* abundance is associated with loss of leaf processing downstream of a motorway runoff discharge outlet (Forrow and Maltby, 2000). Both *Gammarus* and *Asellus* species also serve as important prey for various game and coarse fish species, including trout, perch, bullheads, and stone loach (Rask and Hiisivuori, 1985; Copp et al., 2005) as well as smaller species of fish and invertebrate predators (Har and Gill, 1992). The foraging behaviour of fish on *Gammarus* and *Asellus* can differ between species, but carnivorous fish often select their prey based on the availability of their preferred prey amongst the assemblage of freshwater invertebrates available (Dodrill et al., 2021). Gut content studies have shown that perch tend to favour asellids, while trout prefer gammarids, although these preferences are largely shaped by the relative availability of each species in their environment (Newman & Waters, 1984). Shifts in species composition within the community can influence fish foraging behaviour. Consequently, changes in the diversity and abundance of shredder invertebrates may impact the performance of ecological functions and processes carried out by invertebrates within the system.

The impact of interspecific competition for resources on the impacts of chemical stress have been demonstrated in both laboratory (Knillman et al., 2012; Foit et al., 2012; del Arco et al., 2015a&b) and mesocosm studies (Allen et al., 2021). Interspecific competition can enhancethe direct effects of a chemicals on a sensitive species, often benefitting the more tolerant species (Lüring and Roessink, 2006; Liess et al., 2013). However, the enhanced effect of a chemical on one species in a co-species exposure may also be influenced by the competitive ability of the sensitive species (del Arco et al., 2015a). While many studies thus far have focussed on lethal effects, sublethal effects (occurring at concentrations lower than lethal ones), can also alter interactions between species populations (Schnuck and Liess, 2024; Saaristo et al., 2018). Resource competition, along with predation (Brookes et al., 2009), is an important factor influencing the indirect effects of chemicals (Preston 2002; Gessner and Tilli, 2016). Since these factors shape population dynamics (Van den Brink, 2013), ignoring them in ecological risk assessments may underestimate chemical risks (Forbes and Galic, 2016).

In Chapter 4, it was found that both *Gammarus* and *Asellus* populations, with intraspecific competition for resources, were resistant to feeding inhibition up to the 50% effect level, in part due to reduced intraspecific competition. While this phenomenon may mitigate the effects of feeding inhibition within single populations of a species, in a multispecies context, interspecific competition for food resources could exacerbate the consequences of individual feeding inhibition. More tolerant species may capture the released resources (Knillman et al., 2012; Liess et al., 2013; Schnuck and Liess, 2024), which is expected to accelerate the time to extinction by exclusion.

This chapter aims to investigate how interspecific competition for resources, within a Service Providing Unit (SPU), influences the structure of the hypothetical SPU and the performance of its ecological functions (Figure 5.1). This is accomplished by coupling the Individual Based Dynamic Energy Budget Models (DEB IBMs) for *Gammarus pulex* and *Asellus aquaticus*, allowing these species to compete for resources within a single patch.

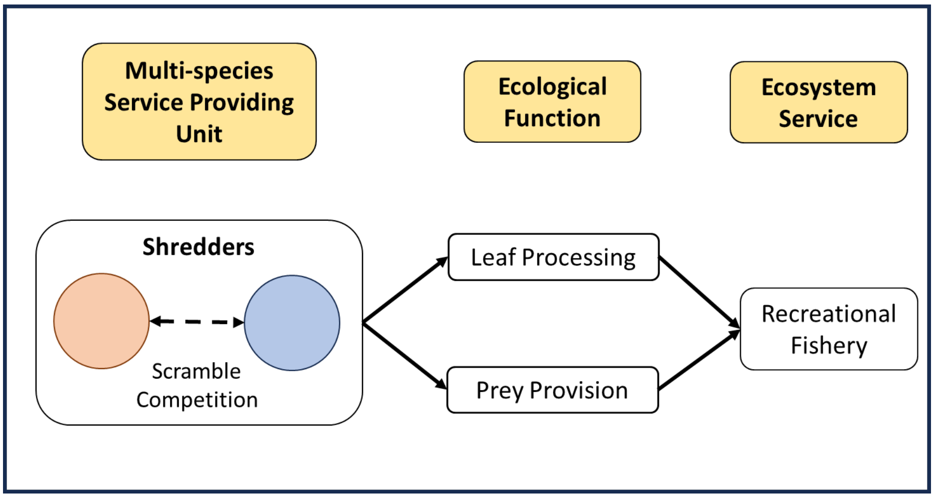


Figure 5.1: Schematic showing how interspecific competition for resources, within a Service Providing Unit (SPU), may influence the structure of the hypothetical SPU and the performance of its ecological functions

A preliminary study showed that initial ratios of *Gammarus:Asellus* and density of shredders on a patch influence the coexistence of species on that patch: coexistence is observed only within a specific range of initial densities. Outside of this range, one species typically excludes the other.

This chapter will explore how feeding inhibition, such as that induced by chemical stressors, in either species and differences in relative sensitivity between the two species affect:

- The conditions that allow for coexistence versus exclusion between the species.
- In cases of coexistence, the relative abundance of the two species.
- In cases of exclusion, the time it takes for one species to dominate completely.
- Finally, this chapter will address how changes the structure of the SPU due to feeding inhibition translate into alterations in the ecological functions within the SPU.

5.2 Methods

5.2.1 Modelling

Gammarus and *Asellus* DEB IBMs were coupled in NetLogo, whereby both species share, and subsequently compete for, the resource on a single patch Within NetLogo, the two species are defined and implemented as separate 'Breeds'. The model code was tested to ensure that each species population exhibited the same dynamics in the coupled environment as in the single species environment (i.e. relative abundance of 100%). Interspecific competition was neither validated nor calibrated as it is an emergent property of the model design. The model simulates a form of scramble competition where food resources are equally accessible to all individuals, regardless of species. This is implemented by randomly 'calling' asellids and gammarids to feed from the shared resource pool within each time step. As this implementation of competition is essentially a lottery-like process among individuals, no explicit equation for interspecific competition is specified in the model. Entities, state variables, and scales for each species are the same as those outlined in Chapter 3. The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual-based models (Grimm et al., 2006; Grimm et al., 2010).

The purpose of this model is to explore how simulated reductions in feeding rates of freshwater *Gammarus pulex* and *Asellus aquaticus*, along with differences in their relative sensitivities, affect the structure of the SPU. This is examined under varying densities and ratios of the two species, competing for resources on a simulated one-square-metre patch. The information is then used to investigate how thresholds of effect for a reduction in feeding rate at the single-species level may change when interspecific competition for resources is considered, how this affects the structure and the performance of ecological functions by the SPU.

5.2.1.1 Design concepts

Basic principles: Key processes in the model follow the basic principles of Dynamic Energy Budget theory (Kooijman, 2010), which posits that uptake of resources by individuals scales with their surface area, and the allocation of energy scales with the volume of the organism. The theory is based on conservation of mass and energy. Individuals do not move on or between patches.

Emergence: Individual life-history traits, such as growth, maturation time, and reproductive effort, emerge from rules of metabolic organisation. Population dynamics emerge from indirect interactions between individuals via competition for the resource and presence of hypothetical toxicant in the form of reduced individual feeding rates.

Interaction: Individuals in the model interact with each other indirectly through resource competition. Population growth is constrained by the amount of resource in the system (carrying capacity); when population densities go beyond available resource, modelled individuals experience starvation mortality. The amount of resource in the model never reaches zero. Density dependence in the model emerges from modelled indirect interactions. Embryos in broods are explicitly linked to females, resulting in embryo mortality when females die due to starvation or background mortality.

Stochasticity: Species specific background mortality is implemented as a stochastic process that occurs daily. Furthermore, as DEB parameters are constants, a scatter multiplier is added to the surface area-specific ingestion rate to implement a measure of variation between individuals. The scatter multiplier is a random number pulled from a log-normal distribution (Kooijman et al., 1989; Martin et al., 2013) with a standard deviation of 0.1.

Observation: The number of individuals from each species was reported every 30 days for each simulation scenario. Simulations were run for 15 years or until one species went extinct. Then the abundance of the two species was noted and if exclusion occurred, the time to exclusion noted.

Initialisation: DEB parameters for *Asellus aquaticus* and *Gammarus pulex* were obtained from the add my pet database collection (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/index.html). Simulations start with a user defined number of individuals, sampled from a pool population, as outlined below.

5.2.2 Experimental Set up

Initial conditions consisted of different densities of *Gammarus* and *Asellus*, with each species population consisting of individuals varying in length and age. The initial amount of resource was set to 400 mg per m^2, equal to the carrying capacity of the resource and to that used in simulations in Chapter 4. Simulations were run with different initial number of *Gammarus* and *Asellus*, from 10 to 200 individuals of each species increasing in increments of 10 individuals, resulting in 400 starting patch conditions. Each set of conditions was repeated 50 times, with individuals sampled from pools of mixed populations obtained by running single species populations models for 10 years and sampling the population around the peak population abundance. For each pool population, properties of around 1400 individuals of each species were taken from the baseline situation. The pool populations were a mix of adults and juveniles of different lengths (Figure 5.2 and 5.3).

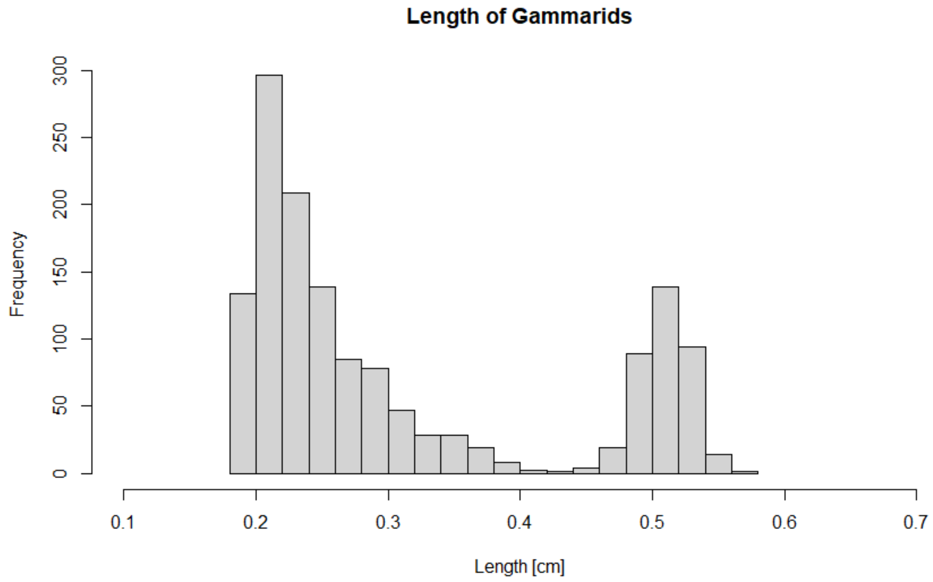


Figure 5.2: Size distribution of the pool population of *Gammarus pulex*, used to sample the initial gammarids for the competition experiments, consisting of 1456 individuals.

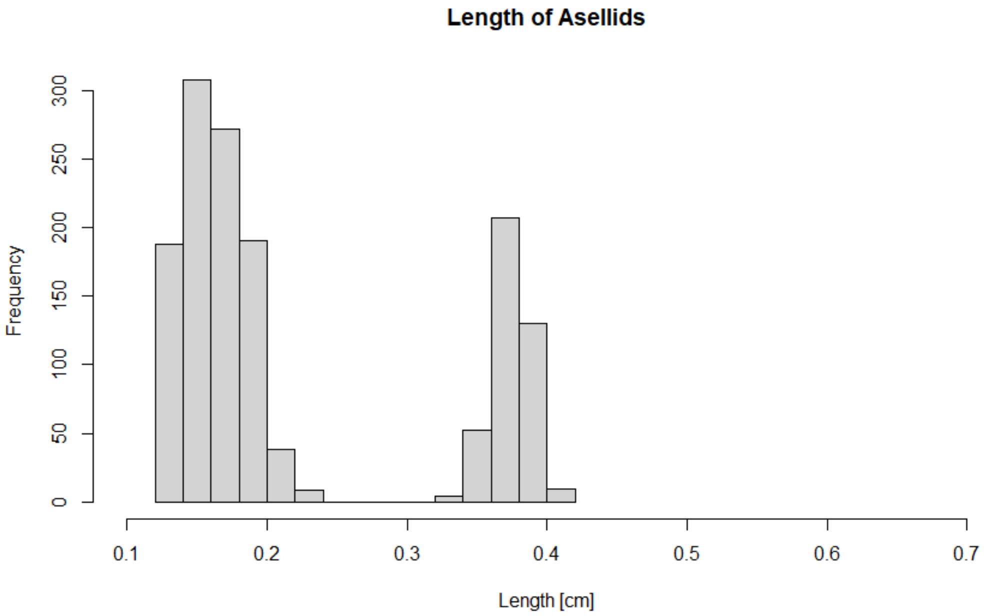


Figure 5.3: Size distribution of the pool population of *Asellus aquaticus* used to sample the initial asellids for experiment competition experiments, consisting of 1408 individuals.

5.2.3 Effect Scenario

Feeding inhibition, as described in Chapter 4 (Eqn 4.5), was applied to *Gammarus* and *Asellus* that the difference in sensitivity, increasing absolute stress, and a combination of difference in sensitivity within increasing absolute stress. Feeding inhibition, when applied, was applied constantly from the first timestep for the duration of the experiment.

5.2.4 Analysis

Within each replicate, the abundance of the two species at the end of the simulation was noted. If both species were present, this was considered to be coexistence. The number of replicates within each patch where coexistence or exclusion occurred was counted and the percentage coexistence or exclusion was reported and plotted in a state space plot. Of the patches where coexistence occurred, the mean relative abundance of gammarids at the end of the simulation period was calculated for each patch:

$$Relative\ abundance\ of\ Gammarus = \frac{\#\ gammarids}{(\#\ gammarids + \#\ asellids)}$$

The mean relative abundance of *Gammarus* was then calculated for each patch and plotted where values < 0.5 denote *Asellus* dominance, while values > 0.5 denote *Gammarus* dominance. Of the patches where coexistence did not occur, the mean time to exclusion, whereby only one species was present in the system, was calculated for each patch.

For the interpretation, the state space plot was split into areas of *Gammarus* dominant, *Asellus* dominant, or equal where the initial ratio of the two species is less than one, equal to one, and more than one, respectively. Combined shredder density within these areas was also compared, with values < 100 indicating low density and those > 100 indicating high density. The distribution of the occurrence of coexistence, change in *Gammarus* relative abundance, mean shredder abundance at the end of the simulation, and time to exclusion were then compared between these areas for different feeding inhibition regimes. The time to exclusion was also compared between instances of exclusion by *Asellus* and exclusion by *Gammarus*.

5.3 Results

5.3.1 Coexistence and Exclusion

In the baseline situation, i.e. no feeding inhibition, coexistence occurred in 32% of all experiments (all 400 patch conditions, each with 50 replicates = 20,000 experiments) with coexistence occurring on 338 of 400 patches. Coexistence occurred more often on *Asellus* dominant patches (41%) (i.e. below the 1:1) than on *Gammarus* dominant patches (21%). Where the initial densities of *Gammarus* and *Asellus* were equal, on the 1:1 line, coexistence occurred on all patches and in 54% of experiments (Figure 5.4, top left).

The occurrence of coexistence decreased with a relative difference in sensitivity between the two species. When *Gammarus* feeding rates were inhibited by 10% the occurrence of coexistence decreased to 22% of all experiments, occurring on 172 of the 400 patches with 163 of these *Gammarus* dominant patches (i.e. Above the 1:1 line), and only 4 on *Asellus* dominant patches (Figure 5.4, top middle). Here, 37% of experiments on *Gammarus* dominant patches resulted in coexistence. When densities of each species were equal, coexistence occurred on 5 patches, with low total shredder density. With a 20% *Gammarus* feeding inhibition, coexistence did not occur on any patches (Figure 5.4, top right).

Similarly, when *Asellus* feeding rates were reduced by 10%, coexistence occurred on 48 patches representing only 0.3% of replicates (Figure 5.5). Almost all of these, except one, were on *Asellus* dominated patches (below the 1:1 line) where it occurred in 0.6% of experiments. Coexistence did not occur on any patches with equal densities of both species. With a 20% reduction in *Asellus* feeding rates, coexistence did not occurr on any patches (Figure 5.5).

The occurrence of coexistence increases with increasing absolute stress with no difference in the relative sensitivity to feeding inhibition between the two species (Figure 5.4, left hand side). With 10% feeding inhibition for both species, coexistence was observed in 358 out of 400 patches, up from 338 in the baseline. This number rose to 385 with 20% feeding inhibition and 397 patches with 30% inhibition. At 50% feeding inhibition of both species, coexistence occurred in all 400 patches (94% of all experiments). The increase in coexistence was particularly notable on *Asellus*-dominated patches, where the number of such patches rose from 135 at baseline to 154 with 10% inhibition, 177 with 20%, and 190 (all) with 30% inhibition (Figure 5.4). In contrast, the conditions for coexistence on *Gammarus*-dominated patches did not show an increase until the 40% effect level, but the number of replicates with coexistence did rise. The percentage of replicates showing coexistence on *Gammarus*-dominated patches increased from 40% at baseline to 46% with 10% feeding inhibition and 64% with 30% inhibition, rising to 90% with 50% feeding inhibition of both species (Figure 5.6).

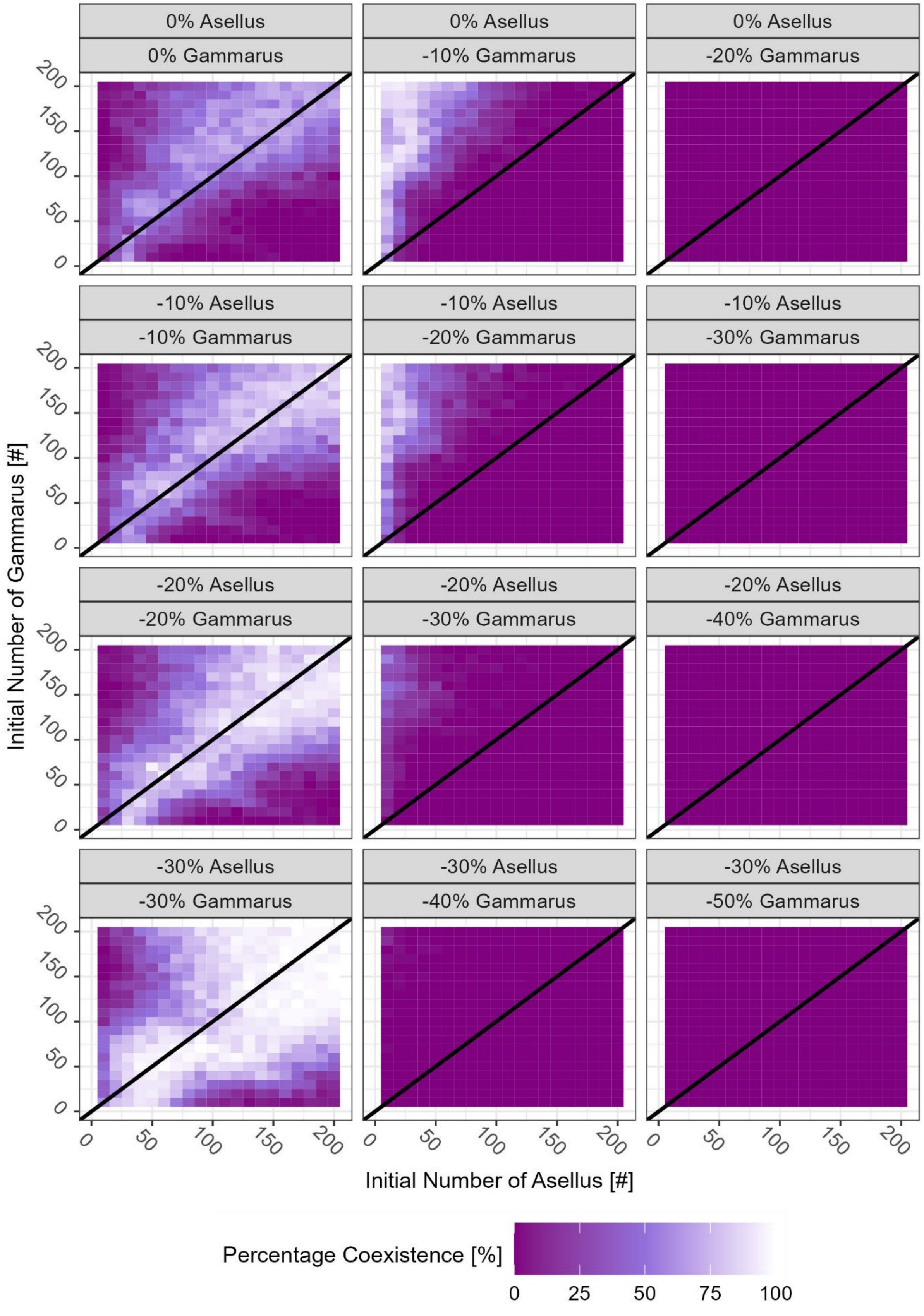


Figure 5.4: The percentage of occurrence of coexistence between *Gammarus* and *Asellus* populations after 15 years under varying initial population sizes [#] and increasing levels of feeding (grey panels) inhibition for both species. The diagonal black line separates regions where

initial *Asellus* population sizes are greater than *Gammarus* (above the line) and vice versa (below the line). Lighter shades represent higher coexistence percentages, while darker shades indicate lower coexistence.

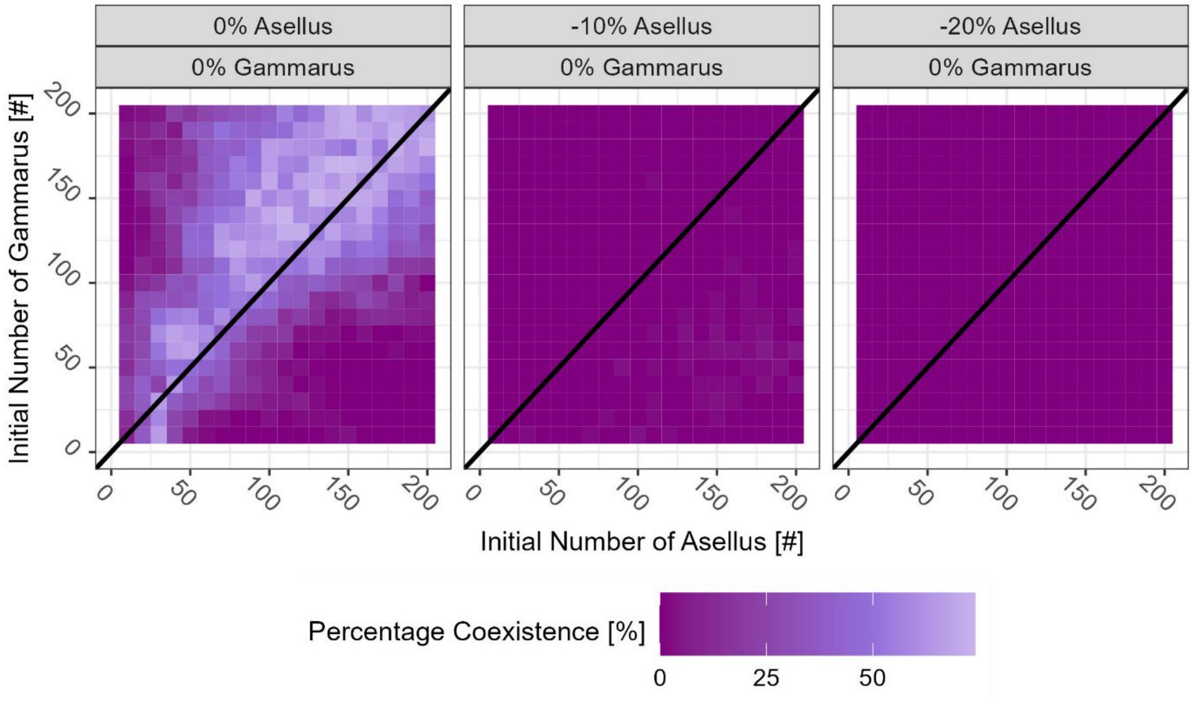


Figure 5.5: The percentage of occurrence of coexistence between *Gammarus* and *Asellus* with increasing feeding inhibition of *Asellus* for populations after 15 years under varying initial population sizes and increasing levels of feeding inhibition (grey panels) for both species. The diagonal black line separates regions where initial *Asellus* population sizes are greater than *Gammarus* (above the line) and vice versa (below the line). Lighter shades represent higher coexistence percentages, while darker shades indicate lower coexistence

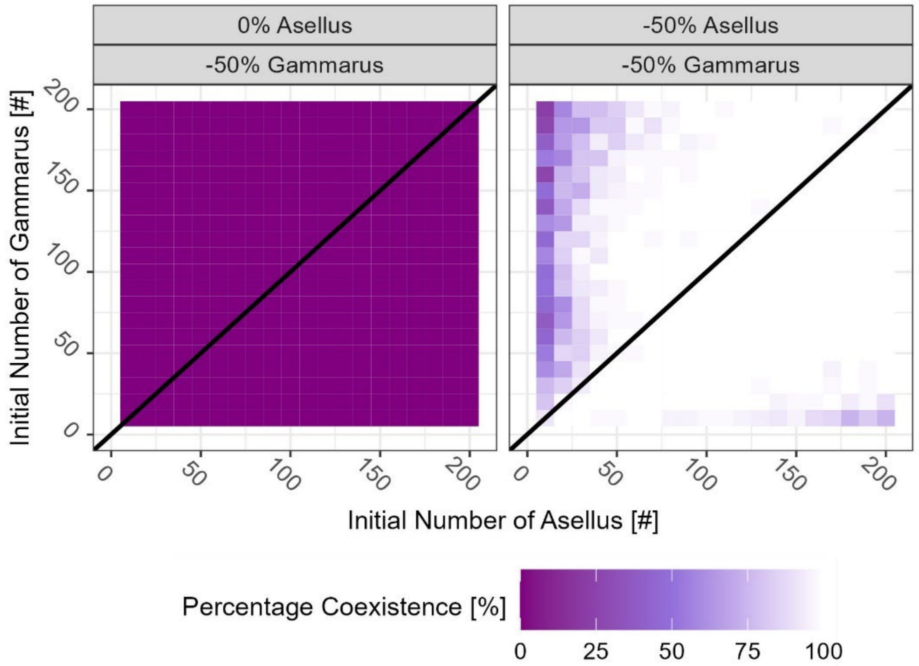


Figure 5.6: The percentage of occurrence of coexistence between *Gammarus* and *Asellus* populations after 15 years under varying initial population sizes with a 50% feeding inhibition of *Gammarus* (left), and both species (right). The diagonal black line separates regions where initial *Asellus* population sizes are greater than *Gammarus* (above the line) and vice versa (below the line). Lighter shades represent higher coexistence percentages, while darker shades indicate lower coexistence.

5.3.2 Relative abundance of *Gammarus*

Of the patches where exclusion occurred, the mean total shredder abundance at the end of the simulation period remained relatively stable across treatments, with the median shredder abundance across patches ranging from 585 to 653 individuals with a median of 615 individuals (Appendix 5.1). In the baseline scenario, the mean total shredder abundance ranged from 528 to 742 individuals per patch, with a median of 616. The largest variability in shredder abundance occurred in patches initially dominated by *Asellus*, whereas the lowest variability was seen in patches with equal initial dominance by both species, showing a range of 600 to 631 individuals and a median of 615 (Appendix 5.1).

The mean relative abundance of the tolerant species increases with increasing feeding inhibition. Figure 5.7 shows the frequency distribution of the mean relative abundance of *Gammarus* across patches. In the baseline situation, the mean relative abundance of *Gammarus* ranges from 16 to 99% with a median of 95% (Figure 5.7, top left panel). The greatest range in mean relative abundance of *Gammarus* occurs on patches initially dominated by *Asellus* (AselDom) (16-99%) with a median of 93% (Figure 5.7). While the mean relative abundance of *Gammarus* on patches initially dominated by *Gammarus* (GamDom) ranges from 90 to 100% with a median of 91% (Figure 5.7).

As *Gammarus* feeding inhibition increases in relation to that of *Asellus*, the relative abundance of *Gammarus* deceases (The frequency distribution shifts to the left in Figure 5.7) from 95% in the baseline situation to 0.2% with 20% *Gammarus* feeding inhibition (Figure 5.7). This indicates a shift from *Gammarus* to *Asellus* dominance with the pattern differring between patches of different initial relative abundance of species. In patches initially dominated by *Asellus*, this decreases from 93% (16-99%) to 2% (1-5%) while in *Gammarus* dominant patches this decreases from 97% (90-100%) to 3% (0-22%). Furthermore, high shredder density patches are slightly more sensitive (Figure 5.7) with no coexistence occurring on *Asellus* dominant patches with high shredder density while on *Gammarus* dominant patches, the *Gammarus* relative abundance decreases from 97% (93-100%) to 3% (0-18%) compared to 4% (0-22%).

Similar patterns were observed for *Asellus* feeding inhibition, however with a 10% inhibition of *Asellus* feeding, *Asellus* were excluded on all patches but those initially dominated by *Asellus* (Figure 5.7). Here, patches with low shredder density were more resistant to shifts in relative abundance, with the minimum relative abundance of *Gammarus* increasing from 16 to 33% compared to 75 to 87% in high density patches. The median values did not differ between high and low shredder densities.

With increasing absolute stress, the relative abundance of *Gammarus* decreases slightly (Figure 5.7, down the left-hand panels). While *Gammarus*-dominant patches remain relatively stable, the median relative abundance of *Gammarus* drops marginally to 96% with 10 and 20% feeding inhibition of both species, and 94% at the 30% stress level, with the range narrowing to 88-99%. In patches where dominance is either equal or favours *Asellus*, the decline in *Gammarus* populations is more noticeable. In equal-dominance patches, under moderate stress, the *Gammarus* median abundance decreases slightly to 94% (89–97%), falling to 90% at the 30% stress level. The decline is more pronounced in *Asellus*-dominant patches, where *Gammarus* abundance is generally lower. Initially, the median is 93% with a wide range (16-99%), reflecting greater variability. As stress increases, the mean *Gammarus* abundance median drops to 91%, with a minimum of 29%. At the 30% stress level, the *Gammarus* median declines further to 83%, and the range narrows to 8-93%.

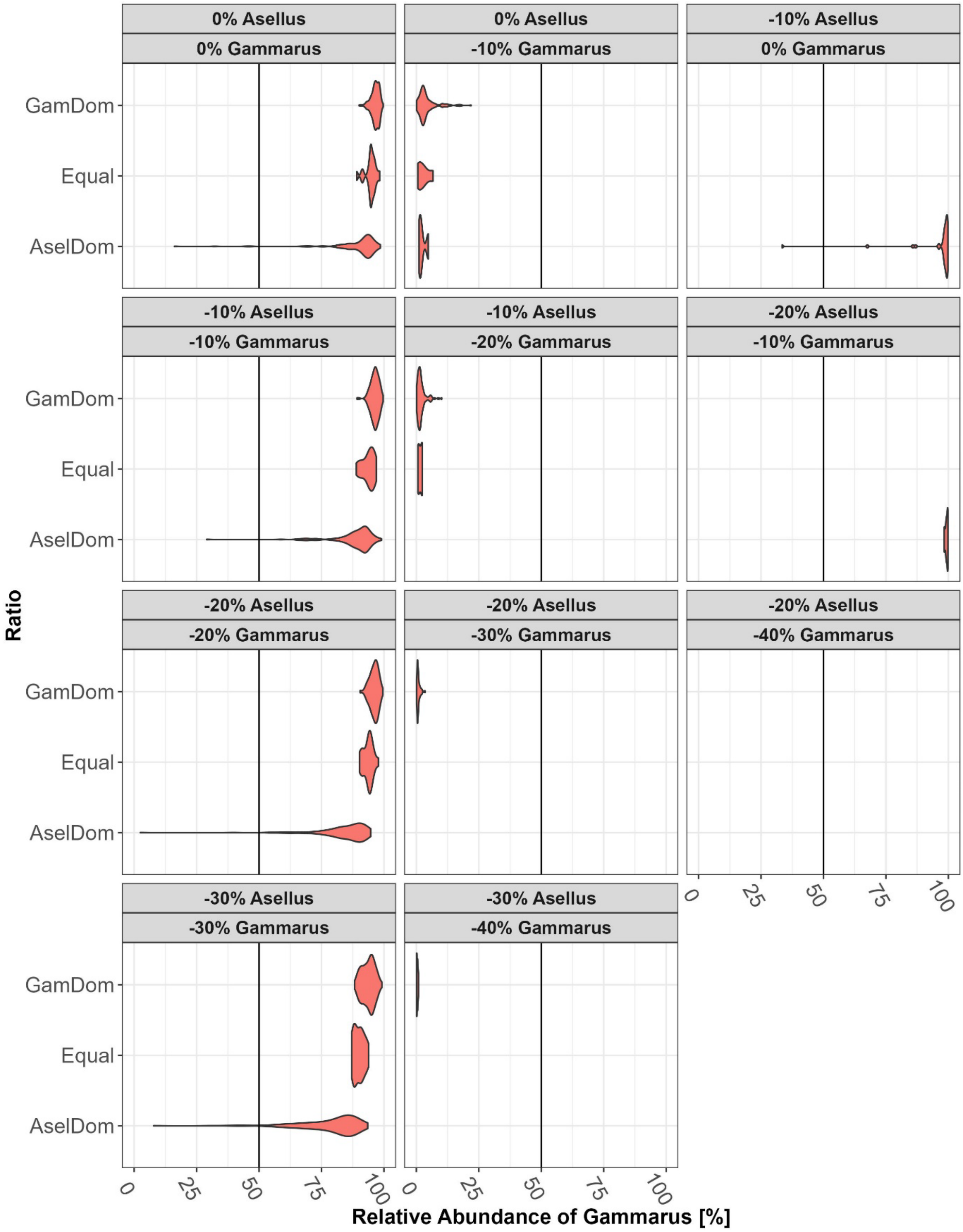


Figure 5.7: The frequency distribution of the relative abundance of *Gammarus* populations under varying levels of feeding inhibition and density across initial conditions. The x-axis represents the relative abundance of *Gammarus* (%), while the y-axis shows the initial dominance ratio: *Gammarus*-dominant (GamDom), *Asellus*-dominant (AselDom), and equal dominance (Equal). Each panel represents different combinations of feeding inhibition levels for *Gammarus* and *Asellus*, with stress levels ranging from 0% to -40%.

5.3.3 Time to Exclusion

Patches where coexistence did not occur experienced exclusion. The time to exclusion decreased with increasing relative difference in feeding inhibition between species (Figure 5.8). In the baseline situation, the median mean time to exclusion across patches was 6 years (range: 8 months – 12.5 years). Exclusion by *Gammarus* occurred in 289 patch conditions where the median mean time to exclusion was 11.3 years (range: 1.6 years – 12.5 years), while exclusion by *Asellus* occurred in 300 patch conditions, with the median mean time to exclusion 3.3 years (range: 8 months – 10.5 years). Time to exclusion differed between the different initial ratios of *Gammarus* and *Asellus*. Exclusion by *Gammarus* lasted longest overall in patches initially dominated by *Asellus*, with a median of 13.1 years (range: 8.4 years– 15 years), while in patches initially dominated by *Gammarus*, it took 10 years (range: 1.6 years – 13.5 years). Conversely, exclusion by *Asellus* was quicker than by *Gammarus*, being fastest in *Asellus*-dominated patches at 2 years (range: 8 months – 6.9 years) and longest in patches initially dominated by *Gammarus*, taking 5.3 years (range: 1.2 years – 10.5 years).

The time to exclusion decreased with increasing relative differences in feeding inhibition. *Gammarus* feeding inhibition led to longer exclusion times than exclusion by *Asellus*. As feeding inhibition increased, time to exclusion generally decreased across all density and dominance conditions. *Gammarus* feeding inhibition resulted in greater differences in exclusion times between *Gammarus*- and *Asellus*-dominated patches compared to *Asellus* feeding inhibition (Figure 5.8). With increasing *Gammarus* feeding inhibition, where *Asellus* generally began to exclude *Gammarus*, time to exclusion by *Asellus* remained relatively stable on *Gammarus*-dominated patches, with a median of 6 years (range: 1.3 years – 14.6 years) (Figure 5.8). However, on patches initially dominated by *Asellus*, this time decreased significantly, dropping to 1 year and 2 months (range: 8 months – 4.2 years) (Figure 5.8, top panel). Where *Gammarus* populations were resistant to exclusion, time to exclusion fell to 2.1 years (range: 1.1 years – 7.6 years). This decreased further with 20% feeding inhibition to 1 year (range: 3 months – 2.1 years).

Exclusion by *Asellus* occurred within 1 year and 4 months (range: 7 months – 7 years and 5 months), again taking 1 year and 1 month (range: 7 months – 2.9 years) on *Asellus*-dominated patches. On *Gammarus*-dominated patches, time to exclusion by *Asellus* was 1 year and 11 months (range: 1 year – 7.4 years). By 30% *Gammarus* feeding inhibition, exclusion by *Asellus* occurred within 1 year and 2 months (range: 5 months – 2.7 years), 10 months (range: 4 months – 1.6 years) at 40% feeding inhibition, and 6 months (range: 3 months – 1.1 years) at 50% feeding inhibition. This was consistently quickest on *Asellus*-dominated patches (Figure 5.8, top panel).

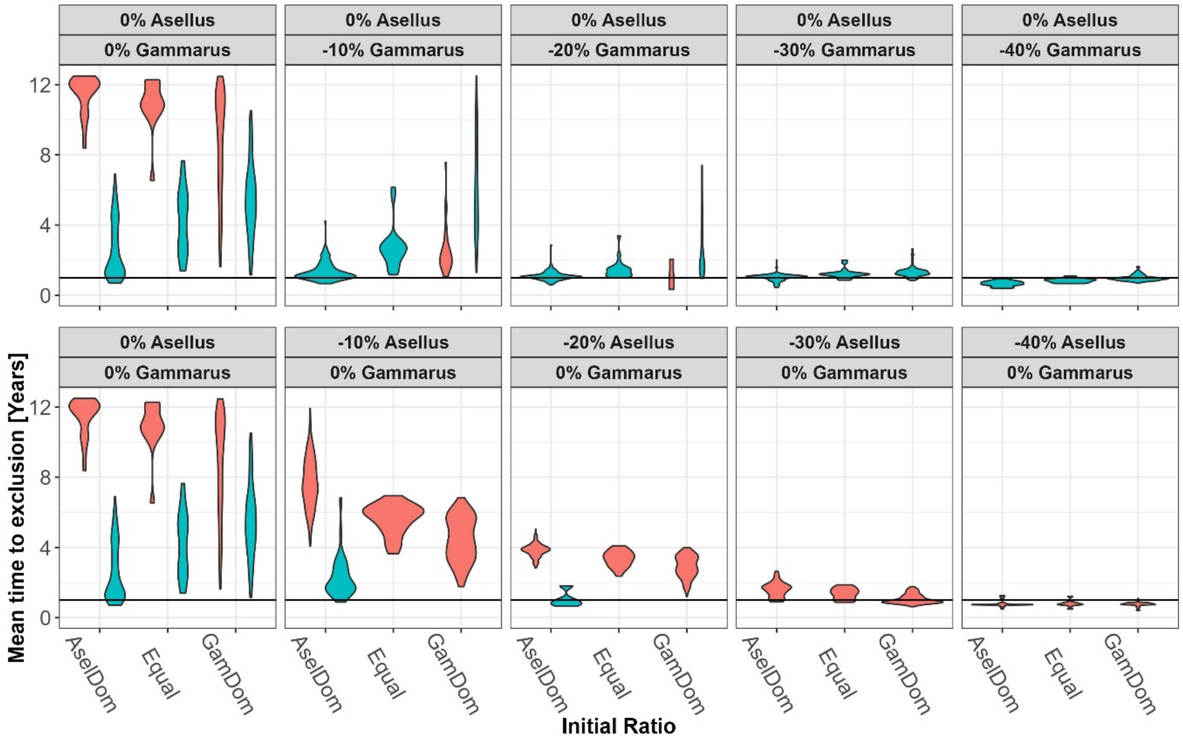


Figure 5.8: The mean time to exclusion (in years) under different initial conditions and varying levels of *Gammarus* and *Asellus* feeding inhibition. The x-axis represents the initial ratio of *Gammarus* and *Asellus* (e.g., *Gammarus*-dominant, *Asellus*-dominant, or equal) with results stratified by exclusion by *Gammarus* (red) and exclusion by *Asellus* (blue). The black horizontal line represents a time to exclusion of 1 year.

Similar patterns were observed with *Asellus* feeding inhibition, where the time to exclusion by *Gammarus* decreased as *Asellus* feeding inhibition increased (Figure 5.7, bottom panel). With 10% feeding inhibition of *Asellus*, time to exclusion by *Gammarus* fell to 6 years (range: 1.7 years – 11.9 years), further decreasing to 3.5 years (range: 1.2 years – 5 years) with 20% inhibition, 1.3 years (range: 7 months – 2.7 years) at 30%, and 9 months (range: 5 months – 1.3 years) with 40% feeding inhibition. Exclusion by *Asellus* also decreased over time, falling from 3.4 years (range: 8 months – 10.5 years) in the baseline to 1 year and 11 months (range: 10 months – 6.8 years) with 10% inhibition, and 11 months (range: 8 months – 1.8 years) with 20% inhibition. Notably, *Asellus* exclusion only occurred in patches initially dominated by *Asellus*.

As absolute stress increased, both the occurrence of coexistence and the time to exclusion rose accordingly (Figure 5.9). Variability in time to exclusion also increased with greater stress, especially on patches initially dominated by *Gammarus*. While *Asellus* was generally excluded faster than *Gammarus*, the exclusion times converged at higher levels (50%) of feeding inhibition. For

Gammarus, the median time to exclusion was initially 11.3 years (range: 1.7 years – 15 years) with no inhibition, decreasing slightly to 10.8 years (range: 1.8 years – 15 years) at 20% inhibition, and then increasing to 11.1 years (range: 1.4 years – 15 years) at 30% inhibition. It dropped to 7 years and 10 months (range: 3.8 years – 15 years) at 50% inhibition. In *Asellus*-dominated patches, *Gammarus* exclusion times remained relatively stable across inhibition levels, staying between 12.7 years to 13.2 years, with minimal impact from increasing inhibition levels. However, in *Gammarus*-dominated patches, *Gammarus* exclusion times varied more widely, decreasing from 10.1 years at 0% inhibition to 7.7 years at 50% inhibition.

Similarly, for *Asellus*, the median time to exclusion increased from 3.3 years (range: 8 months – 10.5 years) with no inhibition to 8.8 years (range: 3.8 years – 13.8 years) at 50% inhibition. In *Asellus*-dominated patches (AselDom), *Asellus* exclusion times increased progressively with higher inhibition levels, from 2 years at 0% inhibition to 8.8 years at 50% inhibition. In *Gammarus*-dominated patches (GamDom), *Asellus* exhibited a somewhat similar pattern, with time to exclusion increasing from 5.3 years at 0% inhibition to 6.7 years at 20% inhibition. However, at 30% inhibition, *Asellus* was excluded more quickly (5.5 years), suggesting a non-linear relationship in *Gammarus*-dominated patches.

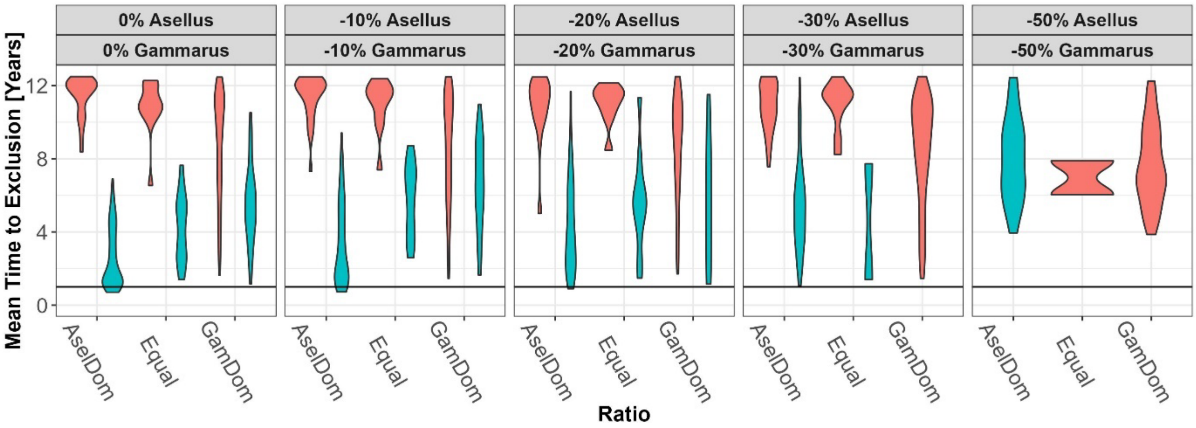


Figure 5.9: The mean time to exclusion (in years) under different initial conditions and equally increasing levels feeding inhibition for both species. The x-axis represents the initial ratio of *Gammarus* and *Asellus* (e.g., *Gammarus*-dominant, *Asellus*-dominant, or equal) with results stratified by exclusion by *Gammarus* (red) and exclusion by *Asellus* (blue). The black horizontal line represents a time to exclusion of 1 year.

5.4 Discussion

The aim of this chapter was to assess how interspecific competition for resources, within a SPU, affects species population responses to chemical induced feeding inhibition and the subsequent impacts on the performance ecological functions. Interspecific competition for resources between the two species results in species exclusion with 20% feeding inhibition for both species, compared to 70 and 80% at the single species level (Chapter 4). The impacts of chemical-induced feeding inhibition on patches was influenced by the initial species ratio and density within those patches. Patches with greater differences in initial species densities, particularly those with a higher density of sensitive species, demonstrated the greatest resistance to exclusion. This was also dependent on the level of absolute stress in the system. Specifically, the degree of feeding inhibition leading to the exclusion of *Gammarus* populations increased as the level of feeding inhibition in *Asellus* populations also increased. The resulting effect on the performance of ecological functions, assuming that one species occupies each patch, using model outputs, is likely to be very slight, with greater impacts on prey provision. If the more sensitive *Gammarus* is excluded, leaf processing rates are inferred to slightly decrease as *Asellus* become the dominant species. While for prey provision, leads to more biomass for prey, but a reduction in the size of prey available, a key determinant of fish foraging. Conversely, if *Asellus* is more sensitive, a shift to *Gammarus*-dominated systems increases leaf processing rates slightly but reduces the availability of prey biomass.

5.4.1 Coexistence and Exclusion

In the absence of feeding inhibition in either species, coexistence is more pronounced when the initial populations of both species are relatively equal, and the initial density of the two species remains high, representing great *Gammarus* dominance across patches. This reflects ratios observed in the field where the ratio of *Gammarus* to *Asellus* is greater when water quality is good (Whitehurst et al., 2001). As expected, as the relative difference in sensitivity to feeding inhibition between the two species increases, the conditions for coexistence become narrower, occurring only when there is a greater difference in their initial densities as the tolerant species excludes the sensitive one. Sublethal effects at the individual level can result in a loss in species diversity at the community level. This agrees with findings of Liess et al. (2021) where there was severe degradation of invertebrate community composition, in response to pesticide exposure three orders of magnitude below the EC_{50}, with a loss of the most sensitive species. This is observed here, albeit in a two species system, as the relative abundance of *Gammarus* decreases with increasing *Gammarus* feeding inhibition, and vice versa, with both species populations collapsing at 20% feeding inhibition. However, coexistence is more frequent with reduced *Gammarus* feeding inhibition compared to reduced *Asellus* feeding inhibition. This indicates that high initial densities of *Gammarus* may make them more resistant to exclusion than *Asellus* when their feeding is inhibited. This is further supported by the observation that exclusion times are longer in *Gammarus*-dominant patches with *Gammarus* feeding inhibition compared to *Asellus*-dominant patches with equivalent *Asellus* feeding inhibition. This difference is likely attributed to differences in consumption rates and reproductive output between the two species.

The occurrence of coexistence increases with increasing absolute feeding inhibition of the two species. Coexistence increases, primarily, in patches initially dominated by *Asellus*, patches where, in the baseline situation, *Gammarus* excluded *Asellus*. There, as *Gammarus* is the dominant species in the model, occupying most patches in the baseline simulation, feeding inhibition of both species favours *Asellus* more than *Gammarus*. These findings are consistent with those of Schnuck and Liess (2024), which demonstrated that exposure of two zooplankton species, both exhibiting similar sensitivities to the pyrethroid insecticide esfenvalerate, to concentrations 3–4 orders of magnitude below the acute EC_{50} significantly reduced competitive interactions between the species. Similarly, Cordeiro et al. (2014), found that when organophosphates were applied at acute lethal concentrations to competing maize beetle species, the competitive advantage of the dominant species was diminished, reducing the likelihood of competitive exclusion. However, the beetles in the study differed in the sensitive greatly, suggesting that the life history strategies of species, not just the feeding rates play a role in chemical impacts on population dynamics of competition species.

Population fitness is strongly influenced by reproductive strategies and the number of offspring produced (Brockelman, 1975), which in turn affect the species' ability to compete, survive, and thrive in varying environmental conditions. In this context, *Asellus* produces more eggs per female compared to *Gammarus* of the same body size. This means that *Asellus* has a higher reproductive output, which can be advantageous in environments such as these where high reproductive rates are essential for population growth. On the other hand, *Gammarus* compensates with higher feeding rates, which can enhance its energy acquisition, growth, and survival, providing a competitive edge in environments where food resources are abundant. However, if *Gammarus* experiences a decrease in its feeding rate this balance shifts. As *Gammarus*'s ability to obtain food diminishes, its competitive advantage decreases. In such scenarios, *Asellus*, with its higher reproductive output per individual, gains a competitive advantage, potentially leading to an increase in its population size relative to *Gammarus*. This shift could alter the species composition and dynamics of the ecosystem, as *Asellus* becomes more dominant while *Gammarus* populations decline. This illustrates the importance of individual fitness, particular when already chemically sensitive species are in competition for resources, and not just survival when predicting chemical impact on species populations (Kliot and Ghanim, 2012; Straub et al., 2020).

Reductions in *Gammarus* feeding activity have been shown to reflect species abundance in natural environments. For example, a 50% reduction in in situ *Gammarus* feeding was linked to declines in both species' diversity and ecosystem functioning (Baird et al., 2007). While in Chapter 4 it was found that *Gammarus* populations were somewhat resistant to 50% feeding inhibition, in the current chapter, when interspecific competition is considered, *Gammarus* relative abundance and persistence decreased with just 10% feeding inhibition. This agrees with previous findings that interspecific competition can enhance the impact of feeding inhibition on sensitive populations (Knillman et al., 2012; Foit et al., 2012; Liess, 2012; del Arco et al., 2015b; Boutin et al., 2019). Results here suggest that the initial densities of the competing species can influence the level of feeding in inhibition that causes the exclusion of one species. Similar results were found in Kim et al. (2018), a modelling study, where initial cell densities of algae species *Pseudokirchneriella subcapitata* and *Chlorella vulgaris* affected the impact of copper exposure had on the dynamics between the two species. In Kim et al. (2018), *C. vulgaris* became less competitive than *P. subcapitata* with increase copper concentrations in most initial cell density combinations, but were resistant where initial densities were highest, resulting in a shift in competitive dominance to the species that initially had the competitive disadvantage. These findings suggest that the effects of chemical stress on competing species are highly context-dependent, influenced not only by the stressor itself but also by the initial abundance of the affected species and the overall density of shredders within the ecosystem.

In the model, *Gammarus* and *Asellus* compete indirectly for resource through resource exploitation. However, in the laboratory *Gammarus* has been observed to exhibit cannibalistic and predatory behaviour towards *Asellus* (Blockwell et al.,1997; Kelly et al.,2002; del Arco et al.,2016, Van den Brink et al.,2017), meaning that in reality both asellids and gammarids may experience interference. Despite this, this model only considers exploitation competition. The exclusion of interference competition, particularly predation and cannibalism by *Gammarus*, may lead to an underestimation of its competitive advantage over *Asellus*. This may lead to an underestimated mortality in *Asellus* populations, particularly under high *Gammarus* density or an overestimation of coexistence potential, as interference could further shift the competitive balance toward *Gammarus*. Nevertheless, lack of empirical data on the frequency and ecological relevance of these behaviours limits their incorporation into the model in a meaningful and effective way. However, it has been shown that chemical exposure can alleviate such interactions between *Gammarus* and *Asellus* (del Arco et al.,2016a; Van den Brink et al., 2017)

Similarly, there are few studies studying the chemical impact of between *Gammarus* and *Asellus* specifically with which to validate results against. However, the results are consistent with those studied with other species where differences in sensitivity between competition species result in greater impacts on sensitive populations compared to when studied in isolation (Liess, 2013; del Arco et al., 2015b; Saaristo et al., 2018; Schnuck and Liess, 2024). The lack of empirical studies with *Gammarus* and *Asellus* is partly due to the aggressive and predatory behaviour of *Gammarus* observed in the laboratory (Kelly et al., 2002). Of those that did study the competitive interaction, Blockwell et al. (1997) studied the effect of lindane on the competitive interaction with A. *aquaticus* on the feeding response of juvenile *G. pulex*. Lindane reduced the feeding activity of the gammarids. At 4.0 ug/L lindane, the competition from *Asellus* was excluded and the level of stress experienced by *G. pulex* similar to that of the control treatment. While del Arco et al. (2016b) found that the impacts of Carbendazim benefits *Asellus* populations not through reduced competition for food, but through reduced predation from the more sensitive *Gammarus*. However, habitat heterogeneity has been shown to mitigate certain behaviours in *Gammarus*, such as reducing cannibalism among adults and juveniles (McGrath et al., 2007), or predation on other crustacea (Kley et al., 2009). This indicates that the aggressive behaviours commonly observed in laboratory settings may be artifacts of experimental conditions. Assuming this also applies to *Gammarus*'s predatory behaviour, it is plausible that habitat heterogeneity in natural environments could reduce direct predatory and competitive interactions between *Gammarus* and *Asellus*. In such cases, competition between the two species may become more exploitative, with both species focusing on resource acquisition rather than direct conflict.

Furthermore, it is important to note that while the model assumes closed patches, invertebrates have the ability and opportunity to move between patches, escaping competition and repopulating patches where extinction has occurred (Blakely et al., 2006; Galic et al., 2012). These processes are not modelled here but, in the field, they can enhance the competitive ability of sensitive populations on a landscape level. In the field, microhabitat utilisation is similar between the two species, with *Gammarus* favouring smaller substrates and *Asellus* preferring weeds near larger substrates (Graca et al., 1994). Studies also noted the preference of *Asellus* for reed beds and littoral zones in lakes (Hargeby et al., 2004; Marcus et al., 1978). Therefore, habitat heterogeneity could facilitate the persistence of species populations under chemical stress. *Gammarus*, being more mobile than *Asellus* (Resh et al., 2008), cover a larger range due to their stronger swimming ability. This mobility gives *Gammarus* access to more resources and greater opportunities to escape unfavourable conditions. In contrast, *Asellus* have limited mobility (Resh et al., 2008), reducing their ability to repopulate patches (Galic et al., 2012, 2013) or avoid chemical exposure (O'Callaghan et al., 2019). Therefore, in the field, exclusion of *Gammarus* populations by *Asellus* following chemical exposure induced feeding inhibition found here may not be as low. While *Asellus* is often less sensitive to a wide range of chemical stressors than *Gammarus* (Chapter 3), in cases in which they are the more sensitive species, they may face greater impacts from chemical exposure. This reduction in interspecific competition could lessen the impact of chemical stress on species population dynamics, particularly in more heterogeneous habitats, where the buffering effects of complex environments may play a key role in maintaining species coexistence.

5.4.2 Time to Exclusion

As expected, for both species, increasing difference in feeding inhibition between species population led to a decrease in the time to exclusion. Increasing difference in relative sensitivity to chemical stress therefore enhanced the impact competitive interactions, leading to the rapid decline in abundance and exclusion of the more sensitive species. While there are few studies with which to compare the time to exclusion, similar results were found in Viaene et al. (2015), however on a much smaller scale with *Daphnia magna* excluding *Brachionus calyciflorus* between 1 – 3 weeks days in in the absence of chemical stress (Gilbert, 1985), but reduced to less than 10 days with the addition of pyrene 110 µg L^{-1}. However, the results in this study are context dependent with the initial density of both species influencing the time to exclusion. In patches initially dominated by *Asellus*, exclusion took a minimum of 7 months, whereas in patches initially dominated by *Gammarus*, exclusion could take over 7 years. Therefore, the dominant species in a patch significantly influences how each species responds to increased feeding inhibition. The results demonstrate that the combination of competitive dynamics and environmental stress can either prolong or hasten species exclusion, depending on the interaction of these factors.

While exclusion of sensitive populations occurs with feeding inhibition of 10% (or a 10% relative difference in feeding inhibition), the time to exclusion takes, on average, several hundred days. Not until a 40% inhibition of *Gammarus* feeding does the exclusion of *Gammarus* occur within 144 days. This occurs particularly on patches where the initial relative abundance of *Asellus* was low (GamDom). For some chemicals such as pesticides, such prolonged exposure durations are unlikely to occur in natural environments, as organisms are typically exposed to pulsed, intermittent stress from chemicals rather than continuous exposure (Reinert et al., 2002). Other chemicals, such as pharmaceuticals (Burns et al., 2018), may result in continuous low-level exposures or frequent pulses with little time to recover between stress events (Naddy and Klaine, 2000; Schnuck and Liess, 2022), particularly, from chemical exposures from converging streams across interconnected landscapes (Norman et al., 2020). Foit et al. (2012) found that interspecific competition for food between *Daphnia magna* and *Culex pipens* larvae insignificantly increased recovery times following exposure to pyrethroid insecticide fenvalerate, suggesting that the risk of population collapse from repeated stress events rises when species are already competing for limited resources. This implies that populations subjected to multiple, closely spaced, pulses of chemical stress may be more vulnerable to collapse, especially when there is little recovery time between pulses. The results of this study indicate that even low-level, prolonged exposure or frequent pulses with little recovery time can lead to significant impacts on the structure of species populations. For example, just low levels of continuous stress were enough to shift competitive dynamics and affect species persistence. Although such prolonged exposures are unlikely to occur naturally, they highlight the vulnerability of ecosystems to chronic stress, particularly when recovery time is limited. Additionally, while time to exclusion at low levels of feeding inhibition often exceeds one year, the strict definition of exclusion—when only one species remains—may overestimate the actual collapse timeline. Exclusion may occur sooner, once a population declines to an unrecoverable level, even if a few individuals remain. Therefore, these results present a liberal view of species exclusion, and the effective exclusion times may be shorter than the analysis suggests.

5.4.3 Potential consequences for the performance of ecological functions

5.4.3.1 Leaf litter processing

Although changes in the structure of the shredder processing unit (SPU) occur with increasing feeding inhibition in either species, based on results of the single species models, shifts from one *Gammarus* to *Asellus* dominated systems, and visa verse, have minimal impact on the overall consumption rate by shredders in the SPU. In these models, *Gammarus* populations exhibit marginally higher consumption rates (mg/day) compared to *Asellus* populations (Table 3.14). Nonetheless, the results suggest a degree of redundancy in the SPU regarding leaf processing, indicating that both species can fulfil this ecological function. However, in field conditions, functional efficiency as well as their functional role plays a more significant role in leaf processing (Jonsson and Malmqvist, 2003). *Gammarus* individuals not only have higher consumption rates than *Asellus* but are also more effective shredders (Graca et al., 1994). Therefore, in the field, shifts from *Gammarus*-dominated to *Asellus*-dominated patches could lead to a reduction in the rate of leaf litter processing. This is supported by evidence that decreased *Gammarus* abundance due to water quality degradation is associated with lower leaf decomposition rates (Farrow and Maltby, 2000).

It is important to interpret potential changes in leaf processing by these two detritivores with caution. As discussed throughout this thesis, the model used is closed, reaching an equilibrium where population dynamics are driven solely by food consumption and availability. This constrains food consumption across the population, resulting in similar consumption rates between *Gammarus* and *Asellus.* A limitation of this model is that it does not account for the multiple biotic and abiotic factors influencing leaf litter processing in the field. Abiotic factors include temperature (Cummins et al., 2024; Ferreira et al., 2015a) and nutrient availability (Woodward et al., 2012; Ferreira et al., 2015b), while biotic factors encompass microbial colonisation (Ferreira et al., 2012), detritivore community composition (Rubio-Rios et al., 2021), and the species of leaf litter present (Cummins et al., 2024). These factors, particularly the biotic ones, are interdependent, and changes in one can affect others. In field conditions, reductions in *Gammarus* populations due to stressors may significantly impact leaf litter processing rates (Forrow and Maltby, 2000; Maltby et al., 2002).

5.4.3.2 Prey provision

Prey selection by fish is influenced by a combination of factors such as prey size, absolute abundance, relative abundance, and microhabitat. Larger prey often provides more energy that smaller prey, meaning fish such as brown trout and rainbow trout, which prey on both *Gammarus* and *Asellus* (Dodrill et al., 2021; Andersen et al., 2016), and perch, which primarily feed on *Asellus* (Rask and Hiisivuori, 1985; Copp et al., 2005), demonstrate size-selective foraging. In these species, prey size is often biased towards larger individuals (Newman and Waters, 1984; Elliot, 1970, 1973). However, relative availability also influences their choices. Larger trout may prefer larger prey, such as caddisfly larvae and chironomids, when *Gammarus* numbers decline, whereas smaller brown trout show a stronger preference for *Gammarus* than their larger counterparts (Anderson et al., 2016). In the absence of *Gammarus*, juvenile brown trout may turn to *Asellus* as an alternative food source (Elliot, 1973). While Enefalk et al. (2019) observed that *Asellus* appeared in 39% of trout stomachs, making it the fourth most common prey item after Trichoptera (encased and free living) and chironomid larvae. Therefore, changes in the relative abundance, or total shredder abundance influence the provision of prey by *Gammarus* and *Asellus* in a recreational fishery.

With increasing *Gammarus* feeding inhibition, the relative abundance of *Gammarus* declines and *Asellus* prevalence increases. With predatory fish showing preferences for different prey, (Chalcraft and Resetarits, 2003), shifts from *Gammarus* to *Asellus* dominated patches may negatively impact trout populations as their preferred prey declines (Wilzbach et al., 1986; Romaniszyn et al., 2007; Tyson and Knight, 2001). While they may still benefit from the provision of *Asellus*, selecting them based on their increased relative availability, *Asellus* populations consist of smaller individuals (Table 3.14, Figure 5.1) and therefore, in the absence of alternative prey, trout and other drift feeding fish may expend more energy foraging for less energetically beneficial *Asellus*. This could lead to energy imbalances for larger trout, as they would need to expend more energy foraging on smaller or less abundant prey (Newman and Waters, 1984), potentially triggering prey switching or reduced growth rates in those populations. However, due to differences in microhabitat between *Gammarus* and *Asellus* (Graca et al., 1994a), the increased proportion of *Asellus* available due to *Gammarus* feeding inhibition may benefit benthic feeding fish such as perch, stone loach, and bullhead (Rask and Hiisivuori, 1985; Copp et al., 2005) and, to an extent, juvenile trout that reside and feed in the benthos (Elliot, 1973). Conversely, *Asellus* feeding inhibition results in the increased prevalence of *Gammarus*, potentially benefiting drift feeding fish through microhabitat partitioning of *Gammarus* and *Asellus* (Graca et al., 1995).

Increases in absolute stress and chemical induced feeding inhibition resulted in increased occurrence of coexistence across patches. Coupled with the fact that there was very little if any change in the median shredder abundance across patches, this suggests that the shredder community becomes more diverse with increasing absolute stress in the system. For foraging fish, given different species of fish often prefer different species, this may result in increased prey diversity, could support a greater diversity of fish species and resource partitioning for fish (Sánchez-Hernández et al., 2017), particularly when *Gammarus* and *Asellus* differ in their microhabitat distribution (Graca et al., 1995).

5.5 Conclusion

The results highlight that species responses to chemical stress are context-dependent with chemical effects on the SPU influenced by initial population densities and the difference in sensitivity to chemical stress. Interspecific competition for resources is an important factor when assessing chemical impacts on SPUs. In contrast to findings presented in Chapter 4, where single species dynamics were examined, this chapter demonstrates that interspecific competition amplifies the impacts of feeding inhibition on populations of shredders, with greater differences in species sensitivity to chemical stress leading to more pronounced impacts on SPU structure. While *Gammarus* initially holds a competitive advantage due to its higher feeding rates, increased feeding inhibition exacerbates its vulnerability, allowing *Asellus* to potentially dominate due to its higher reproductive output. However, the buffering effects of habitat heterogeneity and species mobility between patches may facilitate coexistence, indicating that natural settings may support resilience not fully captured by the models used in this research. The findings further emphasise the intricate relationship between competition, chemical stress, and ecosystem function, including leaf litter processing, and prey availability for fish species. Differences in feeding inhibition alters the structure of the SPU, which has the potential to affect the foraging strategies and abundance of benthic-feeding fish. Ultimately, this study underscores the need for a more nuanced understanding of chemical impacts within competitive ecological contexts. By integrating species-specific sensitivities, and interspecific competitions we can enhance our ability to predict and manage the effects of chemical stress on freshwater ecosystems.

Chapter 6 – General Discussion

The aim of this thesis was to explore how information on chemical impacts on the feeding activity of freshwater invertebrates can be used to predict population level responses of ecosystem functions and associated ecosystem services, examining the implication for ecological risk assessment. This was addressed through a case study of a recreational fishery, where the structure and activity of invertebrate populations are critical for maintaining prey availability and processing organic matter, both of which support fish populations. This was achieved by focussing on chemical induced effects of feeding inhibition on the performance of ecological functions by freshwater invertebrates. The thesis first examined the impacts of chemical stress on individual freshwater invertebrates, assessing differences in sensitivity between different functional feeding groups. The research then focused on freshwater shredders, *Gammarus pule*x and *Asellus aquaticus,* exploring how chemical impacts on individual energy uptake translate to population-level responses and the performance of ecological functions. This was explored both in single-species populations and then when interspecific competition for food resource between *G. pulex* and *A. aquaticus* is considered.

This chapter synthesises the findings of previous chapters to examine how assessing effects of feeding inhibition across different levels of biological organisation influences the prediction of impacts on ecological functions within a recreational fishery. It further explores how insights into feeding behaviour responses to chemical stress, combined with extrapolatory modelling, can be used to assess chemical impacts on ecosystem service delivery.

6.1 Main Findings

Chemical impacts on ecological functions are highly context dependent (Clements et al., 2016). Results of this thesis suggest that impacts of chemical stress on the performance of ecological functions within a recreational fishery can be influenced by the functional feeding group in question (Chapter 2), the chemical mode of action of the exposure chemical, or pathway of impact in a consumer resource system (Chapter 4), species life history traits (Chapter 4), the presence of interspecific competition (Chapter 5), and the initial densities of competing species (Chapter 5).

The first chapter aimed to assess how chemical stressors impact the feeding activity of individual freshwater invertebrates, and how functional feeding groups (FFGs) differ in their sensitivity to these stressors. While of the 1500+ chemicals in the curated RIVM toxicity database (Oginah et al., 2023), only 48 had sufficient data to evaluate differences in sensitivity between FFGs. Of those 48, significant differences were detected between FFGs in 30%. This lack of difference can largely be attributed to the widespread presence of arthropods across functional groups. Arthropods exhibit considerable variation in their sensitivity to chemical stressors, with both crustaceans and insects encompassing a comparable number of sensitive and tolerant genera (Van den Berg et al., 2019). Therefore, FFGs rich in arthropods are unlikely to exhibit differences in sensitivity. Where differences did emerge, often for chemicals with the most data available, differences were primarily driven by taxonomic distinctions level of phylum, such as between molluscs and arthropods. For example, filterers, largely comprising molluscs (primarily bivalves) and zooplankton, demonstrated heightened sensitivity to metals, particularly to cadmium and zinc. In contrast, gatherers composed solely by arthropods were vulnerable to acetylcholinesterase (AChE) inhibitors; e.g. carbaryl, diazinon, and malathion, aligning with findings of Maltby et al., (2005). Herbivores, predominantly represented by gastropod molluscs, exhibited greater tolerance to neurotoxicants and AChE inhibitors, aligning with Maltby et al., (2005). This signals to potential functional redundancy in systems with great arthropod diversity and the vulnerability of filterers to metal exposure. With filterers important for improving water quality by removing excess nutrients (Faber et al., 2019), these results highlight the vulnerability of water clarity and nutrient regulation to metal exposure. Furthermore, these results of this thesis support that fact that the ecological status and distribution of functional traits within the invertebrate community—whether species-rich or functionally diverse—play a key role in determining the impact of chemical stress on ecological function performance (Baert et al., 2017).

Since feeding activity of freshwater invertebrates is not only linked to but drives many ecological processes and functions in freshwater systems (Graça et al., 2001; Bloor et al., 2005) and is a sensitive ecotoxicological endpoint (Agatz et al., 2014), feeding is a useful endpoint to extrapolate from individual to functional level impacts (Bloor et al., 2005; Ford et al., 2021). A systematic review of the peer-reviewed literature revealed that feeding is a toxicity endpoint that can be measured on a wide range of taxa, across all functional feeding groups studied, in response to a range of chemical stressors. However, there is scarce information about the effects of single chemicals on a range of taxa, making it difficult to draw conclusions about chemical impacts on the ecological functions, using feeding data alone. Data are concentrated on a limited number of chemicals and standard species (e.g., *Daphnia spp.*, *Gammarus spp.*, *Dreissena sp.*, *Brachionus sp.*), mirroring the distribution of toxicity data for other well-studied endpoints (Oginah et al., 2023). This lack of comprehensive data continues to hinder the implementation of an ecosystem services approach to risk assessment (Maltby et al., 2021), highlighting the ongoing need for cross-species extrapolation (van den Berg et al., 2021). However, a strong positive correlation was found between feeding sensitivity and lethality for neurotoxicants—indicating that lethality data could be used to infer feeding sensitivity for these chemicals—the relationship was less clear for other contaminants. This supported by the fact that feeding inhibition is a general stress response (Hellou et al., 2010), rather than one driven by specific biochemical mechanisms. This lack of specificity complicates mechanistic predictions of how chemical exposure affects the feeding activity of individual invertebrates. Furthermore, the available data are heavily concentrated on filter feeders, limiting the ability to extrapolate findings across different functional feeding groups (FFGs). The scarcity of feeding data and the absence of standardised feeding assays across species made it difficult to assess species-specific chemical sensitivities or to link these sensitivities to specific chemical modes of action. Nonetheless, while changes in feeding activity may be an endpoint that can be measured with a wide range of freshwater invertebrates, across functional feeding groups.

The thesis then examined how individual-level impacts on energy uptake translate to population-level responses and the performance of ecological functions. This was done using dynamic energy budget (DEB) individual-based models (IBMs) for two key freshwater shredders, *Gammarus pulex* and *Asellus aquaticus*, adapted from the *G. pseudolimnaeus* DEB IBM of Galic et al., (2017). These species were identified as important for studying the effects of individual feeding activity on broader ecological functions (Chapter 3).

In Chapter 4, single consumer population responses were assessed in the context of impacts on consumers (reduced feeding rates and assimilation efficiency) and on resources (food quality and availability). Population-level responses varied in response to different pathways of impact. Both *G. pulex* and *A. aquaticus* populations were highly responsive to and similarly affected by changes in food availability and assimilation efficiency. The maximum deviation in median population abundance decreased almost linearly with reduced food availability, consistent with previous field studies demonstrating a positive correlation between shredder density and leaf litter availability (Cummins et al., 1973; Murphy and Giller, 2000). The reduction in assimilation efficiency represented declines in both food quality and consumer digestion efficiency; however, as these factors were modelled identically, it was not possible to distinguish between them. Chemicals like fungicides and copper can impair both the digestive enzymes of consumers and microbial communities on leaf litter, affecting the quality of resources to shredders (Dedourge-Geffard et al., 2009; Zubrod et al., 2011, 2015). While few population studies have focused on species abundance in response to chemical impacts on nutritional quality or assimilation efficiency (Zubrod et al., 2019), long-term fungicide exposure in streams has been linked to reductions in macroinvertebrate communities (Lin et al., 2012; Fernández et al., 2015), particularly in colder climates where fungal growth rates are slower (Graça et al., 2023). Similarly, mesocosm studies have shown that fungicide exposure can lead to declines in gammarid density due to the loss of fungal biomass (Zubrod et al., 2014). These findings highlight the importance of indirect pathways of effect on consumer resource systems and sub organism effects having potentially far-reaching impacts on populations than individual level responses.

Single-species populations were, however, resistant to feeding inhibition up to a 50% threshold (Chapter 4), beyond which mortality rates sharply increased and population abundance declined substantially. However, thresholds of population level collapse (70 and 80% for *Gammarus* and *Asellus* respectively) were comparable to those reported in modelling studies (Baird et al., 2007; Gabsi et al., 2014; Galic et al., 2017) but higher than those from short term studies in field conditions (Maltby et al., 2005). This discrepancy may stem from lack of environmental factors such as variable temperature and resource availability in the model assumptions, or system-level factors, such as interspecific competition for resources, which can increase the sensitivity of the more sensitive species (Knillman et al., 2012).

When interspecific competition for resources was introduced, both the difference in relative sensitivity and the initial density of the competing species were found to be important factors in population response to feeding inhibition (Chapter 6). When species differed in their sensitivity to stress, the effects of feeding inhibition became more pronounced compared to the single population level, agreeing with previous empirical studies where, when competition species differ in sensitivity, interspecific competition for resources exacerbated the impacts of chemical stress on populations (Knillman et al., 2012; Foit et al., 2012; Liess, 2013; Boutin et al., 2019). However, results here suggest that the initial ratio of the two species also influences the impact of chemical stress on the system, with exclusion times shortest when the tolerant species was most abundant. This indicates that assemblage structure, not only composition, plays an important role in the in the impact of chemical stress on competing species. However, when both species had similar sensitivity to chemical stress and experienced equal levels of feeding inhibition, the occurrence of coexistence between them increased. These results agree with empirical findings of del Arco et al. (2015a) and Schnuck and Liess (2024), where chemical stress elevated interspecific competition between species, increasing coexistence. However, whether a chemical stressor elevates or enhances the impact of interspecific competition depends on not only on the difference in sensitivity between species but also the difference in their competitive abilities or strength (Cordeiro et al., 2014; Van Den Brink et al., 2017). This supports the fact that life history and functional traits of competing species also influence the impact of chemical stress in multispecies systems.

With regard to consequences on the performance of ecological functions, while both species are involved in leaf processing, they differ significantly in their sensitivity to chemical exposure (Chapter 3) and their efficiency in performing this function (Graça et al., 1994). At the single species level, food availability had the most significant impact on leaf processing rates, decreasing almost linearly with reduced food levels, while reductions in feeding rates and assimilation efficiency had a lesser impact on leaf consumption, especially for *Gammarus* populations. This resilience in leaf processing suggests that these populations may compensate for lower feeding rates through mechanisms like competitive release. Leaf processing by *Gammarus* and *Asellus* emerged as the most sensitive endpoint to stressors compared to population abundance and prey provision, underscoring the ecological importance of macroinvertebrate-driven decomposition and its role as an indicator of chemical stress in aquatic ecosystems. In the coupled scenario, while total leaf processing rates were not calculated, it is inferred that changes in SPU structure could have consequences for leaf processing due to differences in functional efficiency between species. These findings support the use of invertebrate-driven leaf loss as an indicator of chemical stress (Gessner and Chauvet, 2002; Young et al., 2008). *Gammarus* feeding rates, a known ecological endpoint, are often used in situ as water quality indicators and are analogous to leaf processing rates (Maltby et al., 2002; Bloor et al., 2006). The study highlights the importance of leaf litter processing rates as indicators of chemical stress, responsive to various toxicity pathways, though population-level effects may vary due to intraspecific interactions.

Prey provision was found to be more sensitive than population abundance, particularly for *Asellus*, as the DEB model prioritises energy for growth and maintenance over reproduction (Chapter 3). Both *Gammarus* and *Asellus* are significant prey for fish species like trout and perch, with potential ecosystem impacts; for example, chemical-induced reductions in food resources could reduce fish populations that rely on these invertebrates (Rask and Hiisivuori, 1985; Wilzbach et al., 1986; Tyson and Knight, 2001). The study found cumulative impacts (total area under the effect curve) to be a more comprehensive measure of long-term prey provision declines than maximum deviation alone, as this method captures gradual reductions in prey over time, which may more accurately predict impacts on fish populations. While in the coupled scenario, there was little impact of feeding inhibition on total shredder abundance, shifts in SPU structure could have impacts on the foraging activity of fish due to prey preferences (Chalcraft and Resetarits, 2003).

6.2 Evaluation of the use of the models

Both species models underpredicted the reproductive output of individuals (Chapter 3). Given that reproduction is a critical factor in population dynamics, fitness, and recovery (Galic et al., 2012), it is essential that DEB models accurately capture this process. The underprediction of reproductive output introduces uncertainty into model predictions, particularly when reproductive differences between species are a focus. While theoretically, both *Gammarus* and *Asellus* should exhibit metabolic acceleration (Kooijman, 2014), this is not always observed in laboratory growth studies (Galic et al., 2016). It is important to note that the primary aim of this study was not to develop DEB IBMs for use in regulatory ERA, but rather to understand the broader ecological impacts of chemically induced effect on the feeding behaviour of individuals. This study offers an important contribution by demonstrating how ecological dynamics unfold across different levels of biological organisation, all within a consistent modelling framework. By systematically incorporating ecological interactions and factors that could influence chemical impacts on the ecological functions of two freshwater shredder species, this research sheds light on how these species' performance may be affected.

Since the development of the models used in this thesis, Mangold-Döring et al. (2024) published a DEB IBM for *Gammarus pulex,* encountering similar challenges with reproductive output under the abj model (with metabolic acceleration). To address this, they applied a correction factor to the fecundity function by adjusting the calibration of the reproduction buffer. Given this study was published after the development of the models, this approach was not utilised in this thesis. However, this is a viable and necessary solution to the development of the mode and underscores the ongoing need for refinement in DEB models to ensure accurate predictions of reproductive dynamics (Jager and Ashauer, 2022).

A limitation of the DEB IBMs in this study is the use of a closed system with fixed environmental conditions, resulting in stable consumption rates for both populations. Unlike the original *Gammarus* model by Galic et al., (2017), this model did not account for temporal dynamics like seasonal recruitment cycles, which are crucial for functions such as prey provision. For example, winter population growth and spring resource availability can significantly influence individual reproductive success and population structures (Gee, 1988; Biro et al. 2003). Without incorporating these seasonal dynamics, the model's ability to simulate real-world ecological processes is limited. Nonetheless, these findings highlight the need to consider both ecological structure and function in environmental risk assessments, as shifts in species interactions and population dynamics can have cascading effects on ecosystem services like food web stability and nutrient cycling. The model offers insights into species dynamics under resource-limited conditions by offering a controlled framework for studying key ecological processes that may influence chemical induced effect on the feeding of *Gammarus* and *Asellus*. The absence of seasonal environmental variation was intentional, as the primary goal was to investigate the mechanisms of species interactions in a stable, resource-constrained environment.

Nonetheless, with the limitation of the models, the question is are the results of this study valid? Models have long been used to test hypotheses and used in stress ecology to identify processes and ecological interactions that have fundamental repercussions for ecosystems (de Laender et al., 2015; Rico et al., 2016). DEB IBMs continue to do that in a more detailed way, enabling the user to test increasing complex scenarios. This study highlights key factors that influence the extrapolation of individual chemical stress effects to impacts on ecological functions, which in turn underpin ecosystem service delivery. If single-species models were refined to better represent reproductive output by adjusting fecundity functions, it is expected that while the exact quantitative outcomes might differ, the overall patterns of impact would remain consistent. For example, in the single-species model, an increase in reproductive output for both species could lead to larger population sizes and higher growth rates. This might affect the percentage change in population abundance, potentially amplifying the impacts due to an already high reproductive output. In coupled species models, where coexistence dynamics are influenced by both feeding rates and reproduction, therefore modifying reproductive parameters could alter the predicted range of conditions under which coexistence or exclusion occurs. These changes may even shift the specific thresholds of population exclusion. However, the broader patterns of impact—such as how species ratios and population densities influence outcomes in environments where species compete for resources—are likely to remain.

One limitation in the implementation of the models in this study, particularly for the coupled analysis (Chapter 6), is that DEB IBMs are computationally demanding. NetLogo, the model language used in this thesis, is a generic and accessible programming language for the implementation of individual based and individual based DEB models (Martin et al., 2012). Its simplicity and relative ease of use make it especially valuable in regulatory chemical risk assessment contexts, where risk assessors and managers may have limited programming expertise. However, NetLogo is not the most powerful or efficient programming language for developing complex models like DEB IBMs, particularly when coupling them (as done in Chapter 6), or in multi-patch environments (which was trialled and unsuccessful in the development of the model in chapter 6). In this case, more powerful and efficient languages such as Python or Julia could be better suited to handle such complexity, however agent-based modelling in these languages, particularly Julia, is still relatively new (Vahdati, 2019). Furthermore, there is a gap in the availability of knowledge, experience, and documentation for Julia and a notable absence of Python implementation within the field of ERA. Consequently, models implemented in these languages remain largely inaccessible at the present time. The implementation of more efficient programming languages, designed with user-friendly interfaces, could broaden accessibility to modelling tools and enhance the scope and quality of modelling in ERA.

6.3 Implications for the application of an ecosystem services approach to risk assessment?

The ecosystem services approach to chemical risk assessment aims to link chemical induced effect on individuals or service providing unit to impacts on ecological functions that underpin ecosystem service delivery (Maltby, 2013; Maltby et al., 2017; Devos et al., 2019). By addressing spatial and temporal variations in hazard and exposure, the ecosystem services approach allows for localised risk assessments. This enables risk managers to balance chemical use with ecological costs, shifting from the goal of protecting "everything everywhere all the time" (Holt et al.,2016) to a more targeted, context dependent protection strategy (Devos et al., 2015).

Given that the impact of chemical stress on ecosystems is dependent of ecological context (Clements et al., 2016), incorporating context dependent chemical effects in an ecological risk assessment requires a well-defined ecological scenario. While scenarios have been developed for chemical fate assessments (FOCUS, 2005), they have yet to be defined for ecological scenarios (Rico et al.,2016; Franco et al., 2017). Developing such scenarios for ERA involves identifying key ecological factors that influence the outcomes of risk assessments. Results of this thesis highlight the importance of species identity, chemical mode of action (or pathway of impact) (Figure 6.1), community structure as well as composition (Figure 6.2) when assessing chemical impacts on ecological functions in a recreational fishery.

6.3.1 Linking what we measure to what we want to protect

A central challenge in ERA lies in determining whether observed effects on standard test species are reliable indicators of broader impacts on ecosystem functioning (Maltby et al.,2018). This question becomes particularly relevant when attempting to extrapolate species-level responses to changes in ecosystem processes.

Firstly, it was proposed that feeding behaviour would be an appropriate endpoint to link individual level effects to population level response and impacts on ecological functions. Feeding behaviour is sensitive ecotoxicological measure and a general response to chemical exposure (Hellou, 2010). Feeding inhibition, for example, can lead to both individual reproductive failure and mortality (Agatz et al., 2013). However, measuring such standard endpoints may not fully capture the sublethal and cumulative consequences of feeding inhibition due to individual buffering processes. While these endpoints play a fundamental role in ERA, they may overlook early-warning indicators of ecological stress that feeding may detect (Hellou et al., 2010) and underestimate long term impacts on function (Ford et al., 2024), such as organic matter processing and population structure which is important for size selective foraging of predators. Feeding inhibition, for example, can lead to both individual reproductive failure and mortality (Agatz et al., 2013) yet results of this thesis suggest that its ecological implications may differ depending on how feeding is impacted (i.e. pathway of impact), the relative sensitivity of species in the assemblage, and the relative abundance of competing species. In particular, these findings show that the pathway through which energy uptake by invertebrates is reduced can lead to varying population and functional consequences, with reductions in food availability and assimilation efficiency having a greater impact on individual populations than reductions in ingestion. The population modelling outcomes of this thesis therefore highlight two significant gaps in current risk assessment frameworks for an ecosystem services approach to risk assessment: first, interspecific competition can alter individual-level impact extrapolations to population-level responses, and second, the specific impact pathway is crucial in determining the extent of ecological disruption. Therefore, assessments should consider not only the physiological mode of action (Ashauer and Jager, 2018) but also the ecological pathway of impact, which can be conceptualised through evidence-based logic chains (Hayes et al., 2018; Fleeger, 2020).

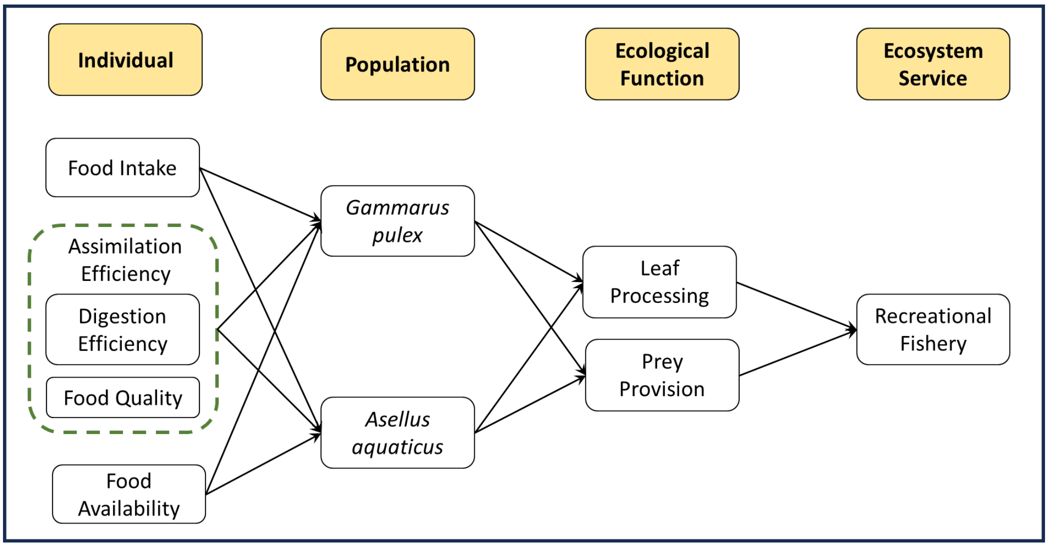
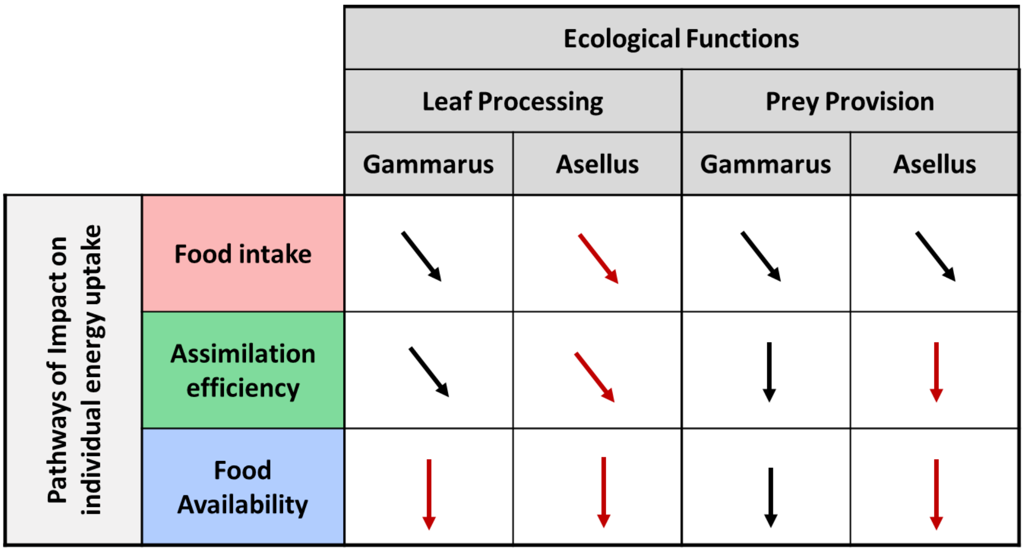


Figure 6.1: Conceptual model illustrating the connections from chemical induced change in individual energy uptake to ecosystem services in a freshwater fishery. Pathways of impact on individual energy uptake (food intake, assimilation efficiency, digestion efficiency, food quality, and food availability) impact two key shredders species populations, *Gammarus pulex* and *Asellus aquaticus*. These populations contribute to ecological functions, leaf processing and prey provision, which ultimately support the ecosystem service of recreational fishery.



Pathways of Impact on individual energy uptake		Ecological Functions			
		Leaf Processing		Prey Provision	
		Gammarus	Asellus	Gammarus	Asellus
	Food intake	↘	↘	↘	↘
	Assimilation efficiency	↘	↘	↓	↓
	Food Availability	↓	↓	↓	↓

Figure 6.2: Summary of results of how different pathways of effect on individual energy uptake can influence the relative consequences of the performance of ecological functions (Leaf processing and Prey Provision) of single populations of *Gammarus pulex* and *Asellus aquaticus*

One of the key challenges in applying the ecosystem services approach to ERA is the mismatch between the species used in single species toxicity tests—typically standard model organisms—and the species that perform the ecological functions of interest (Maltby et al., 2018). To address this gap, various methods have been developed to enable cross-species extrapolation of toxicity data to non-model organisms. The most established and widely used approach is the SSD, which uses toxicity data from broad range of taxonomic groups to estimate the distribution of species sensitivities (Postuma et al., 2001). These can be used to estimate a hazardous concentration (HC_x) for a specified protection level (e.g., HC_5, protecting 95% of species). While SSDs are broadly applicable, they may underestimate the risk for chemicals with specific modes of action targeting particular taxonomic groups (Oginah et al., 2023). Trait-based approaches offer an alternative, using sensitivity-related traits to estimate responses in untested species (Van den Berg et al., 2019), while phylogenetic methods infer sensitivity based on taxonomic relatedness (Craig, 2013; Spurgeon et al., 2020). However, such approaches have limitations: trait-based methods are constrained by the lack of trait data for many non-model species and may not capture all relevant ecological or physiological factors (Van den Berg et al., 2021), while phylogenetic relatedness may not reflect ecological or functional differences.

Current ERAs often rely heavily on taxonomic, not functional, species classifications to evaluate chemical impacts, typically focusing on a limited set of model species (e.g. algae, fish, and invertebrates). While this approach simplifies assessments, it can overlook ecological variability, particularly regarding species' roles in ecosystem functioning. In this thesis, while *Gammarus* and *Asellus* exhibited similar overall patterns of response to chemical exposure, the impact on functional performance differed (Figure 6.2). This highlights a key limitation in conventional ERAs: taxonomic identity alone does not adequately capture differences in ecological function or chemical sensitivity. Categorising species based on their function rather than taxonomic identity can reduce complexity in ERAs, while maintaining predictive accuracy when assessing chemical impacts on key ecological functions. For example, Rumschlag et al. (2020) demonstrated that pesticide impacts in outdoor experimental ponds showed consistent patterns across assemblages when species were grouped by functional feeding roles and pesticides by mode of action. However, ecological function is not defined solely by feeding. Functional efficiency and life history traits also play an important role (Jonsson and Malmqvist, 2003). In this thesis, although *Gammarus* and *Asellus* are both classified as shredders (Tachet et al., 2010) (in the literature, *Gammarus* is sometimes also classified as a predator Kelly et al. (2002), and *Asellus* a gatherer Kunz et al. (2021)), the results illustrate that population-level responses to chemical impacts on energy uptake are shaped by species-specific life histories and individual sensitivities. Impacts on ecological function performance are influenced not only by population-level effects but also by changes in population structure and individual functional efficiency. Furthermore, while functional feeding group classifications provide some insight into changes in assemblages structure, they may overlook the broader ecological roles of individual species such as preferred prey (Chalcraft and Resetarits, 2003). So, while grouping species by functional feeding groups can streamline ecological risk assessments and enhance predictive power, by emphasising ecological roles over taxonomic identity, this approach may overlook key interspecies differences in chemical sensitivity. Relying solely on functional feeding group classifications risks obscuring critical nuances, potentially limiting our understanding of the broader ecological impacts of pesticide exposure.

Currently, ERAs typically focus on direct toxic effects on individual species, often overlooking the indirect, food web mediated pathways through which chemicals can alter ecosystem functioning (Fleeger, 2020). This approach can miss key ecological interactions, such as resource availability and quality, that significantly influence organismal responses. For example, shredder populations were shown in this thesis to be particularly sensitive to changes in food availability and assimilation efficiency—both of which are affected by the microbial composition of conditioned leaf litter (Bärlocher et al., 1979). These findings support the need to integrate food web-level considerations into ERAs (Rico et al., 2016). Further to their importance of ecosystem services (Seena et al., 2020), including ecotoxicological data from microbial species could provide critical insights into resource-related changes affecting shredding activity in these species, as impacts on lower trophic levels tend to propagate throughout the food web (Relyea and Hoverman, 2006). Although linking dose-response curves to changes in leaf litter quality remains complex (Lebrun et al., 2020), a tiered approach to ecological assessment—where lower-level impacts signal potential higher-order effects—could improve sensitivity in detecting resource-related disruptions to ecological functions performed by populations of species. Consequently, incorporating food web-level assessments and microbial ecotoxicological data could offer a clearer, more comprehensive view of resource-based chemical impacts (Rico et al., 2016). While such assessments add additional complexity and data demands, incorporating food web dynamics and microbial data can lead to a more holistic understanding of how chemical stressors affect ecosystem functions.

Conventional ecological risk assessments and modelling approaches often look at species populations in isolation, overlooking how interspecific interactions—such as competition within functional feeding groups—can shape ecological outcomes. This simplified approach risks underestimating the complexity of chemical effects at the population and community levels. This findings in this thesis demonstrate that interspecific competition within a functional feeding group, can substantially alter predicted population level outcomes of individual feeding inhibition. The difference in sensitivity and initial densities in competing species also impact the predictions (Figure 6.3), emphasising the need to incorporate these interactions within risk assessment frameworks. For example, results from Chapter 5 suggest that in a *Gammarus*-dominated system, a 10% reduction in *Gammarus* feeding activity due to chemical exposure may shift competitive dynamics, gradually leading to *Asellus* dominance over approximately one year. This shift significantly impacts ecosystem functions: as *Gammarus* is a more efficient shredder (Graça et al., 1994) with its decline correlated with reduced leaf litter processing (Forrow and Maltby, 2000; Maltby et al., 2002), disrupting energy flow. Additionally, although total prey biomass may increase due to greater shredder abundance (Table 3.14), the prevalence of the smaller *Asellus* prey could negatively affect fish growth, which prefer larger prey items (Newman and Waters, 1984; Anderson et al., 2016). Conversely, in an *Asellus*-dominated system, a 10% reduction in *Gammarus* feeding has limited effects on shredder dynamics, maintaining stable leaf processing rates and ecosystem function due to little shift in community structure. While *Asellus* dominance supports steady prey availability for fish, the lower biomass of *Asellus* yields and smaller prey sizes (Table 3.14), which may subtly influence fish diet quality without significantly impacting overall prey provision. While these results represent only a subset of factors that influence chemical effects on the performance of ecological functions, they demonstrate how population and community level responses to individual feeding inhibition can differ. Furthermore, exclusion of sensitive species occurred within 1 year from the 20% effect level. This highlights the need to incorporate ecological interactions and longer-term population dynamics into ERAs.

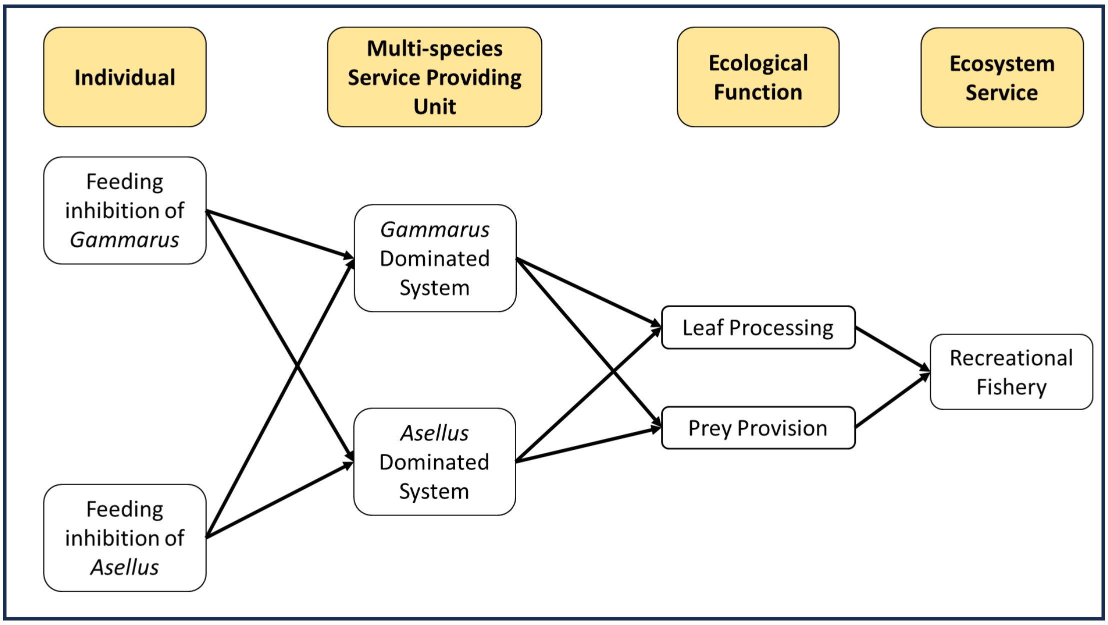


Figure 6.3: Conceptual model illustrating the connections from chemical induced change in feeding of *Gammarus* or *Asellus* may lead to changes in the delivery of ecosystem services in a freshwater fishery.

A key consideration in ERA moving forward is the appropriate application of peak effects and time variable effects (Ashauer and Brown, 2013; Jager, 2024), here captured by cumulative impacts. While peak effects describe the maximum observed deviation from baseline conditions, cumulative impacts account for the total magnitude and duration of the effect, often expressed as the area under the effect curve. These metrics serve different purposes and are suited to different types of stressors and ecological endpoints (Ashauer and Brown, 2013). The findings of this thesis suggest that cumulative impacts may serve as a more ecologically relevant measure of long-term ecosystem service disruptions, particularly in relation to prey provision. While peak deviations may indicate acute effects, the cumulative decline in prey availability—reflected as a gradual reduction over time—is likely a more accurate predictor of impacts on higher trophic levels, such as fish populations. The choice between using peak effects or cumulative impact metrics might depend largely on the chemical exposure profile (Ashauer and Brown, 2013), the type of ecosystem service or function being assessed (Devos et al., 2019) which is also encompassed by the scale of the observation (Simmons et al., 2021). Integrating these considerations into traditional ERA frameworks may be challenging due to the lack of specific protection goals in higher tiers. However, within an ecosystem services-based framework, where services of interest can be explicitly defined in space and time, selecting the appropriate metric becomes not a question of *whether* to incorporate such complexity, but *when* and *how* to do so.

Peak effects may be more appropriate in scenarios involving short-lived high concentration exposure events, particularly where lethal toxicity thresholds are exceeded for short periods (i.e. days), causing acute harm to sensitive species. This is especially relevant for key ecological functions that are temporally constrained, such as for the presence of keystone, provisioning, or culturally significant species during specific life stages or seasons. In contrast, cumulative impacts may be more suitable for the assessment of ecosystem services that are temporally driven, such as prey availability, population size structure (Gee, 1988; Biro et al., 2003), or organic matter processing. This may be of particular interest for continuous, low-level or repeated exposures where impacts accumulate over time. Such scenarios are commonly observed in systems with chronically poor water quality, where reduced processing rates (Maltby et al., 2002; Peters et al., 2013) or change in species composition (Liess et al., 2021) are indicative of long-term ecological change. It is therefore important to select the appropriate impact metric to accurately capture the risk of chemical exposure to ecosystem services.

Conventional ERAs often rely on short-term toxicity tests and fixed thresholds—such as a >10% deviation in feeding rate over 28 days—to determine acceptable chronic effects (Van den Brink, 2008; EFSA, 2013). However, this approach may overlook cumulative and indirect effects that emerge over longer timeframes. The findings in this thesis highlight that such short-term tests can miss ecologically meaningful impacts: exclusion of one species occurred only after one year of sustained 10% feeding inhibition, well below typical toxicity thresholds. This highlights the potential for long-term, sublethal effects to alter community structure and ecosystem function—outcomes that are not captured by standard assays (Neinstedt et al., 2012; Franco et al., 2016). Moreover, indirect ecological interactions can have impacts equal to or greater than those observed in direct toxicity tests (Gessner and Tlili, 2016; Fleeger et al., 2020). While these findings suggest that the current 10% threshold may be overly protective in some contexts, a more ecologically informed interpretation is that chemical impacts should be evaluated not only by the magnitude of individual responses but also by their ecological context. By incorporating information about species' functional efficiency—such as *Gammarus* being a more effective shredder (Graça et al., 1994b)—and projected population structures derived from single-species models, we can better understand how subtle changes in population composition (e.g., in structure of the SPU) may cascade into meaningful disruptions in ecological function. This supports a move toward more ecologically integrated ERAs that account for long-term dynamics and functional outcomes.

Standard toxicity tests that link chemical concentrations to individual level effects are typically used in ecological risk assessments. However, this approach may not capture impacts on ecological processes in complex systems often involving multiple species and their interactions (Peters et al.,2013), such as decomposition and nutrient cycling. This oversimplification therefore may limit the ability of ERAs to account for the resilience and function of ecological systems under chemical stress. The insurance hypothesis proposes that species diversity promotes functional diversity which, in turn, enables functional redundancy - offering a buffer against the loss of ecosystem functions (Yachi and Loreau, 1999; Loreau et al., 2020). According to this hypothesis, species rich systems should be more resilient to stress as multiple species can perform multiple functions. However, this relationship is not linear nor consistent across all environments (Laureto et al., 2015). Instead, diversity of functional traits often provides a more robust explanation for ecosystem performance than species diversity alone (Laureto et al., 2015). Consequently, loss of species can have little or great impact on the performance of ecosystem functions, depending on which species are loss. Nonetheless, empirical evidence indicates that changes in proxy measures of function, such as invertebrate feeding activity, can correspond to functional impairments in aquatic systems (Forrow and Maltby, 2000; Rasmussen et al., 2008). This highlights the importance of integrating functional endpoints into ERAs. Contrary to typical assumptions in ERA, functional diversity alone is not necessarily an indicator of resilience (Biggs et al., 2020). The effectiveness of functional redundancy depends on the scale of observation—spatially and temporally— given that species populations exhibit different life cycles and population dynamics (Loreau et al., 2020). Therefore, moving toward an assessment framework that explicitly considers functional traits and redundancy across scales could greatly improve the ecological realism and long-term predictive power of ERAs.

Given that ecosystem services are frequently spatially explicit, this study underscores the importance of incorporating assemblage status into ERA frameworks. Furthermore, the findings emphasise the need to consider species identity and inter-trophic interactions, as these factors can amplify the ecological impacts of chemical exposure. This thesis reinforces the call for clearer definitions of ecological scenarios when evaluating chemical effects on ecosystem services (Neinstedt et al., 2012; Franco et al., 2016), particularly in addressing spatial variations in the ecological status of freshwater systems (Holmes et al., 2022). For more robust ERAs, it is crucial to integrate functional traits and inter-trophic interactions, as these elements significantly influence ecosystems' resilience to chemical stressors.

6.4 Conclusions

In conclusion, this thesis illustrates that impacts on the feeding activity of freshwater invertebrates can have far reaching consequences to impacts on ecosystem services delivery. However, the impacts of chemical stressors on the performance of ecological functions in freshwater systems are highly context dependent. Impacts on ecological structure and functions can be influenced by combination of factors including functional feeding group, chemical mode of action, species life history traits, interspecific competition, and initial species densities.

Feeding activity emerged as a useful indicator of chemical impacts at both individual and population levels, revealing the importance of indirect pathways affecting consumer-resource systems and suggest that sub-organism effects may have more substantial impacts on populations than individual-level responses. While there is little feeding data available for most species in response to many chemicals, the relative sensitivity of feeding in response to chemical stress can be inferred from lethality data, for a few specific chemical modes of action. Furthermore, the thesis highlights the relevance of feeding activity for understanding broader ecosystem effects on processes such as leaf decomposition and prey availability. Through extrapolatory modelling, this research illustrates how individual changes in energy uptake can lead to varying impacts on ecological functions. By applying dynamic energy budget (DEB) individual-based models (IBMs) to key species, the study emphasises the significance of interspecies interactions and competitive dynamics in predicting chemical effects on ecosystem function.

However, results from this thesis suggest that impacts on feeding activity only led to significant adverse consequences greater than those predicted from individual toxicity tests when interspecific competition for resources is considered, while impacts on the resource reveal impacts at the single population level. These findings both suggest that ecological interactions, not only direct effects on the consumer, have great impact on the outcome of a risk assessment and should therefore, if not be included, be considered when assessing risk of chemical impact on ecosystem services. The study highlights the critical need to consider both ecological and environmental contexts in risk assessments, as variations in species richness and differences in species sensitivity within the same functional feeding group can profoundly influence the structure of species that perform essential ecosystem functions.

References

Accolla, C., Vaugeois, M., Grimm, V., Moore, A.P., Rueda-Cediel, P., Schmolke, A. and Forbes, V.E., 2021. A review of key features and their implementation in unstructured, structured, and agent-based population models for ecological risk assessment. Integrated Environmental Assessment and Management, 17(3), pp.521-540.

Accolla, C. and Forbes, V.E., 2021. Temperature dependence of population responses to competition and metabolic stress: An agent-based model to inform ecological risk assessment in a changing climate. Science of the Total Environment, 763, p.144096.

Adam, O., Degiorgi, F., Crini, G. and Badot, P.M., 2010. High sensitivity of *Gammarus* sp. juveniles to deltamethrin: outcomes for risk assessment. Ecotoxicology and environmental safety, 73(6), pp.1402-1407.

Adcock, J.A., 1982. Energetics of a population of *Asellus aquaticus* (Crustacea, Isopoda): respiration and energy budgets. Freshwater biology, 12(3), pp.257-269.

Adriaenssens, V., Goethals, P.L. and De Pauw, N., 2006. Fuzzy knowledge-based models for prediction of *Asellus* and *Gammarus* in watercourses in Flanders (Belgium). Ecological Modelling, 195(1-2), pp.3-10.

Agatz, A. and Brown, C.D., 2013. Evidence for links between feeding inhibition, population characteristics, and san

Agatz, A., Ashauer, R. and Brown, C.D., 2014. Imidacloprid perturbs feeding of *Gammarus pulex* at environmentally relevant concentrations. Environmental toxicology and chemistry, 33(3), pp.648-653.

Agatz, A., Cole, T. A., Preuss, T. G., Zimmer, E., & Brown, C. D., 2013. Feeding inhibition explains effects of imidacloprid on the growth, maturation, reproduction, and survival of *Daphnia* magna. Environmental science & technology, 47(6), pp2909-2917.

Ågerstrand, M., Arnold, K., Balshine, S., Brodin, T., Brooks, B.W., Maack, G., McCallum, E.S., Pyle, G., Saaristo, M. and Ford, A.T., 2020. Emerging investigator series: use of behavioural endpoints in the regulation of chemicals. Environmental Science: Processes & Impacts, 22(1), pp.49-65.

Allen, J., Gross, E.M., Courcoul, C., Bouletreau, S., Compin, A., Elger, A., Ferriol, J., Hilt, S., Jassey, V.E., Laviale, M. and Polst, B.H., 2021. Disentangling the direct and indirect effects of agricultural runoff on freshwater ecosystems subject to global warming: A microcosm study. Water Research, 190, p.116713.

Alonso, Á. and Romero-Blanco, A., 2022. Same sensitivity with shorter exposure: behavior as an appropriate parameter to assess metal toxicity. Ecotoxicology, 31(8), pp.1254-1265.

Alonso, Á., De Lange, H.J. and Peeters, E.T., 2010. Contrasting sensitivities to toxicants of the freshwater amphipods *Gammarus pulex* and G. fossarum. Ecotoxicology, 19, pp.133-140.

Amiard-Triquet, C., 2009. Behavioral disturbances: the missing link between sub-organismal and supra-organismal responses to stress? Prospects based on aquatic research. Human and Ecological Risk Assessment, 15(1), pp.87-110.

Amiard-Triquet, C., 2015. How to improve toxicity assessment? From single-species tests to mesocosms and field studies. In Aquatic ecotoxicology (pp. 127-151). Academic Press.

Andersen, T., Færøvig, P.J. and Hessen, D.O., 2007. Growth rate versus biomass accumulation: different roles of food quality and quantity for consumers. Limnology and Oceanography, 52(5), pp.2128-2134.

Anderson, N.H. and Cummins, K.W., 1979. Influences of diet on the life histories of aquatic insects. Journal of the Fisheries Board of Canada, 36(3), pp.335-342.

Anderson, A.M., Mittag, E., Middleton, B., Vondracek, B. and Ferrington Jr, L.C., 2016. Winter diets of brown trout populations in southeastern Minnesota and the significance of winter-emerging invertebrates. Transactions of the American Fisheries Society, 145(1), pp.206-220.

Arakelova, K.S., 2001. The evaluation of individual production and scope for growth in aquatic sow bugs (*Asellus aquaticus*). Aquatic Ecology, 35, pp.31-42.

Arco, A., Rico, A. and den Brink, P., 2015. Effects of intra-and interspecific competition on the sensitivity of *Daphnia* magna populations to the fungicide carbendazim. Ecotoxicology, 24(6).

Arsuffi, T.L. and Suberkropp, K., 1985. Selective feeding by stream caddisfly (Trichoptera) detritivores on leaves with fungal-colonized patches. Oikos, pp.50-58.

Arsuffi, T.L. and Suberkropp, K., 1989. Selective feeding by shredders on leaf-colonizing stream fungi: comparison of macroinvertebrate taxa. Oecologia, 79, pp.30-37.

Ashauer, R. and Brown, C.D., 2013. Highly time-variable exposure to chemicals—toward an assessment strategy. Integrated Environmental Assessment and Management, 9(3), pp.e27-e33.

Ashauer, R. and Jager, T., 2018. Physiological modes of action across species and toxicants: the key to predictive ecotoxicology. Environmental Science: Processes & Impacts, 20(1), pp.48-57.

Ashauer, R., Agatz, A., Albert, C., Ducrot, V., Galic, N., Hendriks, J., Jager, T., Kretschmann, A., O'Connor, I., Rubach, M.N. and Nyman, A.M., 2011. Toxicokinetic-toxicodynamic modeling of quantal and graded sublethal endpoints: A brief discussion of concepts. Environmental Toxicology and Chemistry, 30(11), pp.2519-2524.

Ashauer, R., Hintermeister, A., Potthoff, E. and Escher, B.I., 2011. Acute toxicity of organic chemicals to *Gammarus pulex* correlates with sensitivity of *Daphnia* magna across most modes of action. Aquatic toxicology, 103(1-2), pp.38-45.

Atkinson, C.L., Capps, K.A., Rugenski, A.T. and Vanni, M.J., 2017. Consumer-driven nutrient dynamics in freshwater ecosystems: From individuals to ecosystems. Biological Reviews, 92(4), pp.2003-2023.

Atkinson, C.L., Hopper, G.W., Kreeger, D.A., Lopez, J.W., Maine, A.N., Sansom, B.J., Schwalb, A. and Vaughn, C.C., 2023. Gains and gaps in knowledge surrounding freshwater mollusk ecosystem services. Freshwater Mollusk Biology and Conservation, 26(1), pp.20-31.

Au, S.Y., Bruce, T.F., Bridges, W.C. and Klaine, S.J., 2015. Responses of Hyalella azteca to acute and chronic microplastic exposures. Environmental toxicology and chemistry, 34 (11), pp.2564-2572.

Augusiak, J., Van den Brink, P.J. and Grimm, V., 2014. Merging validation and evaluation of ecological models to 'evaludation': A review of terminology and a practical approach. Ecological Modelling, 280, pp.117-128.

Augusiak, J. and Van den Brink, P.J., 2015. Studying the movement behavior of benthic macroinvertebrates with automated video tracking. Ecology and Evolution, 5(8), pp.1563-1575.

Bacher, C. and Gangnery, A., 2006. Use of dynamic energy budget and individual based models to simulate the dynamics of cultivated oyster populations. Journal of Sea Research, 56(2), pp.140-155.

Baert, J.M., De Laender, F. and Janssen, C.R., 2017. The consequences of nonrandomness in species-sensitivity in relation to functional traits for ecosystem-level effects of chemicals. Environmental Science & Technology, 51(12), pp.7228-7235.

Baird, D.J., Brown, S.S., Lagadic, L., Liess, M., Maltby, L., Moreira-Santos, M., Schulz, R. and Scott, G.I., 2007. In situ-based effects measures: Determining the ecological relevance of measured responses. Integrated Environmental Assessment and Management: An International Journal, 3(2), pp.259-267.

Baird, D.J., Maltby, L., Greig-Smith, P.W. and Douben, P.E., 1996. Putting the 'ECO-'into ECOtoxicology. In ECOtoxicology: Ecological Dimensions (pp. 1-4). Dordrecht: Springer Netherlands.

Bandow, C. and Weltje, L., 2012. Development of an embryo toxicity test with the pond snail Lymnaea stagnalis using the model substance tributyltin and common solvents. Science of the Total Environment, 435, pp.90-95.

Bärlocher, F., 1985. The role of fungi in the nutrition of stream invertebrates. Botanical journal of the Linnean Society, 91(1-2), pp.83-94.

Barnes, A.D., Jochum, M., Lefcheck, J.S., Eisenhauer, N., Scherber, C., O'Connor, M.I., de Ruiter, P. and Brose, U., 2018. Energy flux: the link between multitrophic biodiversity and ecosystem functioning. Trends in ecology & evolution, 33(3), pp.186-197.

Barnett, L.A., Branch, T.A., Ranasinghe, R.A. and Essington, T.E., 2017. Old-growth fishes become scarce under fishing. Current biology, 27(18), pp.2843-2848.

Barnthouse, L.W., Suter, G.W. and Rosen, A.E., 1988. Inferring population-level significance from individual-level effects: An extrapolation from fisheries science to ecotoxicology. In Aquatic toxicology and environmental fate: Eleventh Volume. ASTM International.

Baste, I.A. and Watson, R.T., 2022. Tackling the climate, biodiversity and pollution emergencies by making peace with nature 50 years after the Stockholm Conference. Global Environmental Change, 73, p.102466.

Baudy, P., Zubrod, J.P., Konschak, M., Röder, N., Nguyen, T.H., Schreiner, V.C., Baschien, C., Schulz, R. and Bundschuh, M., 2021. Environmentally relevant fungicide levels modify fungal community composition and interactions but not functioning. Environmental Pollution, 285, p.117234.

Baveco, J.M., Norman, S., Roessink, I., Galic, N. and Brink, P.J.V.D., 2014. Comparing population recovery after insecticide exposure for four aquatic invertebrate species using models of different complexity. Environmental toxicology and chemistry, 33(7), pp.1517-1528.

Beaudouin, R., Dias, V., Bonzom, J.M. and Péry, A., 2012. Individual-based model of Chironomus riparius population dynamics over several generations to explore adaptation following exposure to uranium-spiked sediments. Ecotoxicology, 21, pp.1225-1239.

Beggel, S., Hinzmann, M., Machado, J. and Geist, J., 2017. Combined impact of acute exposure to ammonia and temperature stress on the freshwater mussel Unio pictorum. Water, 9(7), p.455.

Beketov, M.A. and Liess, M., 2005. Acute contamination with esfenvalerate and food limitation: chronic effects on the mayfly, Cloeon dipterum. Environmental Toxicology and Chemistry: An International Journal, 24(5), pp.1281-1286.

Beketov, M.A. and Liess, M., 2012. Ecotoxicology and macroecology–time for integration. Environmental Pollution, 162, pp.247-254.

Belanger, S., Barron, M., Craig, P., Dyer, S., Galay-Burgos, M., Hamer, M., Marshall, S., Posthuma, L., Raimondo, S. and Whitehouse, P., 2017. Future needs and recommendations in the development of species sensitivity distributions: Estimating toxicity thresholds for aquatic ecological communities and assessing impacts of chemical exposures. Integrated environmental assessment and management, 13(4), pp.664-674.

Benke, A.C., 2018. River food webs: an integrative approach to bottom‐up flow webs, top‐down impact webs, and trophic position. Ecology, 99(6), pp.1370-1381.

Berezina, N.A., Litvinchuk, L.F. and Maximov, A.A., 2021. Relations between the food spectrum of fishes and the composition of zooplankton and benthos in a subarctic lake. Inland Water Biology, 14, pp.438-448.

Bernhardt, E.S., Rosi, E.J. and Gessner, M.O., 2017. Synthetic chemicals as agents of global change. Frontiers in Ecology and the Environment, 15(2), pp.84-90.

Bernot, R.J., Kennedy, E.E. and Lamberti, G.A., 2005. Effects of ionic liquids on the survival, movement, and feeding behavior of the freshwater snail, Physa acuta. Environmental Toxicology and Chemistry: An International Journal, 24(7), pp.1759-1765.

Biggs, C.R., Yeager, L.A., Bolser, D.G., Bonsell, C., Dichiera, A.M., Hou, Z., Keyser, S.R., Khursigara, A.J., Lu, K., Muth, A.F. and Negrete Jr, B., 2020. Does functional redundancy affect ecological stability and resilience? A review and meta‐analysis. Ecosphere, 11(7), p.e03184.

Bilbo, T.R., Dawson, D.E. and Salice, C.J., 2024. The challenge of assessing multiple stressors in freshwater ecosystems: nonintuitive interactions between pesticide exposure and larval crowding. Frontiers in Freshwater Science, 1, p.1302240.

Birdsong, M., Hunt, L.M. and Arlinghaus, R., 2021. Recreational angler satisfaction: What drives it?. Fish and Fisheries, 22(4), pp.682-706.

Birk, S., Chapman, D., Carvalho, L., Spears, B.M., Andersen, H.E., Argillier, C., Auer, S., Baattrup-Pedersen, A., Banin, L., Beklioğlu, M. and Bondar-Kunze, E., 2020. Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. Nature Ecology & Evolution, 4(8), pp.1060-1068.

Biro, P.A., Post, J.R. and Parkinson, E.A., 2003. Population consequences of a predator‐induced habitat shift by trout in whole‐lake experiments. Ecology, 84(3), pp.691-700.

Blakely, T.J., Harding, J.S., McIntosh, A.R. and Winterbourn, M.J., 2006. Barriers to the recovery of aquatic insect communities in urban streams. Freshwater Biology, 51(9), pp.1634-1645.

Blarer, P. and Burkhardt-Holm, P., 2016. Microplastics affect assimilation efficiency in the freshwater amphipod *Gammarus* fossarum. Environmental science and pollution research, 23(23), pp.23522-23532.

Blaum, N., Mosner, E., Schwager, M. and Jeltsch, F., 2011. How functional is functional? Ecological groupings in terrestrial animal ecology: towards an animal functional type approach. Biodiversity and Conservation, 20, pp.2333-2345.

Blockwell, S.J., Taylor, E.J., Jones, I. and Pascoe, D., 1998. The influence of fresh water pollutants and interaction with *Asellus aquaticus* (L.) on the feeding activity of *Gammarus pulex* (L.). Archives of Environmental Contamination and Toxicology, 34, pp.41-47.

Blondel, J., 2003. Guilds or functional groups: does it matter?.

Bloor, M.C. and Banks, C.J., 2006. An evaluation of mixed species in-situ and ex-situ feeding assays: The altered response of *Asellus aquaticus* and *Gammarus pulex*. Environment international, 32(1), pp.22-27.

Bloor, M.C., 2011. Dietary preference of *Gammarus pulex* and *Asellus aquaticus* during a laboratory breeding programme for ecotoxicological studies. International Journal of Zoology, 2011.

Boag, D.A. and Pearlstone, P.S.M., 1979. On the life cycle of Lymnaea stagnalis (Pulmonata: Gastropoda) in southwestern Alberta. Canadian Journal of Zoology, 57(2), pp.353-362.

Boxall, A.B., Collins, R., Wilkinson, J.L., Swan, C., Bouzas‐Monroy, A., Jones, J., Winter, E., Leach, J., Juta, U., Deacon, A. and Townsend, I., 2024. Pharmaceutical Pollution of the English National Parks. Environmental Toxicology and Chemistry.

Boyle, T.P., Fairchild, J.F., Haverland, P.S., Lebo, J.A. and Robinson‐Wilson, E.F., 1996. Ecological restructuring in experimental aquatic mesocosms due to the application of diflubenzuron. Environmental Toxicology and Chemistry: An International Journal, 15(10), pp.1806-1814.

Bratman, G.N., Anderson, C.B., Berman, M.G., Cochran, B., De Vries, S., Flanders, J., Folke, C., Frumkin, H., Gross, J.J., Hartig, T. and Kahn Jr, P.H., 2019. Nature and mental health: An ecosystem service perspective. Science advances, 5(7), p.eaax0903.

Brock, T.C., Arts, G.H., Maltby, L. and Van den Brink, P.J., 2006. Aquatic risks of pesticides, ecological protection goals, and common aims in European Union legislation. Integrated Environmental Assessment and Management: An International Journal, 2(4), pp.e20-e46.

Brockelman, W.Y., 1975. Competition, the fitness of offspring, and optimal clutch size. The American Naturalist, 109(970), pp.677-699.

Brodie, J.F., Redford, K.H. and Doak, D.F., 2018. Ecological function analysis: incorporating species roles into conservation. Trends in Ecology & Evolution, 33(11), pp.840-850.

Brooks, A.C., Gaskell, P.N. and Maltby, L.L., 2009a. Importance of prey and predator feeding behaviors for trophic transfer and secondary poisoning. Environmental science & technology, 43(20), pp.7916-7923.

Brooks, A.C., Gaskell, P.N. and Maltby, L.L., 2009b. Sublethal effects and predator-prey interactions: Implications for ecological risk assessment. Environmental Toxicology and Chemistry: An International Journal, 28(11), pp.2449-2457.

Brown, A.R., Whale, G., Jackson, M., Marshall, S., Hamer, M., Solga, A., Kabouw, P., Galay-Burgos, M., Woods, R., Nadzialek, S. and Maltby, L., 2017. Toward the definition of specific protection goals for the environmental risk assessment of chemicals: A perspective on environmental regulation in Europe. Integrated environmental assessment and management, 13(1), pp.17-37.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. and West, G.B., 2004. Toward a metabolic theory of ecology. Ecology, 85(7), pp.1771-1789.

Bruins, R.J., Canfield, T.J., Duke, C., Kapustka, L., Nahlik, A.M. and Schäfer, R.B., 2017. Using ecological production functions to link ecological processes to ecosystem services. Integrated Environmental Assessment and Management, 13(1), pp.52-61.

Bundschuh, M., Appeltauer, A., Dabrunz, A. and Schulz, R., 2012. Combined effect of invertebrate predation and sublethal pesticide exposure on the behavior and survival of *Asellus aquaticus* (Crustacea; Isopoda). Archives of environmental contamination and toxicology, 63, pp.77-85.

Bundschuh, M., Hahn, T., Gessner, M.O. and Schulz, R., 2017. Antibiotic mixture effects on growth of the leaf-shredding stream detritivore *Gammarus* fossarum. Ecotoxicology, 26, pp.547-554.

Bundschuh, M., Mesquita-Joanes, F., Rico, A. and Camacho, A., 2023. Understanding Ecological Complexity in a Chemical Stress Context: A Reflection on Recolonization, Recovery, and Adaptation of Aquatic Populations and Communities. Environmental Toxicology and Chemistry, 42(9), pp.1857-1866.

Burns, C.W., 1995. Effects of crowding and different food levels on growth and reproductive investment of *Daphnia*. Oecologia, 101, pp.234-244.

Burns, E.E., Carter, L.J., Kolpin, D.W., Thomas-Oates, J. and Boxall, A.B., 2018. Temporal and spatial variation in pharmaceutical concentrations in an urban river system. Water research, 137, pp.72-85.

Burns, F, Mordue, S, al Fulaij, N, Boersch-Supan, PH, Boswell, J, Boyd, RJ, Bradfer-Lawrence, T, de Ornellas,P, de Palma, A, de Zylva, P, Dennis, EB, Foster, S, Gilbert ,G, Halliwell, L, Hawkins, K, Haysom, KA, Holland, MM, Hughes, J, Jackson, AC, Mancini, F, Mathews, F, McQuatters-Gollop, A, Noble, DG, O'Brien, D, Pescott, OL, Purvis, A, Simkin, J, Smith, A, Stanbury, AJ, Villemot, J, Walker, KJ, Walton, P, Webb, TJ, Williams, J, Wilson, R, Gregory, RD, 2023. State of Nature 2023, The State of Nature partnership, Available at: www.stateofnature.org.uk

Cadmus, P., Kotalik, C.J., Jefferson, A.L., Wheeler, S.H., McMahon, A.E. and Clements, W.H., 2019. Size-dependent sensitivity of aquatic insects to metals. Environmental Science & Technology, 54(2), pp.955-964.

Cadotte, M.W., Carscadden, K. and Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of applied ecology, 48(5), pp.1079-1087.

Calow, P., 1985. Adaptive aspects of energy allocation. In *Fish energetics: new perspectives* (pp. 13-31). Dordrecht: Springer Netherlands.

Cairns Jr, J., 1988. Putting the eco in ecotoxicology. Regulatory Toxicology and Pharmacology, 8(2), pp.226-238.

Camp, A.A. and Buchwalter, D.B., 2016. Can't take the heat: Temperature-enhanced toxicity in the mayfly Isonychia bicolor exposed to the neonicotinoid insecticide imidacloprid. Aquatic Toxicology, 178, pp.49-57.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A. and Kinzig, A.P., 2012. Biodiversity loss and its impact on humanity. Nature, 486(7401), pp.59-67.

Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'connor, M.I. and Gonzalez, A., 2011. The functional role of producer diversity in ecosystems. American journal of botany, 98(3), pp.572-592.

Carlisle, D.M. and Clements, W.H., 2005. Leaf litter breakdown, microbial respiration and shredder production in metal-polluted streams. Freshwater biology, 50(2), pp.380-390.

Carpenter, S.R., Mooney, H.A., Agard, J., Capistrano, D., DeFries, R.S., Díaz, S., Dietz, T., Duraiappah, A.K., Oteng-Yeboah, A., Pereira, H.M. and Perrings, C., 2009. Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. Proceedings of the National Academy of Sciences, 106(5), pp.1305-1312.

Carson, R., 2009. Silent spring. 1962. New York.

CEFIC, Safe and Sustainable-by-Design: Boosting innovation and growth within the European chemical industry, 2021

Chapman, P.M., 2002. Integrating toxicology and ecology: putting the "eco" into ecotoxicology. Marine pollution bulletin, 44(1), pp.7-15.

Chapman, P.M., Fairbrother, A. and Brown, D., 1998. A critical evaluation of safety (uncertainty) factors for ecological risk assessment. Environmental Toxicology and Chemistry: An International Journal, 17(1), pp.99-108.

Charles, S., Billoir, E., Lopes, C. and Chaumot, A., 2009. Matrix population models as relevant modeling tools in ecotoxicology. Ecotoxicology Modeling, pp.261-298.

Charron, L., Geffard, O., Chaumot, A., Coulaud, R., Jaffal, A., Gaillet, V., Dedourge-Geffard, O. and Geffard, A., 2014. Influence of molting and starvation on digestive enzyme activities and energy storage in *Gammarus* fossarum. *Plos one*, *9*(4), p.e96393.

Chesson, P., 2000. General theory of competitive coexistence in spatially-varying environments. Theoretical population biology, 58(3), pp.211-237.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annual review of Ecology and Systematics, 31(1), pp.343-366.

Clark, J.L. and Clements, W.H., 2006. The use of in situ and stream microcosm experiments to assess population- and community-level responses to metals. Environmental Toxicology and Chemistry: An International Journal, 25(9), pp.2306-2312.

Clements, W.H. and Rohr, J.R., 2009. Community responses to contaminants: using basic ecological principles to predict ecotoxicological effects. Environmental Toxicology and Chemistry: An International Journal, 28(9), pp.1789-1800.

Clements, W.H., Cadmus, P. and Brinkman, S.F., 2013. Responses of aquatic insects to Cu and Zn in stream microcosms: understanding differences between single species tests and field responses. Environmental Science & Technology, 47(13), pp.7506-7513.

Clements, W.H., Kashian, D.R., Kiffney, P.M. and Zuellig, R.E., 2016. Perspectives on the context-dependency of stream community responses to contaminants. Freshwater Biology, 61(12), pp.2162-2170.

Concepción, E.D., Moretti, M., Altermatt, F., Nobis, M.P. and Obrist, M.K., 2015. Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. Oikos, 124(12), pp.1571-1582.

Congdon, J.D., Dunham, A.E., Hopkins, W.A., Rowe, C.L. and Hinton, T.G., 2001. Resource allocation-based life histories: a conceptual basis for studies of ecological toxicology. Environmental Toxicology and Chemistry: An International Journal, 20(8), pp.1698-1703.

Copp, G.H., Spathari, S. and Turmel, M., 2005. Consistency of diel behaviour and interactions of stream fishes and invertebrates during summer. River Research and Applications, 21(1), pp.75-90.

Cordeiro, E.M.G., Correâ, A.S. and Guedes, R.N.C., 2014. Insecticide-mediated shift in ecological dominance between two competing species of grain beetles. PloS one, 9(6), p.e100990.

Covich, A.P., Palmer, M.A. and Crowl, T.A., 1999. The role of benthic invertebrate species in freshwater ecosystems: zoobenthic species influence energy flows and nutrient cycling. BioScience, 49(2), pp.119-127.

Crane, M. and Maltby, L., 1991. The lethal and sublethal responses of *Gammarus pulex* to stress: sensitivity and sources of variation in an in situ bioassay. Environmental Toxicology and Chemistry: An International Journal, 10(10), pp.1331-1339.

Cumming, G.S., Buerkert, A., Hoffmann, E.M., Schlecht, E., von Cramon-Taubadel, S. and Tscharntke, T., 2014. Implications of agricultural transitions and urbanization for ecosystem services. Nature, 515(7525), pp.50-57.

Cummins, K.W., 1974. Structure and function of stream ecosystems. BioScience, 24(11), pp.631-641.

Cummins, K.W., Petersen, R.C., Howard, F.O., Wuycheck, J.C. and Holt, V.I., 1973. The utilization of leaf litter by stream detritivores. Ecology, 54(2), pp.336-345.

Cummins, K.W. and Klug, M.J., 1979. Feeding ecology of stream invertebrates. Annual review of ecology and systematics, 10(1), pp.147-172.

Cummins, C.S., Rosemond, A.D., Tomczyk, N.J., Wenger, S.J., Bumpers, P.M., Gulis, V., Helton, A.M. and Benstead, J.P., 2024. Temperature dependence of leaf breakdown in streams differs between organismal groups and leaf species. Ecology, p.e4405.

Dahl, J., 1998. Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. Oecologia, 116(3), pp.426-432.

Dahms, H.U., Hagiwara, A. and Lee, J.S., 2011. Ecotoxicology, ecophysiology, and mechanistic studies with rotifers. Aquatic toxicology, 101(1), pp.1-12.

Daily, G.C., 1997. Introduction: what are ecosystem services. Nature's services: Societal dependence on natural ecosystems, 1(1).

Daily, G.C., Polasky, S., Goldstein, J., Kareiva, P.M., Mooney, H.A., Pejchar, L., Ricketts, T.H., Salzman, J. and Shallenberger, R., 2009. Ecosystem services in decision making: time to deliver. Frontiers in Ecology and the Environment, 7(1), pp.21-28.

Dalkvist, T., Topping, C.J. and Forbes, V.E., 2009. Population-level impacts of pesticide-induced chronic effects on individuals depend more on ecology than toxicology. Ecotoxicology and Environmental Safety, 72(6), pp.1663-1672.

Dallimer, M., Irvine, K.N., Skinner, A.M., Davies, Z.G., Rouquette, J.R., Maltby, L.L., Warren, P.H., Armsworth, P.R. and Gaston, K.J., 2012. Biodiversity and the feel-good factor: understanding associations between self-reported human well-being and species richness. BioScience, 62(1), pp.47-55.

Dallinger, R. and Kautzky, H., 1985. The importance of contaminated food for the uptake of heavy metals by rainbow trout (*Salmo gairdneri*): a field study. Oecologia, pp.82-89.

Dasgupta, P. (2021), The Economics of Biodiversity: The Dasgupta Review. (London: HM Treasury)

Davey, A.J., Bailey, L., Bewes, V., Mubaiwa, A., Hall, J., Burgess, C., Dunbar, M.J., Smith, P.D. and Rambohul, J., 2020. Water quality benefits from an advice-led approach to reducing water pollution from agriculture in England. Agriculture, Ecosystems & Environment, 296, p.106925.

Dawoud, M., Bundschuh, M., Goedkoop, W. and McKie, B.G., 2017. Interactive effects of an insecticide and a fungicide on different organism groups and ecosystem functioning in a stream detrital food web. Aquatic Toxicology, 186, pp.215-221.

de Assis Barros, L., Venter, M., Elkin, C. and Venter, O., 2022. Managing forests for old-growth attributes better promotes the provision of ecosystem services than current age-based old-growth management. Forest Ecology and Management, 511, p.120130.

De Groot, R.S., Wilson, M.A. and Boumans, R.M., 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. Ecological economics, 41(3), pp.393-408.

De Laender, F. and Janssen, C.R., 2013. Brief communication: The ecosystem perspective in ecotoxicology as a way forward for the ecological risk assessment of chemicals. Integrated Environmental Assessment and Management, 9(3), pp.e34-e38.

De Laender, F., De Schamphelaere, K.A., Vanrolleghem, P.A. and Janssen, C.R., 2008. Do we have to incorporate ecological interactions in the sensitivity assessment of ecosystems? An examination of a theoretical assumption underlying species sensitivity distribution models. Environment international, 34(3), pp.390-396.

De Laender, F., Rohr, J.R., Ashauer, R., Baird, D.J., Berger, U., Eisenhauer, N., Grimm, V., Hommen, U., Maltby, L., Meliàn, C.J. and Pomati, F., 2016. Reintroducing environmental change drivers in biodiversity–ecosystem functioning research. Trends in ecology & evolution, 31(12), pp.905-915.

De Laender, F., van den Brink, P.J., Janssen, C.R. and Di Guardo, A., 2014. The ChimERA project: coupling mechanistic exposure and effect models into an integrated platform for ecological risk assessment. Environmental Science and Pollution Research, 21, pp.6263-6267.

de Roos, A.M., 1997. A gentle introduction to physiologically structured population models. In Structured-population models in marine, terrestrial, and freshwater systems (pp. 119-204). Boston, MA: Springer US.

de Villemereuil, P.B. and López-Sepulcre, A., 2011. Consumer functional responses under intra-and inter-specific interference competition. Ecological modelling, 222(3), pp.419-426.

DeAngelis, D.L. and Grimm, V., 2014. Individual-based models in ecology after four decades. F1000prime reports, 6.

Dedourge-Geffard, O., Palais, F., Biagianti-Risbourg, S., Geffard, O. and Geffard, A., 2009. Effects of metals on feeding rate and digestive enzymes in *Gammarus* fossarum: an in situ experiment. Chemosphere, 77(11), pp.1569-1576.

Del Arco et al 2015a - Del Arco, A.I., Parra, G., Rico, A. and Van den Brink, P.J., 2015. Effects of intra-and interspecific competition on the sensitivity of aquatic macroinvertebrates to carbendazim. Ecotoxicology and environmental safety, 120, pp.27-34.

Del Arco et al 2015b - Del Arco, A.I., Rico, A. and van den Brink, P.J., 2015. Effects of intra-and interspecific competition on the sensitivity of *Daphnia* magna populations to the fungicide carbendazim. Ecotoxicology, 24, pp.1362-1371.

Del Signore, A., Hendriks, A.J., Lenders, H.R., Leuven, R.S. and Breure, A.M., 2016. Development and application of the SSD approach in scientific case studies for ecological risk assessment. Environmental Toxicology and Chemistry, 35(9), pp.2149-2161.

Devos, Y., Munns Jr, W.R., Forbes, V.E., Maltby, L., Stenseke, M., Brussaard, L., Streissl, F. and Hardy, A., 2019. Applying ecosystem services for pre-market environmental risk assessments of regulated stressors. EFSA Journal, 17, p.e170705.

Devos, Y., Romeis, J., Luttik, R., Maggiore, A., Perry, J.N., Schoonjans, R., Streissl, F., Tarazona, J.V. and Brock, T.C., 2015. Optimising environmental risk assessments: Accounting for ecosystem services helps to translate broad policy protection goals into specific operational ones for environmental risk assessments. EMBO reports, 16(9), pp.1060-1063.

Di Guardo, A., Gouin, T., MacLeod, M. and Scheringer, M., 2018. Environmental fate and exposure models: advances and challenges in 21 st century chemical risk assessment. Environmental Science: Processes & Impacts, 20(1), pp.58-71.

Díaz, S., Fargione, J., Chapin III, F.S. and Tilman, D., 2006. Biodiversity loss threatens human well-being. PLoS biology, 4(8), p.e277.

Dick, J.T., 1995. The cannibalistic behaviour of two *Gammarus* species (Crustacea: Amphipoda). Journal of Zoology, 236(4), pp.697-706.

Dick, J.T., Montgomery, I. and Elwood, R.W., 1993. Replacement of the indigenous amphipod *Gammarus* duebeni celticus by the introduced G. *pulex*: differential cannibalism and mutual predation. Journal of Animal Ecology, pp.79-88.

Dimitrov, M.R., Kosol, S., Smidt, H., Buijse, L., Van den Brink, P.J., Van Wijngaarden, R.P., Brock, T.C. and Maltby, L., 2014. Assessing effects of the fungicide tebuconazole to heterotrophic microbes in aquatic microcosms. Science of the Total Environment, 490, pp.1002-1011.

Dodrill, M.J., Yackulic, C.B., Kennedy, T.A., Yard, M.D. and Korman, J., 2021. As the prey thickens: rainbow trout select prey based upon width not length. Canadian Journal of Fisheries and Aquatic Sciences, 78(7), pp.809-819.

Dolciotti, I., Foit, K., Herkelrath, A. and Liess, M., 2014. Competition impedes the recovery of *Daphnia* magna from repeated insecticide pulses. Aquatic toxicology, 147, pp.26-31.

Ducrot, V., Teixeira-Alves, M., Lopes, C., Delignette-Muller, M.L., Charles, S. and Lagadic, L., 2010. Development of partial life-cycle experiments to assess the effects of endocrine disruptors on the freshwater gastropod Lymnaea stagnalis: a case-study with vinclozolin. Ecotoxicology, 19(7), pp.1312-1321.

Dudgeon, D., 2019. Multiple threats imperil freshwater biodiversity in the Anthropocene. Current Biology, 29(19), pp.R960-R967.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L. and Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological reviews, 81(2), pp.163-182.

Duffy, J.E., 2002. Biodiversity and ecosystem function: the consumer connection. Oikos, 99(2), pp.201-219.

Durance, I., Bruford, M.W., Chalmers, R., Chappell, N.A., Christie, M., Cosby, B.J., Noble, D., Ormerod, S.J., Prosser, H., Weightman, A. and Woodward, G., 2016. The challenges of linking ecosystem services to biodiversity: lessons from a large-scale freshwater study. In Advances in ecological research (Vol. 54, pp. 87-134). Academic Press.

ECHA May, 2008. Guidance on information requirements and chemical safety assessment. Chapter R19, uncertainty analysis. Guidance for the implementation of REACH.

EEA, 2018, European waters — Assessment of status and pressures 2018, EEA Report, 7/2018, European Environment Agency.

EFSA Guidance for Those Carrying out Systematic Reviews European Food Safety Authority, 2010. Application of systematic review methodology to food and feed safety assessments to support decision making. EFSA journal, 8(6), p.1637.

EFSA Panel on Plant Protection Products and their Residues (PPR), 2013. Guidance on tiered risk assessment for plant protection products for aquatic organisms in edge-of-field surface waters. EFSA Journal, 11(7), p.3290.

EFSA Scientific Committee, 2016. Guidance to develop specific protection goals options for environmental risk assessment at EFSA, in relation to biodiversity and ecosystem services. Efsa Journal, 14(6), p.e04499.

EFSA Panel on Plant Protection Products and their Residues (PPR), Ockleford, C., Adriaanse, P., Berny, P., Brock, T., Duquesne, S., Grilli, S., Hernandez-Jerez, A.F., Bennekou, S.H., Klein, M. and Kuhl, T., 2018. Scientific Opinion on the state of the art of Toxicokinetic/Toxicodynamic (TKTD) effect models for regulatory risk assessment of pesticides for aquatic organisms. EFSA journal, 16(8), p.e05377.

Elliott, J.M., 1970. Diel changes in invertebrate drift and the food of trout Salmo trutta L. Journal of Fish Biology, 2(2), pp.161-165.

Elliott, J.M., 1973. The food of brown and rainbow trout (Salmo trutta and S. gairdneri) in relation to the abundance of drifting invertebrates in a mountain stream. Oecologia, 12, pp.329-347.

Elmqvist, T., Tuvendal, M., Krishnaswamy, J. and Hylander, K., 2013. Managing trade-offs in ecosystem services. In Values, payments and institutions for ecosystem management (pp. 70-89). Edward Elgar Publishing.

Enefalk, Å., Huusko, A., Louhi, P. and Bergman, E., 2019. Fine stream wood decreases growth of juvenile brown trout (Salmo trutta L.). Environmental biology of fishes, 102, pp.759-770.

Environment Agency (EA). (2018). A survey of freshwater angling in England. Phase 1 Report.Environment Agency. Retrieved from https://www.gov.uk/government/publications/a-survey-of-freshwater-angling-in-england

Environment Agency. 2021. River Basin Management Plans 2021-Challenges and Choices consultation: Summary report. Accessed 30.08.24 https://www.gov.uk/government/consultations/river-basin-planning-challenges-and-choices

Environmental Audit Committee (EAC). 2022. Water quality in rivers. HC 74. UK Parliament. https://committees.parliament.uk/publications/8460/documents/88412/default/

European Commission, Chemicals Strategy for Sustainability Towards a Toxic-Free Environment, 2020

European Commission, Regulation (EC) No 1907/2006 of the European Parliament and of the Council of 18 December 2006 concerning the Registration, Evaluation, Authorisation and Restriction of Chemicals (REACH), establishing a European Chemicals Agency, amending Directive 1999/4. Vol. 10, Ec 2074/2005, 2006

Faber, J.H., Marshall, S., Brown, A.R., Holt, A., Van den Brink, P.J. and Maltby, L., 2021. Identifying ecological production functions for use in ecosystem services-based environmental risk assessment of chemicals. Science of the Total Environment, 791, p.146409.

Fang, W., Peng, Y., Muir, D., Lin, J. and Zhang, X., 2019. A critical review of synthetic chemicals in surface waters of the US, the EU and China. Environment international, 131, p.104994.

Feckler, A., Goedkoop, W., Konschak, M., Bundschuh, R., Kenngott, K.G., Schulz, R., Zubrod, J.P. and Bundschuh, M., 2018. History matters: Heterotrophic microbial community structure and function adapt to multiple stressors. Global Change Biology, 24(2), pp.e402-e415.

Feckler, A., Goedkoop, W., Zubrod, J.P., Schulz, R. and Bundschuh, M., 2016. Exposure pathway-dependent effects of the fungicide epoxiconazole on a decomposer-detritivore system. Science of the Total Environment, 571, pp.992-1000.

Fernández, D., Voss, K., Bundschuh, M., Zubrod, J.P. and Schäfer, R.B., 2015. Effects of fungicides on decomposer communities and litter decomposition in vineyard streams. Science of the Total Environment, 533, pp.40-48.

Ferreira, V., Encalada, A.C. and Graça, M.A., 2012. Effects of litter diversity on decomposition and biological colonization of submerged litter in temperate and tropical streams. Freshwater Science, 31(3), pp.945-962.

Ferreira, V., Chauvet, E. and Canhoto, C., 2015a. Effects of experimental warming, litter species, and presence of macroinvertebrates on litter decomposition and associated decomposers in a temperate mountain stream. Canadian Journal of Fisheries and Aquatic Sciences, 72(2), pp.206-216.

Ferreira, V., Castagneyrol, B., Koricheva, J., Gulis, V., Chauvet, E. and Graça, M.A., 2015b. A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. Biological Reviews, 90(3), pp.669-688.

Filla A, Hiripi L, Elekes K. Role of aminergic (serotonin and dopamine) systems in the embryogenesis and different embryonic behaviors of the pond snail, Lymnaea stagnalis. Comp Biochem Physiol C Toxicol Pharmacol. 2009 Jan;149(1):73-82. doi: 10.1016/j.cbpc.2008.07.004. Epub 2008 Jul 16. PMID: 18682301.

Fisher, B., Turner, R.K. and Morling, P., 2009. Defining and classifying ecosystem services for decision making. Ecological economics, 68(3), pp.643-653.

Fleeger, J.W., Carman, K.R. and Nisbet, R.M., 2003. Indirect effects of contaminants in aquatic ecosystems. Science of the total environment, 317(1-3), pp.207-233.

Fleeger, J.W., 2020. How do indirect effects of contaminants inform ecotoxicology? A review. Processes, 8(12), p.1659.

FOCUS. Boesten, J.J.T.I., Aden, K., Beigel, C., Beulke, S., Dust, M., Dyson, J.S., Fomsgaard, I.S., Jones, R.L., Karlsson, S., Van der Linden, A.M.A. and Richter, O., 2005. Guidance document on estimating persistence and degradation kinetics from environmental fate studies on pesticides in EU registration. Report of the FOCUS Work Group on Degradation Kinetics, EC Doc. Ref. Sanco/10058/2005, version, 1, pp.68-106.

Foit, K., Kaske, O. and Liess, M., 2012. Competition increases toxicant sensitivity and delays the recovery of two interacting populations. Aquatic Toxicology, 106, pp.25-31.

Fong, P.P. and Ford, A.T., 2014. The biological effects of antidepressants on the molluscs and crustaceans: a review. Aquatic toxicology, 151, pp.4-13.

Forbes, V.E. and Calow, P., 1999. Is the per capita rate of increase a good measure of population-level effects in ecotoxicology?. Environmental Toxicology and Chemistry: An International Journal, 18(7), pp.1544-1556.

Forbes, V.E., Sibly, R.M. and Calow, P., 2001. Toxicant impacts on density-limited populations: A critical review of theory, practice, and results. Ecological Applications, 11(4), pp.1249-1257.

Forbes, V.E. and Calow, P., 2002. Population growth rate as a basis for ecological risk assessment of toxic chemicals. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 357(1425), pp.1299-1306.

Forbes, V.E., Calow, P. and Sibly, R.M., 2008. The extrapolation problem and how population modeling can help. Environmental Toxicology and Chemistry: An International Journal, 27(10), pp.1987-1994.

Forbes, V.E., Calow, P., Grimm, V., Hayashi, T., Jager, T., Palmqvist, A., Pastorok, R., Salvito, D., Sibly, R., Spromberg, J. and Stark, J., 2010. Integrating population modeling into ecological risk assessment.

Forbes, V.E., Calow, P., Grimm, V., Hayashi, T.I., Jager, T., Katholm, A., Palmqvist, A., Pastorok, R., Salvito, D., Sibly, R. and Spromberg, J., 2011. Adding value to ecological risk assessment with population modeling. Human and Ecological Risk Assessment, 17(2), pp.287-299.

Forbes, V.E. and Calow, P., 2013. Use of the ecosystem services concept in ecological risk assessment of chemicals. Integrated environmental assessment and management, 9(2), pp.269-275.

Forbes, V.E. and Galic, N., 2016. Next-generation ecological risk assessment: Predicting risk from molecular initiation to ecosystem service delivery. Environment international, 91, pp.215-219.

Forbes, V.E., Galic, N., Schmolke, A., Vavra, J., Pastorok, R. and Thorbek, P., 2016. Assessing the risks of pesticides to threatened and endangered species using population modeling: A critical review and recommendations for future work. Environmental toxicology and chemistry, 35(8), pp.1904-1913.

Forbes, V.E., Salice, C.J., Birnir, B., Bruins, R.J., Calow, P., Ducrot, V., Galic, N., Garber, K., Harvey, B.C., Jager, H. and Kanarek, A., 2017. A framework for predicting impacts on ecosystem services from (sub) organismal responses to chemicals. Environmental toxicology and chemistry, 36(4), pp.845-859.

Forbes, V.E., Railsback, S., Accolla, C., Birnir, B., Bruins, R.J., Ducrot, V., Galic, N., Garber, K., Harvey, B.C., Jager, H.I. and Kanarek, A., 2019. Predicting impacts of chemicals from organisms to ecosystem service delivery: A case study of endocrine disruptor effects on trout. Science of the total environment, 649, pp.949-959.

Forbes, V.E., Agatz, A., Ashauer, R., Butt, K.R., Capowiez, Y., Duquesne, S., Ernst, G., Focks, A., Gergs, A., Hodson, M.E. and Holmstrup, M., 2021. Mechanistic effect modeling of earthworms in the context of pesticide risk assessment: synthesis of the FORESEE workshop. Integrated Environmental Assessment and Management, 17(2), pp.352-363.

Ford, A.T., Ågerstrand, M., Brooks, B.W., Allen, J., Bertram, M.G., Brodin, T., Dang, Z., Duquesne, S., Sahm, R., Hoffmann, F. and Hollert, H., 2021. The role of behavioral ecotoxicology in environmental protection. Environmental Science & Technology, 55(9), pp.5620-5628.

Forrow, D.M. and Maltby, L., 2000. Toward a mechanistic understanding of contaminant-induced changes in detritus processing in streams: Direct and indirect effects on detritivore feeding. Environmental Toxicology and Chemistry: An International Journal, 19(8), pp.2100-2106.

Forsman, A. and Wennersten, L., 2016. Inter-individual variation promotes ecological success of populations and species: Evidence from experimental and comparative studies. Ecography, 39(7), pp.630-648.

Foucreau, N., Puijalon, S., Hervant, F. and Piscart, C., 2013. Effect of leaf litter characteristics on leaf conditioning and on consumption by G ammarus *pulex*. Freshwater Biology, 58(8), pp.1672-1681.

Friberg, N. and Jacobsen, D., 1994. Feeding plasticity of two detritivore-shredders. Freshwater Biology, 32(1), pp.133-142.

Frost, T.M., Carpenter, S.R., Ives, A.R. and Kratz, T.K., 1995. Species compensation and complementarity in ecosystem function. In Linking species & ecosystems (pp. 224-239). Boston, MA: Springer US.

Fulford, R., Yoskowitz, D., Russell, M., Dantin, D. and Rogers, J., 2016. Habitat and recreational fishing opportunity in Tampa Bay: Linking ecological and ecosystem services to human beneficiaries. Ecosystem Services, 17, pp.64-74.

Gabsi, F., Hammers-Wirtz, M., Grimm, V., Schäffer, A. and Preuss, T.G., 2014. Coupling different mechanistic effect models for capturing individual-and population-level effects of chemicals: Lessons from a case where standard risk assessment failed. Ecological Modelling, 280, pp.18-29.

Gabsi, F., Schäffer, A. and Preuss, T.G., 2014. Predicting the sensitivity of populations from individual exposure to chemicals: the role of ecological interactions. Environmental toxicology and chemistry, 33(7), pp.1449-1457.

Gagic, V., Kleijn, D., Báldi, A., Boros, G., Jørgensen, H.B., Elek, Z., Garratt, M.P., de Groot, G.A., Hedlund, K., Kovács-Hostyánszki, A. and Marini, L., 2017. Combined effects of agrochemicals and ecosystem services on crop yield across Europe. Ecology Letters, 20(11), pp.1427-1436.

Galic, N., Hommen, U., Baveco, J.M. and Van Den Brink, P.J., 2010. Potential application of population models in the European ecological risk assessment of chemicals II: Review of models and their potential to address environmental protection aims. Integrated environmental assessment and management, 6(3), pp.338-360.

Galic, N., Baveco, H., Hengeveld, G.M., Thorbek, P., Bruns, E. and Van Den Brink, P.J., 2012. Simulating population recovery of an aquatic isopod: Effects of timing of stress and landscape structure. Environmental Pollution, 163, pp.91-99.

Galic, N., Schmolke, A., Forbes, V., Baveco, H. and van den Brink, P.J., 2012. The role of ecological models in linking ecological risk assessment to ecosystem services in agroecosystems. Science of the Total Environment, 415, pp.93-100.

Galic, N., Hengeveld, G.M., Van den Brink, P.J., Schmolke, A., Thorbek, P., Bruns, E. and Baveco, H.M., 2013. Persistence of aquatic insects across managed landscapes: effects of landscape permeability on re-colonization and population recovery. PLoS One, 8(1), p.e54584.

Galic, N., Ashauer, R., Baveco, H., Nyman, A.M., Barsi, A., Thorbek, P., Bruns, E. and Van den Brink, P.J., 2014. Modeling the contribution of toxicokinetic and toxicodynamic processes to the recovery of *Gammarus pulex* populations after exposure to pesticides. Environmental toxicology and chemistry, 33(7), pp.1476-1488.

Galic, N., Grimm, V. and Forbes, V.E., 2017. Impaired ecosystem process despite little effects on populations: modeling combined effects of warming and toxicants. Global change biology, 23(8), pp.2973-2989.

Galic, N., Salice, C.J., Birnir, B., Bruins, R.J., Ducrot, V., Jager, H.I., Kanarek, A., Pastorok, R., Rebarber, R., Thorbek, P. and Forbes, V.E., 2019. Predicting impacts of chemicals from organisms to ecosystem service delivery: A case study of insecticide impacts on a freshwater lake. Science of the total Environment, 682, pp.426-436.

Gamfeldt, L. and Källström, B., 2007. Increasing intraspecific diversity increases predictability in population survival in the face of perturbations. Oikos, 116(4), pp.700-705.

Gee, J.H., 1982. Resource utilization by *Gammarus pulex* (Amphipoda) in a Cotswold stream: a microdistribution study. The Journal of Animal Ecology, pp.817-831.

Gee, J.H., 1988. Population dynamics and morphometries of *Gammarus pulex* L.: evidence of seasonal food limitation in a freshwater detritivore. Freshwater Biology, 19(3), pp.333-343.

Gergs, A. and Jager, T., 2014a. Body size-mediated starvation resistance in an insect predator. Journal of Animal Ecology, 83(4), pp.758-768.

Gergs, A., Preuss, T.G. and Palmqvist, A., 2014b. Double trouble at high density: cross-level test of resource-related adaptive plasticity and crowding-related fitness. PloS one, 9(3), p.e91503.

Gergs, A., Gabsi, F., Zenker, A. and Preuss, T.G., 2016. Demographic toxicokinetic–toxicodynamic modeling of lethal effects. Environmental science & technology, 50(11), pp.6017-6024.

Gergs, A., Hager, J., Bruns, E. and Preuss, T.G., 2021. Disentangling mechanisms behind chronic lethality through toxicokinetic–toxicodynamic modeling. Environmental Toxicology and Chemistry, 40(6), pp.1706-1712.

Gessner, M.O., Chauvet, E. and Dobson, M., 1999. A perspective on leaf litter breakdown in streams. Oikos, pp.377-384.

Gessner, M.O. and Chauvet, E., 2002. A case for using litter breakdown to assess functional stream integrity. Ecological applications, 12(2), pp.498-510.

Gessner, M.O. and Tlili, A., 2016. Fostering integration of freshwater ecology with ecotoxicology. Freshwater biology, 61(12), pp.1991-2001.

Glazier, D.S. and Calow, P., 1992. Energy allocation rules in *Daphnia magna*: clonal and age differences in the effects of food limitation. *Oecologia*, *90*, pp.540-549.

Gómez, A., Cecchine, G. and Snell, T.W., 1997. Effect of pentachlorophenol on predator-prey interaction of two rotifers. Aquatic Toxicology, 37(4), pp.271-282.

González, J.M. and Graça, M.A.S., 2003. Conversion of leaf litter to secondary production by a shredding caddis-fly. Freshwater Biology, 48(9), pp.1578-1592.

Goodchild, C.G., Simpson, A.M., Minghetti, M. and DuRant, S.E., 2019. Bioenergetics-adverse outcome pathway: Linking organismal and suborganismal energetic endpoints to adverse outcomes. Environmental toxicology and chemistry, 38(1), pp.27-45.

Graça, M.A.S., Maltby, L. and Calow, P., 1993a. Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus* I: feeding strategies. Oecologia, 93, pp.139-144.

Graça, M.A.S., Maltby, L. and Calow, P., 1993b. Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus*: II. Effects on growth, reproduction and physiology. Oecologia, 96, pp.304-309.

Graça, M.A.S., Maltby, L. and Calow, P., 1994a. Comparative ecology of *Gammarus pulex* (L.) and *Asellus aquaticus* (L.) II: fungal preferences. Hydrobiologia, 281, pp.163-170.

Graça, M.A.S., Maltby, L. and Calow, P., 1994b. Comparative ecology of *Gammarus pulex* (L.) and *Asellus aquaticus* (L.) I: population dynamics and microdistribution. Hydrobiologia, 281, pp.155-162.

Graça, M.A., 2001. The role of invertebrates on leaf litter decomposition in streams–a review. International Review of Hydrobiology: A Journal Covering all Aspects of Limnology and Marine Biology, 86(4-5), pp.383-393.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G. and Huth, A., 2006. A standard protocol for describing individual-based and agent-based models. Ecological modelling, 198(1-2), pp.115-126.

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X. and Briggs, J.M., 2008. Global change and the ecology of cities. science, 319(5864), pp.756-760.

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J. and Railsback, S.F., 2010. The ODD protocol: a review and first update. Ecological modelling, 221(23), pp.2760-2768.

Grimm, V. and Martin, B.T., 2013. Mechanistic effect modeling for ecological risk assessment: where to go from here?. Integrated environmental assessment and management, 9(3), pp.e58-e63.

Grimm, V. and Railsback, S.F., 2013. Individual-based modeling and ecology. In Individual-based modeling and ecology. Princeton university press.

Grimm, V., Augusiak, J., Focks, A., Frank, B.M., Gabsi, F., Johnston, A.S., Liu, C., Martin, B.T., Meli, M., Radchuk, V. and Thorbek, P., 2014. Towards better modelling and decision support: Documenting model development, testing, and analysis using TRACE. Ecological modelling, 280, pp.129-139.

Grimm, V., Ayllón, D. and Railsback, S.F., 2017. Next-generation individual-based models integrate biodiversity and ecosystems: yes we can, and yes we must. Ecosystems, 20, pp.229-236.

Grizzetti, B., Lanzanova, D., Liquete, C., Reynaud, A. and Cardoso, A.C., 2016. Assessing water ecosystem services for water resource management. Environmental Science & Policy, 61, pp.194-203.

Groh, K., Vom Berg, C., Schirmer, K. and Tlili, A., 2022. Anthropogenic chemicals as underestimated drivers of biodiversity loss: scientific and societal implications. Environmental Science & Technology, 56(2), pp.707-710.

Guasch, H., Ivorra, N., Lehmann, V., Paulsson, M., Real, M. and Sabater, S., 1998. Community composition and sensitivity of periphyton to atrazine in flowing waters: the role of environmental factors. Journal of applied phycology, 10, pp.203-213.

Gulis, V., Suberkropp, K. and Rosemond, A.D., 2008. Comparison of fungal activities on wood and leaf litter in unaltered and nutrient-enriched headwater streams. Applied and environmental microbiology, 74(4), pp.1094-1101.

Gunn, I.D.M.; Carvalho, L.; Davies, C.E.; Edwards, F.K.; Furse, M.T.; Maitland, P.S.; Raper, C.; Siriwardena, G.M.; Winfield, I.J. (2018). UK Checklist of freshwater species. NERC Environmental Information Data Centre. https://doi.org/10.5285/57653719-434b-4b11-9f0d-3bd76054d8bd

Gurney, W.S., Middleton, D.A., Nisbet, R.M., McCauley, E., Murdoch, W.W. and DeRoos, A., 1996. Individual energetics and the equilibrium demography of structured populations. theoretical population biology, 49(3), pp.344-368.

Gust, K.A., Kennedy, A.J., Melby, N.L., Wilbanks, M.S., Laird, J., Meeks, B., Muller, E.B., Nisbet, R.M. and Perkins, E.J., 2016. *Daphnia* magna's sense of competition: intra-specific interactions (ISI) alter life history strategies and increase metals toxicity. Ecotoxicology, 25, pp.1126-1135.

Haase, P., Bowler, D.E., Baker, N.J., Bonada, N., Domisch, S., Garcia Marquez, J.R., Heino, J., Hering, D., Jähnig, S.C., Schmidt-Kloiber, A. and Stubbington, R., 2023. The recovery of European freshwater biodiversity has come to a halt. Nature, 620(7974), pp.582-588.

Haines-Young, R. and Potschin-Young, M., 2018. Revision of the common international classification for ecosystem services (CICES V5. 1): a policy brief. One Ecosystem, 3, p.e27108.

Hanna, D.E., Tomscha, S.A., Ouellet Dallaire, C. and Bennett, E.M., 2018. A review of riverine ecosystem service quantification: Research gaps and recommendations. Journal of Applied Ecology, 55(3), pp.1299-1311.

Hansul, S., Fettweis, A., Smolders, E. and De Schamphelaere, K., 2021. Interactive metal mixture toxicity to *Daphnia* magna populations as an emergent property in a dynamic energy budget individual-based model. Environmental Toxicology and Chemistry, 40(11), pp.3034-3048.

Hargeby, A., 1990. Effects of pH, humic substances and animal interactions on survival and physiological status of *Asellus aquaticus* L. and *Gammarus pulex* (L.). Oecologia, 82(3), pp.348-354.

Harrison, L.J., Pearson, K.A., Wheatley, C.J., Hill, J.K., Maltby, L., Rivetti, C., Speirs, L. and White, P.C., 2022. Functional measures as potential indicators of down-the-drain chemical stress in freshwater ecological risk assessment. Integrated Environmental Assessment and Management, 18(5), pp.1135-1147.

Harrison, P.A., Berry, P.M., Simpson, G., Haslett, J.R., Blicharska, M., Bucur, M., Dunford, R., Egoh, B., Garcia-Llorente, M., Geamănă, N. and Geertsema, W., 2014. Linkages between biodiversity attributes and ecosystem services: A systematic review. Ecosystem services, 9, pp.191-203.

Harrison, P.A., Vandewalle, M., Sykes, M.T., Berry, P.M., Bugter, R., De Bello, F., Feld, C.K., Grandin, U., Harrington, R., Haslett, J.R. and Jongman, R.H., 2010. Identifying and prioritising services in European terrestrial and freshwater ecosystems. Biodiversity and conservation, 19, pp.2791-2821.

Harrison, P.A., Vandewalle, M., Sykes, M.T., Berry, P.M., Bugter, R., de Bello, F., Feld, C.K., Grandin, U., Harrington, R., Haslett, J.R. and Jongman, R.H., 2010. Identifying and prioritising services in European terrestrial and freshwater ecosystems. Biodiversity and conservation, 19, pp.2791-2821.

Hayes, F., Spurgeon, D.J., Lofts, S. and Jones, L., 2018. Evidence-based logic chains demonstrate multiple impacts of trace metals on ecosystem services. Journal of environmental management, 223, pp.150-164.

Heinis, F., Timmermans, K.R. and Swain, W.R., 1990. Short-term sublethal effects of cadmium on the filter feeding chironomid larva Glyptotendipes pallens (Meigen)(Diptera). Aquatic toxicology, 16(1), pp.73-85.

Hessen, D.O., Elser, J.J., Sterner, R.W. and Urabe, J., 2013. Ecological stoichiometry: an elementary approach using basic principles. Limnology and Oceanography, 58(6), pp.2219-2236.

Hieber, M. and Gessner, M.O., 2002. Contribution of stream detrivores, fungi, and bacteria to leaf breakdown based on biomass estimates. Ecology, 83(4), pp.1026-1038.

Higgins, P.J., 1980. Effects of food availability on the valve movements and feeding behavior of juvenile Crassostrea virginica (Gmelin). I. Valve movements and periodic activity. Journal of Experimental Marine Biology and Ecology, 45(2), pp.229-244.

Hixon, M.A., Johnson, D.W. and Sogard, S.M., 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science, 71(8), pp.2171-2185.

Hoefnagel, K.N. and Verberk, W.C., 2015. Is the temperature-size rule mediated by oxygen in aquatic ectotherms?. Journal of thermal biology, 54, pp.56-65.

Hoekstra, A.Y. and Wiedmann, T.O., 2014. Humanity's unsustainable environmental footprint. Science, 344(6188), pp.1114-1117.

Hölker, F. and Breckling, B., 2001. An individual-based approach to depict the influence of the feeding strategy on the population structure of roach (Rutilus rutilus L.). Limnologica, 31(1), pp.69-78.

Holland, D.G., 1976. The distribution of the freshwater Malacostraca in the area of the Mersey and Weaver River Authority. Freshwater Biology, 6(3), pp.265-276.

Holmes, C.M., Maltby, L., Sweeney, P., Thorbek, P., Otte, J.C. and Marshall, S., 2022. Heterogeneity in biological assemblages and exposure in chemical risk assessment: Exploring capabilities and challenges in methodology with two landscape-scale case studies. Ecotoxicology and Environmental Safety, 246, p.114143.

Holt, A.R., Alix, A., Thompson, A. and Maltby, L., 2016. Food production, ecosystem services and biodiversity: We can't have it all everywhere. Science of the Total Environment, 573, pp.1422-1429.

Hommen, U., Baveco, J.M., Galic, N. and van den Brink, P.J., 2010. Potential application of ecological models in the European environmental risk assessment of chemicals I: Review of protection goals in EU directives and regulations. Integrated environmental assessment and management, 6(3), pp.325-337.

Hooper, D.U., 2011. Biodiversity, ecosystem functioning, and global change. Serpentine: the evolution and ecology of a model system. University of California Press, Berkeley, California, USA, pp.329-357.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S. and Schmid, B., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological monographs, 75(1), pp.3-35.

Huang, A., Mangold-Döring, A., Guan, H., Boerwinkel, M.C., Belgers, D., Focks, A. and Van den Brink, P.J., 2023. The effect of temperature on toxicokinetics and the chronic toxicity of insecticides towards *Gammarus pulex*. Science of the Total Environment, 856, p.158886.

Huang, A., Roessink, I., van den Brink, N.W. and van den Brink, P.J., 2022. Size-and sex-related sensitivity differences of aquatic crustaceans to imidacloprid. Ecotoxicology and Environmental Safety, 242, p.113917.

Hultin, L., 1971. Upstream movements of *Gammarus pulex pulex* (Amphipoda) in a South Swedish stream. Oikos, pp.329-347.

Hynes, H.B.N., 1955. The reproductive cycle of some British freshwater Gammaridae. The Journal of Animal Ecology, pp.352-387.

Hynes, H.B.N. and Harper, F., 1972. The life histories of *Gammarus lacustris* and *G. pseudolimnaeus* in southern Ontario. Crustaceana. Supplement, pp.329-341.

IPBES, W., 2019. Intergovernmental science-policy platform on biodiversity and ecosystem services. Summary for Policy Makers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn, Germany.

Isbell, F., Cowles, J., Dee, L.E., Loreau, M., Reich, P.B., Gonzalez, A., Hector, A. and Schmid, B., 2018. Quantifying effects of biodiversity on ecosystem functioning across times and places. Ecology Letters, 21(6), pp.763-778.

Iversen, T.M. and Jessen, J., 1977. Life-cycle, drift and production of *Gammarus pulex* L.(Amphipoda) in a Danish spring. Freshwater Biology, 7(3), pp.287-296.

Iversen, T.M. and Thorup, J., 1988. A three years' study of life cycle, population dynamics and production of *Asellus aquaticus* L. in a macrophyte rich stream. Internationale Revue der gesamten Hydrobiologie und Hydrographie, 73(1), pp.73-94.

Iversen, T.M., Thorup, J. and Skriver, J., 1982. Inputs and transformation of allochthonous particulate organic matter in a headwater stream. Ecography, 5(1), pp.10-19.

Jager, T., Heugens, E.H. and Kooijman, S.A., 2006. Making sense of ecotoxicological test results: towards application of process-based models. Ecotoxicology, 15(3), pp.305-314.

Jager, T., 2012. Making sense of chemical stress application of dynamic energy budget theory in ecotoxicology and stress ecology.

Jager, T., Barsi, A., Hamda, N.T., Martin, B.T., Zimmer, E.I. and Ducrot, V., 2014. Dynamic energy budgets in population ecotoxicology: Applications and outlook. Ecological Modelling, 280, pp.140-147.

Jager, T. and Ashauer, R., 2018. Modelling survival under chemical stress: a comprehensive guide to the GUTS framework.

Jager, T., 2020. Revisiting simplified DEBtox models for analysing ecotoxicity data. Ecological Modelling, 416, p.108904.

Jager, T., Trijau, M., Sherborne, N., Goussen, B. and Ashauer, R., 2022. Considerations for using reproduction data in toxicokinetic–toxicodynamic modelling. Integrated Environmental Assessment and Management, 18(2), pp.479-487.

Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D.E., Coscieme, L., Golden, A.S., Guerra, C.A., Jacob, U., Takahashi, Y., Settele, J. and Díaz, S., 2022. The direct drivers of recent global anthropogenic biodiversity loss. Science advances, 8(45), p.eabm9982.

Jax, K., 2005. Function and "functioning" in ecology: what does it mean?. Oikos, 111(3), pp.641-648.

Jimenez, M.P., DeVille, N.V., Elliott, E.G., Schiff, J.E., Wilt, G.E., Hart, J.E. and James, P., 2021. Associations between nature exposure and health: a review of the evidence. International journal of environmental research and public health, 18(9), p.4790.

Johnsen, K., Jacobsen, C.S., Torsvik, V. and Sørensen, J., 2001. Pesticide effects on bacterial diversity in agricultural soils–a review. Biology and Fertility of Soils, 33, pp.443-453

Johnston, A.S.A., Hodson, M.E., Thorbek, P., Alvarez, T. and Sibly, R.M., 2014. An energy budget agent-based model of earthworm populations and its application to study the effects of pesticides. *Ecological Modelling*, *280*, pp.5-17.

Johnston, A.S., Sibly, R.M., Hodson, M.E., Alvarez, T. and Thorbek, P., 2015. Effects of agricultural management practices on earthworm populations and crop yield: validation and application of a mechanistic modelling approach. Journal of Applied Ecology, 52(5), pp.1334-1342.

Jones, L.B. and Burns, C.J., 2024. REACHing for divergence?—UK chemical regulation post-Brexit. Integrated Environmental Assessment and Management.

Jonsson, M. and Malmqvist, B., 2003. Importance of species identity and number for process rates within different stream invertebrate functional feeding groups. Journal of Animal Ecology, pp.453-459.

Kasprzyk-Hordern, B., Dinsdale, R.M. and Guwy, A.J., 2008. The occurrence of pharmaceuticals, personal care products, endocrine disruptors and illicit drugs in surface water in South Wales, UK. Water research, 42(13), pp.3498-3518.

Kaval, P., 2019. Integrated catchment management and ecosystem services: A twenty-five year overview. Ecosystem Services, 37, p.100912.

Keeler, B.L., Polasky, S., Brauman, K.A., Johnson, K.A., Finlay, J.C., O'Neill, A., Kovacs, K. and Dalzell, B., 2012. Linking water quality and well-being for improved assessment and valuation of ecosystem services. Proceedings of the National Academy of Sciences, 109(45), pp.18619-18624.

Kefford, B.J., Botwe, P.K., Brooks, A.J., Kunz, S., Marchant, R., Maxwell, S., Metzeling, L., Schäfer, R.B. and Thompson, R.M., 2020. An integrated database of stream macroinvertebrate traits for Australia: Concept and application. Ecological Indicators, 114, p.106280.

Kelly, D.W., Dick, J.T. and Montgomery, W.I., 2002. The functional role of *Gammarus* (Crustacea, Amphipoda): shredders, predators, or both?. Hydrobiologia, 485, pp.199-203.

Kemper, N., 2008. Veterinary antibiotics in the aquatic and terrestrial environment. Ecological indicators, 8(1), pp.1-13.

Kidd, K.A., Paterson, M.J., Rennie, M.D., Podemski, C.L., Findlay, D.L., Blanchfield, P.J. and Liber, K., 2014. Direct and indirect responses of a freshwater food web to a potent synthetic oestrogen. Philosophical Transactions of the Royal Society B: Biological Sciences, 369(1656), p.20130578.

Kienzler, A., M. G. Barron, S. E. Belanger, A. Beasley and M. R. Embry (2017). "Mode of Action (MOA) Assignment Classifications for Ecotoxicology: An Evaluation of Approaches." Environ Sci Technol 51(17): 10203- 10211.

Kim, Y., Son, J., Mo, H.H., Lee, Y.S. and Cho, K., 2018. Modeling the influence of initial density and copper exposure on the interspecific competition of two algal species. Ecological Modelling, 383, pp.160-170.

Kim, Y., Son, J., Lee, Y.S., Lee, M., Hong, J. and Cho, K., 2019. Integration of an individual-oriented model into a system dynamics model: an application to a multi-species system. Environmental Modelling & Software, 112, pp.23-35.

Kley, A., Kinzler, W., Schank, Y., Mayer, G., Waloszek, D. and Maier, G., 2009. Influence of substrate preference and complexity on co-existence of two non-native gammarideans (Crustacea: Amphipoda). Aquatic Ecology, 43, pp.1047-1059.

Kliot, A. and Ghanim, M., 2012. Fitness costs associated with insecticide resistance. Pest management science, 68(11), pp.1431-1437.

Knapp, J.L., Bates, A., Jonsson, O., Klatt, B., Krausl, T., Sahlin, U., Svensson, G.P. and Rundlöf, M., 2022. Pollinators, pests and yield—Multiple trade-offs from insecticide use in a mass-flowering crop. Journal of Applied Ecology, 59(9), pp.2419-2429.

Knillmann, S., Stampfli, N.C., Beketov, M.A. and Liess, M., 2012a. Intraspecific competition increases toxicant effects in outdoor pond microcosms. Ecotoxicology, 21, pp.1857-1866.

Knillmann, S., Stampfli, N.C., Noskov, Y.A., Beketov, M.A. and Liess, M., 2012b. Interspecific competition delays recovery of *Daphnia* spp. populations from pesticide stress. Ecotoxicology, 21, pp.1039-1049.

Konschak, M., Zubrod, J.P., Baudy, P., Fink, P., Kenngott, K.G.J., Englert, D., Röder, N., Ogbeide, C., Schulz, R. and Bundschuh, M., 2021. Chronic effects of the strobilurin fungicide azoxystrobin in the leaf shredder *Gammarus* fossarum (Crustacea; Amphipoda) via two effect pathways. Ecotoxicology and Environmental Safety, 209, p.111848.

Konschak, M., Zubrod, J.P., Duque Acosta, T.S., Bouchez, A., Kroll, A., Feckler, A., Röder, N., Baudy, P., Schulz, R. and Bundschuh, M., 2021. Herbicide-induced shifts in the periphyton community composition indirectly affect feeding activity and physiology of the gastropod grazer Physella acuta. Environmental Science & Technology, 55(21), pp.14699-14709.

Kontogianni, A., Luck, G.W. and Skourtos, M., 2010. Valuing ecosystem services on the basis of service-providing units: A potential approach to address the 'endpoint problem' and improve stated preference methods. Ecological Economics, 69(7), pp.1479-1487.

Kontogianni, A., Tourkolias, C., Machleras, A. and Skourtos, M., 2012. Service providing units, existence values and the valuation of endangered species: A methodological test. Ecological Economics, 79, pp.97-104.

Kooijman, S.A., 2014. Metabolic acceleration in animal ontogeny: an evolutionary perspective. Journal of Sea Research, 94, pp.128-137.

Kooijman, S.A.L.M., 2010. Dynamic energy budget theory for metabolic organisation. Cambridge university press.

Kostalos, M. and Seymour, R.L., 1976. Role of microbial enriched detritus in the nutrition of *Gammarus* minus (Amphipoda). Oikos, pp.512-516.

Kramer, V.J., Etterson, M.A., Hecker, M., Murphy, C.A., Roesijadi, G., Spade, D.J., Spromberg, J.A., Wang, M. and Ankley, G.T., 2011. Adverse outcome pathways and ecological risk assessment: Bridging to population-level effects. Environmental Toxicology and Chemistry, 30(1), pp.64-76.

Kremen, C., 2005. Managing ecosystem services: what do we need to know about their ecology?. Ecology letters, 8(5), pp.468-479.

Kremen, C., 2020. Ecological intensification and diversification approaches to maintain biodiversity, ecosystem services and food production in a changing world. Emerging Topics in Life Sciences, 4(2), pp.229-240.

Kremer, P., Hamstead, Z., Haase, D., McPhearson, T., Frantzeskaki, N., Andersson, E., Kabisch, N., Larondelle, N., Rall, E.L., Voigt, A. and Baró, F., 2016. Key insights for the future of urban ecosystem services research. Ecology and Society, 21(2).

Lallas, P.L., 2001. The Stockholm Convention on persistent organic pollutants. American Journal of International Law, 95(3), pp.692-708.

Larras, F., Beaudouin, R., Berny, P., Charles, S., Chaumot, A., Corio-Costet, M.F., Doussan, I., Pélosi, C., Leenhardt, S. and Mamy, L., 2022. A meta-analysis of ecotoxicological models used for plant protection product risk assessment before their placing on the market. Science of the Total Environment, 844, p.157003.

Larras, F., Charles, S., Chaumot, A., Pelosi, C., Le Gall, M., Mamy, L. and Beaudouin, R., 2022. A critical review of effect modeling for ecological risk assessment of plant protection products. Environmental Science and Pollution Research, 29(29), pp.43448-43500.

Laureto, L.M.O., Cianciaruso, M.V. and Samia, D.S.M., 2015. Functional diversity: an overview of its history and applicability. Natureza & Conservação, 13(2), pp.112-116.

Lebrun, J.D., De Jesus, K. and Tournebize, J., 2021. Individual performances and biochemical pathways as altered by field-realistic exposures of current-use fungicides and their mixtures in a non-target species, *Gammarus* fossarum. Chemosphere, 277, p.130277.

Leduc, A.O., Da Silva, E.M. and Rosenfeld, J.S., 2015. Effects of species vs. functional diversity: Understanding the roles of complementarity and competition on ecosystem function in a tropical stream fish assemblage. Ecological Indicators, 48, pp.627-635.

Lemm, J.U., Venohr, M., Globevnik, L., Stefanidis, K., Panagopoulos, Y., van Gils, J., Posthuma, L., Kristensen, P., Feld, C.K., Mahnkopf, J. and Hering, D., 2021. Multiple stressors determine river ecological status at the European scale: Towards an integrated understanding of river status deterioration. Global Change Biology, 27(9), pp.1962-1975.

Leuzinger, S. and Rewald, B., 2021. The who or the how? Species vs. ecosystem function priorities in conservation ecology. Frontiers in Plant Science, 12, p.758413.

Lewis, S.E., Piatt, J.J. and Lewis, A.S., 2017. Amphipods (*Gammarus* pseudolimnaeus) prefer but are harmed by a diet of non-native leaves. Freshwater Science, 36(4), pp.739-749.

Liang, R. and Maltby, L., 2024. Spatial variation in the recovery potential of freshwater macroinvertebrate assemblages: Moving towards spatially defined assemblage vulnerability to chemicals. Science of The Total Environment, 909, p.168402.

Liang, R., Sinclair, T.M., Craig, P.S. and Maltby, L., 2024. Spatial variation in the sensitivity of freshwater macroinvertebrate assemblages to chemical stressors. Water Research, 248, p.120854.

Liess, M., 2002. Population response to toxicants is altered by intraspecific interaction. Environmental Toxicology and Chemistry: An International Journal, 21(1), pp.138-142.

Liess, M. and Beketov, M., 2011. Traits and stress: keys to identify community effects of low levels of toxicants in test systems. Ecotoxicology, 20, pp.1328-1340.

Liess, M., Gerner, N.V. and Kefford, B.J., 2017. Metal toxicity affects predatory stream invertebrates less than other functional feeding groups. Environmental Pollution, 227, pp.505-512.

Liess, M., Liebmann, L., Vormeier, P., Weisner, O., Altenburger, R., Borchardt, D., Brack, W., Chatzinotas, A., Escher, B., Foit, K. and Gunold, R., 2021. Pesticides are the dominant stressors for vulnerable insects in lowland streams. Water Research, 201, p.117262.

Little, C.J. and Altermatt, F., 2018. Species turnover and invasion of dominant freshwater invertebrates alter biodiversity–ecosystem-function relationship. Ecological Monographs, 88(3), pp.461-480.

Lombardo, A., Franco, A., Pivato, A. and Barausse, A., 2015. Food web modeling of a river ecosystem for risk assessment of down-the-drain chemicals: A case study with AQUATOX. Science of the Total Environment, 508, pp.214-227.

Loos, R., Gawlik, B.M., Locoro, G., Rimaviciute, E., Contini, S. and Bidoglio, G., 2009. EU-wide survey of polar organic persistent pollutants in European river waters. Environmental pollution, 157(2), pp.561-568.

Lopes, C., Péry, A.R.R., Chaumot, A. and Charles, S., 2005. Ecotoxicology and population dynamics: Using DEBtox models in a Leslie modeling approach. Ecological Modelling, 188(1), pp.30-40.

Loreau, M., 1995. Consumers as maximizers of matter and energy flow in ecosystems. The American Naturalist, 145(1), pp.22-42.

Loreau, M., 2014. Reconciling utilitarian and non-utilitarian approaches to biodiversity conservation. Ethics in Science and Environmental Politics, 14(1), pp.27-32.

Lotka, A.J., 1925. Elements of physical biology. Williams & Wilkins.

Louati, D., BenMiled, S. and Saoud, N.B.B., 2020. HermaDEB: an evolutionary IBM for energy allocation in hermaphrodites. Ecological Modelling, 424, p.109008.

Luck, G.W., Daily, G.C. and Ehrlich, P.R., 2003. Population diversity and ecosystem services. Trends in Ecology & Evolution, 18(7), pp.331-336.

Luck, G.W., Harrington, R., Harrison, P.A., Kremen, C., Berry, P.M., Bugter, R., Dawson, T.P., De Bello, F., Díaz, S., Feld, C.K. and Haslett, J.R., 2009. Quantifying the contribution of organisms to the provision of ecosystem services. Bioscience, 59(3), pp.223-235.

Lukančič, S., Žibrat, U., Mezek, T., Jerebic, A., Simčič, T. and Brancelj, A., 2010. Effects of exposing two non-target crustacean species, *Asellus aquaticus* L., and *Gammarus* fossarum Koch., to atrazine and imidacloprid. Bulletin of environmental contamination and toxicology, 84(1), pp.85-90.

Lürling, M. and Roessink, I., 2006. On the way to cyanobacterial blooms: impact of the herbicide metribuzin on the competition between a green alga (Scenedesmus) and a cyanobacterium (Microcystis). Chemosphere, 65(4), pp.618-626.

Macadam, C.R. and Stockan, J.A., 2015. More than just fish food: ecosystem services provided by freshwater insects. Ecological Entomology, 40, pp.113-123.

MacKay, N.A. and Elser, J.J., 1998. Factors potentially preventing trophic cascades: Food quality, invertebrate predation, and their interaction. Limnology and Oceanography, 43(2), pp.339-347.

MacNeil, C., Dick, J.T. and Elwood, R.W., 1997. The trophic ecology of freshwater *Gammarus* spp.(Crustacea: Amphipoda): problems and perspectives concerning the functional feeding group concept. Biological Reviews, 72(3), pp.349-364.

MacNeil, C., Dick, J.T., Bigsby, E., Elwood, R.W., Montgomery, W.I., Gibbins, C.N. and Kelly, D.W., 2002. The validity of the *Gammarus*: *Asellus* ratio as an index of organic pollution: abiotic and biotic influences. Water research, 36(1), pp.75-84.

Maes, J., Egoh, B., Willemen, L., Liquete, C., Vihervaara, P., Schägner, J.P., Grizzetti, B., Drakou, E.G., La Notte, A., Zulian, G. and Bouraoui, F., 2012. Mapping ecosystem services for policy support and decision making in the European Union. Ecosystem services, 1(1), pp.31-39.

Maes, J., Liquete, C., Teller, A., Erhard, M., Paracchini, M.L., Barredo, J.I., Grizzetti, B., Cardoso, A., Somma, F., Petersen, J.E. and Meiner, A., 2016. An indicator framework for assessing ecosystem services in support of the EU Biodiversity Strategy to 2020. Ecosystem services, 17, pp.14-23.

Malaj, E., von Der Ohe, P.C., Grote, M., Kühne, R., Mondy, C.P., Usseglio-Polatera, P., Brack, W. and Schäfer, R.B., 2014. Organic chemicals jeopardize the health of freshwater ecosystems on the continental scale. Proceedings of the National Academy of Sciences, 111(26), pp.9549-9554.

Maltby, L., Naylor, C. and Calow, P., 1990a. Effect of stress on a freshwater benthic detritivore: scope for growth in *Gammarus pulex*. Ecotoxicology and Environmental Safety, 19(3), pp.285-291.

Maltby, L., Naylor, C. and Calow, P., 1990b. Field deployment of a scope for growth assay involving *Gammarus pulex*, a freshwater benthic invertebrate. Ecotoxicology and Environmental Safety, 19(3), pp.292-300.

Maltby, L. and Naylor, C., 1990. Preliminary observations on the ecological relevance of the *Gammarus* scope for growth assay: effect of zinc on reproduction. Functional Ecology, pp.393-397.

Maltby, L. and Crane, M., 1994. Responses of *Gammarus pulex* (Amphipoda, Crustacea) to metalliferous effluents: identification of toxic components and the importance of interpopulation variation. Environmental Pollution, 84(1), pp.45-52.

Maltby, L., 1995. Sensitivity of the crustaceans *Gammarus pulex* (L.) and *Asellus aquaticus* (L.) to short-term exposure to hypoxia and unionized ammonia: observations and possible mechanisms. Water research, 29(3), pp.781-787.

Maltby, L., Clayton, S.A., Wood, R.M. and McLoughlin, N., 2002. Evaluation of the *Gammarus pulex* in situ feeding assay as a biomonitor of water quality: Robustness, responsiveness, and relevance. Environmental Toxicology and Chemistry: An International Journal, 21(2), pp.361-368.

Maltby, L., Blake, N., Brock, T.C. and Van den Brink, P.J., 2005. Insecticide species sensitivity distributions: importance of test species selection and relevance to aquatic ecosystems. Environmental Toxicology and Chemistry: An International Journal, 24(2), pp.379-388.

Maltby, L., Brock, T.C. and Van den Brink, P.J., 2009. Fungicide risk assessment for aquatic ecosystems: importance of interspecific variation, toxic mode of action, and exposure regime. Environmental Science & Technology, 43(19), pp.7556-7563.

Maltby, L., 2013. Ecosystem services and the protection, restoration, and management of ecosystems exposed to chemical stressors. Environmental Toxicology and Chemistry, 32(5), pp.974-983.

Maltby, L., Jackson, M., Whale, G., Brown, A.R., Hamer, M., Solga, A., Kabouw, P., Woods, R. and Marshall, S., 2017. Is an ecosystem services-based approach developed for setting specific protection goals for plant protection products applicable to other chemicals?. Science of the Total Environment, 580, pp.1222-1236.

Maltby, L., van den Brink, P.J., Faber, J.H. and Marshall, S., 2018. Advantages and challenges associated with implementing an ecosystem services approach to ecological risk assessment for chemicals. Science of the Total Environment, 621, pp.1342-1351.

Maltby, L., Brown, R., Faber, J.H., Galic, N., Van den Brink, P.J., Warwick, O. and Marshall, S., 2021. Assessing chemical risk within an ecosystem services framework: Implementation and added value. Science of the Total Environment, 791, p.148631.

Mangold-Döring, A., Buddendorf, W.B., van den Brink, P.J. and Baveco, J.M., 2024. How relevant are temperature corrections of toxicity parameters in population models for environmental risk assessment of chemicals?. Ecological Modelling, 498, p.110880.

Marcus, J.H., Sutcliffe, D.W. and Willoughby, L.G., 1978. Feeding and growth of *Asellus aquaticus* (Isopoda) on food items from the littoral of Windermere, including green leaves of Elodea canadensis. Freshwater Biology, 8(6), pp.505-519.

Marshall, D.J., Heppell, S.S., Munch, S.B. and Warner, R.R., 2010. The relationship between maternal phenotype and offspring quality: do older mothers really produce the best offspring?. Ecology, 91(10), pp.2862-2873.

Martin, B.T., Jager, T., Nisbet, R.M., Preuss, T.G., Hammers-Wirtz, M. and Grimm, V., 2013. Extrapolating ecotoxicological effects from individuals to populations: a generic approach based on Dynamic Energy Budget theory and individual-based modeling. Ecotoxicology, 22, pp.574-583.

Martinuzzi, S., Januchowski-Hartley, S.R., Pracheil, B.M., McIntyre, P.B., Plantinga, A.J., Lewis, D.J. and Radeloff, V.C., 2014. Threats and opportunities for freshwater conservation under future land use change scenarios in the United States. Global change biology, 20(1), pp.113-124.

McCahon, C.P. and Pascoe, D., 1988. Cadmium toxicity to the freshwater amphipod *Gammarus pulex* (L.) during the moult cycle. Freshwater Biology, 19(2), pp.197-203.

McCauley, E.M.W.W., Murdoch, W.W. and Nisbet, R.M., 1990. Growth, reproduction, and mortality of *Daphnia pulex* Leydig: life at low food. Functional Ecology, pp.505-514.

McGrath, K.E., Peeters, E.T., Beijer, J.A. and Scheffer, M., 2007. Habitat-mediated cannibalism and microhabitat restriction in the stream invertebrate *Gammarus pulex*. Hydrobiologia, 589, pp.155-164.

Melvin, S.D. and Wilson, S.P., 2013. The utility of behavioral studies for aquatic toxicology testing: a meta-analysis. Chemosphere, 93(10), pp.2217-2223.

Millennium Ecosystem Assessment (MEA), 2005, Millennium Ecosystem Assessment, Ecosystems and Human Well-being: A Framework for Assessment Island Press, Washington, DC, USA (2005)

Mintram, K.S., Brown, A.R., Maynard, S.K., Liu, C., Parker, S.J., Tyler, C.R. and Thorbek, P., 2018. Assessing population impacts of toxicant-induced disruption of breeding behaviours using an individual-based model for the three-spined stickleback. Ecological Modelling, 387, pp.107-117.

Moe, S.J., De Schamphelaere, K., Clements, W.H., Sorensen, M.T., Van den Brink, P.J. and Liess, M., 2013. Combined and interactive effects of global climate change and toxicants on populations and communities. Environmental toxicology and chemistry, 32(1), pp.49-61.

Mohr, S., Berghahn, R., Schmiediche, R., Hübner, V., Loth, S., Feibicke, M., Mailahn, W. and Wogram, J., 2012. Macroinvertebrate community response to repeated short-term pulses of the insecticide imidacloprid. Aquatic Toxicology, 110, pp.25-36.

Mora-Zamorano, F.X., Klingler, R., Basu, N., Head, J., Murphy, C.A., Binkowski, F.P., Larson, J.K. and Carvan III, M.J., 2017. Developmental methylmercury exposure affects swimming behavior and foraging efficiency of yellow perch (Perca flavescens) Larvae. Acs Omega, 2(8), pp.4870-4877.

Muller, E.B., Nisbet, R.M. and Berkley, H.A., 2010. Sublethal toxicant effects with dynamic energy budget theory: model formulation. Ecotoxicology, 19, pp.48-60.

Müller, K., 1963. Diurnal rhythm in 'organic drift' of *Gammarus pulex*. Nature, 198(4882), pp.806-807.

Munns Jr, W.R., 2006. Assessing risks to wildlife populations from multiple stressors: overview of the problem and research needs. Ecology and Society, 11(1).

Munns Jr, W.R., Rea, A.W., Suter, G.W., Martin, L., Blake-Hedges, L., Crk, T., Davis, C., Ferreira, G., Jordan, S., Mahoney, M. and Barron, M.G., 2016. Ecosystem services as assessment endpoints for ecological risk assessment. Integrated environmental assessment and management, 12(3), pp.522-528.

Murphy, J.F. and Giller, P.S., 2000. Seasonal dynamics of macroinvertebrate assemblages in the benthos and associated with detritus packs in two low-order streams with different riparian vegetation. Freshwater Biology, 43(4), pp.617-631.

Murphy, C.A., Nisbet, R.M., Antczak, P., Garcia-Reyero, N., Gergs, A., Lika, K., Mathews, T., Muller, E.B., Nacci, D., Peace, A. and Remien, C.H., 2018. Incorporating suborganismal processes into dynamic energy budget models for ecological risk assessment. Integrated environmental assessment and management, 14(5), pp.615-624.

Naddy, R.B. and Klaine, S.J., 2001. Effect of pulse frequency and interval on the toxicity of chlorpyrifos to *Daphnia* magna. Chemosphere, 45(4-5), pp.497-506.

Naeem, S., 1998. Species redundancy and ecosystem reliability. Conservation biology, 12(1), pp.39-45.

Naeem, S., Chazdon, R., Duffy, J.E., Prager, C. and Worm, B., 2016. Biodiversity and human well-being: an essential link for sustainable development. Proceedings of the Royal Society B: Biological Sciences, 283(1844), p.20162091.

Natural Capital Coalition: Natural Capital Coalition. 2016. "Natural Capital Protocol". Available at: www.naturalcapitalcoalition.org/business-insights-pilot-testing-the-natural-capital-protocol.

Naylor, C., Pindar, L. and Calow, P., 1990. Inter-and intraspecific variation in sensitivity to toxins; the effects of acidity and zinc on the freshwater crustaceans *Asellus aquaticus* (L.) and *Gammarus pulex* (L.). Water research, 24(6), pp.757-762.

Newman, R.M. and Waters, T.F., 1984. Size-selective predation on *Gammarus* pseudolimnaeus by trout and sculpins. Ecology, 65(5), pp.1535-1545.

Nienstedt, K.M., Brock, T.C., van Wensem, J., Montforts, M., Hart, A., Aagaard, A., Alix, A., Boesten, J., Bopp, S.K., Brown, C. and Capri, E., 2012. Development of a framework based on an ecosystem services approach for deriving specific protection goals for environmental risk assessment of pesticides. Science of the Total Environment, 415, pp.31-38.

Nilsson, L.M., 1974. Energy budget of a laboratory population of *Gammarus pulex* (Amphipoda). Oikos, pp.35-42.

Nisbet, R.M., Muller, E.B., Brooks, A.J. and Hosseini, P., 1997. Models relating individual and population response to contaminants. Environmental Modeling & Assessment, 2, pp.7-12.

Nisbet, R.M., McCauley, E., Gurney, W.S., Murdoch, W.W. and Wood, S.N., 2004. Formulating and testing a partially specified dynamic energy budget model. *Ecology*, *85*(11), pp.3132-3139.

Nõges, P., Argillier, C., Borja, Á., Garmendia, J.M., Hanganu, J., Kodeš, V., Pletterbauer, F., Sagouis, A. and Birk, S., 2016. Quantified biotic and abiotic responses to multiple stress in freshwater, marine and ground waters. Science of the Total Environment, 540, pp.43-52.

Nyman, A.M., Hintermeister, A., Schirmer, K. and Ashauer, R., 2013. The insecticide imidacloprid causes mortality of the freshwater amphipod *Gammarus pulex* by interfering with feeding behavior. PloS one, 8(5), p.e62472.

O'Callaghan, I., Harrison, S., Fitzpatrick, D. and Sullivan, T., 2019. The freshwater isopod *Asellus aquaticus* as a model biomonitor of environmental pollution: A review. Chemosphere, 235, pp.498-509.

OECD (2004)a, Test No. 218: Sediment-Water Chironomid Toxicity Using Spiked Sediment, OECD Guidelines for the Testing of Chemicals, Section 2, OECD Publishing, Paris, https://doi.org/10.1787/9789264070264-en.

OECD (2004)b, Test No. 219: Sediment-Water Chironomid Toxicity Using Spiked Water, OECD Guidelines for the Testing of Chemicals, Section 2, OECD Publishing, Paris, https://doi.org/10.1787/9789264070288-en.

Office for National Statistics (ONS), released 25 January 2023, ONS website, statistical bulletin. Accessed on 30.08.24: https://www.ons.gov.uk/economy/environmentalaccounts/bulletins/uknaturalcapitalaccounts/2023

Oginah, S.A., Posthuma, L., Hauschild, M., Slootweg, J., Kosnik, M. and Fantke, P., 2023a. To split or not to split: Characterizing chemical pollution impacts in aquatic ecosystems with species sensitivity distributions for specific taxonomic groups. Environmental Science & Technology, 57(39), pp.14526-14538.

Oginah, S.A., Posthuma, L., Maltby, L., Hauschild, M. and Fantke, P., 2023b. Linking freshwater ecotoxicity to damage on ecosystem services in life cycle assessment. Environment International, 171, p.107705.

Oliver, T.H., Isaac, N.J., August, T.A., Woodcock, B.A., Roy, D.B. and Bullock, J.M., 2015. Declining resilience of ecosystem functions under biodiversity loss. Nature communications, 6(1), p.10122.

Oseid, D.M. and Smith, L.L., 1979. The effects of hydrogen cyanide on *Asellus commuais* and *Gammarus pseudolimnaeus* and changes in their competitive response when exposed simultaneously. Bulletin of Environmental Contamination and Toxicology, 21(1), pp.439-447.

Outhwaite, C.L., Gregory, R.D., Chandler, R.E., Collen, B. and Isaac, N.J., 2020. Complex long-term biodiversity change among invertebrates, bryophytes and lichens. Nature ecology & evolution, 4(3), pp.384-392.

Pastorok, R.A., Akçakaya, R., Regan, H., Ferson, S. and Bartell, S.M., 2003. Role of ecological modeling in risk assessment. Human and Ecological Risk Assessment, 9(4), pp.939-972.

Pastorok, R.A., Bartell, S.M., Ferson, S. and Ginzburg, L.R. eds., 2016. Ecological modeling in risk assessment: chemical effects on populations, ecosystems, and landscapes. CRC Press.

Pereira, C.M., Vlaeminck, K., Viaene, K. and De Schamphelaere, K.A., 2019. The unexpected absence of nickel effects on a *Daphnia* population at 3 temperatures is correctly predicted by a dynamic energy budget individual-based model. Environmental toxicology and chemistry, 38(7), pp.1423-1433.

Pereira, J.L. and Gonçalves, F., 2007. Effects of food availability on the acute and chronic toxicity of the insecticide methomyl to *Daphnia* spp. Science of the total environment, 386(1-3), pp.9-20.

Perrin, N. and Sibly, R.M., 1993. Dynamic models of energy allocation and investment. *Annual Review of Ecology and Systematics*, pp.379-410.

Persson, L., 1983. Food consumption and competition between age classes in a perch Perca fluviatilis population in a shallow eutrophic lake. Oikos, pp.197-207.

Persson, L., Carney Almroth, B.M., Collins, C.D., Cornell, S., De Wit, C.A., Diamond, M.L., Fantke, P., Hassellöv, M., MacLeod, M., Ryberg, M.W. and Søgaard Jørgensen, P., 2022. Outside the safe operating space of the planetary boundary for novel entities. Environmental science & technology, 56(3), pp.1510-1521.

Pestana, J.L., Novais, S.C., Lemos, M.F. and Soares, A.M., 2014. Cholinesterase activity in the caddisfly Sericostoma vittatum: Biochemical enzyme characterization and in vitro effects of insecticides and psychiatric drugs. Ecotoxicology and environmental safety, 104, pp.263-268.

Pestana, J.L.T., Alexander, A.C., Culp, J.M., Baird, D.J., Cessna, A.J. and Soares, A.M.V.M., 2009. Structural and functional responses of benthic invertebrates to imidacloprid in outdoor stream mesocosms. Environmental Pollution, 157(8-9), pp.2328-2334.

Peters, F., Lippe, M., Eguiguren, P. and Günter, S., 2023. Forest ecosystem services at landscape level–Why forest transition matters?. Forest Ecology and Management, 534, p.120782.

Peters, K., Bundschuh, M. and Schäfer, R.B., 2013. Review on the effects of toxicants on freshwater ecosystem functions. Environmental pollution, 180, pp.324-329.

Pilière, A.F.H., Verberk, W.C.E.P., Gräwe, M., Breure, A.M., Dyer, S.D., Posthuma, L., De Zwart, D., Huijbregts, M.A.J. and Schipper, A.M., 2016. On the importance of trait interrelationships for understanding environmental responses of stream macroinvertebrates. Freshwater biology, 61(2), pp.181-194.

Postaski, L.L., Capelli, G.M. and Chambers, R.M., 2013. Occurrence and distribution of the freshwater amphipods *Gammarus* pseudolimnaeus and *Gammarus* fasciatus in Southeastern Virginia. Northeastern Naturalist, 20(4), pp.609-623.

Postma, J.F., Buckert-de Jong, M.C., Staats, N. and Davids, C., 1994. Chronic toxicity of cadmium to Chironomus riparius (Diptera: Chironomidae) at different food levels. Archives of Environmental Contamination and Toxicology, 26, pp.143-148.

Posthuma, L., Suter II, G.W. and Traas, T.P. eds., 2001. Species sensitivity distributions in ecotoxicology.

Posthuma, L., van Gils, J., Zijp, M.C., van De Meent, D. and de Zwart, D., 2019. Species sensitivity distributions for use in environmental protection, assessment, and management of aquatic ecosystems for 12 386 chemicals. Environmental Toxicology and Chemistry, 38(4), pp.905-917.

Posthuma, L., Zijp, M.C., De Zwart, D., Van de Meent, D., Globevnik, L., Koprivsek, M., Focks, A., Van Gils, J. and Birk, S., 2020. Chemical pollution imposes limitations to the ecological status of European surface waters. Scientific reports, 10(1), p.14825.

Poteat, M.D., Jacobus, L.M. and Buchwalter, D.B., 2015. The importance of retaining a phylogenetic perspective in traits-based community analyses. Freshwater biology, 60(7), pp.1330-1339.

Potschin, M. and Haines-Young, R., 2016. Defining and measuring ecosystem services. In Routledge handbook of ecosystem services (pp. 25-44). Routledge.

Pouso, S., Borja, Á., Fleming, L.E., Gómez-Baggethun, E., White, M.P. and Uyarra, M.C., 2021. Contact with blue-green spaces during the COVID-19 pandemic lockdown beneficial for mental health. Science of The Total Environment, 756, p.143984.

Preston, B.L., 2002. Indirect effects in aquatic ecotoxicology: implications for ecological risk assessment. Environmental Management, 29(3), pp.311-323.

Pretty, J.L., Giberson, D.J. and Dobson, M., 2005. Resource dynamics and detritivore production in an acid stream. Freshwater

Preuss, T.G., Hammers-Wirtz, M., Hommen, U., Rubach, M.N. and Ratte, H.T., 2009. Development and validation of an individual based *Daphnia* magna population model: the influence of crowding on population dynamics. Ecological Modelling, 220(3), pp.310-329.

Public Health England. (2020). Improving access to greenspace. A new review for 2020.

Radchuk, V., De Laender, F., Van den Brink, P.J. and Grimm, V., 2016. Biodiversity and ecosystem functioning decoupled: invariant ecosystem functioning despite non-random reductions in consumer diversity. Oikos, 125(3), pp.424-433.

Raimondo, S. and Forbes, V.E., 2022. Moving beyond risk quotients: Advancing ecological risk assessment to reflect better, more robust and relevant methods. Ecologies, 3(2), pp.145-160.

Raimondo, S., Etterson, M., Pollesch, N., Garber, K., Kanarek, A., Lehmann, W., & Awkerman, J. (2018). A framework for linking population model development with ecological risk assessment objectives. Integrated environmental assessment and management, 14(3), 369-380.

Ramírez, A. and Gutiérrez-Fonseca, P.E., 2014. Functional feeding groups of aquatic insect families in Latin America: a critical analysis and review of existing literature. Revista de Biología Tropical, 62, pp.155-167.

Rask, M. and Hiisivuori, C., 1985. The predation on *Asellus aquaticus* (L.) by perch, Perca fluviatilis (L.), in a small forest lake. Hydrobiologia, 121, pp.27-33.

Reiber, L., Foit, K., Liess, M., Karaoglan, B., Wogram, J. and Duquesne, S., 2022. Close to reality? Micro-/mesocosm communities do not represent natural macroinvertebrate communities. Environmental Sciences Europe, 34(1), p.65.

Reiber, L., Foit, K., Liess, M., Karaoglan, B., Wogram, J. and Duquesne, S., 2022. Close to reality? Micro-/mesocosm communities do not represent natural macroinvertebrate communities. Environmental Sciences Europe, 34(1), p.65.

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J. and Smol, J.P., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological reviews, 94(3), pp.849-873.

Reinert, K.H., Giddings, J.M. and Judd, L., 2002. Effects analysis of time-varying or repeated exposures in aquatic ecological risk assessment of agrochemicals. Environmental Toxicology and Chemistry: An International Journal, 21(9), pp.1977-1992.

Resh, V.H., 2008. Which group is best? Attributes of different biological assemblages used in freshwater biomonitoring programs. Environmental Monitoring and Assessment, 138, pp.131-138.

Rico, A., Van den Brink, P.J., Gylstra, R., Focks, A. and Brock, T.C., 2016. Developing ecological scenarios for the prospective aquatic risk assessment of pesticides. Integrated environmental assessment and management, 12(3), pp.510-521.

Rittschof, D. and McClellan-Green, P., 2005. Molluscs as multidisciplinary models in environment toxicology. Marine pollution bulletin, 50(4), pp.369-373.

Robinson, A., Lahive, E., Short, S., Carter, H., Sleep, D., Pereira, G., Kille, P. and Spurgeon, D., 2021. Chemicals with increasingly complex modes of action result in greater variation in sensitivity between earthworm species. Environmental Pollution, 272, p.115914.

Rodrigues, A., Bordalo, M.D., Golovko, O., Koba, O., Barata, C., Soares, A.M. and Pestana, J.L., 2018. Combined effects of insecticide exposure and predation risk on freshwater detritivores. Ecotoxicology, 27(7), pp.794-802.

Roex, E.W., Van Gestel, C.A., Van Wezel, A.P. and Van Straalen, N.M., 2000. Ratios between acute aquatic toxicity and effects on population growth rates in relation to toxicant mode of action. Environmental Toxicology and Chemistry: An International Journal, 19(3), pp.685-693.

Rohr, J.R., Salice, C.J. and Nisbet, R.M., 2016. The pros and cons of ecological risk assessment based on data from different levels of biological organization. Critical Reviews in Toxicology, 46(9), pp.756-784.

Rohr, J.R., Salice, C.J. and Nisbet, R.M., 2017. Chemical safety must extend to ecosystems. Science, 356(6341), pp.917-917.

Romaniszyn, E.D., Hutchens Jr, J.J. and Bruce Wallace, J., 2007. Aquatic and terrestrial invertebrate drift in southern Appalachian Mountain streams: implications for trout food resources. Freshwater Biology, 52(1), pp.1-11.

Romero-Blanco, A. and Alonso, Á., 2022. Laboratory versus wild populations: the importance of population origin in aquatic ecotoxicology. Environmental Science and Pollution Research, 29(16), pp.22798-22808.

Root, R.B., 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecological monographs, 37(4), pp.317-350.

Rorije, E., Wassenaar, P.N., Slootweg, J., van Leeuwen, L., van Broekhuizen, F.A. and Posthuma, L., 2022. Characterization of ecotoxicological risks from unintentional mixture exposures calculated from European freshwater monitoring data: Forwarding prospective chemical risk management. Science of the Total Environment, 822, p.153385.

Rubach, M.N., Baird, D.J., Boerwinkel, M.C., Maund, S.J., Roessink, I. and Van den Brink, P.J., 2012. Species traits as predictors for intrinsic sensitivity of aquatic invertebrates to the insecticide chlorpyrifos. Ecotoxicology, 21, pp.2088-2101.

Rubio-Ríos, J., Pérez, J., Salinas, M.J., Fenoy, E., López-Rojo, N., Boyero, L. and Casas, J.J., 2021. Key plant species and detritivores drive diversity effects on instream leaf litter decomposition more than functional diversity: A microcosm study. Science of the Total Environment, 798, p.149266.

Rumschlag, S.L., Mahon, M.B., Hoverman, J.T., Raffel, T.R., Carrick, H.J., Hudson, P.J. and Rohr, J.R., 2020. Consistent effects of pesticides on community structure and ecosystem function in freshwater systems. Nature Communications, 11(1), p.6333.

Saaristo, M., Brodin, T., Balshine, S., Bertram, M.G., Brooks, B.W., Ehlman, S.M., McCallum, E.S., Sih, A., Sundin, J., Wong, B.B. and Arnold, K.E., 2018. Direct and indirect effects of chemical contaminants on the behaviour, ecology and evolution of wildlife. Proceedings of the Royal Society B, 285(1885), p.20181297.

Sánchez-Hernández, J., Gabler, H.M. and Amundsen, P.A., 2017. Prey diversity as a driver of resource partitioning between river-dwelling fish species. Ecology and Evolution, 7(7), pp.2058-2068.

Schäfer, R.B., Caquet, T., Siimes, K., Mueller, R., Lagadic, L. and Liess, M., 2007. Effects of pesticides on community structure and ecosystem functions in agricultural streams of three biogeographical regions in Europe. Science of the total environment, 382(2-3), pp.272-285.

Schäfer, R.B., Kühn, B., Malaj, E., König, A. and Gergs, R., 2016. Contribution of organic toxicants to multiple stress in river ecosystems. Freshwater Biology, 61(12), pp.2116-2128.

Scherer, C., Brennholt, N., Reifferscheid, G. and Wagner, M., 2017. Feeding type and development drive the ingestion of microplastics by freshwater invertebrates. Scientific reports, 7(1), pp.1-9.

Schindler, D.W., 1988. Effects of acid rain on freshwater ecosystems. Science, 239(4836), pp.149-157.

Schlief, J. and Mutz, M., 2006. Palatability of leaves conditioned in streams affected by mine drainage: a feeding experiment with *Gammarus pulex* (L.). Hydrobiologia, 563(1), pp.445-452.

Schmera, D., Heino, J. and Podani, J., 2022. Characterising functional strategies and trait space of freshwater macroinvertebrates. Scientific Reports, 12(1), p.12283.

Schmera, D., Podani, J., Heino, J., Erős, T. and Poff, N.L., 2015. A proposed unified terminology of species traits in stream ecology. Freshwater Science, 34(3), pp.823-830.

Schmitt-Jansen, M., Veit, U., Dudel, G. and Altenburger, R., 2008. An ecological perspective in aquatic ecotoxicology: Approaches and challenges. Basic and Applied Ecology, 9(4), pp.337-345.

Schoch CL, et al.,. NCBI Taxonomy: a comprehensive update on curation, resources and tools. Database (Oxford). 2020: baaa062.

Schoener, T.W., 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. science, 331(6016), pp.426-429.

Schuijt, L.M., Peng, F.J., van den Berg, S.J., Dingemans, M.M. and Van den Brink, P.J., 2021. (Eco) toxicological tests for assessing impacts of chemical stress to aquatic ecosystems: facts, challenges, and future. Science of the total environment, 795, p.148776.

Schulz, R., 2004. Field studies on exposure, effects, and risk mitigation of aquatic nonpoint-source insecticide pollution: A review. Journal of environmental quality, 33(2), pp.419-448.

Schunck, F. and Liess, M., 2022. Time between sequential exposures to multiple stress turns antagonism into synergism. Environmental Science & Technology, 56(20), pp.14660-14667.

Schunck, F. and Liess, M., 2024. Ultra-low esfenvalerate exposure may disrupt interspecific competition. Science of The Total Environment, 906, p.167455.

Seyoum, A., Kharlyngdoh, J.B., Paylar, B. and Olsson, P.E., 2021. Sublethal effects of DBE-DBCH diastereomers on physiology, behavior, and gene expression of *Daphnia* magna. Environmental pollution, 284, p.117091.

Shahid, N., Becker, J.M., Krauss, M., Brack, W. and Liess, M., 2018. Adaptation of *Gammarus pulex* to agricultural insecticide contamination in streams. Science of the Total Environment, 621, pp.479-485.

Sherborne, N., Galic, N. and Ashauer, R., 2020. Sublethal effect modelling for environmental risk assessment of chemicals: Problem definition, model variants, application and challenges. Science of the Total Environment, 745, p.141027.

Sherborne, N., Jager, T., Goussen, B., Trijau, M. and Ashauer, R., 2022. The application and limitations of exposure multiplication factors in sublethal effect modelling. Scientific Reports, 12(1), p.6031.

Sibly, R.M. and Hone, J., 2002. Population growth rate and its determinants: an overview. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 357(1425), pp.1153-1170.

Silva, C.O., Novais, S.C., Alves, L.M., Soares, A.M., Barata, C. and Lemos, M.F., 2019. Linking cholinesterase inhibition with behavioural changes in the sea snail Gibbula umbilicalis: Effects of the organophosphate pesticide chlorpyrifos. Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology, 225, p.108570.

Simmons, B.I., Blyth, P.S., Blanchard, J.L., Clegg, T., Delmas, E., Garnier, A., Griffiths, C.A., Jacob, U., Pennekamp, F., Petchey, O.L. and Poisot, T., 2021. Refocusing multiple stressor research around the targets and scales of ecological impacts. Nature Ecology & Evolution, 5(11), pp.1478-1489.

Smith, A.C., Harrison, P.A., Soba, M.P., Archaux, F., Blicharska, M., Egoh, B.N., Erős, T., Domenech, N.F., György, Á.I., Haines-Young, R. and Li, S., 2017. How natural capital delivers ecosystem services: A typology derived from a systematic review. Ecosystem Services, 26, pp.111-126.

Soares, S., Moreira, S., Andrade, S., Guilhermino, L. and Ribeiro, R., 2005. Freshwater-saltwater interface and estuarine sediment in situ assays based on post-exposure feeding of chironomids and polychaetes. Estuaries, 28, pp.314-319.

Soga, M. and Gaston, K.J., 2016. Extinction of experience: the loss of human–nature interactions. Frontiers in Ecology and the Environment, 14(2), pp.94-101.

Sokolova, I.M., Frederich, M., Bagwe, R., Lannig, G. and Sukhotin, A.A., 2012. Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. Marine environmental research, 79, pp.1-15.

Sousa, T., Domingos, T., Poggiale, J.C. and Kooijman, S.A.L.M., 2010. Dynamic energy budget theory restores coherence in biology. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1557), pp.3413-3428.

Spaak, J.W., Baert, J.M., Baird, D.J., Eisenhauer, N., Maltby, L., Pomati, F., Radchuk, V., Rohr, J.R., Van den Brink, P.J. and De Laender, F., 2017. Shifts of community composition and population density substantially affect ecosystem function despite invariant richness. Ecology Letters, 20(10), pp.1315-1324.

Stanley, D.A., Garratt, M.P., Wickens, J.B., Wickens, V.J., Potts, S.G. and Raine, N.E., 2015. Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. Nature, 528(7583), pp.548-550.

Stark, J.D., 2005. How closely do acute lethal concentration estimates predict effects of toxicants on populations?. Integrated Environmental Assessment and Management: An International Journal, 1(2), pp.109-113.

Steel, E.A., 1961, July. Some observations on the life history of *Asellus aquaticus* (L.) and *Asellus meridianus Racovitza* (Crustacea: Isopoda). In Proceedings of the Zoological Society of London (Vol. 137, No. 1, pp. 71-87). Oxford, UK: Blackwell Publishing Ltd.

Stendera, S., Adrian, R., Bonada, N., Cañedo-Argüelles, M., Hugueny, B., Januschke, K., Pletterbauer, F. and Hering, D., 2012. Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: a review. Hydrobiologia, 696, pp.1-28.

Stock, S., Bu, F., Fancourt, D. and Mak, H.W., 2022. Longitudinal associations between going outdoors and mental health and wellbeing during a COVID-19 lockdown in the UK. Scientific Reports, 12(1), p.10580.

Straub, L., Strobl, V. and Neumann, P., 2020. The need for an evolutionary approach to ecotoxicology. Nature ecology & evolution, 4(7), pp.895-895.

Sutcliffe, D.W., 1993. Reproduction in *Gammarus* (Crustacea, Amphipoda): female strategies.

Sutcliffe, D.W., Carrick, T.R. and Willoughby, L.G., 1981. Effects of diet, body size, age and temperature on growth rates in the amphipod *Gammarus pulex*. Freshwater biology, 11(2), pp.183-214.

Swan, C.M. and Palmer, M.A., 2004. Leaf diversity alters litter breakdown in a Piedmont stream. Journal of the North American Benthological Society, 23(1), pp.15-28.

Swan, C.M. and Palmer, M.A., 2006. Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. Oecologia, 147, pp.469-478.

Tachet H., Bournaud M., Richoux P. & Usseglio-Polatera P. (2010): Invertébrés d'eau douce - systématique, biologie, écologie. CNRS Editions, Paris. Accessed through www.freshwaterecology.info - the taxa and autecology database for freshwater organisms, version 8.0 (accessed on 25.11.2021).

Takano, T., Nakamura, K. and Watanabe, M., 2002. Urban residential environments and senior citizens' longevity in megacity areas: the importance of walkable green spaces. Journal of Epidemiology & Community Health, 56(12), pp.913-918.

Tallis, H. and Polasky, S., 2009. Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. Annals of the New York Academy of Sciences, 1162(1), pp.265-283.

TEEB, 2010. TEEB, the economics of ecosystems and biodiversity: Ecological and economic foundations (Edited by Kumar, P.).

Thorpe, J.E., Miles, M.S. and Keay, D.S., 1984. Developmental rate, fecundity and egg size in Atlantic salmon, Salmo salar L. Aquaculture, 43(1-3), pp.289-305.

Tickner, D., Opperman, J.J., Abell, R., Acreman, M., Arthington, A.H., Bunn, S.E., Cooke, S.J., Dalton, J., Darwall, W., Edwards, G. and Harrison, I., 2020. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. BioScience, 70(4), pp.330-342.

Tilman, D., 1982. Resource competition and community structure (No. 17). Princeton university press.

Tilman, D., Isbell, F. and Cowles, J.M., 2014. Biodiversity and ecosystem functioning. Annual review of ecology, evolution, and systematics, 45(1), pp.471-493.

Topping, C.J., Dalkvist, T., Forbes, V.E., Grimm, V. and Sibly, R.M., 2009. The potential for the use of agent-based models in ecotoxicology. Ecotoxicology Modeling, pp.205-235.

Traas, T.P., Janse, J.H., Van den Brink, P.J., Brock, T.C. and Aldenberg, T., 2004. A freshwater food web model for the combined effects of nutrients and insecticide stress and subsequent recovery. Environmental Toxicology and Chemistry: An International Journal, 23(2), pp.521-529.

Tyson, J.T. and Knight, R.L., 2001. Response of yellow perch to changes in the benthic invertebrate community of western Lake Erie. Transactions of the American Fisheries Society, 130(5), pp.766-782.

Vahdati, A.R., 2019. Agents. jl: Agent-based modeling framework in Julia. Journal of Open Source Software, 4(42), p.1611.

Van Allen, B., Jones, N., Gilbert, B., Carscadden, K. and Germain, R., 2021. Maternal effects and the outcome of interspecific competition. Ecology and Evolution, 11(12), pp.7544-7556.

Van den Berg, S.J., Baveco, H., Butler, E., De Laender, F., Focks, A., Franco, A., Rendal, C. and Van den Brink, P.J., 2019. Modeling the sensitivity of aquatic macroinvertebrates to chemicals using traits. Environmental science & technology, 53(10), pp.6025-6034.

Van den Berg, S.J., Rendal, C., Focks, A., Butler, E., Peeters, E.T., De Laender, F. and Van den Brink, P.J., 2020. Potential impact of chemical stress on freshwater invertebrates: A sensitivity assessment on continental and national scale based on distribution patterns, biological traits, and relatedness. Science of the Total environment, 731, p.139150.

Van den Brink, P.J., Alix, A., Thorbek, P., Baveco, H., Agatz, A., Faber, J.H., Brown, A.R., Marshall, S. and Maltby, L., 2021. The use of ecological models to assess the effects of a plant protection product on ecosystem services provided by an orchard. Science of the Total Environment, 798, p.149329.

Van den Brink, P.J., Baveco, J.M., Verboom, J. and Heimbach, F., 2007. An individual-based approach to model spatial population dynamics of invertebrates in aquatic ecosystems after pesticide contamination. Environmental Toxicology and Chemistry: An International Journal, 26(10), pp.2226-2236.

Van den Brink, P.J., Klein, S.L. and Rico, A., 2017. Interaction between stress induced by competition, predation, and an insecticide on the response of aquatic invertebrates. Environmental toxicology and chemistry, 36(9), pp.2485-2492.

Van den Brink, P.J., Sibley, P.K., Ratte, H.T., Baird, D.J., Nabholz, J.V. and Sanderson, H., 2008. Extrapolation of effects measures across levels of biological organization in ecological risk assessment. Extrapolation Practice for Ecotoxicological Effect Characterization of Chemicals, SETAC Press & CRC Press, Boca Raton, Fl, USA, pp.105-133.

van der Geest, H.G., Greve, G.D., Kroon, A., Kuijl, S., Kraak, M.H.S. and Admiraal, W., 2000. Sensitivity of characteristic riverine insects, the caddisfly Cyrnus trimaculatus and the mayfly Ephoron virgo, to copper and diazinon. Environmental Pollution, 109(2), pp.177-182.

van der Linden, P., Shinn, C., Moreira-Santos, M., Oehlmann, J., Ribeiro, R. and Müller, R., 2019. Aquatic mesocosms exposed to a fungicide in warm and cold temperate European climate zones: Long-term macroinvertebrate response. Science of The Total Environment, 681, pp.133-142.

Van Dievel, M., Janssens, L. and Stoks, R., 2020. Effects of pesticide exposure and predation risk on nutrient cycling and primary production. Science of The Total Environment, 705, p.135880.

Varpe, Ø., 2017. Life history adaptations to seasonality. *Integrative and comparative biology*, *57*(5), pp.943-960.

Vaugeois, M., Venturelli, P.A., Hummel, S.L., Accolla, C. and Forbes, V.E., 2020. Population context matters: predicting the effects of metabolic stress mediated by food availability and predation with an agent-and energy budget-based model. Ecological modelling, 416, p.108903.

Verheyen, J. and Stoks, R., 2023. Thermal performance curves in a polluted world: too cold and too hot temperatures synergistically increase pesticide toxicity. Environmental Science & Technology, 57(8), pp.3270-3279.

Viaene, K.P., De Laender, F., Rico, A., Van den Brink, P.J., Di Guardo, A., Morselli, M. and Janssen, C.R., 2015. Species interactions and chemical stress: Combined effects of intraspecific and interspecific interactions and pyrene on *Daphnia* magna population dynamics. Environmental toxicology and chemistry, 34(8), pp.1751-1759.

Vlaeminck, K., Viaene, K.P., Van Sprang, P., Baken, S. and De Schamphelaere, K.A., 2019. The use of mechanistic population models in metal risk assessment: Combined effects of copper and food source on Lymnaea stagnalis populations. Environmental toxicology and chemistry, 38(5), pp.1104-1119.

Vlaeminck, K., Viaene, K.P., Van Sprang, P. and De Schamphelaere, K.A., 2021. Development and validation of a mixture toxicity implementation in the dynamic energy budget–individual-based model: Effects of copper and zinc on *Daphnia* magna populations. Environmental Toxicology and Chemistry, 40(2), pp.513-527.

Vlaeminck, K., Viaene, K.P., Van Sprang, P. and De Schamphelaere, K.A., 2022. Predicting Combined Effects of Chemical Stressors: Population-Level Effects of Organic Chemical Mixtures with a Dynamic Energy Budget Individual-Based Model. Environmental Toxicology and Chemistry, 41(9), pp.2240-2258.

Volterra, V., 1926. Fluctuations in the abundance of a species considered mathematically. Nature, 118(2972), pp.558-560.

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R. and Davies, P., 2010. Global threats to human water security and river biodiversity. nature, 467(7315), pp.555-561.

Wallace, J.B. and Webster, J.R., 1996. The role of macroinvertebrates in stream ecosystem function. Annual review of entomology, 41(1), pp.115-139.

Wallace, J.B., Eggert, S.L., Meyer, J.L. and Webster, J.R., 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science, 277(5322), pp.102-104.

Wallace, J.B., Eggert, S.L., Meyer, J.L. and Webster, J.R., 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological monographs, 69(4), pp.409-442.

Wallace, J.B., Webster, J.R. and Cuffney, T.F., 1982. Stream detritus dynamics: regulation by invertebrate consumers. Oecologia, 53, pp.197-200.

Weir, S.M. and Salice, C.J., 2021. Investigating potential toxic effects of pollutants on population growth rates and probability of extinction for a representative squamate. Ecotoxicology, 30, pp.175-186.

Weir, S.M., Suski, J.G. and Salice, C.J., 2010. Ecological risk of anthropogenic pollutants to reptiles: evaluating assumptions of sensitivity and exposure. Environmental Pollution, 158(12), pp.3596-3606.

Weitere, M., Altenburger, R., Anlanger, C., Baborowski, M., Bärlund, I., Beckers, L.M., Borchardt, D., Brack, W., Brase, L., Busch, W. and Chatzinotas, A., 2021. Disentangling multiple chemical and non-chemical stressors in a lotic ecosystem using a longitudinal approach. Science of the Total Environment, 769, p.144324.

Weltje, L., Rufli, H., Heimbach, F., Wheeler, J., Vervliet-Scheebaum, M. and Hamer, M., 2010. The chironomid acute toxicity test: development of a new test system. Integrated Environmental Assessment and Management: An International Journal, 6(2), pp.301-307.

Welton, J.S., 1979. Life-history and production of the amphipod *Gammarus pulex* in a Dorset chalk stream. Freshwater Biology, 9(3), pp.263-275.

Werner, E.E. and Hall, D.J., 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology, 55(5), pp.1042-1052.

Whelan, M.J., Linstead, C., Worrall, F., Ormerod, S.J., Durance, I., Johnson, A.C., Johnson, D., Owen, M., Wiik, E., Howden, N.J. and Burt, T.P., 2022. Is water quality in British rivers "better than at any time since the end of the Industrial Revolution"?. Science of the Total Environment, 843, p.157014.

Whitehurst, I.T., 1991. The effects of sampling techniques on the *Gammarus*: *Asellus* ratio. Water research, 25(6), pp.745-748.

Whittaker, R.H. and Niering, W.A., 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. Ecology, 56(4), pp.771-790.Wilkinson, J.L., Boxall, A.B., Kolpin, D.W., Leung, K.M., Lai, R.W., Galbán-Malagón, C., Adell, A.D., Mondon, J., Metian, M., Marchant, R.A. and Bouzas-Monroy, A., 2022. Pharmaceutical pollution of the world's rivers. Proceedings of the National Academy of Sciences, 119(8), p.e2113947119.

Wilson, J.J., Trott, M., Tully, M.A., Lindsay, R.K., Fossey, M., Godier-McBard, L., Butler, L.T., Torrance, A. and Smith, L., 2023. Mental health and recreational angling in UK adult males: a cross-sectional study. Epidemiologia, 4(3), pp.298-308.

Wilzbach, M.A., Cummins, K.W. and Hall, J.D., 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology, 67(4), pp.898-911.

Winfield, I.J., 2016. Recreational fisheries in the UK: natural capital, ecosystem services, threats, and management. Fisheries Science, 82, pp.203-212.

Wong, B.B. and Candolin, U., 2015. Behavioral responses to changing environments. Behavioral Ecology, 26(3), pp.665-673.

Woodward, G., Gessner, M.O., Giller, P.S., Gulis, V., Hladyz, S., Lecerf, A., Malmqvist, B., McKie, B.G., Tiegs, S.D., Cariss, H. and Dobson, M., 2012. Continental-scale effects of nutrient pollution on stream ecosystem functioning. Science, 336(6087), pp.1438-1440.

Worischka, S., Schmidt, S.I., Hellmann, C. and Winkelmann, C., 2015. Selective predation by benthivorous fish on stream macroinvertebrates–The role of prey traits and prey abundance. Limnologica, 52, pp.41-50.

WWF (2020) Living Planet Report 2020 -Bending the curve of biodiversity loss.Almond, R.E.A., Grooten M. and Petersen, T. (Eds). WWF, Gland, Switzerland.

Yachi, S. and Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proceedings of the National Academy of Sciences, 96(4), pp.1463-1468.

Yardy, L. and Callaghan, A., 2020. What the fluff is this?-*Gammarus pulex* prefer food sources without plastic microfibers. Science of the total environment, 715, p.136815.

Young, R.G., Matthaei, C.D. and Townsend, C.R., 2008. Organic matter breakdown and ecosystem metabolism: functional indicators for assessing river ecosystem health. Journal of the North American Benthological Society, 27(3), pp.605-625.

Zeeshan, M., Murugadas, A., Ghaskadbi, S., Ramaswamy, B.R. and Akbarsha, M.A., 2017. Ecotoxicological assessment of cobalt using Hydra model: ROS, oxidative stress, DNA damage, cell cycle arrest, and apoptosis as mechanisms of toxicity. Environmental pollution, 224, pp.54-69.

Zhao, Q., De Laender, F. and Van den Brink, P.J., 2020. Community composition modifies direct and indirect effects of pesticides in freshwater food webs. Science of the total environment, 739, p.139531.

Zhao, Q., Van den Brink, P.J., Xu, C., Wang, S., Clark, A.T., Karakoç, C., Sugihara, G., Widdicombe, C.E., Atkinson, A., Matsuzaki, S.I.S. and Shinohara, R., 2023. Relationships of temperature and biodiversity with stability of natural aquatic food webs. Nature Communications, 14(1), p.3507.

Zubrod, J.P., Bundschuh, M. and Schulz, R., 2010. Effects of subchronic fungicide exposure on the energy processing of *Gammarus* fossarum (Crustacea; Amphipoda). Ecotoxicology and Environmental Safety, 73(7), pp.1674-1680.

Zubrod, J.P., Bundschuh, M., Feckler, A., Englert, D. and Schulz, R., 2011. Ecotoxicological impact of the fungicide tebuconazole on an aquatic decomposer-detritivore system. Environmental Toxicology and Chemistry, 30(12), pp.2718-2724.

Zubrod, J.P., Baudy, P., Schulz, R. and Bundschuh, M., 2014. Effects of current-use fungicides and their mixtures on the feeding and survival of the key shredder *Gammarus fossarum*. Aquatic toxicology, 150, pp.133-143.

Zubrod, J.P., Englert, D., Rosenfeldt, R.R., Wolfram, J., Lüderwald, S., Wallace, D., Schnetzer, N., Schulz, R. and Bundschuh, M., 2015a. The relative importance of diet-related and waterborne effects of copper for a leaf-shredding invertebrate. Environmental Pollution, 205, pp.16-22.

Zubrod, J.P., Englert, D., Wolfram, J., Wallace, D., Schnetzer, N., Baudy, P., Konschak, M., Schulz, R. and Bundschuh, M., 2015b. Waterborne toxicity and diet-related effects of fungicides in the key leaf shredder *Gammarus fossarum* (Crustacea: Amphipoda). Aquatic Toxicology, 169, pp.105-112.

Zubrod, J.P., Englert, D., Luderwald, S., Poganiuch, S., Schulz, R. and Bundschuh, M., 2017. History matters: pre-exposure to wastewater enhances pesticide toxicity in invertebrates. Environmental Science & Technology, 51(16), pp.9280-9287.

Zubrod, J.P., Bundschuh, M., Arts, G., Brühl, C.A., Imfeld, G., Knäbel, A., Payraudeau, S., Rasmussen, J.J., Rohr, J., Scharmüller, A. and Smalling, K., 2019. Fungicides: an overlooked pesticide class?. Environmental science & technology, 53(7), pp.3347-3365.

Appendices

Appendix for Chapter 2

Table A2.1: Search parameters and results of search for feeding assays in the US Environmental Protection Agency ECOTOX database (conducted on 21.12.2022)

Search Parameters

Category	Parameters	Value
Habitat	Aquatic	Aquatic
Chemicals		All
Effect Measurements	Behavior Group	Avoidance
		Behavior
		Feeding Behavior
Species	Animals	Insects/Spiders
		Other Invertebrates
		Crustaceans
		Molluscs
		Worms
Test Conditions	Exposure Media	Water - Fresh Water
	Test Locations	Lab

Results

Filter	No. Endpoints	No. Studies	Endpoints	1 endpoint / chemical / species / study
Aquatic-Export	4991	641		
FeedingEndpoints+ExposureType	606	94	321	212

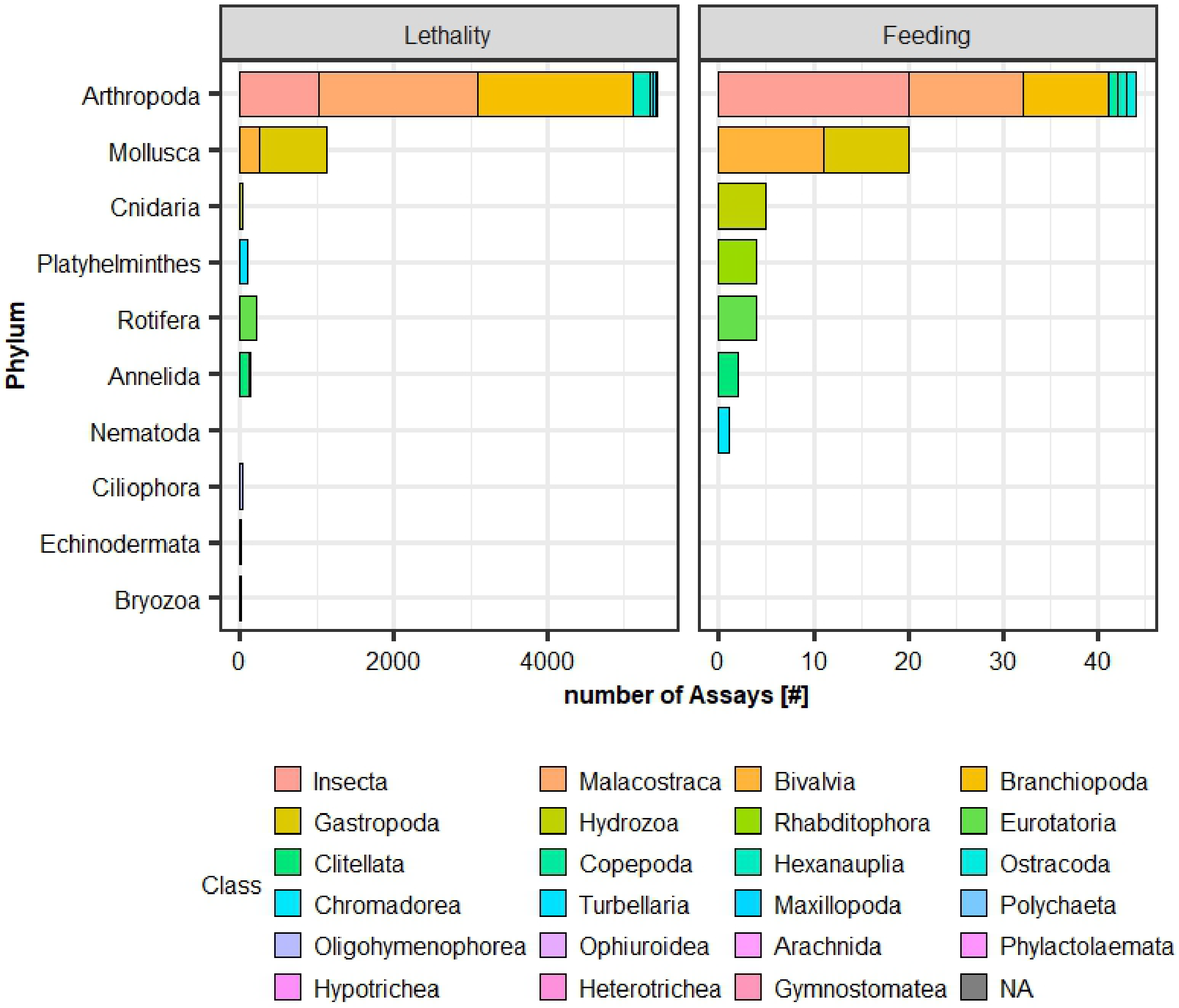


Figure A2.0.1: Count of assays per taxonomic group in the feeding (left) and lethality (right) datasets. Colours represent the Class.

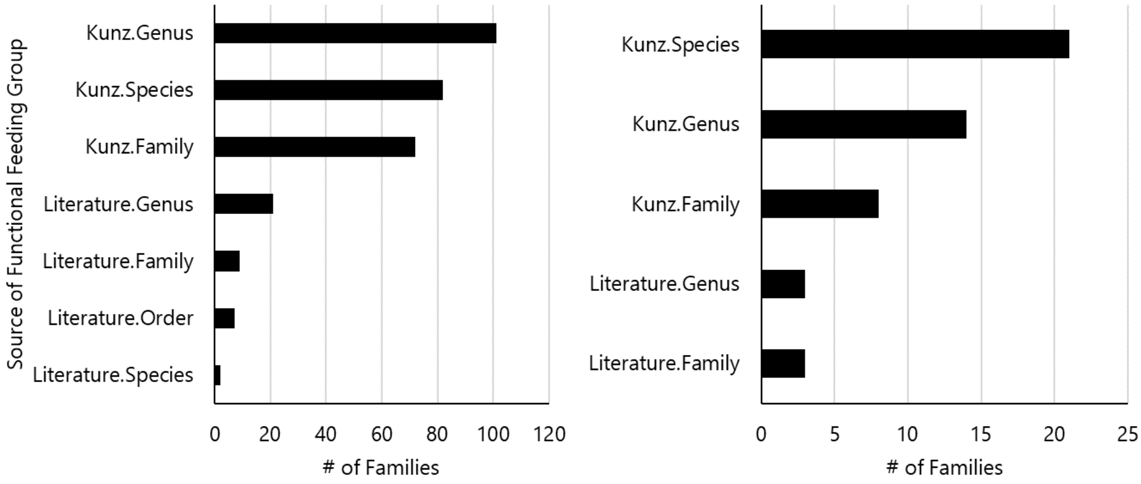


Figure A2.0.2: Functional feeding groups (FFGs) were assigned to species within families in the lethality (Left) and Feeding (Right) datasets. This figure represents the number of families assigned per source of FFG information.

Table A2.2: The taxonomic distribution of lethality data within taxonomic levels (phylum, class, and order) for each functional feeding group and then across all available data (Total). Values reflect the proportion of available for that taxonomic group within the greater taxonomic level (i.e. across classes within a phylum, across orders within a class)

Taxa	Filterer	Gatherer	Herbivore	Predator	Shredder	Grand Total
Annelida		**4.5**		**3.8**		**1.6**
Clitellata		**78.7**		**70.2**		**75.4**
Arhynchobdellida				90.9		32.6
Lumbriculida		100.0				64.1
Rhynchobdellida				9.1		3.3
Polychaeta		**21.3**		**29.8**		**24.6**
Amphinomida		25.0				13.3
Phyllodocida		31.3		100.0		63.3
uncertain order		43.8				23.3
Arthropoda	**84.6**	**90.3**	**36.8**	**86.3**	**91.1**	**79.1**
Arachnida				**1.3**		**0.2**
Sarcoptiformes				7.1		7.1
Trombidiformes				92.9		92.9
Branchiopoda	**62.2**	**0.1**				**21.3**
Anostraca	15.8					15.8
Diplostraca	84.2					84.1
Notostraca		100.0				0.1
Hexanauplia	**8.6**			**4.8**		**3.8**
Cyclopoida	35.4			100.0		49.8
Harpacticoida	56.4					43.8
Sessilia	8.3					6.4
Insecta	**4.1**	**25.9**	**41.9**	**21.6**	**17.1**	**17.5**
Coleoptera			8.0	14.2	5.2	5.4
Diptera	62.8	75.3	20.6	22.4	22.7	44.5
Ephemeroptera	20.9	16.3	23.1	5.6	2.3	13.4
Hemiptera	12.8	4.3	7.0	19.4		8.0
Hymenoptera				0.4		0.1
Lepidoptera				0.9		0.2
Megaloptera				3.0		0.6
Odonata				14.2		3.1
Plecoptera		4.1	40.2	18.5	69.2	23.9
Trichoptera	3.5		1.0	1.3	0.6	0.8
Malacostraca	**21.1**	**74.0**	**58.1**	**72.3**	**82.9**	**55.8**
Amphipoda	8.3	31.9	0.4	5.9	52.8	25.5
Decapoda	14.1	29.2	95.7	49.4	37.6	39.1
Isopoda		7.9	4.0		9.6	5.2
Mysida	77.6	31.0		44.7		30.2
Maxillopoda	**2.5**					**0.8**
Calanoida	100.0					100.0

Ostracoda	**1.6**					**0.5**
Podocopida	100.0					100.0
Bryozoa	**0.5**					**0.2**
Phylactolaemata	**100.0**					**100.0**
Plumatellida	100.0					100.0
Ciliophora	**1.1**					**0.4**
Gymnostomatea	**3.6**					**3.6**
Pleurostomatida	100.0					100.0
Heterotrichea	**14.3**					**14.3**
Heterotrichida	100.0					100.0
Hypotrichea	**21.4**					**21.4**
Euplotida	100.0					100.0
Oligohymenophorea	**60.7**					**60.7**
Hymenostomatida	52.9					52.9
Peritrichida	47.1					47.1
Cnidaria				**2.5**		**0.4**
Hydrozoa				**100.0**		**100.0**
Anthoathecata				100.0		100.0
Echinodermata				**0.8**		**0.1**
Ophiuroidea				**100.0**		**100.0**
Amphilepidida				100.0		100.0
Mollusca	**7.5**	**1.1**	**63.2**		**8.9**	**14.3**
Bivalvia	**100.0**	**5.3**				**16.8**
Mytiloida	33.7					33.5
Unionoida	44.9					44.7
Venerida	21.4	100.0				21.8
Gastropoda		**94.7**	**100.0**		**100.0**	**83.2**
Architaenioglossa			19.7			17.3
Hygrophila		22.2	61.1		100.0	64.4
Littorinimorpha		16.7	0.6			0.9
Neogastropoda			0.9			0.8
Pleurotomariida			0.2			0.2
Sorbeoconcha		61.1	17.5			16.5
Platyhelminthes		**4.1**		**6.6**		**1.9**
Turbellaria		**100.0**		**100.0**		**100.0**
Rhabdocoela				1.2		0.7
Tricladida		100.0		98.8		99.3
Rotifera	**6.2**					**2.0**
Eurotatoria	**100.0**					**100.0**
Bdelloidea	4.5					4.5
Ploima	95.5					95.5

Table A2.3: The taxonomic distribution of feeding data within taxonomic levels (phylum, class, and order) for each functional feeding group and then across all available data (Total). Values reflect the proportion of available for that taxonomic group within the greater taxonomic level (i.e. across classes within a phylum, across orders within a class)

Taxonomic Group	Filterer	Gatherer	Herbivore	Predator	Shredder	Grand Total
Annelida		**28.6**				**3.1**
Clitellata		**100.0**				**100.0**
Tubificida		100.0				100.0
Naididae		100.0				100.0
Arthropoda	**39.4**	**71.4**		**58.3**	**88.9**	**50.8**
Branchiopoda	**61.5**					**24.2**
Diplostraca	100.0					100.0
Daphniidae	100.0					100.0
Insecta	**7.7**			**57.1**		**15.2**
Diptera	100.0					20.0
Chironomidae	100.0					100.0
Hemiptera				25.0		20.0
Belostomatidae				100.0		100.0
Odonata				75.0		60.0
Coenagrionidae				33.3		33.3
Libellulidae				66.7		66.7
Malacostraca	**23.1**	**100.0**		**42.9**	**100.0**	**57.6**
Amphipoda	100.0	60.0		100.0	75.0	78.9
Gammaridae	100.0	100.0		100.0	100.0	100.0
Decapoda		40.0			25.0	21.1
Atyidae					100.0	50.0
Palaemonidae		100.0				50.0
Ostracoda	**7.7**					**3.0**
Podocopida	100.0					100.0
Cyprididae	100.0					100.0
Cnidaria				**33.3**		**6.2**
Hydrozoa				**100.0**		**100.0**
Anthoathecata				100.0		100.0
Hydridae				100.0		100.0
Mollusca	**36.4**		**100.0**		**11.1**	**26.2**
Bivalvia	**100.0**					**70.6**
Myida	25.0					25.0
Dreissenidae	100.0					100.0
Unionida	50.0					50.0
Unionidae	100.0					100.0
Venerida	25.0					25.0
Cyrenidae	100.0					100.0
Gastropoda			**100.0**		**100.0**	**29.4**
Hygrophilla			100.0		100.0	100.0
Lymnaeidae			75.0			60.0
Planorbidae			25.0		100.0	40.0
Platyhelminthes				**8.3**		**1.5**

Rhabditophora				**100.0**		**100.0**
Tricladida				100.0		100.0
Dugesiidae				100.0		100.0
Rotifera	**24.2**					**12.3**
Eurotatoria	**100.0**					**100.0**
Philodinida	50.0					50.0
Philodinidae	100.0					100.0
Ploima	50.0					50.0
Brachionidae	100.0					100.0
Grand Total	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**

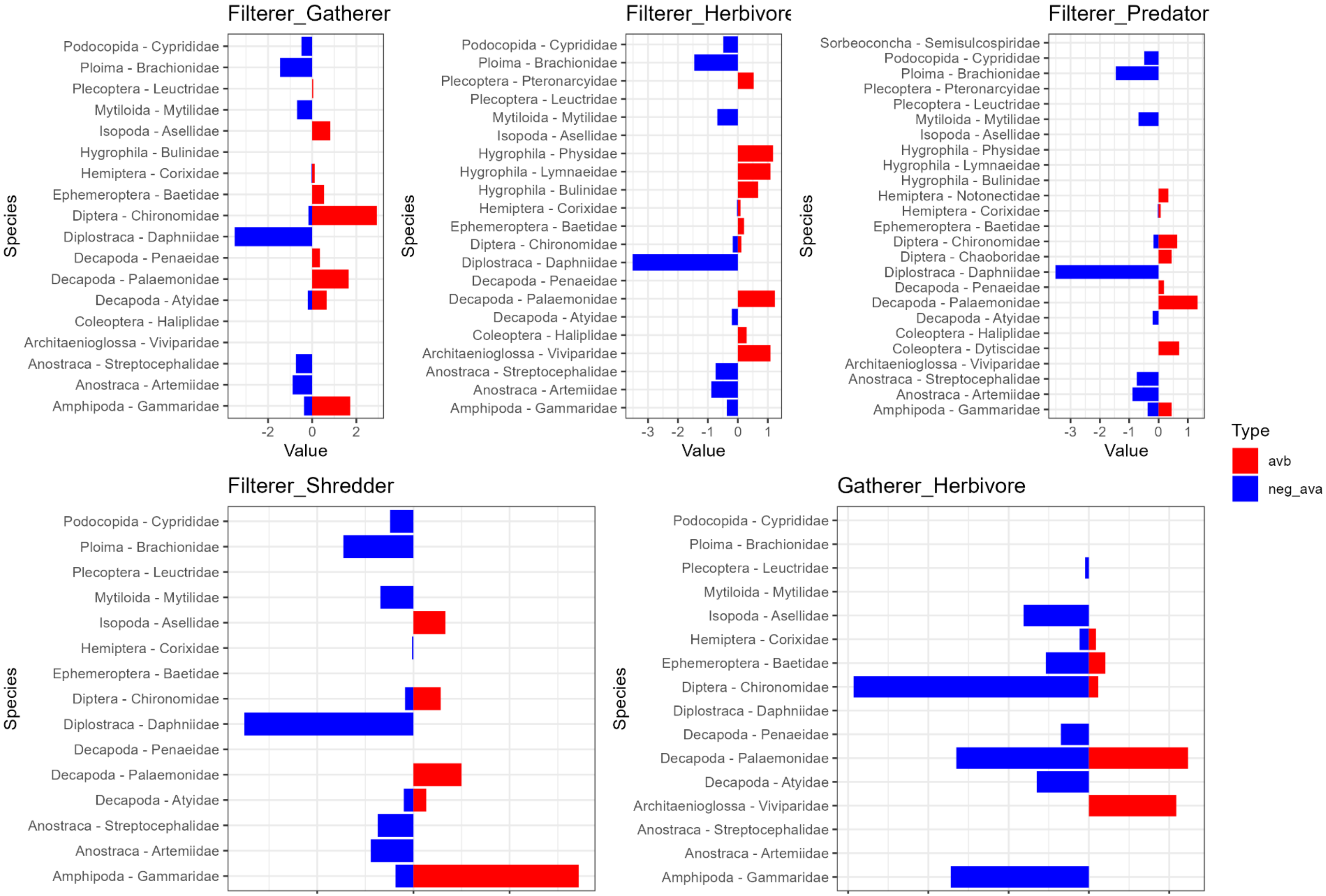


Figure A2.0.3: SIMPER analysis showing the taxonomic similarity of functional feeding group used in the analysis of differences in sensitivity of FFGs for 48 chemicals using acute LC50 from lethality dataset in Oginah et al.2023) pt1.

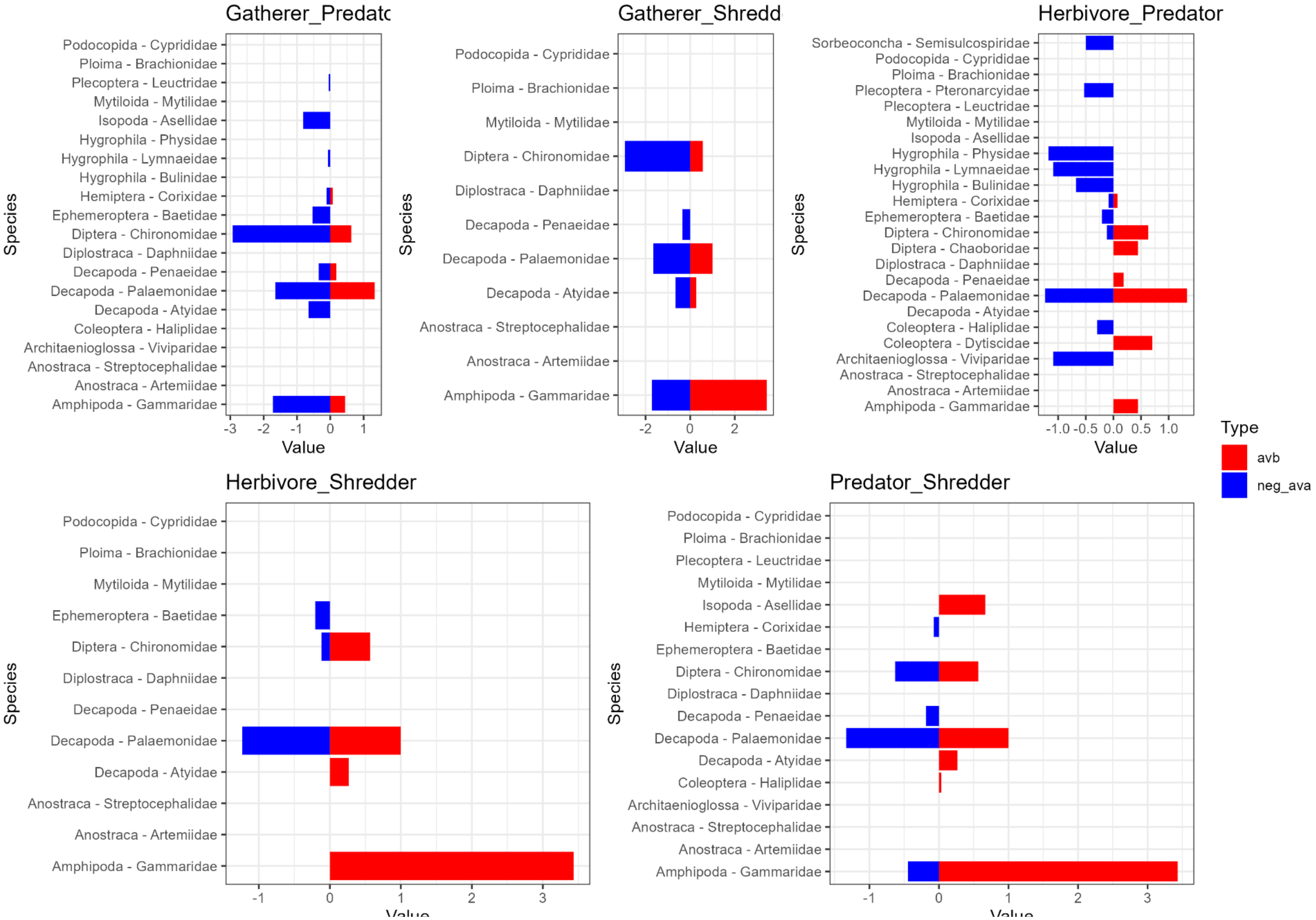


Figure A2.0.4: SIMPER analysis showing the taxonomic similarity of functional feeding group used in the analysis of differences in sensitivity of FFGs for 48 chemicals using acute LC50 from lethality dataset in Oginah et al.2023) pt2

Table A2.4: Results of the test for differences between LC_{50}s from functional feeding groups (FFGs) for 48 chemicals using the protocol of Oginah et al.,(2023). Chemicals that revealed differences in sensitivity between FFGs are highlighted in bold in the "Test column" and the test used to derive its significance also stated

Chemical mode of action	Chemical Name	No. Species	p value	Df	F Value	Test
AChE inhibition	Carbaryl	69	5.67E-04	4	5.675	**ANOVA**
	Diazinon	38	3.08E-02	3	3.401	**ANOVA**
	Fenthion	12	2.01E-03	1	17.152	**ANOVA**
	Malathion	102	3.80E-02	4	2.651	**ANOVA**
	Methomyl	31	3.61E-03	4	5.098	**ANOVA**
	Fenitrothion	49	2.32E-03	4	4.951	**ANOVA**
	Methyl parathion	50	4.99E-02	4	2.595	**ANOVA**
	Parathion	58	1.91E-01		0.191	KW_Rejected
	Azinphos-methyl	25	7.74E-01		0.774	Reject_ANOVA
	Chlorpyrifos	94	2.85E-01		0.285	Reject_ANOVA
	Mexacarbate	12	8.03E-01		0.803	Reject_ANOVA
	Phorate	22	2.10E-01		0.210	Reject_ANOVA
	Fenthion	55	1.13E-01		0.113	Reject_ANOVA
	Dichlorvos	19	9.19E-02		0.092	Reject_ANOVA
	Ammonium sulfamate	31	2.10E-01		0.210	Reject_ANOVA
	Propoxur	12	2.60E-01		0.260	Reject_ANOVA
Dissolved Metal	Cadmium chloride	117	4.08E-03	4	4.067	**ANOVA**
	Mercuric chloride	66	5.17E-04	4	5.784	**ANOVA**
	Zinc sulfate	62	1.78E-03	3	5.672	**ANOVA**
	Zinc chloride	31	1.17E-03	2	8.674	**ANOVA**
	Cadmium sulfate	16	5.47E-01		0.547	Reject_ANOVA
	Lead nitrate	13	4.94E-01		0.494	Reject_ANOVA
	Copper sulfate	85	1.04E-01		0.104	Reject_ANOVA
Iono/Osmoregulatory/ **Circulatory impairment**	Cadmium	28	1.10E-01		0.110	Reject_ANOVA
	Copper	27	1.02E-01		0.102	Reject_ANOVA
	Mercury	15	8.26E-01		0.826	Reject_ANOVA
	Potassium chloride	22	5.68E-01		0.568	Reject_ANOVA
Neurotoxicity	Lindane	59	2.58E-06	4	10.392	**ANOVA**
	Endosulfan	47	1.70E-02	4	3.513	**ANOVA**
	Endrin	41	5.22E-03	KW	0.005	**KW**
	Dieldrin	37	7.22E-01		0.722	Reject_ANOVA

	Cypermethrin	31	4.47E-01		0.447	Reject_ANOVA
	Permethrin	46	8.09E-02		0.081	Reject_ANOVA
Nonpolar Narcosis	Phenol	113	1.34E-03	4	4.796	**ANOVA**
	Rotenone	18	3.00E-02	1	5.672	**ANOVA**
	DDT	68	5.14E-02		0.051	Reject_ANOVA
	Methoxychlor	30	4.22E-01		0.422	Reject_ANOVA
	Pentachlorophenol	68	6.05E-01		0.605	Reject_ANOVA
	Chlorothalonil	40	2.30E-01		0.230	Reject_ANOVA
	Acetone	31	6.74E-01		0.674	Reject_ANOVA
	Aniline	18	2.10E-01		0.210	Reject_ANOVA
	Atrazine	26	2.81E-01		0.281	Reject_ANOVA
	Benzene	13	7.07E-01		0.707	Reject_ANOVA
	Sodium pentachlorophenate	20	3.03E-01		0.303	Reject_ANOVA
Reactivity	Potassium chromate	59	3.80E-01		0.380	Reject_ANOVA
unclassified	Ammonium chloride	33	4.03E-01		0.403	Reject_ANOVA
	Hexabutyldistannoxane	13	1.56E-01		0.156	Reject_ANOVA
	Sodium cyanide	13	1.28E-01		0.128	Reject_ANOVA

Table A2.5: Results of the Kruskal-Wallis and post hoc Dunn's Tests to identify significant differences in the log10-transformed, normalised LC_{50} values across different functional feeding groups (FFGs) for six chemical modes of action. Groups where significant differences ($p<0.05$) were found are highlighted in bold.

Mode of Action	Kruskal Wallis Test	Comparison	Z	P.unadj	p.adj
AChE inhibition	$H_{(4)}$=72.172, p=7.89-E15)	Herbivore - Shredder	6.81	0.00	**0.000**
		Herbivore - Predator	6.13	0.00	**0.000**
		Filterer - Gatherer	1.21	0.23	1.000
		Filterer - Shredder	0.94	0.35	1.000
		Predator - Shredder	0.80	0.42	1.000
		Filterer - Predator	0.11	0.91	1.000
		Gatherer - Shredder	-0.17	0.86	1.000
		Gatherer - Predator	-1.05	0.30	1.000
		Filterer - Herbivore	-6.26	0.00	**0.000**
		Gatherer - Herbivore	-7.51	0.00	**0.000**
Dissolved Metal	$H_{(4)}$=68.522, 4.66E-14	Predator - Shredder	0.51	0.61	1.000
		Gatherer - Herbivore	-0.01	0.99	1.000
		Herbivore - Shredder	-1.44	0.15	1.000
		Gatherer - Shredder	-1.67	0.10	0.958
		Herbivore - Predator	-1.97	0.05	0.487
		Gatherer - Predator	-2.28	0.02	0.226
		Filterer - Herbivore	-3.99	0.00	**0.001**
		Filterer - Gatherer	-5.20	0.00	**0.000**
		Filterer - Shredder	-5.56	0.00	**0.000**
		Filterer - Predator	-6.25	0.00	**0.000**
IOC	$H_{(4)}$=18.55, p=0.0096	Predator - Shredder	2.04	0.04	0.412
		Gatherer - Shredder	1.73	0.08	0.834
		Gatherer - Herbivore	0.87	0.39	1.000
		Herbivore - Shredder	0.24	0.81	1.000
		Filterer - Shredder	-0.23	0.82	1.000
		Filterer - Herbivore	-0.42	0.68	1.000
		Gatherer - Predator	-0.60	0.55	1.000
		Herbivore - Predator	-1.15	0.25	1.000

		Filterer - Gatherer	-3.31	0.00	**0.009**
		Filterer - Predator	-3.32	0.00	**0.009**
Neurotoxicity	$H_{(4)}$=14.25, p=0.006538	Herbivore - Shredder	3.25	0.00	**0.011**
		Herbivore - Predator	2.48	0.01	0.133
		Filterer - Shredder	2.15	0.03	0.313
		Filterer - Gatherer	1.69	0.09	0.918
		Filterer - Predator	1.28	0.20	1.000
		Predator - Shredder	0.90	0.37	1.000
		Gatherer - Shredder	0.52	0.60	1.000
		Gatherer - Predator	-0.40	0.69	1.000
		Filterer - Herbivore	-1.33	0.19	1.000
		Gatherer - Herbivore	-2.85	0.00	**0.044**
None	$H_{(4)}$=47.325, p=1.3E-9	Herbivore - Predator	4.74	0.00	**0.000**
		Herbivore - Shredder	4.39	0.00	**0.000**
		Gatherer - Predator	0.50	0.62	1.000
		Gatherer - Shredder	0.15	0.88	1.000
		Predator - Shredder	-0.30	0.77	1.000
		Filterer - Predator	-0.70	0.48	1.000
		Filterer - Shredder	-1.06	0.29	1.000
		Filterer - Gatherer	-1.62	0.11	1.000
		Gatherer - Herbivore	-5.04	0.00	**0.000**
		Filterer - Herbivore	-6.82	0.00	**0.000**
Nonpolar Narcosis	$H_{(4)}$=24.94, p=5.1E-5	Herbivore - Shredder	3.56	0.00	**0.004**
		Predator - Shredder	3.40	0.00	**0.007**
		Filterer - Shredder	1.16	0.25	1.000
		Gatherer - Shredder	0.65	0.52	1.000
		Filterer - Gatherer	0.49	0.63	1.000
		Herbivore - Predator	0.38	0.71	1.000
		Gatherer - Predator	-3.08	0.00	**0.021**
		Filterer - Predator	-3.12	0.00	**0.018**
		Gatherer - Herbivore	-3.25	0.00	**0.011**
		Filterer - Herbivore	-3.28	0.00	0.010
Reactivity		Predator - Shredder	0.74	0.46	1.000

	$H_{(4)}$=20.39, p=0.0004181	Herbivore - Shredder	0.69	0.49	1.000
		Herbivore - Predator	-0.09	0.92	1.000
		Gatherer - Shredder	-0.15	0.88	1.000
		Gatherer - Herbivore	-0.91	0.36	1.000
		Gatherer - Predator	-0.95	0.34	1.000
		Filterer - Shredder	-2.33	0.02	0.200
		Filterer - Gatherer	-2.52	0.01	0.119
		Filterer - Predator	-3.17	0.00	0.015
		Filterer - Herbivore	-3.36	0.00	0.008
Uncoupler			NA		
Electron transport inhibition			NA		
Polar Narcosis			NA		

Appendix for Chapter 3

Acute LC_{50}s (<7 days) for *Gammarus* and *Asellus* were collected from the US EPA Ecotox Database. Where multiple LC_{50} values were reported for a single contaminant, geometric means were calculated to obtain one LC_{50} for each contaminant for each species (Table A3.1). LC50 values for both species were available for 67 contaminants. LC_{50}s of *Asellus* were plotted against LC_{50}s of *Gammarus* (Figure 1). The black line indicates 1:1 line with intercept at 0. Points above the black line indicate contaminants where *Gammarus* was more sensitive than *Asellus* for 42 of the available 67 contaminants, equally tolerant for 14, and less sensitive for 11 (Figure A3.1).

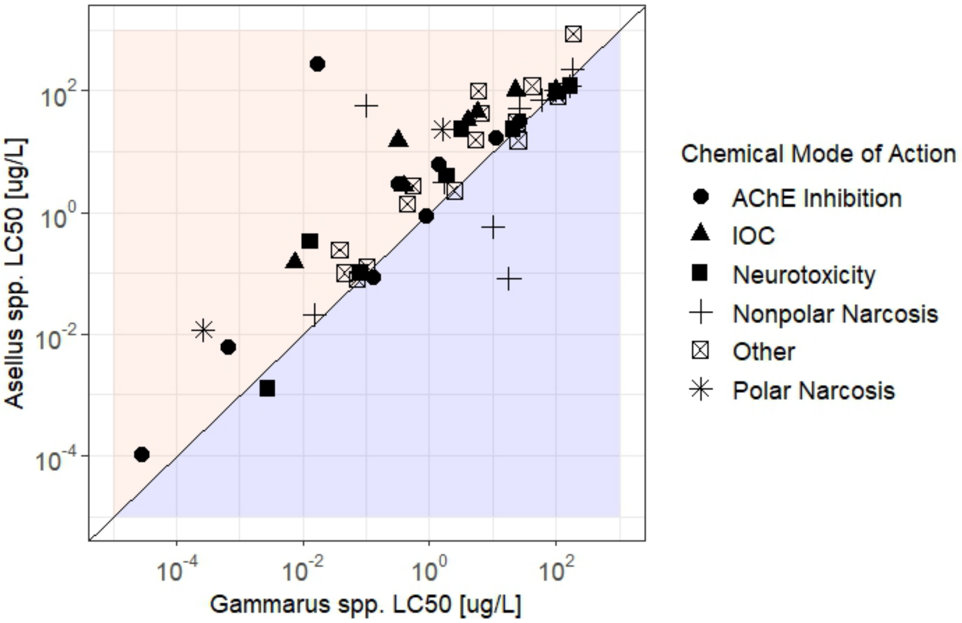


Figure A3.1: Difference in sensitivity of *Asellus spp.* and *Gammarus spp.* to chemical stress. Acute LC_{50}s for each species plotted against each other. Note the log scale of both axes. The black line indicates 1:1 with intercept at 0. The coral shaded area represents the area where *Gammarus spp.* is more sensitive than *Asellus spp.*, while the blue area represents the reverse.

To assess differences between the sensitivity ratio and the chemical mode of action, Levene's test found equal variances between Sensitivity ratio and chemical modes of action ($F_{(9)}$=0.8828, p = 0.5431). A one way ANOVA was used to determine if the ratio of sensitivity of the two species differed between different modes of action. There was no statistical interaction between the ratio of sensitivity and Chemical Mode of Action ($F_{(9)}$=0.915, p-0.516)

Appendix for Chapter 4

Appendix 4.1: Figure 4.7 use of mean deviation rather than maximum deviation explanation

Summary

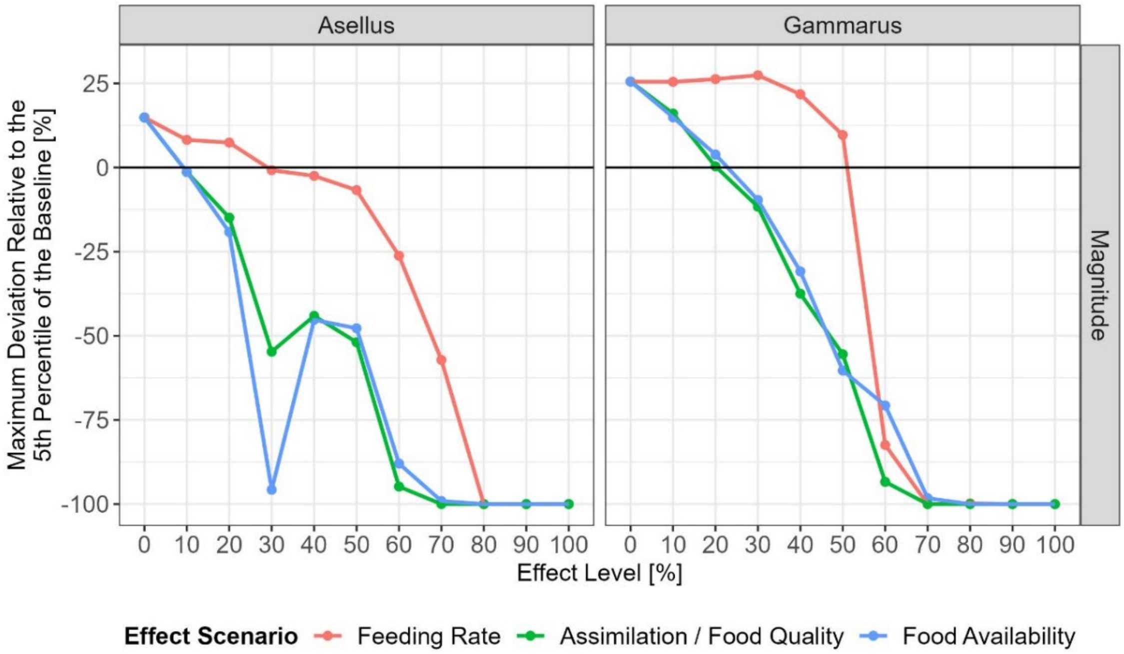
Figure 4.7a presents the mean deviation in prey biomass for three impact pathways on individual feeding, relative to the 5th percentile of the baseline. This metric differs from the one used for population abundance and leaf processing, as it was considered more appropriate given the distinct dynamics of prey biomass. Unlike population abundance, prey biomass exhibits more pronounced oscillations, which, when effects of stress, can lead to phase asynchrony across treatments. In such cases, using metrics like maximum deviation can exaggerate differences due to asynchrony rather than actual treatment effects. The mean deviation, by averaging deviations from the baseline over time, provides a more stable and interpretable measure that better captures the impacts of different impact pathways on prey biomass. The process by which this conclusion was met is outline below.

Problem Definition

When using the maximum deviation in prey biomass relative to the 5th percentile of the baseline, the prey biomass also decreases with increasing effect level. However, there is an anomalous result with a 30% reduction in food availability for *Asellus*. Here, the prey biomass falls to -96% of the 5th percentile of the baseline. This result deviates from the general trend, where the maximum deviation in prey biomass decreases steadily with increasing effect levels: -19% with a 20% reduction in food availability and -45% with a 40% reduction.

This raised the question of whether the observed anomaly represents a real biological effect or if it is an artifact of the model behaviour, its parameters, or the method of analysis. Specifically, is the observed decrease with a 30% reduction in food availability genuine, or is it a model-specific outcome? The purpose of this section is to address this question by considering the following points:

- How does a reduction in food availability affect prey biomass?
- Are the changes in oscillation patterns consistent with the known behaviour of this model type (and other similar models)?
- Does the anomaly disappear when trends are derived from plausible alternative methods of analysis?



Appendix 4.1a: The magnitude of impact of three effect scenarios on *Asellus* and *Gammarus* Prey Provision (Adult Biomass). The plot shows the relationship between the effect level [%] and the maximum deviation of the median relative to the 5th percentile of the baseline, defined as the magnitude.

How does a reduction in food availability affect prey biomass oscillations?

With a reduction in food availability, prey biomass decreases, and its fluctuations become asynchronous with the baseline (Figure A). This shift is most pronounced at the 30% effect level, where the oscillation amplitude slightly decreases and becomes delayed relative to the baseline. Consequently, when comparing the maximum deviation of the median to the 5th percentile of the baseline, the analysis may overestimate the "effect" (Appendix 4.1a). With increasing effect level, the amplitude of the prey biomass oscillations continue to decline until almost not visible at with a 50% reduction in food availability (Figure A).

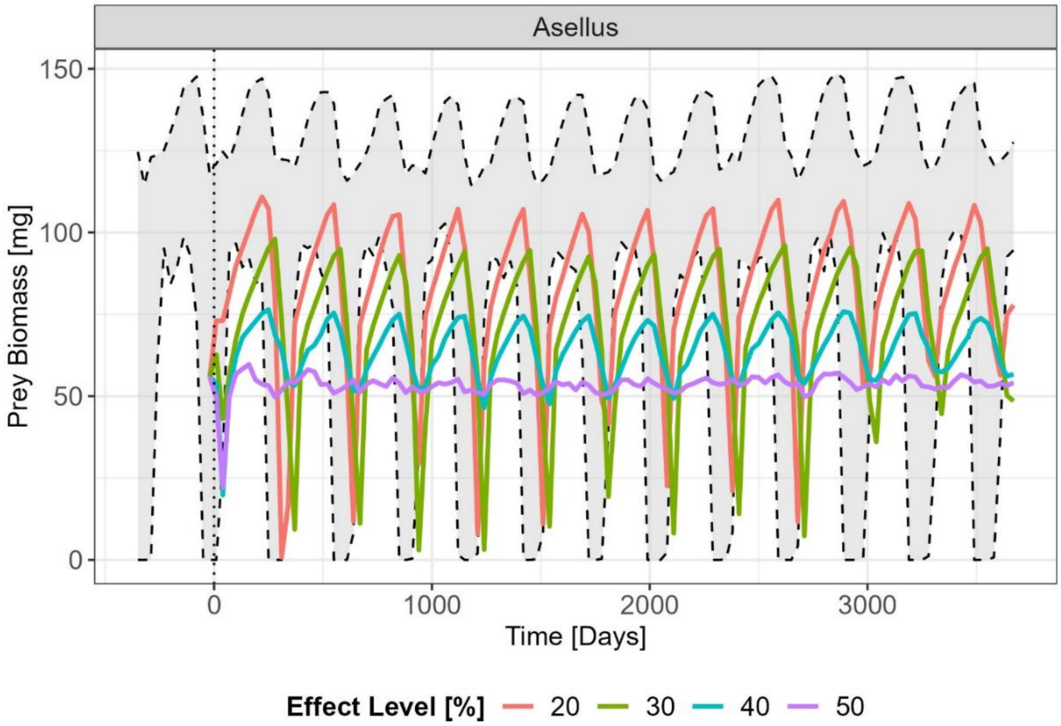


Figure A: Impact on median *Asellus* prey biomass with reduction in food availability by 20, 30 , 40 and 50% compared to the baseline (grey area inside the black dashed lines)

Are the changes in oscillation patterns consistent with the known behaviour of this model type (and other similar models)?

Changes in oscillations are consistent with known behaviour of complex stochastic population models. Individual based dynamic energy budget models (DEB-IBMs) are complex stochastic models that can exhibit oscillatory behaviour driven by changes in both consumer and resource characteristics, like other consumer-resource models (Nisbet et al., 2016). Simulated population dynamics in such models are sensitive to parameter values, particularly resource availability and consumer mortality rate (Rosenzweig, 1971; De Roos, 1997, 1998; Persson et al., 1998).

The "paradox of enrichment" (Rosenzweig, 1971) describes the phenomenon where increasing resource availability can lead to greater instability in predator-prey systems, potentially resulting in large-amplitude population cycles or even extinction. Conversely, a reduction in resource availability, such as decreased resource carrying capacity (K), can stabilise the system. De Roos (1997) demonstrated that populations dynamics of an age structured *Daphnia* population model altered with K and mortality rate. When K is high, classical predator-prey cycles emerge, where the *Daphnia* population fluctuates in response to algal availability. Population dynamics, however, are altered with decreasing K—oscillations lengthen and flatten, transitioning to single-generation cycles before eventually reaching a steady state. Ultimately,, the population collapses with decreasing K due to a lack of resources to sustain the population. Similarly, Hilker and Schmitz (2008) demonstrated that in an oscillating predator-prey system with a saturating functional response, disease transmission, modelled as predator mortality, led to the stabilisation of predator-prey cycles.

For both these DEB IBMs, individual maturation is size dependent with maturation occurring when a particular energy threshold is reached. In these cases, progression through various life stages generally depends on food intake (De Roos et al., 2003). A reduction in food availability can initially result in large mortality (As observed in Figure A), due to starvation. However, as food intake decreases, the time required for maturation and growth may increase. Consequently, fecundity—determined by body length—may also reduce reduced, leading to longer but lower-amplitude population oscillations.

These findings provide a framework for understanding the oscillatory dynamics of the *Asellus* and *Gammarus* models used here, particularly the *Asellus* population. As resource availability declines, oscillation amplitudes initially increase in length before flattening, aligning with theoretical expectations. However, these patterns are partly a result of the experimental system's design and its fixed carrying capacity. In natural environments, additional factors—such as temperature fluctuations, seasonal variations in resource availability, and predation—can influence population dynamics. In particular, mechanisms such as predation, crowding, and spatial heterogeneity may contribute to stability even in enriched systems (Roy & Chattopadhyay, 2007). Therefore, while the dynamics of the populations may differ in field populations, reductions in prey availability from a reduction in food availability is nonetheless biologically plausible due to both reduced population size (Lotka, 1925; Volterra, 1926; Tilman, 1982) and reduced individual growth rates (Sibly and Hone, 2002).

Does the anomaly disappear when trends are derived from different, but reasonable, methods of analysis?

When comparing the difference in the median of the treated population to the 5th percentile of the baseline, the shift in oscillation timing amplifies the apparent deviation. Using an alternative metric, such as cumulative impact (Figure 4.7c), which is less affected by asynchrony, almost eliminates this anomaly. Instead, the effect follows the expected trend of increasing reduction in food availability results in a steady decrease in prey biomass with increasing effect level.

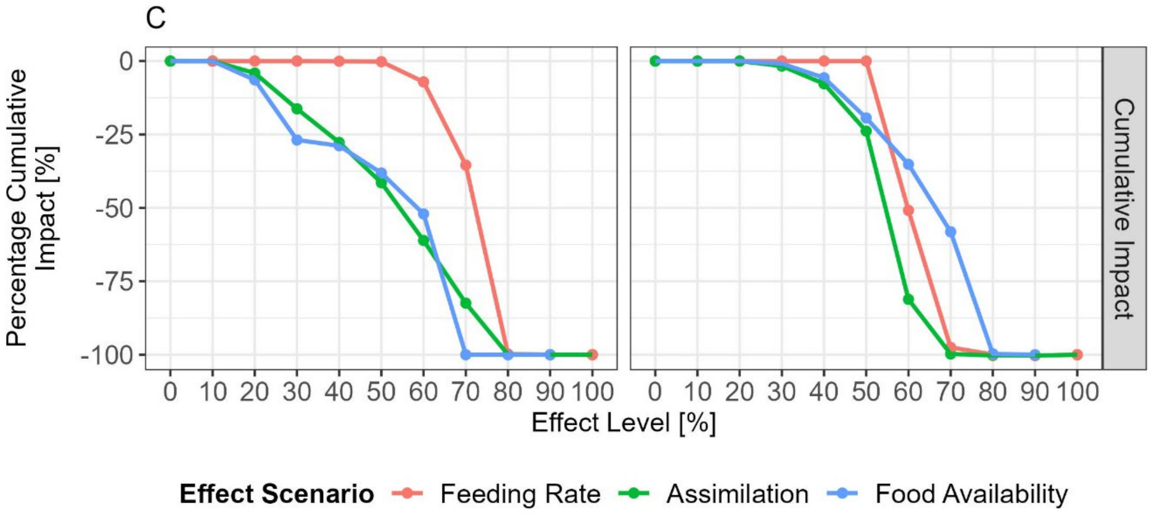


Figure 4.7c: The impact of three effect scenarios on *Asellus* (left) and *Gammarus* (right) Prey Provision (Adult Biomass) evaluated using the Cumulative Impact (percentage cumulative reduction in prey provision). Each subplot shows the relationship between effect level (%) and the respective impact metric for both species.

Alternatively, the mean captures overall trends in prey biomass and is sensitive to all values in the dataset, making it useful for detecting shifts in the entire population. Comparing the means across all replicates for all time points for each treatment enables us to capture trends while being unaffected by asynchrony. Here, comparing the relative of the aggregate mean to that of the baseline results in the disappearance of the anomaly (Figure 4.7a).

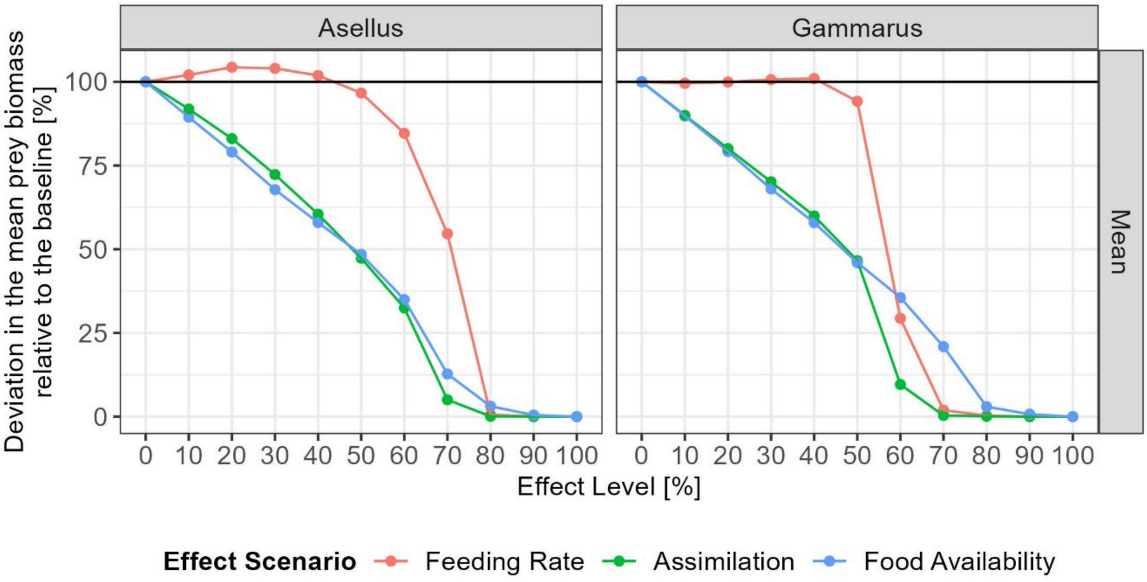


Figure 4.17a: Mean prey biomass [mg] (mean across all replicated and timesteps for the 10 year stress period) relative to the baseline for *Asellus* and *Gammarus*, with increasing reduction in three pathways of impact [%]

Are there any other plausible types of mechanism which could produce this type of sudden drop at a specific food level, and if so are they relevant to this model situation?

While the anomaly observed in Appendix 4.1a is most likely to be an artifact rather than a genuine relative effect, other possible mechanisms that could produce this sudden drop at a specific food level. Mortality events (whether affecting the entire population or specific cohorts) can result in asynchrony due to delayed recovery or recruitment. This disruption can alter the timing of population oscillations relative to the baseline, creating phase mismatches. Alternatively, given these are complex consumer-resource models, mortality in one population influences the dynamics of the other, potentially leading to phase shifts in population cycles (Scheffer and Carpenter, 2003). However, in these simulations, stress is applied constantly rather than as a pulsed disturbance, making it equivalent to a parameter shift rather than a transient disturbance. As a result, the impact extends beyond just altering oscillation timing—it can also affect the amplitude and central tendency of population fluctuations.

Conclusion

The anomaly observed in Appendix 4.1a is determined to be an artifact rather than a genuine relative effect. The decline in prey biomass with decreasing food availability follows expected trends, steadily decreasing with increasing effect levels. This pattern arises primarily due to population asynchrony rather than a significant change in the magnitude of oscillations. This interpretation is further supported by the absence of the anomaly when using alternative assessment methods, such as cumulative impact (i.e., area under the curve) and mean comparisons, both of which are less influenced by asynchrony.

However, conclusions regarding *Gammarus* vary depending on the analytical approach. When using maximum deviation or mean comparisons, the results suggest that the pathway of impact significantly influences prey biomass response. In contrast, when assessing cumulative impact, the differences between pathways of impact become less pronounced.

This highlights a key limitation of the method(s) of analysis: when pathways of impact affect the populations oscillations, comparing the two oscillating populations, taking either the maximum deviation from the which complicates interpretation and may obscure meaningful patterns. This raises the question of whether comparing the median to the 5th percentile of the baseline was the most appropriate method of analysis for this study. While it was initially considered suitable, particularly for evaluating population responsiveness to different impact pathways, its full effectiveness remains unclear, as the planned recovery analysis—defined as the median returning to the baseline operating range—was not completed. As a result, the mean deviation in prey biomass is present in the main text in this thesis (Figure 4.7a)

Appendix 4.1 References

de Roos, A.M., 1997. A gentle introduction to physiologically structured population models. In Structured-population models in marine, terrestrial, and freshwater systems (pp. 119-204). Boston, MA: Springer US.

Hilker, F.M. and Schmitz, K., 2008. Disease-induced stabilization of predator–prey oscillations. Journal of Theoretical Biology, 255(3), pp.299-306.

Lotka, A.J., 1925. The measure of net fertility. Journal of the Washington Academy of Sciences, 15(21), pp.469-472.

Nisbet, R.M., Martin, B.T. and de Roos, A.M., 2016. Integrating ecological insight derived from individual-based simulations and physiologically structured population models. Ecological Modelling, 326, pp.101-112.

Persson, L., Leonardsson, K., De Roos, A.M., Gyllenberg, M. and Christensen, B., 1998. Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. Theoretical population biology, 54(3), pp.270-293.

Rosenzweig, M.L., 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science, 171(3969), pp.385-387.

Roy, S. and Chattopadhyay, J., 2007. The stability of ecosystems: a brief overview of the paradox of enrichment. Journal of biosciences, 32, pp.421-428.

Scheffer, M. and Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in ecology & evolution, 18(12), pp.648-656.

Sibly, R.M. and Hone, J., 2002. Population growth rate and its determinants: an overview. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 357(1425), pp.1153-1170.

Volterra, V., 1928. Variations and fluctuations of the number of individuals in animal species living together. ICES Journal of Marine Science, 3(1), pp.3-51.

Appendix for Chapter 5

Of the patches where exclusion occurred, the mean total shredder abundance at the end of the simulation period remained relatively stable across treatments, with the median shredder abundance across patches ranging from 585 to 653 individuals with a median of 615 individuals (Figure A5.1). In the baseline scenario, the mean total shredder abundance ranged from 528 to 742 individuals per patch, with a median of 616. The largest variability in shredder abundance occurred in patches initially dominated by *Asellus*, whereas the lowest variability was seen in patches with equal initial dominance by both species, showing a range of 600 to 631 individuals and a median of 615 (Figure A5.1).

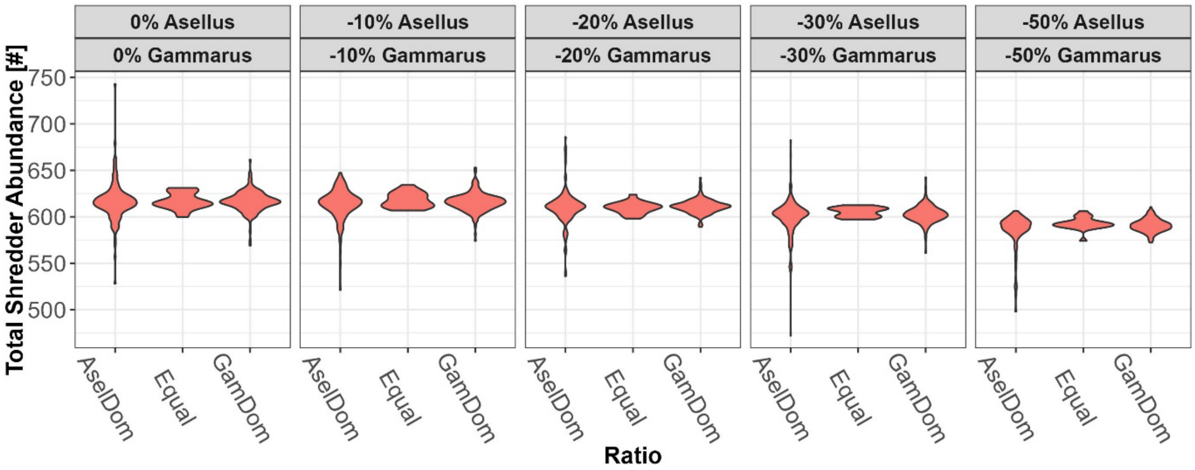


Figure A5.0.5: Frequency distribution of mean shredder abundance across patches where coexistence occurred, with increasing feeding inhibition of both species, grouping patches by different initial dominance ratios of *Gammarus* and *Asellus*. The x-axis represents the relative abundance of *Gammarus* (%), while the y-axis shows the initial dominance ratio: *Gammarus*-dominant (GamDom), *Asellus*-dominant (AselDom), and equal dominance (Equal)