Transfer of Essential Substances from Phytoplankton to Zooplankton in Freshwater Ecosystems (Review)

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Abstract—In freshwater ecosystems, the efficiency of transfer of essential substances from phytoplankton to zooplankton, measured as the ratio of the production of these substances in zooplankton to their production in phytoplankton, determines the functioning of higher trophic levels. In addition to carbon, primary producers transfer essential substances, including polyunsaturated fatty acids (PUFAs), nitrogen (N), and phosphorus (P), up the trophic chain. The transfer efficiency of these substances significantly varies in nature depending on environmental factors, which is reflected in the quality of biological resources. The purpose of this review is to analyze the mechanisms regulating the efficiency of the transfer of essential substances from phytoplankton to zooplankton and establish the main factors that may influence the efficiency of their transfer.

ESSENTIAL SUBSTANCES TRANSFERRED FROM PHYTOPLANKTON TO ZOOPLANKTON

The functioning of trophic chains in freshwater ecosystems depends on the efficiency of transport of essential substances from producers to higher trophic levels. The transfer of carbon up the trophic chain is accompanied by the loss of some portion of the substance due to an incomplete assimilation of the biomass of the previous trophic level by consumers. About 10% of carbon is transferred from one trophic level to the next one (Lindeman, 1942). In addition to carbon (C), physiologically important substances are also transferred through trophic chains; these essential substances include polyunsaturated fatty acids, eicosapentaenoic acid (20:5, omega-3) (EPA) and docosahexaenoic acid (22:6, omega-3) (DHA), N, and P. In nature, a shortage of essential substances in food resources is often observed for zooplankton. This is due to the large difference between their content in food and zooplankton demands (Sterner and Hessen, 1994; Brett and Müller-Navarra, 1997; Twinning et al., 2016). Therefore, it is important to know the efficiency of the transfer of essential substances from phytoplankton to zooplankton, since this determines the quality of zooplankton as a resource for higher trophic levels.

Fatty Acids

Fatty acids are bioactive molecules responsible for many bodily functions. Some of them are used for catabolism and others for physiological processes (Bell and Tocher, 2009; Taipale et al., 2011). In particular, PUFAs included in phospholipids are used as a building material for cell membranes. Planktonic communities are the main suppliers of essential PUFAs up the trophic chain, in particular, to fish. DHA is a priority acid. This molecule is contained in the membranes of nerve tissue cells and is critical for reproductive functions in fish (Izquierdo et al., 2001). Its deficiency can lead to a loss of vision (Bell et al., 1995). EPA is involved in the production of biologically active hormone-like substances, namely, eicosanoids (Heckmann et at., 2008; Schmitz and Ecker, 2008). Eicosanoids serve to regulate the cardiovascular system, blood clotting, and immune response in fish. They can also be used to synthesize DHA (Jardine et al., 2020). It has been repeatedly shown that the deficiency of EPA limits the growth and reproduction of daphnids (Martin-Creuzburg et al., 2010; Sperfeld and Wacker, 2011).

Nitrogen and Phosphorus

Nitrogen and phosphorus determine the physiology of consumers (Frost et al., 2005; Wagner et al.,

2013). Stoichiometric ratios between C, N, and P are important for consumers. Inconsistencies of the stoichiometric C : N : P ratios in food resources to the physiological demands of zooplankton may affect the synthesis of lipids, proteins, and nucleic acids (Wagner et al., 2015). These changes in metabolism entail a decrease in the rates of individual growth, reproduction, and survival (Sterner, 1993; Frost et al., 2005). The C : P ratio in nature often exceeds threshold values, i.e., the level at which the production of crustaceans begins to be limited by phosphorus.

The purpose of this review is to analyze the mechanisms regulating the efficiency of transfer of essential substances from phytoplankton to zooplankton and establish the main factors that may influence the efficiency of their transfer. The transfer efficiency of essential substances depends on their content (i.e., their weight per unit of carbon) and production in both phytoplankton and zooplankton.

CONTENT OF ESSENTIAL SUBSTANCES IN PHYTOPLANKTON

Fatty Acids

The fatty acid profile of phytoplankton varies widely and can depend both on the taxonomic structure and on environmental conditions. M.I. Gladyshev et al. (2007) showed that changes in the indices of food quality in the Bugach eutrophic reservoir, measured in terms of the content of essential substances and stoichiometric ratios, were more correlated with the dynamics of the taxonomic structure of phytoplankton than with the environmental conditions. In particular, the cyanobacterium *Anabaena flos-aquae* (Lyngb.) Breb. contained only α-linolenic acid (18 : 3, omega-3) (ALA), the diatom *Stephanodiscus* spp. contained mainly EPA, and the dinoflagellate *Peridinium* sp. was especially rich in DHA. The data of (Gladyshev et al., 2007) indicate that different algal species have a specific structure of the elemental and PUFA compositions. Therefore, it can be concluded that the quality of food resources largely depends on the taxonomic composition of phytoplankton.

Other researchers have also paid attention to the species specificity of the fatty acid profile in algae (Strandberg et al., 2015). It was shown that dinophytes are characterized by a high content of DHA (Ahlgren et al., 1997; Sushchik et al., 2004; Gutseit et al., 2007). Diatoms are characterized by a high EPA concentration, which can reach 30% of total FAs (Caramujo et al., 2008; Breuer et al., 2013; Bellou et al., 2014), while the content of EPA in cryptophytes and dinophytes does not exceed 10% (Ahlgren et al., 1992, Taipale et al., 2013). Cryptophytes are characterized by stearic acid (STD) (18:4, omega-3) (Ahlgren et al., 1992). Cyanobacteria cannot synthesize PUFAs with a chain length of more than 18 carbon atoms; however, they synthesize PUFAs with 18 carbon atoms (Tocher

et al., 1998). In addition, the content of PUFAs can also significantly vary within the same taxonomic group. N.N. Sushchik et al. (2004) showed that two diatom species significantly differed in EPA content. In particular, the concentration of EPA was insignificant in diatoms *Cyclotella atomus* Hust. and *C. meneghiniana* Kutz, while *Stephanodiscus hantzschii* Grun. and *S. minutulus* (Kutz.) Cleve & Moller contributed greatly to the total EPA content in seston. Among cyanobacteria, two species, *Anabaena flos-aquae* Bréb. ex Born. & Flauh. and *Planktothrix agardhii* (Gom.) Anagn. & Kom., showed a high correlation with α-linolenic acid (ALA), while this FA was absent in two other species, *Aphanizomenon flos-aquae* Ralf. ex. Born. & Flah. and *Microcystis aeruginosa* (Kütz.) Kütz. O. Kormilets (2019) noted a high variability in the FA content depending on the species identity and habitat. For example, freshwater chrysophytes synthesize large amounts of fatty acids of the n-3 and n-6 families, while marine species of Chrysophyceae are poor in fatty acids of the n-6 family.

Species-specific differences in the composition of FAs in algae are determined by the fact that different taxa differ in their sets of enzymes (desaturases); therefore, they synthesize different FAs (Gugger et al., 2002; Dijkman and Kromkamp, 2006; Kelly and Scheibling, 2012; Galloway and Winder, 2015). The availability of a certain set of desaturases is determined by the genotype. Although the differences in the composition of FAs and stoichiometric ratios are great between the taxa, these parameters may also vary depending on environmental conditions.

The amount of PUFAs decreases under stress conditions. For instance, an increase in temperature leads to a decrease in the content of PUFAs both in cyanobacteria and in algae (Sushchik et al., 2003). Global climate warming may lead to a decrease in the production of PUFAs as a result of the capability of algal cells for homeoviscose adaptation, i.e., their ability to maintain a constant viscosity of cell membranes by reducing the proportion of PUFAs in lipids when the environmental temperature increases (Guschina and Harwood, 2006; Hixson and Arts, 2016). This was confirmed by Hixson and Arts (2016), who revealed a significant decrease in the proportion of long-chain omega-3 PUFAs and a simultaneous increase in the proportions of omega-6 FAs and saturated FAs in the total amount of FAs in algal cells with an increase in water temperature. Based on linear regression models, the authors predicted that an increase in water temperature by 2.5°C would lead to a decrease in the global production of EPA and DHA by 8.2 and 27.8%, respectively. On the contrary, the amount of PUFAs is expected to increase in cell membranes under the effect of low temperatures, which is determined by the synthesis of the corresponding desaturases in this case (Guschina and Harwood, 2006). In addition, temperature increase can involve the replacement of the main producers of PUFAs (diatoms, cryptophytes,

and dinophytes) by cyanobacteria of poor quality, which do not produce EPA and DHA (Caramujo et al., 2008). Therefore, the decrease in PUFAs with an increase in temperature may be caused by two factors: a change in the taxonomic composition and the suppression of the synthesis of desaturases. In addition to temperature, the desaturase activity may be induced by the effect of high oxygen concentrations in the water. An increase in temperature leads to a decrease in the concentration of dissolved oxygen, which causes an even greater suppression of the activity of desaturases. These two factors can reinforce each other (Strandberg et al., 2015).

Stoichiometric Ratios

Redfield (1934) noted for the first time that the average N : P ratio for marine algae was 16 : 1. Later, many researchers showed that this ratio was far from constant and depended on the species identity and environmental conditions (Klausmeier et al., 2004). For instance, it was shown that the N : P ratio in biomass varied from 15 to 42 for *Chlorella vulgaris* Beijer, while it was 7−32 for *Scenedesmus obliquus* (Turp.) Kütz. (Beuckels et al., 2015). The content of N and P in algal cells varies over a wide range (Sterner and Hessen, 1994). Thus, the content of P can vary from 0.03 to more than 3% of the dry weight and that of N from 3 to 12% in algal cells (Reynolds, 2006).

Reynolds (2006) noted that the growth of phytoplankton was possibly regulated by the co-limitation of N and P, instead of by either of them individually. His study showed that the growth of phytoplankton was limited at concentrations of dissolved inorganic P below 3−10 µg/L and dissolved N below 100−130 µg/L. These are threshold concentrations of nutrients, below which the growth of phytoplankton slows. Different algal species have their own species-specific demands and, consequently, their own threshold concentrations. This was confirmed by A.P. Levich and N.G. Bulgakov (Levich and Bulgakov, 1992), who showed that the taxonomic and size structures of phytoplankton changed in dependence on the N : P ratio. High N : P values (20−50) were favorable for the development of protococcal algae, while the decrease in the N : P ratio to 5−10 led to the dominance of cyanobacteria in the community (Bulgakov and Levich, 1995). The authors concluded that the ratio of concentrations of nutrients in the environment should be recognized as an independent abiotic factor that regulates the taxonomic and size structure of phytoplankton, thereby changing its quality as a food resource for zooplankton.

The relationship between N and P can be explained by the fact that the assimilation of P by algae depends on the concentration of dissolved inorganic N, while the assimilation of N does not depend on the concentration of inorganic P (Beuckels et al., 2015), which is explained by different functions of N and P in cellular metabolism (Loladze and Elser, 2011). In microalgae,

N is required mainly for protein synthesis. The deficiency in N causes a reduction of protein synthesis, which leads to a decrease in the number of ribosomes and ribosomal RNAs. Since most of the P content in a cell is stored in ribosomal RNA, a decrease in the number of ribosomes leads to a decrease in the demand for P (Beuckels et al., 2015). Therefore, the reduction of N assimilation also entails the reduction of assimilation of P.

The content of N and P in phytoplankton increases with an increase in the concentration of inorganic compounds of these elements in the environment (Sterner and Elser, 2002; Beuckels et al., 2015). In addition, when the concentrations of N and P are excessive, algae can store nutrients for future use (Eixler et al., 2006). Diatoms accumulate nitrates in the central vacuole (Coppens et al., 2014). Some species can accumulate P to 3% of dry weight in the form of polyphosphate granules (Eixler et al., 2006; Powell et al., 2009).

In addition, stoichiometric ratios can depend on cell size (Finkel et al., 2010), since the cell size influences both the absorption of elements and their assimilation (Schulhof et al., 2019). Small cells assimilate nutrients under conditions of their deficiency more efficiently than large cells, since they have a higher ratio of the surface area to the volume and a thinner diffuse boundary layer. However, large cells can store more nutrients. Therefore, small algae gain a competitive advantage under conditions of low trophic level, while large algae are more competitive in an environment with high trophic level and rapidly changing concentrations of nutrients (Edwards et al., 2011; Cloern, 2018). Schulhof et al. (2019) revealed that C : P of the fine-fraction of algae (<30 µm) was lower than that of the coarse-fraction (>30 µm) at low trophic level. C : P in the coarse-fraction of algae decreased in algae with an increase in trophic level, while C : P of the fine-fraction of algae did not change, which indicated a higher sensitivity of large cells to the concentration of inorganic phosphorus in the medium.

It should be noted that the content of nutrients in algae depends on temperature (Schulhof et al., 2019). Climate warming sometimes leads to a decrease in the C : P and N : P ratios in algae, which is explained by an increase in the concentrations of nutrients in the environment as a result of an increase in the rate of their regeneration by consumers or microbial communities with an increase in temperature (Velthuis et al., 2017). Warming can also have opposite effects; i.e., it can increase N : P in phytoplankton, which is explained by an increase in the rate of protein biosynthesis and a decrease in the number of ribosomes (Toseland et al., 2013). Therefore, stoichiometric ratios in phytoplankton depend not only on taxonomic identity, but also on abiotic factors.

CONTENT OF ESSENTIAL SUBSTANCES IN ZOOPLANKTON

Fatty Acids

Zooplankton can synthesize only some PUFAs, while the bulk of PUFAs should be consumed by zooplankton together with food. For instance, daphnids synthesize only 0.5% of EPA from lipoic acid (Twining et al., 2016). Therefore, the composition of PUFAs in consumers may depend on their content in food resources. Hessen and Leu (2006) studied the composition of fatty acids in zooplankton and seston. The results of their study clearly showed that the fatty acid profile in daphnids differed between lakes with different taxonomic structures of phytoplankton; the composition of FAs was correlated with the taxonomic composition of phytoplankton. However, the average content of EPA was 1.7 times higher in daphnids than in phytoplankton, while the content of DHA was 0.08 times lower in daphnids than in seston. Therefore, daphnids can regulate the content of PUFAs. Here, it should be noted that cladocerans require more EPA and less DHA than copepods (Desvilettes et al., 1997a; Weers et al., 1997; Ballantyne et al., 2003; Brett et al., 2009; Ravet et al., 2010; Gladyshev et al., 2015). Therefore, the content of EPA is high and that of DHA is low in zooplankton when it is dominated by daphnids.

It has been repeatedly noted that zooplankton exhibit homeostasis (Hessen and Leu, 2006); i.e., it can maintain a relatively constant elemental and biochemical composition. Therefore, mechanisms regulating the content of essential substances in the body might develop in zooplankton in the process of evolution. There are different mechanisms for increasing the content of these substances in zooplankton.

Essential FAs, i.e., FAs that are not synthesized de novo by zooplankton, are not often consumed in the required amount; however, they can accumulate in the tissues of invertebrates and even exceed their content in food resources. Taipale et al. (2011) studied the patterns of PUFA regulation in cladocerans. When high-quality food (*Cryptomonas ozolinii* Skuja) for daphnids was replaced by lower quality food (*Scenedesmus obliquus*), they began to selectively retain EPA and arachidonic acid (20 : 4, omega-6) (ARA), i.e., more essential FAs. The isotopic method based on δ^{13}C showed that EPA and ARA could be synthesized in the body of *Daphnia magna* (Straus, 1820) from FA precursors received with food. Molecules of some FAs are converted into the molecules of other FAs through the elongation of the carbon chain or the formation of unsaturated bonds as a result of desaturation (Dalsgaard et al., 2003; Brett et al., 2009). The synthesis involves enzymes increasing the length of the carbon chain (elongases) and desaturases (Gladyshev, 2012). Therefore, daphnids can increase the content of essential FAs due to their biosynthesis under conditions of poor quality of food resources.

Different taxa differently regulate the composition and content of PUFAs. For instance, cyclops accumulate predominantly DHA (Desvilettes et al., 1997b), diaptoms convert EPA to DHA (Ravet et al., 2010), and cladocerans biosynthesize EPA and ARA from their precursors (Kainz et al., 2004, Ravet et al., 2010; Taipale et al., 2011). Among all FAs, DHA is characterized by the highest coefficient of accumulation in heterotrophs, since this acid is not catabolized for energy production, unlike less essential FAs (Jardine et al., 2020). With respect to its properties, it is not suitable as a substrate for β-oxidation. It was shown that the content of DHA was higher in zooplankton than in seston to a greater extent than other FAs, including EPA (Sakharova et al., 2021; Feneva et al., 2021). It should be noted that ALA, which can be synthesized by cyanobacteria, can be converted into EPA in crustaceans. Therefore, nontoxic cyanobacteria can support the growth of daphnids.

Other mechanisms for increasing the content of PUFAs in zooplankton are also possible. The selectivity of consumption of more essential food particles is typical mainly for copepods (De Mott, 1986). It is known that the range of food particles consumed by filter-feeding crustaceans is limited only by their size (Sommer and Sommer, 2006). They cannot selectively filter higher quality food particles; however, phytoplankton is vertically distributed so that the most essential algae (cryptophytes) are often dominant in the metalimnion, where filter-feeding crustaceans can also concentrate (Burns et al., 2011). Cladocerans can also differently metabolize food particles; as a result, the diet of filter-feeding crustaceans can be selective (Feniova et al., 2018). The selective feeding of zooplankton is confirmed by data on the isotopic composition (δ^{13}C) of zooplankton and phytoplankton from oligotrophic, mesotrophic, eutrophic, and dystrophic lakes (Taipale et al., 2016). Based on an analysis of stable isotopes, Taipale et al. showed that the δ^{13}C of crustaceans was correlated with the δ^{13}C of individual algal taxa, rather than with δ^{13}C of total phytoplankton. Selective feeding was also noted by Gladyshev et al. under field and experimental conditions (Gladyshev et al., 1999); they showed that *Ceriodaphnia quadrangula* (O.F. Müller, 1785) mainly consumed *Cryptomonas erosa* Ehr., although it was not the only food resource in the environment.

Stoichiometric Ratios

The stoichiometric N : C and P : C ratios in zooplankton species vary within a narrow range; i.e., these parameters are more stable in zooplankton than in phytoplankton (Sterner, 1989; Hessen, 1990; Andersen and Hessen, 1991; Dubovskaya, 2009). Therefore, it can be stated that zooplankton species are characterized by the homeostasis of elemental ratios (Sterner, 1990; Dubovskaya, 2009). In freshwater zooplankton,

the C : N : P atomic ratios are species-specific and vary within a narrow range. In particular, according to Andersen and Hessen (1991), the average value of this ratio is 212 : 39 : 1 in *Acanthodiaptomus denticornis* (Wierzejski, 1887), while it is 85 : 14 : 1 in *Daphnia longispina* (O.F. Müller, 1776). They also showed that the zooplankton species differed less in the content of nitrogen (N : C) than in the content of phosphorus (P : C). And, the content of P increased in the series *Acanthodiaptomus denticornis, Heterocope saliens* (Lilljeborg, 1863), *Bosmina longispina* (Leydig, 1860), *Holopedium gibberum* (Zaddach, 1855), *Diaphanosoma brachyurum* (Liévin, 1848), and *Daphnia longispina*.

It should be added that large and small cladoceran species (the family Daphniidae) differ in stoichiometric ratios. Namely, large daphnids have a lower C : P value and are therefore more sensitive to phosphorus limitation than small species of this family, such as *Ceriodaphnia* sp., which, on the contrary, are more sensitive to nitrogen limitation (Elser et al., 1996, 2000; Iwabuchi and Urabe, 2010). Therefore, the content of these elements in cladocerans is mainly determined by their taxonomic composition.

Similarly to PUFAs, the content of N and P is often higher in zooplankton than in food resources (Urabe and Watanabe, 1992). When the content of N and P is deficient in food, crustaceans can concentrate these elements in their tissues to satisfy their needs. M. Karpowicz et al. (2019) revealed differences in the C : P and C : N ratios between phytoplankton and zooplankton in experimental mesocosms. For instance, the C : P ratio was 2−3 times lower in zooplankton than in seston. The increase in the content of P in zooplankton was accompanied by a decrease in the concentration of phosphates in the water. Therefore, the authors concluded that zooplankton could accumulate P, thereby serving as some kind of phosphorus sink. It should be noted that the level of P accumulation is higher in the tissues of cladocerans than in the tissues of copepods. In particular, the content of P in herbivorous cladocerans (*Bosmina*, *Diaphanosoma*, *Holopedium,* and, in particular, *Daphnia*) is up to 2% of dry weight, while its content in freshwater copepods varies from 0.4 to 0.8% of dry weight (Sterner and Hessen, 1994).

Stoichiometric ratios can be influenced by abiotic factors. An increase in temperature leads to a decrease in C : P as a result of a decrease in C reserves in crustacean tissues, which involves changes in P metabolism (Prater et al., 2018). In addition to temperature, the animal metabolism can also be influenced by other factors, such as light, CO_2, predation, and parasitism (Prater et al., 2018). Therefore, the stoichiometry of zooplankton can vary throughout the season. The effects of abiotic and biotic factors on animal metabolism explains frequently observed differences in the biochemical and elemental compositions of zooplankton from different habitats. However, these differences are less significant than those between different taxa.

There are different mechanisms for regulating the relative constancy of stoichiometric elemental ratios in zooplankton, e.g., by increasing the feeding rate or retaining N or P in tissues when the content of these elements is deficient (Sterner and Elser, 2002). Excess of N or P can be excreted together with waste products (Sterner and Hessen, 1994; Sterner and Elser, 2002). According to the concept of threshold elemental ratios (TERs), the element which is the most deficient is assimilated with greater efficiency. In nature, the content of P is often deficient for zooplankton. Therefore, P is often assimilated with 100% efficiency, while C is assimilated with 60% efficiency; in addition, the efficiency of C assimilation decreases linearly with an increase in C : P (Hessen et al., 2013). The release of P may completely stop if the C : P ratio begins to exceed 320−430 in food resources, i.e., at a low content of P (Olsen et al., 1986; Karpowicz et al., 2019). Another way to regulate stoichiometric ratios is the removal of excess of C during respiration or its release together with organic waste products. In addition, excess of C can either not be assimilated in the gut or accumulate in the form of lipids. Therefore, zooplankton can increase the content of essential substances in its tissues by regulating the rate of food consumption and metabolic and physiological processes.

PRODUCTION OF ESSENTIAL SUBSTANCES IN PHYTOPLANKTON AND ZOOPLANKTON

Since the efficiency of transfer of essential substances from phytoplankton to zooplankton is determined as the ratio of their production in zooplankton to their production in phytoplankton, the higher the production of essential substances in zooplankton, the higher the efficiency of their transfer. The amount of C rarely limits the growth of crustaceans in freshwater ecosystems except for oligotrophic water bodies (White, 1993). Therefore, the production of zooplankton under mesotrophic and eutrophic conditions can be limited by PUFAs (Müller-Navarra et al., 2000, 2004; Persson et al., 2007) and P and N (Prater et al., 2018).

Prater et al. (2018) believe that stoichiometric ratios may influence the production of daphnids. Field studies in two lakes in Ontario (Canada) with different phosphorus loads showed that the stoichiometric ratios in food resources influenced the production of daphnids in the lake with the low phosphorus load (Prater et al., 2018). The production of daphnids in this lake increased with a decrease in the C : P ratio in the food resources of daphnids. In the lake with the high phosphorus load and low C : P ratio in phytoplankton, the production of daphnids was not correlated with the C : P ratio in food resources. Therefore, stoichiometric ratios can influence the production of daphnids only in the range of a low P content in food resources, i.e., in lakes with a low trophic level. As a result, control of the production of daphnids would be shifted to physical factors, e.g., temperature,

or biochemistry, including FAs, with increase of trophic level. Therefore, one should expect limitation by nutrients under oligotrophic conditions, while the production under eutrophic conditions will be regulated by the biochemical composition of resources. Sterner (1997) also noted that factors regulating zooplankton communities replaced each other depending on environmental conditions. If daphnids are starving (i.e., if they lack C), their growth is limited by C; if C does not limit the growth of daphnids, their production begins to depend on food quality.

Prater et al. (2018) showed that stoichiometric ratios in phytoplankton influenced the production of zooplankton in combination with temperature. In Wolf Lake (Ontario, Canada) with a low phosphorus load, the production of planktonic crustaceans was correlated both with food quality (C : P) and with temperature. The highest production of zooplankton was observed at a low C : P ratio and moderate temperatures. Therefore, the effect of temperature can modify the mechanisms of influence of stoichiometric ratios on the production of zooplankton, which may lead to seasonal changes in their production.

Hessen et al. (2013) noted that the difference between phytoplankton and zooplankton was greater in the P content than in the N content. This may be determined by the fact that the C : P ratio varies over a wider range than C : N in phytoplankton and that P directly influences the growth rate of zooplanktonic organisms (Hessen et al., 2013). Different representatives of zooplankton respond differently to P and N limitation. In particular, it has been shown that the biomass of daphnids, which contains more P in their tissues, is significantly correlated with the concentration of mineral P (Andersen and Hessen, 1991; Hesen, 1992). Copepods, which are characterized by a higher N content, are correlated better with the concentration of mineral N. Therefore, when the amount of one of the elements (N or P) is limited, species that are less vulnerable to its shortage gain the advantage. The shift between N or P limitation, which is often observed in nature, may lead to changes in the species structure of zooplankton, which, in turn, will involve changes in the secondary production and efficiency of transfer of substances from phytoplankton to zooplankton (Sterner, 1993).

The limitation of the secondary production of PUFAs, which they receive with food, is explained by a huge discrepancy in nature between the demands of heterotrophs in these substances and their content in food (Twining et al., 2016). It has been shown that a high content of EPA, DHA, and ARA in food would increase the production of zooplankton (Brett and Müller-Navarra, 1997; Sargent et al., 1999; Parrish et al., 2007). For instance, Müller-Navarra et al. (2000) clearly demonstrated that the production of daphnids in a hypereutrophic pond (Davis Pond, California, United States) depended on the content of PUFAs in phytoplankton. Their study showed that the production of daphnids was very low in summer, and the clutch size varied from 0 to 0.5 eggs per clutch despite the high phytoplankton biomass (3.9−9.4 mg C L^{-1}). Cyanobacteria with a negligibly low content of EPA prevailed during that time. In winter, when diatoms with a high content of EPA began to prevail in phytoplankton, the production of daphnids and their average clutch size increased (9.1−17.0 eggs per clutch) compared to the summer values, although the phytoplankton biomass decreased more than two times (up to 1.7−3.8 mg C L^{-1}). The authors explained the absence of the relationship between the biomasses of phytoplankton and zooplankton by the fact that the production of the consumers depended on the quality of food rather than on its amount. This conclusion is also confirmed by the fact that the highest correlation was found between the production of daphnids and content of EPA in seston. Contrary to expectations, chlorophyll *a* did not influence the production of daphnids. Therefore, the authors concluded that the content of EPA in phytoplankton in eutrophic water bodies may be the main factor controlling the secondary production.

It should be noted that small and large zooplankton species can respond differently to the same levels of food quantity and quality. Under experimental conditions, it was shown that the growth rate of the small species *Ceriodaphnia pulchella* (Sars, 1862) was correlated with the amount of food resources, while the production of large daphnids (*Daphnia magna* (Straus, 1820) and *Daphnia pulicaria* (Forbes, 1893)) responded more strongly to EPA shortage (Feniova et al., 2019). Therefore, small and large zooplankton species have different survival strategies under unfavorable food conditions, which leads to a shift in dominance between small and large species depending on environmental conditions.

EFFICIENCY OF TRANSFER OF ESSENTIAL SUBSTANCES FROM PHYTOPLANKTON TO ZOOPLANKTON

An increase in the content of essential substances in zooplankton relative to that in the food provides more efficient transfer of these substances from phytoplankton to zooplankton. It can be assumed that, the higher the content of essential substances in zooplankton relative to that in their resources, the higher their production and, consequently, the higher the efficiency of transfer of these substances from phytoplankton to zooplankton. The results of the work of Gladyshev et al. (2011) on flows of total organic carbon and essential n-3 PUFAs and FAs in the Bugach eutrophic reservoir showed that different substances were transferred from phytoplankton to zooplankton with different efficiencies. In particular, the efficiency of transfer of PUFAs from phytoplankton to zooplankton was two times higher than that of organic

carbon. However, C16-PUFA, which serves only as an energy source for animals, were transferred less efficiently than total organic carbon. In zooplankton, C16-PUFA undergoes mitochondrial β-oxidation more often than essential PUFAs (Leonard et al., 2004). Therefore, less essential FAs are generally used for catabolic processes, while more essential acids are stored. Thus, the content of PUFAs can increase with each level of the trophic chain and, as a result, the trophic pyramid of production of essential PUFAs will expand upwards rather than getting narrower, as in the case of carbon (Gladyshev et al., 2011).

The trophic status and depth of a water body can influence the efficiency of transfer of substances from phytoplankton to zooplankton. Based on the studies of 56 lake with different depths, along the trophic gradient (ultraoligotrophic, oligotrophic, mesotrophic, and eutrophic lakes), the efficiency of transfer of matter from phytoplankton to zooplankton significantly decreased both in shallow and deep lakes (Lacroix et al., 1999). However, patterns of the effect of the trophic status on the efficiency of material transfer differed between shallow and deep lakes. This might be caused, at least partially, by the use of alternative sources of food resources by zooplankton in shallow lakes (benthic and periphytic taxa in addition to planktonic algae). It is likely that the differences in the efficiency of transfer of matter from phytoplankton to zooplankton in water bodies with different trophic levels are attributed to differences in the fish pressure on zooplankton. It was shown that fish pressure on zooplankton enhanced with an increase in trophic level (Downing et al., 1990).

The efficiency of transfer of essential substances from phytoplankton to zooplankton can be influenced by biotic factors. *Dreissena polymorpha* (Pallas, 1771) is a strong biotic factor influencing planktonic communities. The zebra mussel can significantly reduce the quantity of phytoplankton by its filtration activity (Vanni, 2002; Conroy and Culver, 2005; Conroy et al., 2005). It is capable of selective feeding by rejecting low-quality algae; in particular, it can selectively consume seston with a high content of EPA, i.e., diatoms (Makhutova et al., 2013). The zebra mussel can induce the "blooms" of cyanobacteria of *Microcystis* species under conditions of low trophic levels as a result of the excretion of nutrients (Raikow et al., 2004; Knoll et al., 2008; Sarnelle et al., 2012; Vanderploeg et al., 2017); on the contrary, under conditions of high trophic levels, the mollusks reduced the abundance of cyanobacteria as a result of their consumption (Waajen et al., 2016). Experimental studies showed that the zebra mussel increased the concentration of inorganic P in water, which leads to an increase in its content in algae, thereby facilitating the development of large daphnids (Feniova et al., 2015, 2018). It has been shown that the zebra mussel promoted the development of inedible filamentous green algae (Feniova et al., 2020), which suppressed edible phytoplankton fraction. As a

result, it can significantly influence the development of phytoplankton and, consequently, its production and the efficiency of transfer of substances from phytoplankton to zooplankton.

Manipulation with the presence/absence of the zebra mussel in the experiments made it possible to assess its influence on the efficiency of transfer of C, N, P, EPA, DHA, and total FAs from phytoplankton to zooplankton (Sakharova et al., 2021). The zebra mussel reduced the efficiency of transfer of all these substances compared to the control. However, it differently influenced the efficiency of transfer of individual essential substances. In particular, it reduced the transfer efficiency by 6 times for C, by 3 times for EPA, by 4 times for DHA, by 3 times for total fatty acids, by 6 times for N, and by 7 times for P compared to the control (Sakharova et al., 2021). This effect might be related to the negative effect of the zebra mussel on the biomass and production of zooplankton as a result of its competition with zooplankton species for food resources, and to the shift in the structure of phytoplankton towards the filamentous green algae inaccessible to zooplankton.

Another biotic factor influencing the transfer of matter and energy from phytoplankton to zooplankton is fish. Planktivorous fish can change the structure of zooplankton by selectively grazing larger individuals (Gliwicz, 2003) or slow-swimming cladocerans, which, unlike copepods, cannot actively avoid fish attacks (Bohl, 1982; Okun and Mehner, 2005). Fish can also influence the structure of phytoplankton communities by excreting waste products into the water, thereby changing the chemical composition of substances available for phytoplankton (Happey-Wood and Pentecost, 1981; Lin and Schelske, 1981; Brabrand et al., 1984). As a result, fish can cause changes in the production of phytoplankton and zooplankton and, consequently, affect the efficiency of transfer of essential substances from phytoplankton to zooplankton.

Since fish consume zooplankton and significantly reduce its biomass, their effect on zooplankton production should be assessed in terms of zooplankton potential production, i.e., the P/B ratio (production per unit of biomass). I.Yu. Fenieva et al. (2021) determined the effects of fish on the ratio of P/B in zooplankton to that in phytoplankton, which reflects the efficiency of matter transfer per biomass unit. It was found that fish increased the efficiency of C transfer by two times, P by 12.4 times, N by 2.5 times, EPA by 12.4 times, DHA by 7.4, and total FAs by 10 times compared to those in the control. Therefore, zooplankton use food resources more efficiently in the presence of fish likely due to reduction of competition between zooplankton species.

CONCLUSIONS

The efficiency of the transfer of substances from phytoplankton to zooplankton is controlled by many

factors, including food quality (expressed by the content of PUFAs and stoichiometric ratios), the trophic status of the water body, the taxonomic composition of zooplankton and phytoplankton, temperature, etc. However, the analysis of different studies shows that the level of the effects of factors is not as important as the balance between effects of multiple factors. Therefore, ecological stoichiometry as a separate area has appeared in ecology. Sterner and Elser (2002) defined ecological stoichiometry as a science that studies the balance between different chemicals involved in ecological processes. The limiting factor is similar to the element that is insufficient to maintain the balance, like in Liebig's law of minimum. If there is an imbalance between any of the variables regulating plankton, this will affect their production and the efficiency of transfer of substances from producers up the trophic chain.

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CONFLICT OF INTERESTS

The authors declare that they have no conflict of interests.

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