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THE CORRELATION BETWEEN BENTHIC INVERTEBRATE PRODUCTIVITY AND FISH DENSITY AT STREAMS

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Abstract

Within riverine ecosystems, fish and benthic invertebrates have crucial ecological roles, contributing to the overall functioning and biodiversity of these aquatic environments. The purpose of this study is to describe the relationship between the productivity of benthic invertebrate communities and the density of fish populations in upstream and downstream sections across four European countries. Sampling involved the collection of benthic invertebrates and fish. Data analysis included estimation of invertebrate diversity, density, biomass, and growth rates, as well as assessment of fish condition and density. The correlation between invertebrates and fish were examined and linkages between these factors in both organisms were explored. Also, these connections were compared in four countries under investigation. My results suggest that different countries exhibited various relations among the examined factors concerning these two organisms. Most countries showed higher invertebrate density upstream, a trend that aligns with the density and condition of fish in Sweden and France with no reliable relation in other countries. The highest biodiversity in benthic invertebrate groups is observed in France, which positively correlates with fish density and condition in this country. The taxons with the highest biomass included Hemiptera and Odonata, however, the Hydracarina's small size made it difficult to measure them. The highest growth rate of insects was observed in Portugal, showing no correlation with the abundance and condition of fish. Among benthic invertebrates, Diptera showed the highest productivity based on growth rate across all sites, with Trichoptera displayed the lowest. In this study, it is shown that although significant relationships are not found between benthic invertebrates and fish in all countries, invertebrates can be utilized in the evaluation of various domains such as ecological health assessments, water quality monitoring, and ecosystem functioning, all of which can affect the fish.

Introduction

Interactions between predators and prey are fundamental in ecology as they explore the relationship between organisms that consume others and their impact on ecological communities. (Beauchamp et al., 2007). These interactions help us to understand the dynamics of these relationships and their influence on population sizes (Beauchamp et al., 2007). Many species during some phase of their lifetime function as both predators and prey to maximize their chances of survival and reproduction (Heithaus, and Vaudo, 2004). These types of interactions not only affect individual species but also can shape the composition and diversity of species within aquatic communities (Beauchamp et al., 2007). Investigating benthic invertebrates can explain the basis of relationships between various species in streams. Predation by fish plays a significant role in forming the overall composition of the benthic invertebrate community as they control the populations and composition of these invertebrate organisms (Flecker, 1984). This predation pressure can have cascading effects throughout the entirety of the food web, thereby influencing the population densities and distribution of other species, even macrophytes and algae (Mancinelli et al., 2002).

The association between benthic invertebrates and fish can provide important insights into ecological relationships within aquatic ecosystems. Aquatic benthic invertebrates are characterized by their diminutive size, limited mobility, and use of different microhabitats at the bottom substrate of lakes, rivers, and oceans, and they play crucial roles in these ecosystems (Merritt and Wallace, 2009). Fish, on the other hand, are larger vertebrates that occupy various trophic levels within aquatic food webs throughout their life cycle. They are important predators that consume benthic invertebrates as a significant portion of their diet (Diehl, 1992). Benthic invertebrates serve as a primary food source for numerous fish species, especially those fish characterized by using benthic feeding habits or having specialized feeding adaptations (Henseler et al., 2021). This relationship is important for biomass production, food chain, and energy transfer within aquatic ecosystems (Henseler et al., 2021). Benthic invertebrates are primary consumers and feed mostly on detritus, algae, and organic material within sediments. In turn, larger fish function as secondary or tertiary consumers, preying on these benthic invertebrates and regulating their populations (Campanya et al., 2017).

Benthic invertebrates often inhabit specific niches within the aquatic environment (Covich et al., 1999) and various species of benthic invertebrates may be adapted to specific substrate compositions, depths, and water conditions, (Death and Winterbourn, 1995). Similarly, fish species may have specialized feeding and habitat preferences (Järv et al., 2011). The presence and distribution of benthic invertebrates can impact the distribution and behavioral tendencies of fish species within an ecosystem (Järv et al., 2011).

Benthic invertebrates exhibit various modes of distribution, and their spatial distribution is influenced by a multitude of factors (Rousi et al., 2011). Among these factors, habitat characteristics, including the type of substrate, water depth, water velocity, and habitat complexity, can shape their spread, so that different species have specific tolerances to these factors influencing their place of residence (Heino et al., 2017). Additional factors, such as water quality, the availability of food resources, and Predation and Competition can also exert influence on the distribution of benthic invertebrates, as competition for resources and space can limit the dispersion of certain invertebrate species, while predation can influence their distribution patterns and abundance (Mandaville, 2002). Furthermore, climate change (Hiddink et al., 2015), and human activities (Fore et al., 1996), can have implemented an impact on the dispersion of invertebrate species and these disturbances can alter habitat availability, disrupt ecological interactions, and directly affect the survival of invertebrate species. Therefore, the correlation between benthic invertebrates and fish in streams is multifaceted and influenced by various ecological, hydrological, and anthropogenic factors. This interplay encompasses complex trophic relationships, habitat requirements, and responses to environmental stressors (Heino et al., 2017). Furthermore, these relationships are subject to temporal and spatial variations that make the study of these ecosystems challenging (Heino et al., 2017).

In addition, lentic and lotic features within river systems represent a composite of habitat characteristics that influence the distribution and presence of benthic invertebrate species, and the lentic and lotic gradient is effective in structuring aquatic invertebrate communities (Buffagni, 2021). Basically, the upstream parts of the watercourse are fast-flowing, shaded from surrounding vegetation, and have a lotic ecosystem marked by the continuous flow of water, and the downstream parts usually exhibit greater depth, increased turbidity, and have a more lentic ecosystem characterized by standing or slow-moving water bodies (Buffagni, 2021). Previous studies have also detected physiological and behavioral differences between salmonid fish species occupying different stretches along the river (Berry et al., 2024) which potentially could result in a differentiated interaction between fish and benthic invertebrates. These contrasting environmental conditions between the upstream and downstream sections can cause differences in biotic communities between these two sections.

One of the largest groups of benthic invertebrates is insects. Insects are indeed an ecologically significant and diverse group of benthic invertebrates in many freshwater ecosystems (Mandeville, 2002). Well known for their adaptability to aquatic environments during their larval stages. Their diverse feeding habits and adaptations make them key players in nutrient cycling and energy transfer within these ecosystems (Covich et al., 1999). Streambed invertebrates exhibit a wide range of food habits, which can vary depending on their feeding methods and adaptations (Merritt and Wallace, 2009). Benthic invertebrate functional feeding groups include shredders, collectors, grazers, and predators (Ramírez and Gutiérrez, 2014). The diversity of food habits within this group contributes to the overall functioning and stability of aquatic ecosystems and also acts as an important vector of autochthonous energy feeding into the riverine ecosystem (Ramírez and Gutiérrez, 2014).

Benthic invertebrates can also act as indicators of water quality and habitat health. Monitoring the abundance and diversity of benthic invertebrate communities can therefore serve as a valuable tool for the general well-being and ecological status of aquatic ecosystems, which in turn can influence fish populations (Mandeville, 2002). Aquatic insects are one of the most common benthic invertebrates used broadly in freshwater monitoring and assessment (Wahizatul et al., 2011).

Due to the fact that aquatic ecosystems are very complex, the presence of indicator invertebrate species corresponding with a specific condition is necessary to evaluate ecosystem health (Faith and Walker, 1996) which can also affect the presence or absence of fish. Among these groups, the three main dominant orders of aquatic ecosystems are Ephemeroptera, Plecoptera, and Trichoptera. Benthic invertebrates especially aquatic insects are relatively stationary, and associated with water for most parts of their life cycle, and any change in their numbers and population composition may indicate a change in habitat quality (Mandaville, 2002). For example, the larvae of Ephemeroptera are a source of food for fish and used as bioindicators in many monitoring programs because of their sensitivity to oxygen depletion, acidification, and various contaminants was demonstrated (Jacobus et al., 2019). Plecoptera is another important component of water ecosystems both in terms of biomass and diversity, generally indicating well-oxygenated water, therefore declining Plecoptera populations may indicate eutrophication and can threaten the health of aquatic ecosystems as well as the fish population (Choudhary and Ahi, 2015). Further, Trichoptera also has important roles in food webs, stabilizing bed sediment, prey for fish, and bioindicators of water quality (Morse et al., 2019). Other benthic invertebrates can also play a role in the food web and monitoring of freshwater habitats. Diptera larvae especially the Chironomidae family serve as an important food source for fish (Marti et al., 2006) and are used as a bioassessment. It has been observed that many pollution-tolerant Chironomidae family are often indicative of poor water quality (Mandeville, 2002). Many species of fish feed on aquatic Coleoptera larvae as part of their diet, the presence and activities of these invertebrates can influence the structure and composition of water habitats, which may benefit or impact fish populations differently (Mendoza et al., 2012).

Meanwhile, it is not only invertebrates that are subjected to predation by fish, certain aquatic invertebrate taxa may prey upon juvenile fish and the predator-prey relationship can be reversed between these two organisms. In aquatic environments, predatory insects, Hemiptera or Coleoptera groups (Schumann et al., 2012), and sometimes Odonata larvae (Pritchard, 1964) feed on both invertebrates and vertebrates.

The knowledge about the benthic invertebrate species composition can be used in different aspects, For instance, to understand the distribution of the fish species in different parts of the stream, and how to assess and monitor environmental health in aquatic ecosystems. The application of expertise about the species composition of benthic invertebrates is important for understanding their ecological dynamics and making informed decisions related to environmental conservation and management (López and Sedeño, 2015). Monitoring changes in their composition can serve as early warning indicators of ecosystem health and environmental stressors. Also, these biomarkers help sustainable management and make informed decisions related to environmental conservation and management. The correlation between benthic invertebrates and fish is also an aspect of aquatic ecosystems and plays a role in shaping the structure and dynamics of these ecosystems. Detecting this relationship can therefore be effective for the management and conservation of aquatic environments and their associated species (López and Sedeño, 2015).

The composition and abundance of fish populations in streams can be linked to the availability of benthic invertebrate prey. The relationship between these two organisms is affected by many different factors and needs to be studied from different aspects. Many academic investigations commonly use these two categories separately to address inquiries concerning environmental interactions, but a limited number of studies assess the correlation that exists between these two distinct groups. Studies that specifically address the correlation of benthic invertebrate community structure with fish density and size at streams are rare as well as various influential factors on this issue are poorly known (Aguiar et al., 2020).

Aims

The purpose of this thesis is to:

- Investigate whether there is a correlation between fish density and the productivity of benthic invertebrate communities in both upstream and downstream sections of the rivers.
- Assess the secondary productivity of benthic invertebrates by measuring their growth rate.
- A comparative analysis in four European countries is carried out to identify potential variations in these ecological relationships.

Material and Methods

Study Areas

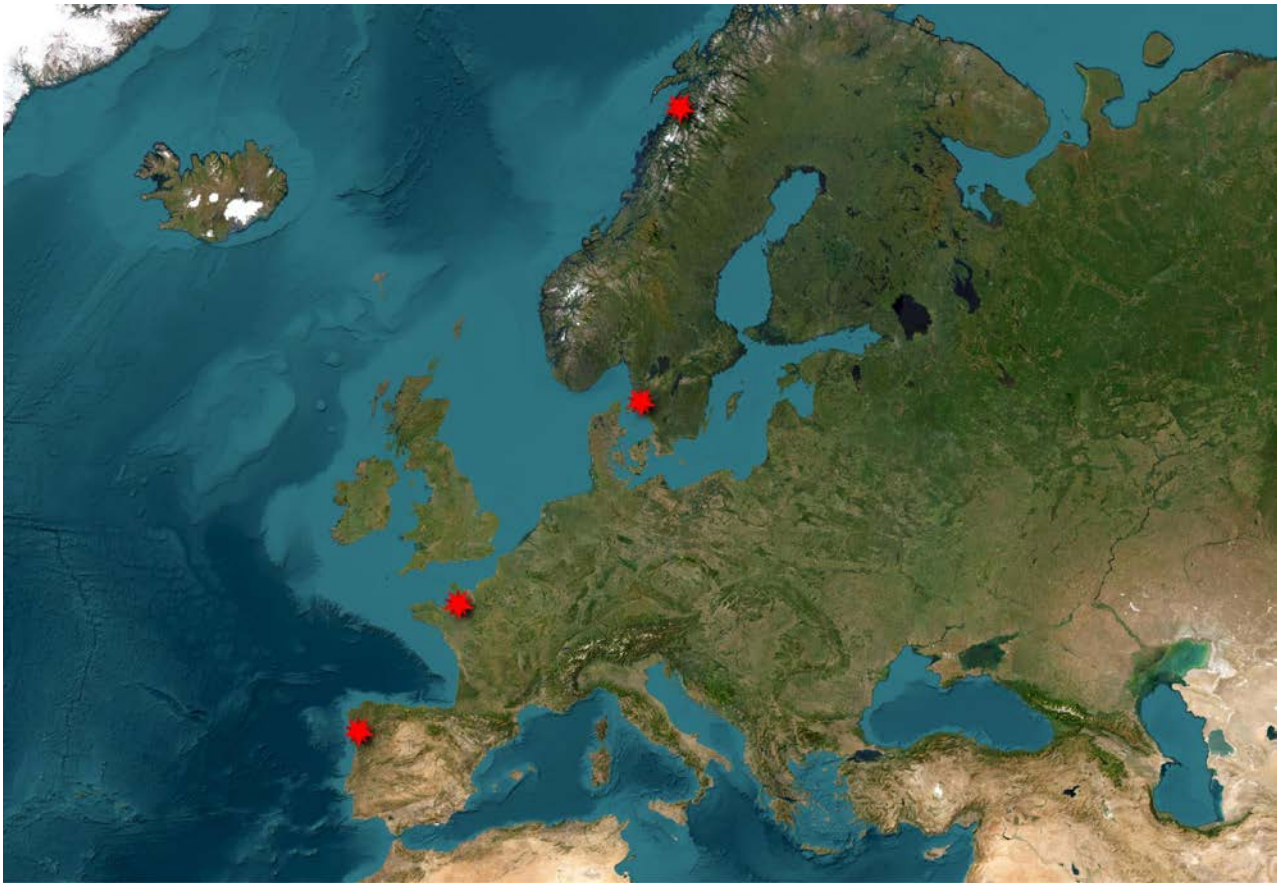

Figure 1. Map of the study area and the locations of streams under investigation (red dots).

The research was conducted in a part of the riverine system in four European countries: Sweden, France, Portugal, and Norway (Figure 1). The sampling range in all sections of upstream and downstream sites was approximately 100 meters along the streams within each location. Sampling was carried out at one site upstream and one site downstream of the rivers in all countries. However, in Norway, due to the presence of a lake upstream, sampling was undertaken at two sites, before and after the lake. In total, sampling was done from nine sites in four countries.

One of the study sites is located in the stream system Haga å, Billdal, Västra Götaland in the southwest of Sweden. It is situated approximately 15 kilometers south of the city center. In France, the La Roche stream was investigated and sampled. It is situated in the Brittany region, in the northwest of France. Another area that was investigated was the Minho stream known as Rio Minho in Portugal. It forms part of the border between Portugal and Spain, running through the northern region of the country. And the last study site is located in Norway along the Fjæreelva stream and the geographic location is in a northerly direction of Norway. (Figure 2)

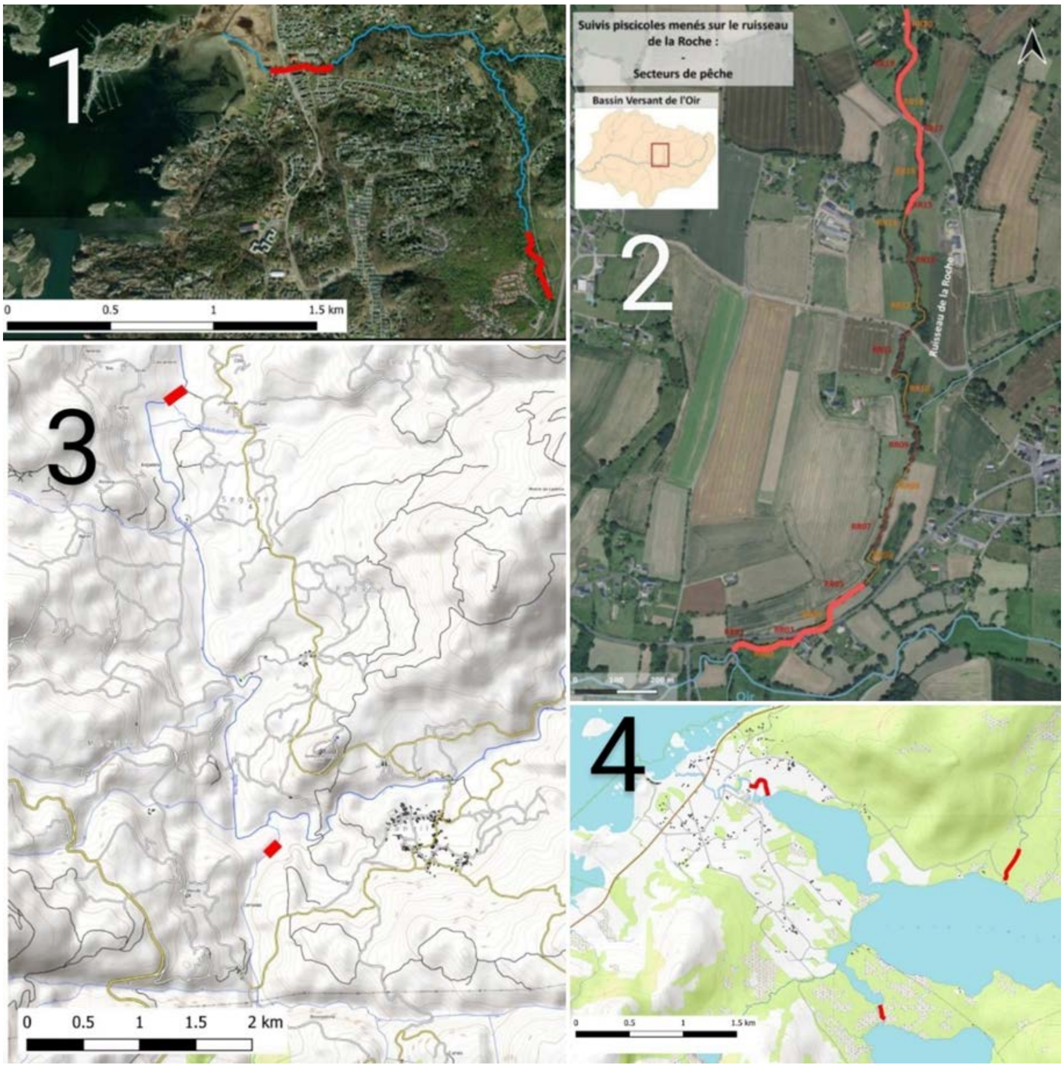

Figure 2. Maps of the study sites. (1): Haga å in Sweden (2): La Roche in France (3): Rio Minho in Portugal (4): Fjæreelva in Norway. Lines marked with red are stretches subjected to sampling of invertebrates and fish.

Sampling Procedure

Sampling was done at all designated sites from benthic invertebrates and fish. Fish were sampled using standardized electrofishing gear to measure population density and individual size criteria. The aquatic invertebrates were collected from the streambed using standardized kick net sampling procedures (Storey et al., 1991). Water temperature at the time of sampling was recorded and to prevent the effects of seasonal fluctuations all samplings were done between the middle of September to the middle of October. All data from downstream and upstream sections of rivers in Norway and France were collected in 2022, and the data from Sweden and Portugal were gathered in 2023.

Benthic invertebrates sampling

For invertebrate Sampling, the standardized kick sampling method, to dislodge and capture benthic invertebrates, was used for collecting benthos in all sampling locations. At each site, three times kick samplings during 30 seconds were performed by a special net. The collected invertebrate samples were preserved in 70% ethanol for subsequent analysis in the laboratory where organisms were identified and sorted using appropriate identification keys (Nilsson, 1996). The population density within individual taxonomic groups of invertebrates was determined. Afterward, the individuals were weighed after being dried in the oven at 60 °C for at least 48 hours. The determination of benthic invertebrate dry weight was conducted to assess their productivity.

Fish collection

A backpack electrofishing unit was used for sampling fish populations within the streams under investigation. Fish captured during electrofishing were collected using dip nets. Captured fish were identified in the field and measurements of their length and weight were undertaken to assess fish conditions. Fish density was determined based on the number of fish per square meter of the river. At each site, about 100 meters along the river section were sampled, and this length was subjected to electrofishing three times in each section.

Data analyses

The density and composition of benthic invertebrates were estimated as the number of organisms in each section of the streams. The number of individuals was evaluated separately in each order of invertebrates. The total biomass in each site was measured by weighing individual dry mass converted to units of mg dry mass for individual body mass. The biomass of all taxa was thereafter summed up to estimate the total biomass of samples in each site. Moreover, daily growth rates were analyzed in relation to body mass and temperature using standardized regression models. The secondary production in terms of daily increase in biomass of benthic invertebrates was obtained by the following formula (Morin and Dumont, 1994):

$$\mathrm{Log}_{10}\, g = a + b \log_{10} W + c\, T$$

With g referring to daily growth rate, W is the weight of individuals (measured for dry mass), and T water temperature (°c). The a,b, and c are constants describing the slope and intersection of the line.

The examination of fish condition was estimated from length and weight of specimens captured at each sampling site. Fulton's condition factor was utilized to assess the condition of the captured fish samples. This factor, calculated as the ratio of the fish's body mass (W, g) to the cube of its length (L, mm), provides insights into the well-being and overall health of the fish population under study:

$$K = W/L^3 * 100$$

Results

Invertebrate abundance

The abundance of benthic invertebrates varied across the study sites, with differences observed between upstream and downstream sections (Table 1). In most countries, the density of invertebrates was higher in the upstream than in the downstream. However, Norway exhibited a reverse trend, with higher invertebrate density observed downstream. The greatest variety of order among benthic invertebrates was in France, which included 12 orders of invertebrates.

A total of 3214 individuals representing 14 taxonomic groups were collected across the study sites. The predominance of taxa based on density among these groups was identified as Ephemeroptera, Plecoptera, Trichoptera, Diptera, and Coleoptera. While the dominant species in terms of environmental sensitivities are Ephemeroptera, Plecoptera, and Trichoptera, these taxa are indicative of relatively pristine aquatic environments, as they are sensitive to pollution and habitat degradation (Mandaville, 2002). In addition, several other orders of invertebrates were identified, including Hydracarina, Eucarida, Bivalvia, Gastropoda, Isopoda, Annelida, Hemiptera, Odonata, and Megaloptera (Table 2).

Table 1. Total density of benthic invertebrates sampled from upstream and downstream sections in four European countries

Sampling	Invertebrate abundance (Individual)	
Countries	Upstream	Downstream
Sweden	184	99
France	606	361
Portugal	153	91
Norway	130 (Site C) 147 (Site B)	1443

Table 2. Total density of benthic invertebrates sampled based on taxons in four European countries

Taxon		Number of Invertebrates
1	Ephemeroptera	251
2	Plecoptera	281
3	Trichoptera	1380
4	Coleoptera	521
5	Diptera	358
6	Hemiptera	15
7	Odonata	13
8	Annelida	23
9	Bivalvia	41
10	Megaloptera	10
11	Gastropoda	35
12	Isopoda	31
13	Eucarida	102
14	Hydracarina	153
Total		3214

Invertebrate biomass

Regarding biomass, the total dry mass of benthic invertebrates varied among taxa and sites, with distinct patterns observed across the studied countries. In two of the countries under study, Sweden and France, upstream sections exhibited the greater total biomass of invertebrates, whereas in the remaining two countries, Portugal and Norway, higher biomass levels were observed downstream (Table 3).

The biomass of each group of invertebrates exhibited diversity with regard to the species, life stage, and environmental conditions. Across taxa, Hemiptera and Odonata emerged as consistently among the highest dry mass, with individuals averaging more than four milligrams in dry weight. Conversely, the order of Hydracarina could not be weighed even as a group due to their so small size and delicate nature. Among the countries under research, individuals from Norway exhibited the lowest dry mass on average, while those from Portugal displayed the highest weight.

Table 3. Total biomass of benthic invertebrates sampled from upstream and downstream sections in four European countries

	Invertebrate dry mass (mg)	
Countries	Upstream	Downstream
Sweden	90.5	55.4
France	264.5	108.5
Portugal	57.4	95.9
Norway	37.8 (Site C) 13.8 (Site B)	480.4

Growth rate of benthic invertebrate

The results of invertebrate growth rates at the upstream and downstream sections reveal substantial variability among insect orders. Specifically, Diptera emerged as the taxon with the highest growth rates and was exceeded based on body mass and temperature at all sites. Diptera consistently exhibited faster growth rates and this pattern was observed at both upstream and downstream sections. Across all sites in the four countries under investigation, Diptera stands out with the highest growth rate and Trichoptera, on the other hand, displayed the lowest growth rate, way below the average.

No samples of Plecoptera were detected in the downstream section of Sweden, thus resulting in an absence of recorded instances. In France also, the growth rates differed between taxa and between upstream and downstream sections and the Plecoptera shows an increase in growth rate from upstream to downstream. Regarding Portugal, it can be asserted that both sites have similar average rates. A general observation is that downstream growth rates tend to be slightly higher than upstream rates in this country. In Norway, the downstream site had the lowest average growth rate. Plots of the Comparative analysis of growth rates for different weights and temperatures allow comparisons of growth rates at various orders in countries under research (Figure 3).

Figure 3. Comparative analysis of growth rates (mg, d^{-1}) across four Countries in the upstream and downstream sections

The performance of the Invertebrate growth rate was analyzed at the upstream and downstream sections across four orders. For Ephemeroptera, Portugal shows the highest downstream and upstream growth rates, while the lowest growth rate was observed in France (Figure 4 - a). In Plecoptera, Portugal demonstrated the highest growth rate, whereas France presented the lowest. The same growth rates appear for both the upstream and downstream in Portugal, suggesting similar growth in both sites. France showed a difference in downstream compared to upstream, this indicates a higher downstream growth. Growth rates varied among Plecoptera at different sites (Figure 4 - b). About the order Trichoptera, the upstream and downstream growth rates differ across countries, and the overall range of the upstream growth rate is less than that of the downstream. However, the average growth rate in Portugal outperforms with the highest rate while Norway lags with the lowest rate (Figure 4 - c). The upstream had a higher average growth rate than the downstream in the Diptera group, although the highest growth rate was recorded in Portugal. The data suggests that while the upstream section performs a higher growth rate on average, the downstream section has a wider variance in growth rates (Figure 4 - d).

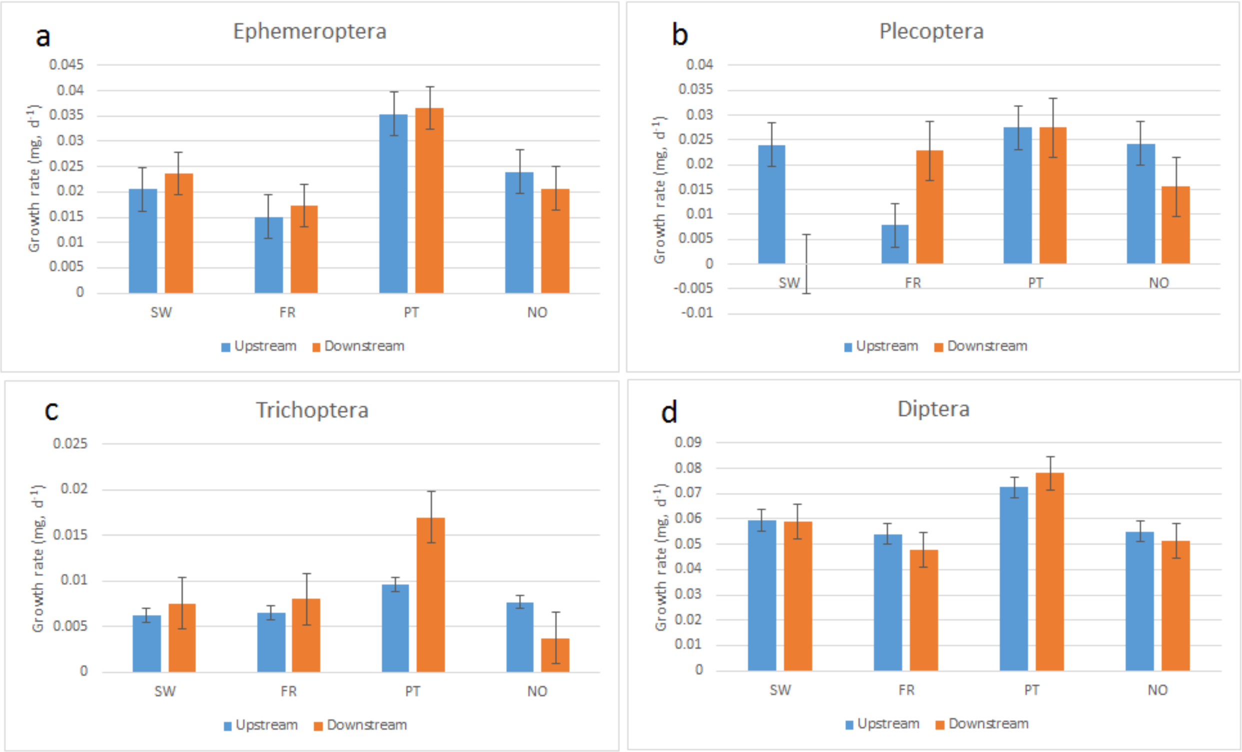

Figure 4. Comparative analysis of growth rates (mg, d^{-1}) across four Orders of insect in the upstream and downstream sections

Fish density

The fish density across the study sites revealed notable variations, particularly between countries (Table 4). France demonstrated the highest fish density both upstream and downstream while Norway has the lowest fish density. Across most countries, fish exhibited a higher density in upstream than downstream sections. However, an exception was observed in Portugal, where a higher density of fish was recorded downstream. Overall, a total of 1307 individual fish were collected from the four countries under investigation. Among these, the highest abundance was observed in upstream France, where a total of 473 individuals were captured.

Table 4. Fish density comparison between upstream and downstream sections across study sites

Sampling Countries	Density /100 m^2	
	Upstream	Downstream
Sweden	23.66	13.66
France	49.78	35.23
Portugal	7.86	9.70
Norway	1.77 (Site C) 4.94 (Site B)	0.76

Fish Condition

The condition of fish, as measured by Fulton's condition factor, serves as an indicator of their overall health and well-being, determined by their body mass in relation to their length. Across the studied countries, the fish condition factor varied from 0.9 to 1.15. In three out of four countries examined, the average fish condition was found to be better in upstream compared to downstream. The France sites seem to have better average fish conditions whereas Portugal's sites had the poorest fish conditions. □Furthermore, a consistent trend of declining fish conditions from upstream to downstream was observed across most sites (Table 5).

Table 5. Average Fish Condition (Fulton Condition Factor)

Sampling	Average Fish Condition (K)	
Countries	Upstream	Downstream
Sweden	1.150	1.013
Portugal	0.907	0.930
France	1.124	1.081
Norway	1.138 (Site C) 1.096 (Site B)	1.058

Discussion

This master thesis have detected differences in invertebrate abundance between upstream and downstream sections which can be attributed to various factors, including differences in habitat quality (Stoll et al., 2016), substrate composition (Hawkins et al, 1982), anthropogenic disturbances (Agra et al, 2021), flow regime and temperature (Chinnayakanahalli et al., 2011). Upstream areas generally have a higher invertebrate abundance and these areas commonly encounter fewer anthropogenic impacts, leading to better water quality and habitat conditions that support increased invertebrate populations. (Allan, 2004). On the contrary, in the downstream sections we often encounter a decrease in the abundance of invertebrates because of receiving pollutant inputs, sediments, and other contaminants from human activities in this section that lead to the degradation of habitat conditions (Dudgeon et al., 2006). In agreement, only in Norway a higher invertebrate density was observed downstream. It is possible that specific environmental factors in the Norwegian study site have influenced this pattern such as the observed generous amount of organic matter in this invertebrate living place (Haapala, 2001). The collected samples contained large amounts of leaves, woody debris, and plant detritus in downstream Norway. Further sampling from the same sites is needed to determine the mechanisms driving this pattern. The dominance of sensitive taxa such as Ephemeroptera, Plecoptera, and Trichoptera across the study sites suggests relatively pristine habitat conditions and good water quality (Mandaville, 2002). However, the presence of other taxa such as Diptera and Coleoptera, which are more tolerant to pollution and habitat degradation, indicates some degree of anthropogenic influence in different sites

(Mandaville, 2002). Monitoring changes in the relative abundance of sensitive and tolerant taxa over time can provide better insights into long-term trends in water quality and ecosystem health.

The variability in biomass of benthic invertebrates observed in this study suggests complex interactions between organisms and their environment within aquatic ecosystems. The contrasting patterns between the upstream and downstream sections suggest the influence of local environmental factors and habitat characteristics on benthic invertebrate biomass (Rosa et al., 2024). One factor for the difference in the average biomass of individuals among countries can be the optimal temperature for the growth of benthic invertebrates (Sundermann et al., 2022). Variations in biomass indicate potential differences in productivity and community composition (Hiddink et al., 2015). The high dry mass of Hemiptera and Odonata suggests that certain species groups by their large size within invertebrate groups may contribute disproportionately to overall biomass (Wesner, 2012). Hemipterans have an intermediate position in the food chain at streams, and the presence of Odonata populations may indicate the abundance of other invertebrates (Choudhary and Ahi, 2015). On the other hand, the inability to weigh Hydracarina due to its small size emphasizes the limitations of traditional methods for evaluating biomass and the need for alternative approaches to assess biomass in certain taxa.

The growth rate analysis provided insights into the productivity dynamics of the invertebrate communities across the study sites. It was observed that Diptera tended to exhibit higher productivity compared to other benthic invertebrates under the same temperature (Morin and Dumont, 1994). Observing the same pattern of high growth rates at Diptera in all sites suggests efficient resource utilization and adaptation to diverse ecological conditions. Similar high growth rates of Diptera have been detected (Levot, Brown and Shipp, 1979) and are often explained as a consequence of their physiological adaptations, effective feeding mechanisms, and modified digestive enzymes. Additionally, they discovered that Diptera larvae usually display high metabolic rates, enabling them to utilize available resources more effectively than other taxa. Conversely, Trichoptera's slower growth rates could mean that they are more sensitive to environmental changes (Hering, 2009). In Cressa and Barrios's (2002) studies, it was reported that the temperature did not affect the growth rate of Trichoptera, a finding that contrasts with our observations. It was shown in our study that temperature impacted the growth rate across all invertebrate groups examined. For instance, in Portugal, where the average temperature during sampling was higher than other countries, around 18 ºC, insect growth rates were recorded about 35 % higher than in other countries with lower temperatures. Fluctuations in the growth rate of invertebrates can directly impact the abundance and health of fish populations. When the growth rate of invertebrates is high, fish populations may benefit from increased food availability, potentially leading to enhanced growth. Conversely, declines in the growth rate of invertebrates can result in reduced food resources for fish, which may lead to decreased fish size and populations (Zimmerman and Vondracek, 2006). However, we did not find a significant relation between invertebrate growth rate and fish condition and population.

The observed variations in fish density across countries reflect the complex interplay of biotic and abiotic factors influencing aquatic environments (Jackson, 2001). This could indicate differing environmental conditions or resources across these sites and could also be the reason for the highest fish density both upstream and downstream in France and the lowest fish density in Norway. The high density of fish upstream in most countries is probably due to upstream habitats typically offering more favorable conditions for fish growth (Rahel and Hubert, 1991).

The better fish condition in France may be due to several factors, including the abundance and biomass of invertebrates within its riverine ecosystems. Which may contribute to improved fish conditions (Hiddink et al., 2011). Furthermore, the observed trend of better fish conditions upstream compared to downstream sites within France accords with the distribution patterns of invertebrate communities along river gradients where upstream sections typically exhibit higher abundances and biomasses of invertebrates (Jones, 2013). As a result, fish residing in upstream habitats have access to greater food resources, leading to enhanced conditions compared to their downstream counterparts. Conversely, the poor fish condition observed in upstream areas of Portugal may be linked to the lower abundance and biomass of invertebrates within this site. Declines in invertebrate productivity may limit the availability of prey for fish populations, resulting in reduced fish conditions (Hiddink et al., 2011). If fish encounter the limitation of benthic invertebrates they should spend more time finding prey, thus they reduce their intake rates while increasing energy consumption (Charnov 1976). However, in our studies, this pattern did not hold true across all countries. For instance, in Norway, despite lower densities and biomasses of invertebrates in upstream sections, fish conditions exhibited improvement. This difference demonstrates the need for further research to dig deeper into additional factors that might have influenced the results.

Conclusion

In this study, the observed disparities in invertebrate abundance and biomass and fish density across upstream and downstream sections reflect the complex interplay of various environmental factors within aquatic ecosystems in different countries. Streams with high habitat complexity and suitable water quality tend to support higher productivity of both benthic invertebrates and fish. While upstream sections generally exhibit higher invertebrate abundance due to better habitat conditions, downstream sections often experience declines in invertebrate populations. The variability in biomass and growth rate of benthic invertebrates exhibit the effect of factors such as optimal temperature and physiological adaptations that influence growth rates across different taxa. The observed variations in fish density across countries present the diverse nature of environmental influences on aquatic systems. While upstream habitats generally support higher fish densities and better conditions due to greater food availability from invertebrate prey, Norway exceptions challenge this pattern, making further investigation necessary into additional factors driving fish populations. The better fish condition observed in France underscores the importance of invertebrate productivity in supporting fish populations, showing the cascading effects of the food webs on aquatic biota. The results of this study can provide insights into the relationships and productivity potential of these aquatic organisms. Understanding these interactions is essential for effective ecosystem management and conservation strategies.

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Appendices

Popular science summary

How streambed invertebrates affect fish density

By Shirin Nozad

Introduction

The relationship between streambed invertebrates and fish indicates an important ecological relationship within aquatic ecosystems, because these organisms depend on each other for food and habitat, contributing to the overall health and balance of the ecosystem. Aquatic benthic (streambed) invertebrates, are characterized by their small size, and limited mobility, and use different microhabitats at the bottom substrate of lakes, rivers, and oceans. They are able to influence the entire food chain. Fish, on the other hand, are larger vertebrates that exist at different levels of a food chain within aquatic food webs throughout their life cycle. They are important predators that consume benthic invertebrates as a large part of their diet.

Insects as keystone contributors

One of the largest groups of benthic invertebrates is insects. Insects are indeed a significant and diverse group of benthic invertebrates in many freshwater ecosystems. They are known for their adaptability to aquatic environments during their larval stages. Some of the more important groups of aquatic insects include: Mayflies (Ephemeroptera), Stoneflies (Plecoptera) and Caddisflies (Trichoptera).

Their diverse feeding habits and adaptations make them key players in nutrient cycling and energy transfer within these ecosystems. Benthic invertebrates especially insects can act as indicators of water quality and habitat health too. Monitoring the abundance and diversity of these invertebrate communities can serve as a valuable tool for the general well-being and ecological status of aquatic ecosystems, which in turn can influence fish populations.

Did you know ...

The species of mayfly known as "Ephemera danica" during the larval stage live in aquatic environments, and after about two years, they undergo the adult stage. How long do you think they live as adults? In the adult stage, they typically live for a very short period, around 24 hours, during which they mate and reproduce to complete their life cycle.

How to evaluate invertebrate productivity at streams?

I investigated whether there is a correlation between fish density and the productivity of benthic invertebrate communities in both upstream and downstream sections of the rivers in four European countries. Stream productivity was evaluated by assessing the biomass, diversity and growth rates of these organisms by collecting samples using standard sampling techniques. As well as fish condition and density were determined to compare with invertebrate data.

What was found?

The streams with high habitat complexity and suitable water quality tend to support higher productivity of both benthic invertebrates and fish. From the analysis of data, it seems that the upstream of most of the countries under investigation had more density and growth rate of invertebrates that show more productivity in these sites, so generally more fish was seen upstream too. It was shown in this study that temperature significantly impacted the growth rate of invertebrates across all groups examined. Also, the larvae of the Diptera group (includes many common insects like mosquitoes and the house fly) tended to exhibit higher productivity compared to other streambed invertebrates. The growth rate of invertebrates can directly impact the abundance and health of fish populations.

Closing remarks

Understanding the dynamics between benthic invertebrates and fish is vital not only for knowing the structure and functioning of stream ecosystems but also for managing and conserving fish populations. Detecting this relationship can be essential for the management and conservation of aquatic environments and their associated species.

Other appendices

Table 6. Average Biomass of invertebrates in the upstream and downstream sections in four European countries

Sampling		Average Dry Mass (mg)		
Country	Taxon	Upstream		Downstream
Sweden	1 (Ephemeroptera)	0.07		0.1
	2 (Plecoptera)	0.12		-
	3 (Trichoptera)	1.01		0.12
	4 (Diptera)	0		0.08
Portugal	1 (Ephemeroptera)	0.1		0.21
	2 (Plecoptera)	0.17		0.16
	3 (Trichoptera)	0.67		0.08
	4 (Diptera)	0.63		2.75
France	1 (Ephemeroptera)	1.1		0.61
	2 (Plecoptera)	0.91		0.09
	3 (Trichoptera)	0.37		0.29
	4 (Diptera)	0.08		0.66
Norway		Site C	Site B	
	1 (Ephemeroptera)	0.12	0.1	0.07
	2 (Plecoptera)	0.05	0.1	0.06
	3 (Trichoptera)	0.35	0.2	0.35
	4 (Diptera)	0.41	0.03	0.14

Table 7. Temperature of water at the time of sampling in the upstream and downstream sections in four European countries

Sampling	Water Temperature (ºC)		
Countries	Upstream		Downstream
Sweden	12.1		11.1
Portugal	17.24		18.81
France	13.1		12.3
Norway	12.49 (Site C)	12.4 (Site B)	12.49

Table 8. Daily growth rate of Invertebrates in the upstream and downstream sections in four European countries

Sampling		Daily Growth Rate (mg, d^{-1})		
Country	Taxon	Upstream		Downstream
Sweden	1 (Ephemeroptera)	0.0205		0.0236
	2 (Plecoptera)	0.0240		-
	3 (Trichoptera)	0.0062		0.0075
	4 (Diptera)	0.0595		0.0591
France	1 (Ephemeroptera)	0.0151		0.0173
	2 (Plecoptera)	0.0078		0.0228
	3 (Trichoptera)	0.0065		0.0080
	4 (Diptera)	0.0541		0.0477
Portugal	1 (Ephemeroptera)	0.0354		0.0366
	2 (Plecoptera)	0.0275		0.0275
	3 (Trichoptera)	0.0096		0.0170
	4 (Diptera)	0.0725		0.0781
Norway		site C	site B	
	1 (Ephemeroptera)	0.0235	0.0245	0.0207
	2 (Plecoptera)	0.0285	0.0201	0.0156
	3 (Trichoptera)	0.0070	0.0084	0.0037
	4 (Diptera)	0.0512	0.0591	0.0515

Table 9. Density of fish in the upstream and downstream sections in four European countries

Sampling	Fish Density (Individual)	
Countries	Upstream	Downstream
Sweden	71	41
Portugal	70	194
France	473	303
Norway	11 (Site C) 94 (Site B)	50

Table 10. Area of fish sampling sites in the upstream and downstream sections in four European countries

Sampling	Fish area (m^2)	
Countries	Upstream	Downstream
Sweden	300	300
France	950	860
Portugal	890	2000
Norway	620 (Site C) 1900 (Site B)	6500