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Understanding the Efficiency of Energy Flow Through Aquatic Food Webs

Benjamin Mooney

Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Department of Aquatic Resources

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Benjamin Mooney, https://orcid.org/0000-0002-4482-8251, Swedish University of Agricultural Sciences (SLU), Department of Aquatic Resources

Supervisor:	**Magnus Huss, Swedish University of Agricultural Sciencies (SLU), Department of Aquatic Resources**
Assistant supervisor:	Anna Gårdmark, Swedish University of Agricultural Sciencies (SLU), Department of Aquatic Resources
Assistant supervisor:	Carolyn Faithful, Swedish University of Agricultural Sciencies (SLU), Department of Aquatic Resources
Reviewer:	Magnus Huss, Swedish University of Agricultural Sciencies (SLU), Department of Aquatic Resources
Responsible for publication:	Noél Holmgren, Department of Aquatic Resources, Swedish University of Agricultural Sciences
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Swedish University of Agricultural Sciences (SLU)
NJ Faculty
Department of Aquatic Resources
Institute of Coastal Research

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Abstract

The efficiency of energy flow through aquatic food webs is crucial for ecosystem functioning. The energy available to higher trophic levels varies across ecosystems and is influenced by factors such as nutrient availability and species composition. Recent research indicates that temperature also plays a significant role in determining energy transfer efficiency. This essay addresses the factors contributing to variability in energy flow efficiency between aquatic ecosystems, with a focus on the impacts of global climate change. It explores how food web characteristics influence energy transfer between trophic levels and examines the challenges in understanding and estimating energy flow due to complex trophic relationships, spatial subsidies, and processes across multiple biological levels. The essay highlights the dynamic response of energy flow efficiency to climate change-related environmental changes, such as rising temperatures, altered precipitation patterns, and nutrient inputs. Additionally, it identifies gaps in our current understanding and suggests important avenues for further research to improve predictions of energy flow changes, essential for informing sustainable management strategies in the face of environmental change.

Table of contents

List of tables **5**

List of figures **6**

Abbreviations **7**

1. Introduction **8**

2. Drivers of Variation in Energy Flow Efficiency Through Aquatic Food Webs **13**

2.1 Environmental Drivers 13

2.1.1 Nutrient Loading and Light Availability 13

2.1.2 Temperature 15

2.1.3 Interactions among Abiotic Variables 17

2.2 Food Web Structure 17

2.2.1 Number of Trophic Levels and Size-dependent Interactions 18

2.2.2 Community Composition 19

3. The Effect of Climate Change on Drivers of Energy Transfer Efficiency **21**

3.1 Consequences of Warming 21

3.2 Consequences of Increase Carbon and Nutrient Loading 24

4. The Necessity of Resolving Energy Flow Efficiency in Aquatic Ecosystems **26**

References **27**

List of tables

Table 1. Definitions of trophic transfer efficiency (TTE) and food web efficiency (FWE), where n denotes trophic position. 9

List of figures

Figure 1. A generalised overview of an aquatic pelagic food web, depicting how basal producers, phytoplankton and bacteria, mobilise energy for higher trophic levels by use of solar energy and dissolved inorganic carbon (DIC) and terrestrially derived dissolved organic carbon (DOC). For simplicity, recycling of carbon and the role of bacteria as decomposers is not shown. 10

Figure 2. A conceptual schematic demonstrating how energy flowing through different pathways can still result in the same trophic transfer efficiency (TTE) and food web efficiency (FWE). Comparing (a) a food web with strong interactions and low connectance and (b) a food web with weak interactions and high connectance..... 100

Figure 3. A conceptual schematic of effects of temperature on autrotrophs (A) and heterotrophs (H) and the ratio between them (H / A ratio). Redrawn and modified from O'Connor *et al*. (2009). 102

Abbreviations

CDOM	Coloured Dissolved Organic Matter
DIC	Dissolved Inorganic Carbon
DOC	Dissolved Organic Carbon
FWE	Food Web Efficiency
TER	Threshold Elemental Ratio
TSR	Temperature Size Rule
TTE	Trophic Transfer Efficiency

1. Introduction

All life depends on the utilisation of an external source of energy (Lindeman, 1942). Autotrophs synthesise carbohydrates from simple inorganic molecules (CO_2 and H_2O) with the help of sunlight energy. In doing so, energy originating from the sun becomes accessible to consumers belonging to higher trophic levels within the complex networks of feeding, or trophic, interactions among diverse species in ecosystems (i.e. food webs, Elton, 1927). The recognition of trophic structure opened the door to understanding causes of variation in ecosystem properties, such as food chain length, biomass distribution across trophic levels, community stability, and the amount of energy that moves from one trophic level to another (Vincent and Anderson, 1979; Post, 2002; Williams and Martinez, 2004; Wootton and Emmerson, 2005; Jia *et al.*, 2021).

Organisms can be classified hierarchically based on their feeding. Primary producers and bacteria represent the total basal energy source for aquatic food webs (Jones, 1992; Pomeroy *et al*., 2007). Autotrophs, including plants and algae, photosynthesise and rely on carbon dioxide as a source of carbon, whereas heterotrophic bacteria rely on oxidising organic molecules as a carbon source (Jansson *et al*., 2007; Pomeroy *et al*., 2007). As consumers graze on the basal trophic level (energy mobilizers), some but not all of the energy transfers to the consecutive trophic level. The remaining energy is lost via respiration, death, excretion or messy feeding (Jones, 1992, Eddy *et al*. 2021). The proportion of energy passed from one trophic level to another is quantified as the trophic transfer efficiency (TTE; table 1), providing a measure of how efficiently energy is transferred from one trophic level to the next, from resources to consumers (Table 1).

It can also be useful to estimate the efficiency of energy transfer from producers to the top trophic level, referred to as food web efficiency (FWE; Table 1). FWE is a measure of overall system energy efficiency, and helps understand the constraints on upper trophic level production. A high FWE means that a greater proportion of the energy produced at the basal trophic level is transferred to the top trophic level. This can influence the number of trophic levels (food chain length; Dickman *et al*., 2008) and the abundance and biomass of top predators (Stock *et al.*, 2017). Top predators are important not only for ecosystem functioning (Lennox *et al*., 2022),

but often serve as food for humans. It is therefore critical to determine and understand the causes and consequences of variation in FWE to utilise aquatic resources sustainably.

Table 1. Definitions of trophic transfer efficiency (TTE) and food web efficiency (FWE), where n denotes trophic position.

Term	Equation	Reference
Trophic Transfer Efficiency	$TTE = \frac{production\ of\ trophic\ level\ (n)}{prodiction\ of\ trophic\ level\ (n+1)}$	Mehner *et al.*, 2022
Food Web Efficiency	$FWE = \frac{production\ of\ highest\ trophic\ level}{bacterial\ production + primary\ production}$	Rand & Stewart, 1998

Understanding and studying processes controlling FWE is not straightforward (Eddy *et al*., 2021); we can attribute this to three main difficulties. First, species interact in complex food webs composed of many interdependent and variable trophic relationships. For example, predators frequently feed on more than one trophic level, including within their own trophic guild, known as intraguild predation, by feeding on a different species that exploit similar resources (Polis *et al*., 1989). Second, energy often crosses between biomes in the form of nutrients, detritus, prey and consumers, known as spatial subsidies (Polis *et al*. 1997). Finally, FWE depends on processes at multiple levels of biological organisation: energy gains, losses and life cycles at the individual level, intraspecific interactions, such as competition, at the population level, and trophic interactions at the community level (Eddy *et al*,. 2021).

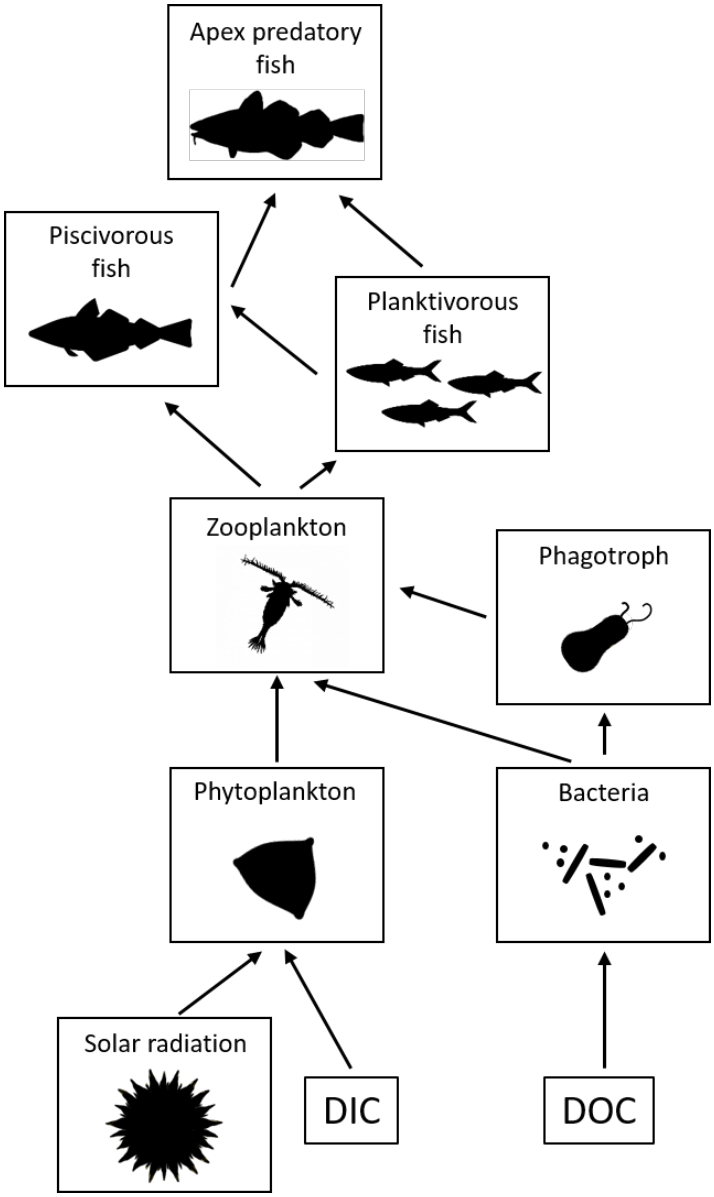

Figure 1. A generalised overview of an aquatic pelagic food web, depicting how basal producers, phytoplankton and bacteria, mobilise energy for higher trophic levels by use of solar energy and dissolved inorganic carbon (DIC) and terrestrially derived dissolved organic carbon (DOC). For simplicity, recycling of carbon and the role of bacteria as decomposers is not shown.

To better understand the processes controlling FWE is becoming increasingly important since they respond dynamically to climate change driven changes in the environment (Dickman *et al*., 2008; Ullah *et al*., 2018; Pontavice *et al*., 2019; Barneche *et al*., 2021; Baruch *et al.*, 2023). Rising global surface temperature is a key component of climate change (Blunden and Arndt, 2016; IPCC, 2023), and is more pronounced towards the earths poles (Manabe and Wetherald, 1975; Holland and Bitz, 2003; Pithan and Mauritsen, 2014; Park *et al*., 2018). For instance, in the

Baltic Sea region, air temperatures are projected to increase on average 1.4 °C to 3.9 °C by the end of this century (HELCOM, 2021; IPCC, 2023). Warming alone has profound consequences on lakes, including loss of ice cover, changes in evaporation and water budgets, warming of surface waters and alterations in mixing regimes (reviewed in Woolway *et al*., 2020). Climate change is also affecting global precipitation patterns (IPCC, 2023). However, these changes vary regionally. Southern Europe is witnessing a decline in annual precipitation, whereas northern Europe is experiencing an increase (IPCC, 2023). In northern latitudes, increased precipitation coupled with changes in land use have led to enhanced surface runoff. This results in greater inflows of terrestrial dissolved organic carbon (DOC) and iron into water bodies (Creed *et al*. 2018, Kritzberg *et al*., 2020), which contain light absorbing components, causing lakes to become browner, known as browning (Monteith *et al*., 2007, Leech *et al*. 2018). An increase in surface runoff can also carry additional nutrients which can cause eutrophication, i.e. excess of nutrients , plant and algal growth (Chapin and Stuart 2002; Malone and Newton, 2020). Eutrophication can cause the proliferation of inedible algae and cyanobacteria, which are often either unviable or poor food sources for zooplankton (Karpowicz *et al*., 2020). This can lead to a very high primary production while a relatively low zooplankton and fish production (Brett and Muller-Navarra, 1997) as less energy flows up to higher trophic levels, i.e. a lower FWE. The potential of climate change to reduce energy flows from basal producers to fish is concerning because it adds to already declining fish stocks, caused mainly by overfishing (e.g. van Rijn *et al*., 2017). Fishing is an essential source of protein for humans, providing an estimated 3.3 billion people with at least 20% of their annual per capita intake of animal protein (FAO, 2022). As we advance our understanding of climate impacts, it is increasingly apparent that we need mitigation measures aimed at preserving biodiversity and the valuable ecosystem services it provides, including the basis for biomass production and food web stability by means of sustained energy transfer (Rinke *et al*., 2019).

A crucial part to developing mitigation strategies is to understand and estimate how energy flows through food webs are responding to environmental changes. Previous studies have estimated TTE as 10% in aquatic food webs (Lindeman, 1942, Pauly and Christensen, 1995, Schulz *et al*., 2004), which many still accept. However, there are discrepancies in this value both within and between food webs. In oligotrophic systems, it is common for TTE between phytoplankton and zooplankton communities to vary between ca. 5 - 30% (Lacroix *et al*., 1999). More recent estimations report FWE ranging from 0 – 40% in aquatic food webs. (Eddy *et al*., 2021). It is therefore apparent we should not apply a general estimation of energy transfer efficiency to all food webs, given there is significant variation this value (Barnes *et al*., 2010; Stock *et al*., 2017; Eddy *et al*., 2021). Such variation in energy transfer efficiency can partly be explained by differences and importance of

nutrient availability in aquatic ecosystems, and in the species composition of aquatic food webs in determining energy transfer efficiency at each trophic coupling (Dickman *et al*., 2008; Baruch *et al*., 2023). Furthermore, recent research suggests temperature might also play an important role in constraining energy transfer efficiency (Barneche *et al*., 2021; Baruch *et al*., 2023).

Changes in the efficiency of energy transfer caused by climate change is predicted to radically alter the function and fuelling of aquatic food webs (Hayden *et al*., 2019). This essay aims to resolve which factors contribute to variability in the efficiency of energy flow between aquatic ecosystems. It discusses the diverse characteristics of food webs and how their differences determine the efficiency of energy transfer between trophic levels. Additionally, it explores the current understanding of how energy transfer efficiency is likely to change under climate change, and the potential consequences this may have for the functioning of food webs. Finally, it identifies gaps in our understanding of energy flow efficiency through aquatic food webs.

2. Drivers of Variation in Energy Flow Efficiency Through Aquatic Food Webs

The efficiency in which energy flows through entire food webs depends on energy transfer efficiencies at each trophic coupling (Hairston and Hairston, 1993). These are the product of multiple ecological and physiological processes, which vary significantly throughout nature. To understand why energy transfer efficiency is not consistent across all food webs, we must therefore understand how ecological and physiological processes vary within and between food webs.

2.1 Environmental Drivers

Seasonal change and location determine intrinsic variation in nutrient availability, light and temperature. Differences in these abiotic variables influence energy transfer efficiency in aquatic food webs, both through bottom up processes by limiting available resources for producers (Hunter and Price, 1992), and by directly affecting consumer physiology (van de Pol *et al.,* 2017; Bernhardt *et al.,*2018; Volkoff and Rønnestad, 2020).

2.1.1 Nutrient Loading and Light Availability

Nutrient and light availability are highly variable across seasonal and spatial gradients in aquatic ecosystems. Nutrient concentration and light availability are influenced by decomposers, the availability and type of organic matter in the surrounding area, the landscape's morphology and to a large extent by climate, (Seekell *et al.* 2014; Lapierre *et al*., 2015; 2018). For example, more intense periods of precipitation can alter water pathways, increasing leaching of organic compounds from surrounding catchment areas into aquatic environments (Ingram, 2016). This is likely to increase loading of associated nutrients and coloured dissolved organic matter (CDOM), which affects both nutrient concentrations and light availability in aquatic environments.

A high level of primary production, induced by high nutient concentrations, might not always result in a high FWE (Friedland *et al*., 2012). Very high levels of primary production can instead have a negative impact on FWE. This is because a

large proportion of primary producers may remain uneaten due to the sheer quantity of phytoplankton, or because eutrophic conditions are usually dominated by cyanobacterial and large inedible algae (Karpowicz *et al.,*2020). These primary producers die and decompose; meaning the energy they produced is not transferred up the food web, albeit some may be re-used as an energy source after decomposition (Fig. 1). Therefore, in cases of exceptionally high nutrient input, which leads to eutrophic conditions, FWE is likely to decline. However, when nutrient concentrations are low,limiting algal growth, increased nutrient input appears to enhance energy transfer efficiency through food webs (Dickman *et al*., 2008), particularly in oligotrophic conditions (Lefebure *et al*., 2013). This is likely because the nutritional quality of primary producers, i.e. their stoichiometry, can be favourably influenced by the addition of nutrients, up until certain concentrations (Falkowski and Davis, 2004).

Nutrient and light availability are both key determinants of primary productivity (Schindler, 1997; Smith, 1979; Karlsson *et al*., 2009) and influence the stoichiometry, and therefore nutritional quality, of primary producers in aquatic ecosystems (Hall *et al.*, 2007). The stoichiometry of primary producers can be a key factor in determining the efficiency of energy transfer between trophic levels (Dickman *et al.,* 2008). The stoichiometric 'light:nutrient hypothesis' states that an ecosystem with a high supply of light in comparison to the supply of phosphorous will yield primary producers with a high tissue C:P ratio (phosphorus poor producers; Sterner *et al*., 1997). The result is a decrease in food quality for grazers since the C and nutrient uptake of herbivores is mediated by the C to nutrient ratio supplied by their food (van de Waal *et al.*, 2009). The theory of ecological stoichiometry predicts that herbivores consuming food with an imbalance in element ratios relative to their requirements (e.g. having a high C:P ratio) will suffer a strongly reduced efficiency of converting ingested carbon in to new biomass (Schindler and Eby, 1997; Elser *et al*., 2000). That is, inadequate supply of one or more mineral elements slows the growth of animals. For instance, several studies have shown that the common zooplankton grazer *Daphnia sp*. exhibit a rapid decline in growth rate when feeding on phosphorous poor producers (Urabe *et al.,* 2002; DeMott *et al*., 1998). The nutritional makeup of food, where the relative shift from one element to another in limiting growth, is termed the threshold elemental ratio (TER) (Sterner, 1997; Frost *et al*., 2006). These stoichiometric constraints generally become less important at higher trophic levels, because the tissue composition of carnivores is more similar to that of their prey (Sterner and Elser, 2002).

Recycled nutrients and carbon, i.e. nutrients that are excreted and returned to the mineral pool by bacteria, plants or consumers, are an often-overlooked but important source of nutrients (Fuhrman *et al.,* 1992; Alongi, 1994; Quevreux *et al*.,

2020). Nutrients and carbon that are not recycled or consumed are lost, and represent energy removed from the food web. Nutrient cycling is therefore likely to preserve energy, because energy that would otherwise be lost has a 'second chance' to be utilised and transferred to consumers (Mehner *et al*. 2022). In periods of extremely high primary productivity, where there is a higher proportion of un-grazed and therefore decomposing phytoplankton, the nutritional make-up of these individuals can be recycled through the bacterial pathway ("microbial loop", Azam *et al*., 1983) and via protozoa feeding on bacteria, providing food for some zooplankton (figure 1; Stoecker and Capuzzo, 1990). Therefore, efficient recycling of nutrients in aquatic food webs may promote higher energy transfer efficiency.

The availability of nutrients also influences the contribution of the microbial pathway relative to that of the autotrophic pathway (Jansson *et al*. 2007, Fig. 1). Bacteria rely on access to organic nutrients from phytoplankton or external carbon sources (i.e. DOC from the terrestrial environment), while phytoplankton can synthesise organic nutrients from inorganic nutrients. Under high DOC concentrations, bacteria can synthesise this external supply of organic nutrients, decoupling their dependence on phytoplankton for organic carbon production and therefore act as competitors to phytoplankton for limited nutrients (Carney *et al.*, 2016). The contribution of bacteria to basal production can consequently increase under high relative to low DOC input (Carney *et al.*, 2016). When energy is produced through the microbial pathway, it often flows to higher trophic levels via more trophic couplings (figure 1). All else equal, this results in lower FWE as energy is lost during each trophic transfer (Berglund *et al*. 2007).

2.1.2 Temperature

In most aquatic systems, temperature is largely the product of latitude, altitude and season. Changes in temperature across space and time can affect aquatic food webs through altering both primary production (Lewandowska *et al*., 2012), internal biological rates (e.g. metabolic costs, Barneche and Allan 2018, Lindmark *et al*. 2022, ecological rates (e.g. species interactions, Gårdmark and Huss 2020) and therefore biomass production (Van Dorst *et al*. 2019) and community composition (Nagelkerken *et al*. 2020).

The temperature size rule (TSR) states that warming leads to shorter developmental times, but smaller adult body sizes in ectotherms (Atkinson, 1994). This pattern has been observed in ectotherms such as fish, and is generally more pronounced in aquatic environments (Ohlberger, 2013; Baudron *et al.,* 2014; Horne *et al.*, 2015, 2017), but there are also examples with no decline in adult body size (Lindmark *et al.*, 2023; Solokas *et al.,* 2023). The most widely accepted explanation for the TSR is based on metabolic rate theory, stating that higher temperatures increase

metabolism, accelerating growth rate but shortening the time fish are growing (Zhang *et al*., 2017). However, the relationship between temperature and growth may vary depending on the size and developmental size of fish (Van Dorst *et al*. 2019) as well as their sex (Van Dorst *et al*. 2024), in line with changes in optimum growth temperature as individuals grow in size (Lindmark *et al*., 2022). This suggests that while more energy can be gained through increased food intake (up to a threshold temperature), fish must spend more energy in warmer environments to keep up with costs for maintenance, which leaves less energy for biomass production (Gårdmark and Huss 2020). The resulting lower efficiency of individual energy production also implies a lower efficiency of energy transfer, as less energy is available for use by higher trophic levels.

At the base of pelagic food webs, phytoplankton communities can respond to warming by shifting to smaller cell size (Hillebrand *et al*. 2022) but sometimes also by shifts in species composition towards larger (Yvon-Durocher *et al.,* 2015; Padfield *et al*., 2018), and more carbon-rich, less palatable species (Woods *et al.,* 2003; Craine *et al.,* 2010; Yvon-Durocher *et al.,* 2015). Accordingly, a recent experiment showed how warming can be detrimental to grazers despite accelerated phytoplankton growth due to the low nutritional value of the latter in warming waters (Diehl *et al*. 2022). Generally, a shift in the edibility of phytoplankton communities induced by warmer water brings a higher proportion of uneaten individuals, whose energy is not transferred to consumers. For instance, cyanobacteria tend to dominate phytoplankton assemblages in warm nutrient-rich environments (O'Neil *et al*., 2012). As some of those taxa are not edible and even toxic, a lower proportion of individuals are eaten and the result is that less of the energy produced at the base of the food web is converted into biomass at higher trophic levels.

Another response of aquatic ecosystems to changes in temperature occurs on a temporal scale, as changes in the seasonal timing of biological events (phenology). This can lead to a temporal mismatch between consumers and their resources (Almén and Tamelander, 2020). For instance, in seasonal climates phytoplankton blooms tend to occur during spring following increased light availability (Almén and Tamelander, 2020), whereas their heterotrophic consumers grow relatively slowly owing to a slower metabolism in the colder waters that are still warming from winter (Irigoien *et al*., 2005). This means phytoplankton can bloom and outgrow consumers with the arrival of spring sunlight, whereafter the bloom is terminated by zooplankton grazing. However, the growth and rate of development of zooplankton grazers is increasing with rising temperatures (Vijverberg, 1980) owing to an increase in respiration, resulting in a higher demand for carbon consumption (Lefébure *et al.*, 2013). This accelerated growth may lead to premature consumption of desirable phytoplankton before they can proliferate

during blooms, reducing carbon fixation by photosynthetic phytoplankton and therefore diminishing energy available for the zooplankton grazer community (Dickman *et al*., 2008). This can, in turn, lead to higher grazer mortality and therefore less energy available for predators at higher trophic levels dependent on these grazers as food resources (Hairston and Hairston, 1993).

2.1.3 Interactions among Abiotic Variables

It is clear that variation in nutrient and light availability (Dickman *et al*. 2008), and potentially temperature, may partly explain the variation in energy transfer efficiency between trophic levels in different ecosystems. However, the additive effects of different abiotic factors alone cannot explain the large variation in energy transfer between food webs (Eddy *et al.,* 2021). Instead, there may be interactive effects among these, as well as between these and other factors. The two-way interaction between nutrient and light availability is complex but is still the most studied (Berglund *et al.*, 2007; Dickman *et al.*, 2008). An example is the effects of light supply on energy transfer efficiency from primary producers to herbivores, which appears to depend on whether or not producers are nutrient limited (Urabe *et al*., 2002). As for interactions with temperature, because temperature influences metabolic rates in ectotherms, we might expect interactive effects with other variables as the ability to cover costs for maintenance may also vary with nutrient demand and availability. However, the role of interactive effects in general, and those including temperature specifically, on energy transfer efficiency remain understudied and inconclusive (Lefébure *et al.,* 2013; Lesutiene *et al*., 2014; Baruch *et al.,* 2023). Given recent findings that suggest changes in carbon use efficiency and increased costs for body growth under warming (Barneche *et al*. 2021), the way in which warming waters may influence energy transfer efficiency may be key to understand and predict the effects of climate change on aquatic food webs.

2.2 Food Web Structure

Food webs are dynamic networks of energy flow, determined by feeding interactions among organisms and their environment. As such, every food web is unique in its structure and composition. The most prominent differences among food webs lie in the number of trophic levels, connectivity and strengths of trophic interactions. Below I outline how such differences in food web structure may contribute to differences in how efficiently energy flows through food webs.

2.2.1 Number of Trophic Levels and Size-dependent Interactions

Energy is lost every time a consumer eats its prey (Polis and Strong, 1996; Berglund *et al*., 2007; Armengol *et al*., 2019); therefore the number of trophic levels in a food web significantly impacts FWE (Dickmann *et al*. 2008). It is generally suggested that the number of trophic levels in food chains is constrained by productivity and basal resource availability, ecosystem size or the combination (Williams and Martinez, 2004, Post 2002). Other theories and observations suggest that in food webs characterised by low levels of size structure, where the predator is not larger than their prey, there are limited benefits for carnivores eating other carnivores, especially when there is an abundance of herbivores as prey (Hastings and Conrad, 1979). For example, lions hunting large mammals on the African savannah. In these food webs, the number of trophic levels is often limited to three. However, most aquatic food webs are size-structured (Cohen *et al*., 1993) where predators are larger than their prey. In these food webs, the number of trophic levels often exceeds three. Even in food webs with a similar number or trophic levels, food webs are often highly variable in connectance (the number of realised links in a food web, Dunne, 2005; van Altena *et al*., 2016) and interaction strength (how frequently trophic interactions occur; Wootton and Emmerson, 2005). These characteristics both contribute to how energy flows through food webs.

Given spatial and temporal overlap, the strength of aquatic predator-prey interactions is often mediated by body size (Brose *et al.,* 2006; DeLong, 2014). For a long time it was thought that a population's mean body size followed a pattern across geographic ranges, with body size increasing with increasing latitude. This is called Bergmann's rule (Bergmann, 1847), and appears to remain valid for birds and mammals and for some (e.g. some zooplankton taxa, Evans *et al*. 2015) but not all other groups (Meiri and Dayan, 2003). While body size in aquatic populations may not be driven by latitude alone, individual body size is partly driven by external pressures including temperature, oxygen availability, mortality and escpecially food availability (Ahti *et al*., 2020). The primary driver of variability in an individual's body size, however, stems from ontogenetic development, which is dependent on the amount of energy consumed. Throughout an individual's ontogeny, body size is ultimately governed by the interplay between food consumption, energy expenditure, and the allocation of net surplus energy toward somatic growth relative to reproduction (de Roos and Persson 2013).

The significance of body size extends beyond individual organisms, and influences community dynamics (de Roos & Person 2013) and food web responses to climate change (Gårdmark & Huss, 2020). Body size therefore potentially plays a part in explaining the efficiency of energy transfer, considering that interaction strengths

play a pivotal role in determining energy flows (Fig. 2). A highly connected web is likely to enhance energy transfer due to increased predation opportunities, while stronger interactions lead to more prey consumption. However, high connectivity alone does not guarantee high FWE, especially with weak interaction strengths. Similarly, strong interactions in a less connected web may result in mediocre FWE (Fig. 2). The efficiency of energy transfer within aquatic ecosystems is therefore shaped by size-dependent dynamics of predator-prey interactions, in conjunction with food web structure and environmental factors. For instance, if aquatic prey grow faster in warmed environments, they might outgrow the size at which they are vulnerable to size specific predation (Rudolf and Roman, 2018).

2.2.2 Community Composition

The species composition of aquatic communities can both be influenced by (e.g. through constraining the number of trophic levels; Dickman *et al*., 2008) and influence FWE. Shifts in community composition have important implications for the transfer of energy through food webs, most notably because some species are more edible and nutritious and of suitable size as prey than others. For instance, during warm and eutrophic conditions, it is typical that cyanobacteria proliferate phytoplankton communities in aquatic environments (O'Neil *et al.*, 2012). Cyanobacteria can potentially divert productivity into alternate food web pathways, such that it is not available to higher trophic levels (Hansson *et al.,* 2013). This is because cyanobacteria often produce allelochemicals that deter feeding (Nagle and Paul, 1998), as well as some species being toxic which sometimes causes mortality in aquatic organisms (O'Neil *et al.,* 2012). Changes in the species composition of predators can also have inferences on the transfer of energy through food webs, due to changes in feeding specialisations, size-dependant interaction strengths and metabolism (Barnes *et al.,* 2010; Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011), all of which affect net energy efficiency at the individual level and therefore biomass production. Climate change is altering the diversity and composition of aquatic communities across the globe (Fujiwara *et al.,* 2019; Zarco-Perello *et al.*, 2020; Pawluk *et al.,* 2021; Palacious-Abrantes *et al.*, 2022), which is inevitably altering the overall and relative biomass, nutrition and edibility of each trophic level. In response, FWE is likely to change too.

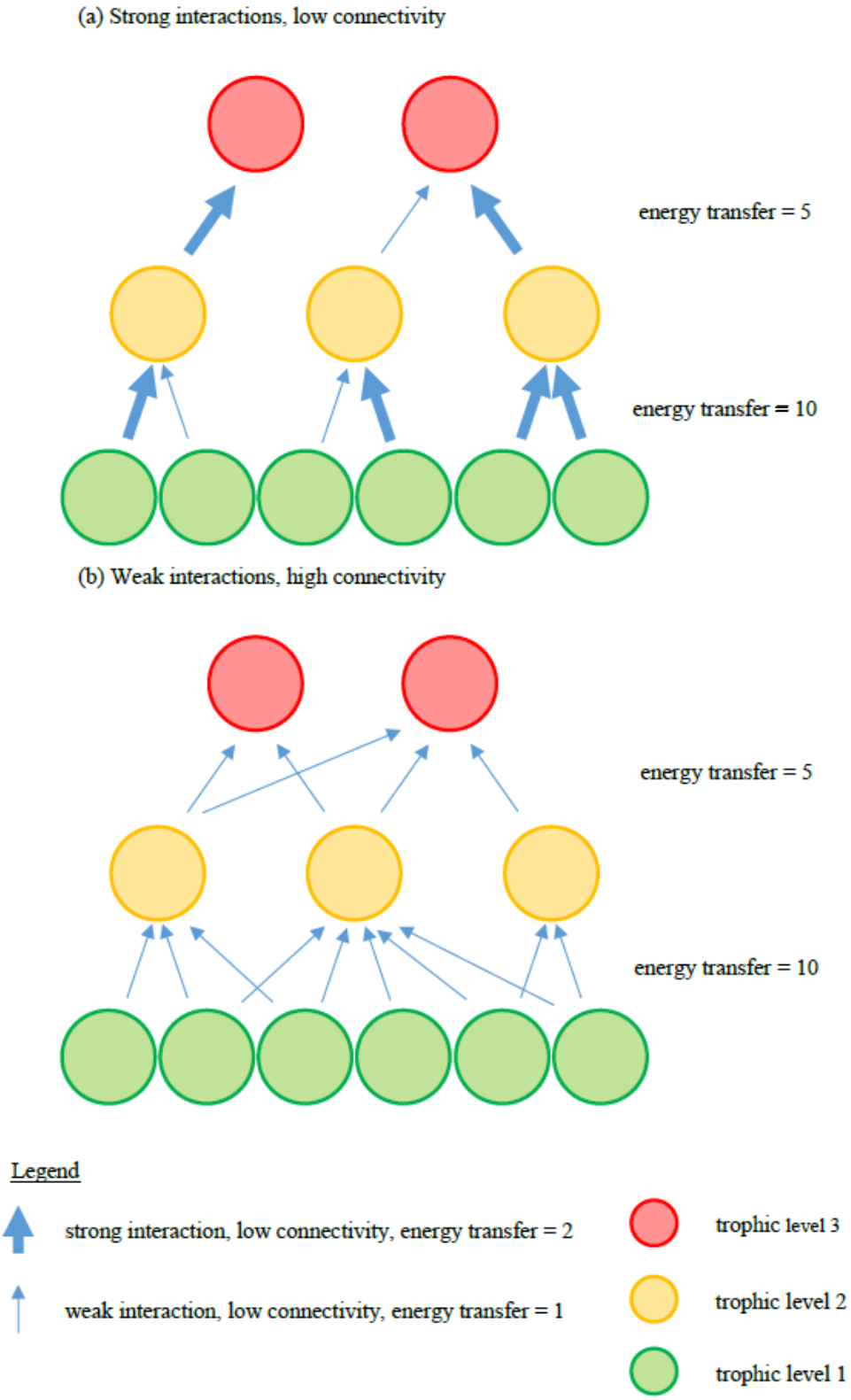

Figure 2. A conceptual schematic demonstrating how energy flowing through different pathways can still result in the same trophic transfer efficiency (TTE) and food web efficiency (FWE). Comparing (a) a food web with strong interactions and low connectance and (b) a food web with weak interactions and high connectance.

3. The Effect of Climate Change on Drivers of Energy Transfer Efficiency

3.1 Consequences of Warming

The consequences of warming on aquatic food web biomass distributions, and especially on FWE, remains unresolved. Primary production is generally predicted to increase with warmer environments (Richardson and Schoeman, 2004; O'Connor *et al*., 2009). When the effects of predation are stripped away, however, warming is thought to decrease the carrying capacity of phytoplankton (Shurin *et al.*, 2012; Atwood *et al.,* 2015; Bernhardt *et al.,* 2018; Kwiatskoweski *et al.,* 2019). This can explain why the ratio of heterotroph to autotroph biomass has been shown to increase under experimental warming (Fig. 3; Muren *et al.,* 2005; O'Connor *et al*., 2009). However, considering that the calorie requirements of heterotrophs are higher when subject to a warmer environment (Brown *et al.*, 2004; O'Gorman *et al.,* 2012; Deutsch *et al.,* 2022), warming may not always favour heterotrophs. Nevertheless, it is apparent that given a higher proportion of heterotrophs to autotrophs, there will be a higher proportion of autotrophs being consumed. Providing the increased metabolic costs of a warmer environment does not outweigh the increased consumption of primary producers, this will result in a higher TTE at this trophic linkage. To complicate matters more, we must also consider that a rise in temperature can affect organisms and food webs in other ways by directly affecting the physiology of organisms. To understand the consequences of warming on aquatic biomass distributions and energy flows through food webs, it is therefore important to consider the interplay between changes in primary production, predator-prey dynamics and the physiological responses of individuals.

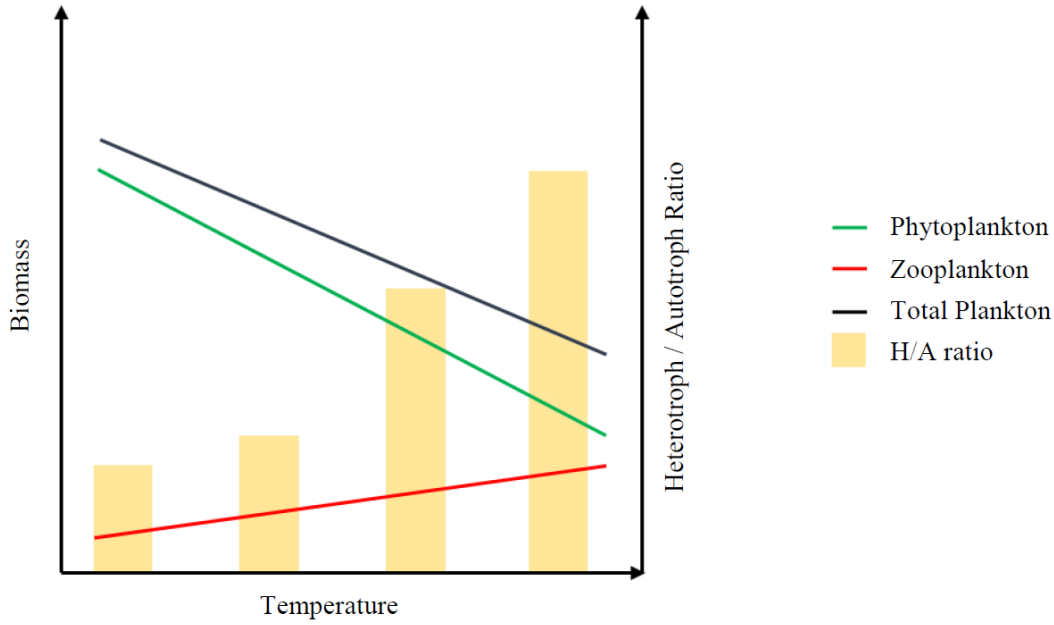

Figure 3. A conceptual schematic of effects of temperature on autrotrophs (A) and heterotrophs (H) and the ratio between them (H / A ratio). Redrawn and modified from O'Connor et al. (2009).

As waters become warmer, the poleward migration of mobile species that seek cooler water (Pinsky *et al.*, 2020; NOAA, 2022) is leading to shifts in species diversity and community composition. For those species that cannot migrate, owing to either immobility or a physically restricted environment, increased temperature can decrease species diversity, as certain species are unable to withstand warmer temperatures (Antão *et al.,* 2020). Accordingly, we see shifts in community composition toward warm water species also at high latitudes (Fossheim *et al*., 2015). To predict how changes in species diversity because of warming will affect FWE, we need to understand the relationships between species diversity and the processes that control FWE. One prediction is that a decrease in species diversity may translate to a decrease in the number of trophic levels and less linkages between trophic levels, as observed by Svensson *et al*. (2017). While there are examples that warming can decrease food web connectivity (O'Gorman *et al*., 2012), it remains unclear how altered connectivity, specifically due to warming-induced shifts in species diversity, affects FWE.

In addition to changes in taxonomic composition, warming-induced changes in body size distributions of aquatic organisms can affect trophic interactions and consequently energy flow within aquatic food webs. Several studies suggest that warming reduces mean body size in aquatic organisms (Horne *et al*. 2015), including several examples with fish (Lema *et al*., 2019; Ahti *et al*., 2020), but also

increases juvenile body growth and overall size-at-age (Huss *et al*., 2019; Lindmark *et al*. 2023). It is therefore clear that warming can result in substantial changes in how fish grow and develop, and therefore in whole fish population and community size distributions. Considering that trophic interactions in aquatic systems are largely driven by body size and associated morphological constraints (Schneider *et al*., 2012, de Roos and Person 2013), shifts in size distributions are likely to alter the way in which energy flows through food webs. For instance, the strong size-dependency of predator-prey interactions suggest that an alteration in the relative size of predators and prey organisms will change the strength of that trophic interaction. Although it seems intuitive that strengthened trophic coupling would increase FWE, it can also increase the reliance of energy to reach higher trophic levels through a single pathway. If such a major trophic coupling collapses, the effect on top predators, such as those targeted in fisheries, would be greater than in a food web where the energy reaching top trophic levels is channelled through several pathways (Fig. 2). Theoretical models have indeed predicted an increased risk for such a collapse of top predators in aquatic systems under warming due to shifts in size-dependent predator-prey interactions (Lindmark *et al*., 2019, Thunell *et al*. 2021).

In addition to shifts in the timing of seasonal events, spatial distribution, species composition and size distributions, rising environmental temperatures may also affect energy flows through food webs in other indirect ways. One example is the expected release of ammonia from sediment under warming (Sanz-Lazaro *et al*., 2015), which coupled with the predicted rise in rainfall and therefore transport of compounds into waterways is likely to contribute to the rise of nutrients in waterways (IPCC 2023). This could set in motion a cascade of negative effects in the form of simultaneous eutrophication and darkening of waters, potentially lowering the efficiency in which energy flows through aquatic food webs.

Finally, the direction and magnitude of change caused by climate warming will vary regionally, one example being that warming will melt permafrost at high latitudes, releasing trapped DOC that may flow into waterways (Zimov *et al*., 2006). At lower latitudes, concentrations of DOC in lakes are instead predicted to fall as droughts intensify and streams dry up (Schindler & Eby, 1997). Consequently, climate change will continue to drastically affect the drivers that control FWE. However we currently largely lack research on how FWE responds to these changes at both regional and local scales.

3.2 Consequences of Increase Carbon and Nutrient Loading

In addition to warming, climate change can indirectly increase nutrient loading in waters across the globe through changes in land use, precipitation and terrestrial productivity (Sinha *et al*., 2017). This affects both the supply of nutrients, such as nitrogen and phosphorous, and the supply of coloured carbon derived from the terrestrial environment, leading to humification and eutrophication. Hummification is the formation of humus produced by decomposition of dead organic matter both in land and in water.

Land use change is altering the amount of water, nutrients and carbon that is entering waterways, e.g. as the ground becomes less permeable through urbanisation, afforestation or areas being deforested and with land being used for agricultural purposes (Kritzberg, 2017). Climate change is generally increasing the frequency and severity of storm events and heavy precipitation around the globe, although this varies spatially (IPCC, 2023). Overall, these processes are acting together to change surface run off, which at high latitudes is increasing the amount of organic matter entering waterways, including coloured carbon (de Wit *et al.,* 2016; Kritzberg *et al*. 2020). This is related to an increase in the severity and frequency of humification, leading to browning (de Wit *et al.,* 2016 and sometimes eutrophication (Karpowicz *et al.,* 2020) of water bodies. Karpowicz *et al*., 2020 reported TTE from phytoplankton to zooplankton as low as 0.001%, owing to very high ("eutrophic") abundances of phytoplankton and blooms of the large-celled flagellate *Gonyostonum semen* under high humification, which is generally inedible for most (at least smaller) species of zooplankton due to its large body size and other physical adaptations (Johansson *et al*. 2013). Hence, under high input of organic matter rich in humic substances, the efficiency of carbon transfer between phytoplankton and zooplankton may decline (Karpowicz *et al.,* 2020).

Organic matter brought by increased surface runoff can favour microbial production in aquatic ecosystems (Jansson *et al*. 2008), potentially altering the efficiency of carbon transfer and therefore affecting higher trophic levels. Microbial production may be favoured because an increase in terrestrially derived organic matter means bacteria are no longer as reliant on organic carbon compounds from phytoplankton. Some consider this will reduce pelagic production at higher trophic levels, as there are more trophic couplings through the bacterial pathway (fig. 1; Blomqvist *et al*., 2001; Berglund *et al*., 2007; Jansson *et al*., 2007). However, the pathway of carbon transfer is highly variable across food webs so this might not always be true (Lefebure *et al*., 2013). Whether an increase in the fraction of microbial production because of surface runoff decreases FWE may therefore depend on the individual food web in question.

In addition to the loading of organic carbon in aquatic ecosystems altering the relative importance of the bacterial energy pathways, the composition of macronutrients in water can also influence energy transfer (e.g. carbon vs. nitrogen; Peacock *et al*. 2022). Furthermore, atmospheric CO_2 concentrations are expected to rise significantly (IPCC, 2023), which can lead to altered C:N:P ratios of phytoplankton and potentially affect the efficiency by which carbon is converted to organismal biomass (van de Waal, 2010). Redfield's famous 'Redfield ratio' (Falkowski and Davis, 2004) suggests that the elemental composition of plankton reflects that of their environment. As atmospheric CO_2 levels rise, so will the concentration of carbonic acid in the ocean and lakes (Doney *et al.,* 2009). This is because of an increase in the gradient between atmospheric CO_2 and dissolved carbon in the water, causing carbon to diffuse from air to water. As a result, it is likely that C:N:P ratios of phytoplankton will be higher as these organisms will have a more ready supply of carbon. Considering the theory of ecological stoichiometry, which predicts that this will reduce the efficiency of converting carbon to new biomass (Schindler and Eby, 1997; Elser *et al*., 2000; Sardans *et al.*, 2021), it is likely that FWE will decrease providing all else is equal.

As outlined above, the consequences of climate-induced changes in carbon and nutrient loading on aquatic food webs is likely to affect energy flows. How and to what extent, however, is likely to depend heavily on specific ecological contexts. For instance, an increase in nutrient loading to aquatic ecosystems can lead to shifts in microbial and pelagic production. Whether or not this shift reflects a change in stoichiometry, or the relative contribution of the microbial versus autotrophic production, the result is a change in how efficiently energy flows from basal producers to higher trophic levels.

4. The Necessity of Resolving Energy Flow Efficiency in Aquatic Ecosystems

The efficiency of energy transfer in aquatic food webs under climate change is a pressing problem to resolve, influenced by many ecological and physiological factors. Environmental drivers, including nutrient and light availability, temperature, and their interactions, are likely to play a significant role in shaping how efficiently energy flows through food webs under climate change.

For example, climate induced warming can lead to increased metabolic costs and shifts in community composition, phenology, and body size, all of which can affect energy flows in food webs. Similarly, climate induced changes in precipitation are affecting nutrient and light availability, which influence microbial and autotrophic primary productivity and stoichiometry. In turn; these changes can affect the efficiency of energy transfer between trophic levels. Even more, the interplay between these abiotic factors are largely unresolved.

The effects of climate change on FWE are likely to be region-specific due to significant biotic variation between food webs, namely large variation in species composition, locally adapted species, and differences in the number of trophic levels. In addition, there are temporal differences in the rate of warming versus nutrient loading and changes in light availability between regions. Additionally, these variables might interact to determine energy transfer efficiency based on their relative change. Also the assumption that warming affects all individuals of a population equally is a simplification that can bias predictions of the biological impacts of climate change, including predictions concerning energy transfer efficiency.

In summary, the efficiency by which energy flows through aquatic food webs is a dynamic and region-dependent process influenced by a wide range of biotic and abiotic factors. The future of aquatic ecosystems and the services they provide, such as fish biomass production, depends on our ability to understand and mitigate the challenges posed by climate change. As global warming incessantly alters aquatic ecosystems, it is crucial to overcome major knowledge gaps in our understanding of how changes in temperature, nutrient loading and light availability interact to affect energy flows through food webs.

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