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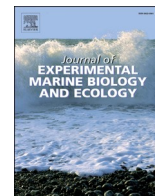
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Diet quality determines blue mussel physiological status: A long-term experimental multi-biomarker approach

Camilla Liénart^{a,b,*}, Michael Tedengren^a, Andrius Garbaras^c, Hwanmi Lim^d, Mathias Chynel^e, Christophe Robinson^a, Tarik Meziane^e, Agnes M.L. Karlson^{a,b}

^a Department of Ecology, Environment and Plant sciences, Stockholm University, Stockholm, Sweden

^b Stockholm University Baltic Sea Centre, Stockholm, Sweden

^c Center for Physical Sciences and Technology, Vilnius, Lithuania

^d Lipidor AB, Svärdvägen 13, SE-182 33 Danderyd, Sweden

^e Muséum National d'Histoire Naturelle, Laboratoire Biologie des Organismes et Ecosystème Aquatiques (UMR 8067 BOREA), Sorbonne Université, CNRS, IRD 207, Université de Caen Normandie, Université des Antilles, 61 rue Buffon, 75005 Paris, France

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ABSTRACT

Cyanobacterial blooms have increased worldwide and decreases in spring blooms of diatoms in temperate aquatic ecosystems are increasingly reported. Whether such shifts in the food base positively or negatively affect primary consumer's physiological status, growth, and more broadly, ecosystem functioning, is poorly known. Here, we test how a widespread filter-feeding blue mussel from the genus *Mytilus* reacts to diatoms, filamentous non-toxic cyanobacteria and a mixture of the two in a 50 day feeding experiment and compare with mussels in the field. We use a multi-tracer approach to assess mussels' nutritional and physiological status. Diatoms had highest relative proportions of the essential fatty acids 20:5 ω 3 (EPA) and 22:6 ω 3 (DHA), but cyanobacteria had a high relative proportion of polyunsaturated FAs (PUFAs) especially 18:3 ω 3, a precursor of ω 3 FAs. Bulk and amino-acid- $\delta^{15}\text{N}$ demonstrated assimilation of cyanobacterial N or diatom N by the mussels, while fatty acid (FA) composition and $\delta^{13}\text{C}$ -FA analyses demonstrated assimilation of C and FAs from diatoms. Still, C and N from both food sources were utilized when mussels were fed the mix and condition index, scope for growth (SFG; measure of energy status) and the elemental N:P ratio of mussels were higher in mussels fed cyanobacteria only, indicating better growth status in this treatment. It seems like mussels fed cyanobacteria, a food with low proportions of essential FAs compared to diatoms, were able to cover the dietary requirements through FA biosynthesis from precursor FAs. The FA composition and $\delta^{15}\text{N}$ -results from mussels fed cyanobacteria agreed well with seasonal field measurements of mussels. Our study provides the first feeding experiment investigating how blue mussels utilize N from cyanobacteria and shows the rather positive response to this type of food. Our results suggest that imbalances in the biochemical composition of diet of consumers can be overcome through biosynthesis of essential FAs. In the context of climate change with shifting biogeochemical baselines, it is crucial to understand the biological effects of such changes in the quality of the production base.

1. Introduction

Worldwide, cyanobacterial blooms increased in frequency, intensity and duration during the last decades, mainly due to eutrophication and global warming (Huisman et al., 2018; Scholz et al., 2017). In temperate aquatic ecosystems, decreases in the spring bloom of diatoms are also being increasingly reported (Hjerne et al., 2019; Klais et al., 2011). Whether such alterations of basal dietary resources positively or negatively affect primary consumer's health, growth and reproduction, and

more broadly, food web structure and nutrient cycling, is poorly known.

Phytoplankton provides primary consumers with essential biomolecules such as vitamins, sterols, fatty acids (FA) and amino acids (AA) (Jónasdóttir, 2019; Peltomaa et al., 2017), the content of which differs among phytoplankton species (Ahlgren et al., 1992). Hence shifts in phytoplankton taxa could have important implications for consumers' growth, survival and reproduction and can be reflected in consumers' FA profiles (Brett and Müller-Navarra, 1997; Müller-Navarra, 2008). It is commonly admitted that for consumers, dietary acquisition of essential

* Corresponding author at: Department of Ecology, Environment and Plant sciences, Stockholm University, Stockholm, Sweden.

E-mail address: camilla.lienart@su.se (C. Liénart).

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compounds is preferred over de novo synthesis due to lower energetic costs and to the fact that some consumers can't perform such synthesis (Ruess and Müller-Navarra, 2019 and references therein). Some specific FAs can be used as trophic tracers in consumers since they are assimilated rather conservatively (i.e., fatty acid trophic markers (FATM); Dalsgaard et al., 2003). On a less detailed level, macronutrients (i.e., carbon (C), nitrogen (N) and phosphorus (P)) and their ratios also differ among phytoplankton, and elemental imbalance may constrain growth in consumers; elemental ratios are used as indicators for condition, growth and diet as it reflects the balance between the organism's requirements and elemental availability (i.e., ecological stoichiometry sensu Elser et al., 2000, 2003; N content is often used as a proxy for proteins, C for lipids and P for RNA).

Traditionally, filamentous cyanobacteria have been considered a poor-quality food source for aquatic organisms due to their low content of essential polyunsaturated FAs (Ahlgren et al., 1992; Galloway and Winder, 2015; Gulati and Demott, 1997; Jónasdóttir, 2019; Müller-Navarra et al., 2000; Peltomaa et al., 2017). Some species of cyanobacteria can also be potentially harmful by producing toxins and other bioactive compounds (Bownik, 2016; Karjalainen et al., 2007; Sivonen and Jones, 1999). In comparison, microalgae such as e.g., diatoms are often considered a high-quality food source, especially for benthic deposit-feeders since they are rich in essential FAs (Galloway and Winder, 2015; Nascimento et al., 2009). In arctic and subarctic regions where the single annual phytoplankton bloom event is dominated by diatoms and in temperate regions with several bloom events, the spring bloom of diatoms is tightly linked to benthic faunal growth (Johnson and Wiederholm, 1992; Lehtonen and Andersin, 1998; Nascimento et al., 2009). However, filamentous cyanobacteria are generally rich in N and P (Walve and Larsson, 2007), essential AAs (Ahlgren et al., 1992; Loick-Wilde et al., 2012), and contain some vitamins (Prasanna et al., 2010) and antioxidants (Pandey and Pandey, 2009). In addition, the rich community of microorganisms associated with the filaments likely increase the nutritional value of cyanobacteria (Hoppe, 1981; Ploug et al., 2011), which is often ignored in simplified laboratory studies where axenic cultures are commonly used. Negative effects of lab cultures of cyanobacteria on aquatic consumers, which are commonly reported (e.g., Engström et al., 2000, 2001; Hedberg et al., 2021), should hence not be directly extrapolated to the field situation. Moreover, some experimental studies also demonstrate negative effects of diatom monoculture diets for invertebrates (e.g., Ban et al., 1997; Ianora et al., 2003; Miralto et al., 1999) due to high amounts of aldehydes which are harmful to invertebrates (Fontana et al., 2007; Leflaivre and Ten-Hage, 2009). Realistic experiments using field collected bloom material is hence needed for evaluation of food quality effects on growth status in consumers (Karlson et al., 2015; Ledesma et al., 2022).

The Baltic Sea, which is affected by eutrophication and climate change (Elmgren et al., 2015; Reusch and others, 2018), has experienced shifts in primary production; both spring and summer blooms start earlier nowadays than in the 1980s resulting in an extended productive season (Kahru et al., 2016). A decrease in the previously dominating phytoplankton group of spring bloom, i.e., diatoms, has been observed (Hjerne et al., 2019), while N₂-fixing filamentous cyanobacteria has increased (Kahru and Elmgren, 2014; Olofsson et al., 2020). Several studies have demonstrated that N from cyanobacterial blooms is assimilated by invertebrate consumers in both pelagic, littoral and benthic food webs (Karlson et al., 2014, 2015; Lesutiene et al., 2014; Rolff, 2000). Gut content, biomarkers and molecular analyses in different pelagic zooplankton grazers provide direct evidence of the ingestion of cyanobacteria (Engström-Öst et al., 2011, 2017; Gorokhova and Engström-Öst, 2009; Motwani et al., 2018; Novotny et al., 2021; Peters et al., 2006). However, the morphology of cyanobacterial filaments (filament length of ca. 130 to 200 µm, width of ca. 4 to 15 µm; Engström et al., 2000; Högländer pers. com.) may prevent direct ingestion in the widespread and abundant filter-feeding key-organism, the blue mussel (ca. 2 to 20 µm particle feeding range; Ward and

Shumway, 2004 and references therein).

Currently, it is unclear whether blue mussels (from the genera *Mytilus*, in the Baltic Sea it forms a species complex often referred to as *Mytilus trossulus edulis*, Stuckas et al., 2009) directly ingest cyanobacterial filaments, or if the N and P exuded by cyanobacterial cells or bacterial degradation are utilized via other pathways (e.g., the microbial loop as discussed for zooplankton and deposit-feeders in Karlson et al., 2015). Recent studies in the Baltic Sea have linked long term changes in the productivity base to blue mussels diet, growth and physiological status at the individual and population levels (Liénart et al., 2020, 2022); Cyanobacterial N is likely utilized by the mussels as shown from the depleted ¹⁵N values in source AAs (Liénart et al., 2022), and over decadal time scales, indications of cyanobacterial feeding was associated with better growth status (as assessed from N:P ratio) but lower condition index (Liénart et al., 2020). To the best of our knowledge, no experimental studies have tested cyanobacterial bloom palatability and nutritional quality when ingested by blue mussels. Only results from toxicity bioassays or short term cyanotoxin bioaccumulation studies performed with toxic cyanobacteria *Nodularia spumigena* are reported (e.g., Kalaitzidou et al., 2021; Kankaanpää et al., 2007; Svensen et al., 2005).

In this study, we experimentally investigated the effects of a diatom-dominated spring bloom versus the most abundant cyanobacteria in the Baltic, the non-toxic *Aphanizomenon* sp., which dominate summer blooms especially in coastal areas (Högländer et al., 2004; Kahru and Elmgren, 2014; Olofsson et al., 2020), on blue mussel scope for growth (SFG, energy budget sensu Gilek et al., 1992; Tedengren et al., 1990; Widdows and Johnson, 1988; Widdows et al., 1995) and condition index (CI, soft tissue:shell ratio). We traced, via a multi-biomarker approach, the assimilation of field-collected bloom material from i) spring, ii) summer and iii) a mix of the two (resulting in 3 diet treatments) in mussels in a 50 day feeding experiment. We took advantage of the natural differences in bulk stable isotope signals in phytoplankton in the region: the diatom-dominated spring bloom was sampled in a bay downstream sewage outfall influence inducing a high $\delta^{15}\text{N}$ signal (Himmejärden bay; see Savage and Elmgren, 2004), whereas the cyanobacteria-dominated summer bloom has a naturally low $\delta^{15}\text{N}$ signal (Rolff, 2000).

In order to confirm food assimilation, we measured the $\delta^{15}\text{N}$ of both bulk tissues and in the source AA Phenylalanine (Phe) in mussels, as the bulk signal is elevated in these slow growing mussels and mask the ultimate N source (Liénart et al., 2022). Phe was targeted since it shows negligible ¹⁵N fractionation during metabolism, which makes it a reliable tracer for tracing diazotrophic nitrogen (Eglite et al., 2018). The $\delta^{13}\text{C}$ of FAs was also measured to explore diet preferences and metabolic pathways of food utilization. Fatty acid profiles (i.e., relative proportions of single FAs to the total FA quantity) were measured to compare diet effects on the mussels' physiological status (e.g., content of essential FAs and its precursors). Cyanobacteria and diatoms were expected to differ in specific FA biomarkers, e.g., higher proportions of the essential fatty acids 20:5 ω 3 (EPA) and 22:6 ω 3 (DHA) in diatoms as well as the typical diatom marker 16:1 ω 7 compared to cyanobacteria (Dalsgaard et al., 2003). Finally, we measured condition index, the scope for growth, and calculated isotope niches as a measure of trophic niche breadth (Jackson et al., 2011; Newsome et al., 2007) in mussels exposed to the different diet regimes, and compared these to isotope, elemental, and FA data in field collected mussels.

We hypothesised that: 1) the assimilation of cyanobacterial N (depleted in ¹⁵N) by mussels would result in a decrease in their $\delta^{15}\text{N}$ values (both for bulk and Phenylalanine) over time while the ¹⁵N-enriched diatom-based diet would instead result in an increase in $\delta^{15}\text{N}$ over time. 2) Mussels fed with the mixed diet will selectively assimilate N or some specific FAs (also traced with $\delta^{13}\text{C}$ -FA) from diatoms or cyanobacteria according to food preferences. 3) A better physiological status, reflected as higher condition index, absolute amount of total FA and proportion of essential FA, and higher scope for growth will be

observed for mussels under the mixed-diet due to complementarity in micronutrients between the two food materials.

2. Material and methods

2.1. Mussels and phytoplankton sampling in the field

Mussels were sampled in 2019 in the bay in front of the Askö Laboratory (N 58° 49' 24, E 17° 37' 59; Baltic Sea, microtidal area; Fig. S1), monthly from April to July, including mussels for start of the experiment (June 26th). After each sampling event, mussels shells were pre-cleaned to remove epibiotic fauna and the mussels were allowed to clear their gills in filtered sea water for 36 h.

Spring bloom material was sampled in early April 2019 with a 41 μm mesh size net at the station H4 in the Himmefjärden Bay (N 58° 59' 02, E 17° 43' 50; Fig. S1). Summer bloom phytoplankton was sampled mid-June 2019 at the station B1 close to the Askö Laboratory (N 58° 48' 18, E 17° 37' 52; Fig. S1) using a 90 μm mesh (filamentous cyanobacteria can be collected with this method). For each sampling, the bloom material was left overnight in a dark and cold room before starting further separation of plankton groups. Zooplankton was removed with a light trap. Fast-sinking diatoms from spring bloom material were carefully collected with a hose from the bottom of the containers. Floating cyanobacterial filaments from summer bloom material were collected from the surface accumulation formed on the top water layer of the containers. After the sorting procedures, microscopic identification was performed on the collected, concentrated sample confirming clear dominance by biovolume of diatoms and cyanobacteria respectively. The spring bloom material was largely dominated by the diatom *Skeletonema marinoi* along with smaller amounts (<20%) of six other diatoms species (*Chaetoceros wighamii*, *Thalassiosira*, *Melosira artica*, *Diatoma tenuis*, *Pauliella taeniata*, *Thalassiosira levanderi*) and two dinoflagellates species (*Peridiniella catenata*, *Scrippsiella complex*). The cyanobacterial material (summer) was entirely dominated by one species, the cyanobacteria *Aphanizomenon* spp. (>95%). The concentrated materials of both diatoms and cyanobacteria were stored in falcon tubes, then frozen ($-20\text{ }^\circ\text{C}$) for further use as food in different experimental treatments.

2.2. Experimental setup, feeding protocol and sampling time points

All blue mussels used for this study were collected from the same large mussel aggregation: for field samples (April, May, June, and July), $n = 70$ mussels in total were sampled, for the feeding experiment, $n = 495$ mussels in total were sampled and divided in three parallel raceways ($n = 165$ mussels randomly selected and placed in each raceway; Fig. 1a). See section 2.6 on experimental design from a statistical perspective. Raceways were supplied with flow through filtered seawater (ca. 30 L; 22 μm pre-filtration sand-system, then 0.5 μm polypropylene yarn filters cartridges changed every 10 days) pumped from 20 m depth at the collection site. Most of the mussels used for the experiment were $12.8 \pm 2\text{ mm}$, shell-free dry weight $15.1 \pm 6.1\text{ mg}$ but those intended for FA analyses were somewhat larger, $17 \pm 2\text{ mm}$. The experiment was run for 50 days in the summer of 2019. Water temperature ($^\circ\text{C}$), salinity (psu) and oxygen concentration ($\text{mg O}_2\text{ L}^{-1}$) were controlled and monitored, and were stable during the experiment, $16.2 \pm 1\text{ }^\circ\text{C}$, $6 \pm 0.1\text{ psu}$ and $9.1 \pm 1.8\text{ mg O}_2\text{ L}^{-1}$ to reflect average summer conditions. The blue mussels were left to form dense clusters attached on small rocks with byssus threads in the raceways as mussels normally do.

The mussels were fed twice a day every 12 h for 90 min during which the water inflow was stopped to allow for consumption of the added food but without allowing oxygen deficiency to develop. Prior to feeding, faeces and pseudo-faeces were manually removed to avoid re-ingestion by mussels. The three diet treatments were: diatom-dominated (D), cyanobacteria-dominated (C) and a mix of both (M) based on organic matter content (mg dw) 50 – 50. During the 50-day experiment, the daily food supply was calculated to cover the basal energy requirement of the mussels as estimated from their oxygen consumption, which was approximately 1.5 mg of carbon or 3 to 5 mg of dry organic material per mussel in the raceway depending on food source. The particle concentration provided in the 30-l raceway was thus decreased as mussels were sacrificed over time and kept below the limit for pseudofaeces production. We initially aimed for a 50 – 50 mix of both food types in the mix diet based on theoretical C content values (i.e., cyanobacteria 45% C dw, diatom 22% C dw; Nascimento et al., 2009), but it turned out being a 75 diatom – 25 cyanobacteria mix based on our own plankton materials elemental composition (cyanobacteria 25% C dw, diatom 21% C dw; Table S1). This also means that the total amount

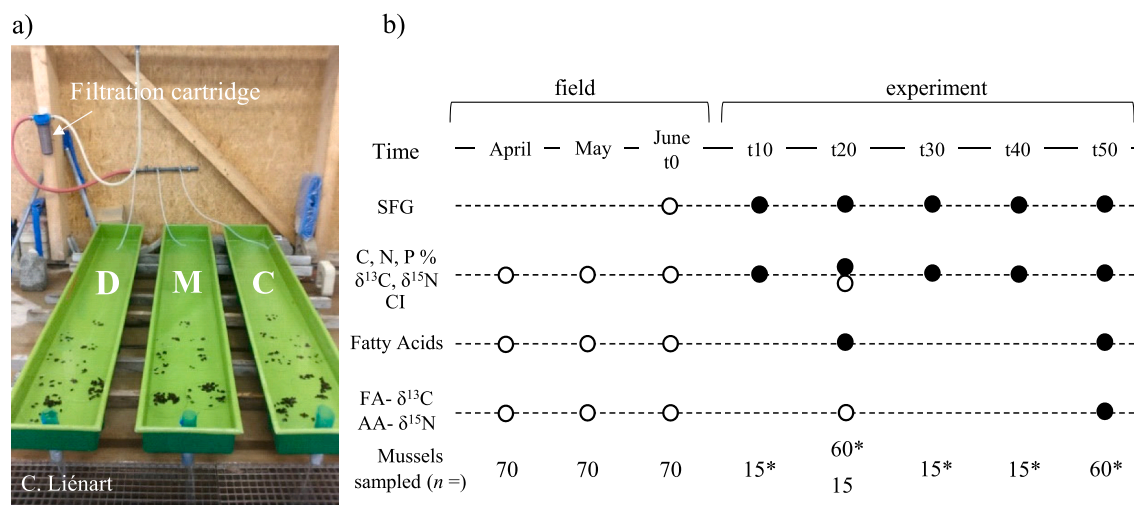


Fig. 1. Experimental setup and sampling timeline. a) Raceways with continuous flow-through system of filtered sea water (0.5 μm , filtration cartridge). Each raceway corresponds to a treatment: diatom diet (D), cyanobacteria diet (C) and mixed diet (M). See statistics section for details. b) Sampling schedule for scope for growth (SFG) measurements, condition index (CI), and chemical analyses (elemental (C, N, P), bulk isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and fatty acid composition (FA) and compound specific isotope analyses of fatty acids and amino acids (FA- $\delta^{13}\text{C}$, AA- $\delta^{15}\text{N}$)) over the 50 days of the experiment. White circles represent field sampling, black circles represent sampling within the experiment. The field sampling from June corresponds to the initial sampling t0 that was used as starting values for the experiment. July sampling was performed in the field at the same time as experimental t20. $n =$ refers to the number of mussels sampled for each time point, with * for the number of mussels for each treatment within the experiment, and when the asterisk is absent, in the field.

of organic matter was higher in the diatom treatment compared to the cyanobacteria treatment so that food quantity was diatoms > mix > cyanobacteria (this actually reflects the seasonal bloom dynamics; e.g., Högländer et al., 2004).

For preservation reasons and since spring and summer blooms do not occur at the same time of the year in the field, both bloom material were kept frozen until the start experiment. We deemed it important to be able to freeze both food sources to avoid comparing fresh and frozen material in the experiment. Even though freezing would decrease cell integrity of the long cyanobacterial filaments to be used as food in the experiment, this reflects the situation in the field at the end of the bloom when the filaments start to decompose/disintegrate. The diatom material collected in spring was freeze-dried, gently grinded (not to break cells but to allow weighing of smaller aliquotes) and suspended in filtered sea water prior to feeding, while cyanobacterial material was thawed overnight in a fridge. For the mixed treatment, spring and summer bloom material were mixed together and suspended in filtered sea water prior to feeding. The amount of food was adjusted as the experiment progressed (i.e., mussels were removed for chemical analysis) so that the amount of food per mussel was constant within each treatment throughout the experiment.

Over the 50 day experiment, mussels were sampled for the following analyses; elemental, stable isotopes, fatty acids (FAs) and isotope analyses on FAs and amino acids (AAs; i.e., compound specific); condition index (CI) and scope for growth measurements (SFG, short term incubations, see below). Briefly, at t_0 (Initial) $n = 70$ mussels were sampled for all the biomarkers and SFG measurements, then every 10 days $n = 15$ mussels for elemental and isotope analysis and SFG measurements (t_{10} , t_{20} , t_{30} , t_{40} , t_{50}); $n = 45$ additional mussels at t_{20} and t_{50} for FAs, and at the end of the experiment (t_{50}) for compound specific isotope analysis (Fig. 1b). See statistical section (2.6.) on how we dealt with the lack of replication of raceways in our analyses. In April and May, $n = 70$ mussels were sampled out in the field for all the biomarkers and $n = 15$ in July for elemental and isotope analysis (mussels intended for FA analyses in July were accidentally lost) (Fig. 1b).

2.3. Bioenergetics

For the assessment of the energy status, 15 similar sized mussels were randomly subsampled from the clusters in the raceways every 10 days for short-term incubations. Mussels were placed in 1 L chambers ($n = 3$ chambers for each treatment, in each chamber 5 mussels were combined) filled with filtered seawater of ambient temperature and salinity and left to acclimatise for one hour with air bubbling. Control chambers without mussels were used to test whether filtered seawater contained picoplankton or heterotrophic bacteria that would confound oxygen measurements or assessments of clearance rates. Air supply was then turned off and the chambers sealed, and respiratory expenditure (ΔO_2) was measured before and after one hour, using an optical oxymeter as a decline in dissolved oxygen concentration ($\Delta mg O_2 V T^{-1}$), with $V =$ volume of water in the chamber (1 L), $T =$ time elapsed between readings (1 h). After this the water was replaced by oxygen saturated seawater but now with a known concentration of seston and the mussels were left to filter-feed for one hour. The particles were counted with a particle counter (Beckman Coulter Multisizer 3) before and after one hour, and the clearance rate (CR; litre h^{-1} for each individual chamber) was calculated as follows: $CR = (\ln C_0 - \ln C_1 V T^{-1})$, where C_0 and $C_1 =$ particle concentration at T_0 and T_1 respectively, $V =$ volume of water in the chamber (1 L) and $T =$ time elapsed between readings (1 h). The assimilation efficiency (AE) was determined according to the method of Conover (1966), which indicates the efficiency by which organic material is absorbed from the ingested food. The aim was to calculate actual energy consumption and compensate for energy losses through faeces production using the Conover ratio (assimilation efficiency, AE): $AE = (F-E)/((1-E) F)$, where $F =$ the organic fraction of the food and $E =$ organic fraction of the faeces. Clearance rate (CR), assimilation

efficiency and respiratory expenditure (ΔO_2) were then used in the balanced energy equation after conversion to energy equivalents (joules, J) to calculate scope for growth (SFG) for each chamber ($n = 3$) as an assessment of the energy status of the mussels under the different diets, every 10 days along the experiment (Fig. 1b, see section 2.5. for calculations and Fig. S2 of the Supplemental material for details on calculations of each variable of SFG). All variables were standardized to per gram of mussel tissue dry weight (shell-free).

2.4. Chemical analyses

Dried ground and homogenized soft tissue (whole mussel, shell not included) of mussels were weighed to measure elemental carbon, nitrogen and phosphorus, bulk carbon and nitrogen isotope, and AA- $\delta^{15}N$ (1.0 ± 0.2 mg total material for C, N and P % and $\delta^{13}C$ and $\delta^{15}N$; 10 ± 0.3 mg for AA- $\delta^{15}N$). Frozen, freeze-dried and ground soft tissue (whole mussel, shell not included, 83 ± 20 mg total material) was used to measure FAs. For each sampling event, 5 or 15 individual mussel were measured for % C and N and $\delta^{13}C$, $\delta^{15}N$, 5 individual mussel were measured for % P, and, in order to get enough material, triplicates of pooled mussels ($n = 3$ individuals per sample) were used for FAs and compound specific analyses (AA- $\delta^{15}N$, FA- $\delta^{13}C$). Dried and ground material from spring and summer blooms were used for all chemical analyses ($n = 5$ replicates). All chemical analyses but the FA measurements were performed on dried material (algae and mussels) which was preserved in a desiccator prior to analysis. Only FA measurements required frozen samples that were preserved at $-20^\circ C$ for a maximum of 8 months.

Carbon and nitrogen elemental and bulk stable isotopes were measured at the Center for Physical Science and Technology (Vilnius, Lithuania) with a Flash EA 1112 Series Elemental Analyzer (Thermo Finnigan) connected to a DeltaV Advantage Isotope Ratio Mass Spectrometer (Thermo Fisher). Phosphorus was analyzed following Larsson et al. (2001) at the Department of Ecology, Environment and Plant Sciences (Stockholm, Sweden), using a Alpkem SFA system (SS-EN ISO 15681-2:2018).

Amino-acid- $\delta^{15}N$ measurements first required the extraction and derivatization of Aas (method in Ledesma et al., 2020), which were then analyzed by gas chromatography combustion isotope ratio mass spectrometry (GC/C/IRMS; method in Liénart et al., 2022) with a Trace GC Ultra Gas Chromatograph (Thermo scientific) coupled to a Delta Advantage Isotope Ratio Mass Spectrometer via GCC III combustion interface (ThermoFinnigan) for the mass spectrometry protocol at the Center for Physical Science and Technology (Vilnius, Lithuania).

Fatty acids analyses were performed by Lipidor AB (Danderyd, Sweden). In brief, after total lipid extraction (following a modified method from Jensen et al. (2003, 2009) see Supplemental methods), FAs were derivatized (i.e., methylation of FAs, resulting in FA methyl ester) and analyzed by gas chromatograph-flame ionization detector (GC/FID) with Agilent 6890 GC (Agilent Technologies Inc.) using Agilent DB-WAX column (30 m length, 0.32 mm internal diameter, 0.25 μm film thickness). Tripentadecanoic with three 15 carbon chain long FAs was added to each sample as internal standard. Results were given in milligram of FA per gram of sample (i.e., semi-quantitative method, relative abundance of FAs to the sample mass dry weight). The $\delta^{13}C$ of FAs were analyzed at the Service de Spectrométrie de Masse Isotopique du Muséum, Paris, France. The FA extracts were analyzed by GC-C-IRMS on an ELEMENTAR VisION interfaced with an Agilent 7890B gas chromatograph equipped with VF WAXms (Agilent Technologies) column (30 m length, 0.25 mm internal diameter, 0.25 μm film thickness). Not all FAs identified from the bulk analysis were detected in the $\delta^{13}C$ -FA analyses due to low concentration and the higher detection limit of GC-CIRMS compared to GC-FID. Detailed methods for FAs bulk and $\delta^{13}C$ analyses are presented in Supplemental methods.

All isotope results are expressed using the conventional delta notation: $\delta^{13}C_{\text{sample}}$ or $\delta^{15}N_{\text{sample}} = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, where $R =$

$^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, with per mil deviation (‰) from international standards, Vienna Pee Dee belemnite for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$. External and internal standards were analyzed as references within each batch of samples. Analytical uncertainties were $<0.15\%$ and $<0.20\%$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively, $<0.30\%$ for AA- $\delta^{15}\text{N}$ and 0.20% for FA- $\delta^{13}\text{C}$. The overall analytical precision was 0.9%, 0.2% and 0.6% for elemental C, N and P respectively.

2.5. Calculations

For each individual mussel used for further chemical analyses, the physiological condition index was calculated as a proxy for physiological status (CI = dry weight soft tissue (g) / dry weight shell (g) 100) according to Lucas and Beninger (1985).

The SFG was calculated according to Widdows and Johnson (1988), Tedengren et al. (1990) and Gilek et al. (1992), using the balanced energy equation: $\text{SFG} = \text{C} - \text{R} - \text{U} - \text{F}$, where C is the total energy consumption, R = respiratory expenditure, and U and F are energy lost as excreta and faeces (F was estimated from loss on ignition of food and faeces respectively and the Conover ratio was then calculated to estimate the assimilation efficiency, see 2.3.). All variables of the equation were expressed in $\text{joules h}^{-1} \text{g}^{-1}$ of mussels' soft tissue dry weight. Details on calculations for each variable of SFG can be found in Supplemental methods section including Fig. S2.

Nitrogen assimilation of diatoms and cyanobacteria by the mussels after 50 days was calculated following a simple two-source mixing model of bulk $\delta^{15}\text{N}$ -data; $\text{N assimilation} = (\text{sample} - \text{source}_2) / (\text{source}_1 - \text{source}_2 + \text{TEF})$, where source_1 is the bulk $\delta^{15}\text{N}$ of the food source (diatom or cyanobacteria), source_2 is the bulk $\delta^{15}\text{N}$ of the mussels at t0, sample is the bulk $\delta^{15}\text{N}$ of the mussels at t50 for each treatment respectively, and TEF is the trophic enrichment factor (theoretical value of 2.4‰ calculated based on an average of McCutchan et al., 2003, Vanderklift and Ponsard, 2003, as in Liénart et al., 2022b).

The overall isotope niche size (i.e., trophic diversity; Newsome et al., 2007) was calculated for mussels from the field and for each of the three treatments at t20 and t50 ($n = 15$ individual mussels) using a Bayesian approach (Bayesian standard ellipse area, or SEA_B , i.e., the δ space area or distant between individuals in a $\delta^{13}\text{C} - \delta^{15}\text{N}$ biplot, R 'SIBER' package version 2.1.5, using standard settings, e.g., ellipses set to 40% of the data; Jackson et al., 2011).

In addition to the absolute amount of total fatty acid (mg FA g^{-1} sample dry weight of all FAs), individual FA markers or FA groups were recalculated to % of FA per sample to allow for comparison between treatments (due to total amount of organic matter given in the experiment which differ between treatments). The 15-carbon chain long FA (15:0) used as internal standard was removed from the dataset. Proportions of different FA groups were computed according their chemical structure (saturated (SFA), monounsaturated (MUFA), polyunsaturated (PUFA), branched (BrFA), $\omega 3$ or $\omega 6$ FAs) or their physiological role: essentials FAs (EFA, which are the 20:4 $\omega 6$ (arachidonic acid, ARA), 20:5 $\omega 3$ (eicosapentaenoic acid, EPA) and 22:6 $\omega 3$ (docosahexaenoic acid, DHA)), precursors of $\omega 3$ and $\omega 6$ PUFAs (18:2 $\omega 6$ and 18:3 $\omega 3$), or from specific origin (produced by bacteria preferentially (BAFA, which includes the odd-numbered chain 17:0 SFA and 15:0 and 17:0r iso and ante-iso FA).

2.6. Experimental design and statistics

The main purpose of the experiment was to confirm and compare assimilation of elements and micronutrients from diatoms versus cyanobacteria in the experimental mussels, with field measurements of mussels over time. Isotope turnover time in the slow growing Baltic mussels is unknown but was expected to be considerable (Liénart et al., 2020). The raceways were not replicated due to logistical constraints and the individuals (bulk isotope and elemental analyses) or composite samples of mussels ($n = 3$ to 5 mussels; scope for growth, FA

composition and compound-specific isotope analyses) formed the replicates; the assumptions on independence were hence violated. The mussels in the raceways attached instantly to the new substrate and formed clusters, as they do in the field. Since the mussels were supplied with filtered flow-through seawater pumped from a location near the original sampling site where mussels were collected, we consider them as representative populations similar to the field sampling where the same site was sampled over time. We explored correlations among the various biomarkers using multivariate and correlative analyses and performed supplemental PERMANOVA and ANOVA tests with factor treatment and time.

Variation in FA profiles between field mussels and mussels in the experimental treatments and over time was visualized with a non-metric multidimensional scaling (NMDS, all functions from R 'vegan' package, version 2.5.6) ordination plot based on Bray-Curtis dissimilarity matrix. After verifying that the dispersion was similar across treatments (PERMDISP2, 9999 permutations, FA: $p = 0.354$), global differences in treatments and time were investigated with permutational multivariate ANOVAs (PERMANOVA, 9999 permutations, based on Bray-curtis dissimilarity matrix, *adonis* function). A similarity percentages (SIMPER, 9999 permutations, based on Bray-curtis dissimilarity matrix, *simper* function) analysis was performed on untransformed data to identify which FA explained the most dissimilarity between significant different levels.

For field samples, the effect of 'time' was considered as a fixed factor with 3 levels (April, May, June) for FA groups and individual FAs, and 4 levels (April, May, June, July) for elemental, isotope and condition index, and was assessed with one-way ANOVA (*aov* function from R 'stats' package version 4.0.6) followed by Tukey's HDS post-hoc test. For experiment samples, the effects of 'treatment', was considered one fixed factor (see above about lack of true replication) with 3 levels (D, C, M) and 'time', as another fixed factor with 2 levels (t20, t50) for FA groups and individual FAs and 5 levels SFG (t10, t20, t30, t40, t50) for elemental, isotope, condition index and. The effect of time, treatment and the interaction between both were assessed with two-way ANOVA (*aov* function from R 'stats' package) followed with a Tukey's HDS post-hoc. For all ANOVAs, normality and homogeneity of variance of the residuals were inspected using Shapiro-Wilk and Levene tests respectively. The ANOVA and Kruskal-Wallis output are reported only in Supplemental material since there was no true replicates in the experiment.

Finally, in order to explore correlations between our different endpoints over time, non-parametric Spearman's rank correlations were performed. We combine two datasets; dataset I is elemental, isotope, condition index, SFG, SEA_B (i.e., Table S1) with $n = 19$ (combining field and experimental sampling time points), dataset II is individual FAs and groups of FAs (i.e., Table S2) with $n = 9$ (field and experimental sampling points). Correlations were tested (see Table 1); i) between all endpoints (datasets I + II, limited by the smallest samples size, $n = 9$, or $n = 7$ or 6 for correlations with SFG and $\delta^{15}\text{N}$ -Phe), ii) focusing on the experiment only using dataset I ($n = 15$), and iii) among selected endpoints (i.e., relevant as diet or condition biomarkers) within dataset II ($n = 9$ for field + experiment). Since our sample size was always very low we did not perform any Bonferroni corrections for the large number of correlations performed and significant results should therefore be carefully interpreted.

3. Results

In addition to the figures, all data (average \pm sd) are presented in Table S1 and S2. Statistical tests are detailed in Table 1 (correlations) and Table S3 (ANOVAs), hereafter we only report significant results (i.e., ANOVAs and relevant correlations).

Table 1

Significant correlations from Spearman's rank correlation tests; rho is the spearman correlation coefficient, p is the p-value, n is the number of observations for a given test using datasets I and/or II (see 2.6. Experimental design and statistics). var1 and var2 denote the variables correlated, p is the p-value, n is the sample size. Please note that Bonferroni correction of the α for multiple tests is not applied since sample size is low; hence these significant correlations should be carefully interpreted.

Proxy for:	var1	var2	rho	p	n		
Growth	P ~	$\omega 6$	-0.70	0.04	9 (dataset I + II)		
		18:2 $\omega 6$	-0.83	0.008			
		20:4 $\omega 6$	-0.73	0.03			
	C:P ~	$\omega 6$	0.63	0.08			
		18:2 $\omega 6$	0.73	0.03			
		20:4 $\omega 6$	0.77	0.02			
	N:P ~	$\omega 6$	0.75	0.03			
		18:2 $\omega 6$	0.73	0.03			
		20:4 $\omega 6$	0.77	0.02			
		SFG ~	$\delta^{15}\text{N}$	-0.81		0.03	7 (dataset I + II)
16:1 $\omega 7$	-0.77	0.04					
BAFA	0.81	0.03					
SFA	0.81	0.03					
Condition	CI ~	$\delta^{13}\text{C}$	-0.92	0.001	9 (dataset I + II)		
		totFA	0.80	0.01			
		MUFA	0.83	0.01			
		PUFA	-0.85	0.01			
		$\omega 3$	-0.83	0.01			
		22:6 $\omega 3$	-0.78	0.02			
	16:1 $\omega 7$	0.83	0.01				
	total FA	$\delta^{13}\text{C}$	-0.88	0.003		9 (dataset I + II)	
		~	22:6 $\omega 3$	-0.82			0.01
		9 (dataset II field + expe)					
9 (dataset I + II)							
Condition / Diet	EFA ~	$\delta^{13}\text{C}$	0.73	0.03	9 (dataset I + II)		
		18:3 $\omega 3$	-0.70	0.04	9 (dataset II field + expe)		
Diet	$\delta^{15}\text{N}$ ~	EFA	0.72	0.04	9 (dataset I + II)		
		MUFA	0.89	0.03	6 (dataset I + II)		
	~	16:1 $\omega 7$	0.94	0.02			
		PUFA	-0.89	0.03			
		$\delta^{13}\text{C}$ ~	$\delta^{15}\text{N}$	0.61	0.02	15 (dataset I, expe only)	
CI	-0.71	0.04					

3.1. Condition status and bioenergetics of blue mussels

During the experiment, the mortality of the mussels was generally very low (<3%), yet with highest mortality in the diatom treatment (2.4%), intermediate for cyanobacteria treatment (1.2%) and lowest for the mixed treatment (0.6%). Visual observations showed that the mussels from the diatom treatment produced more pseudofeces than mussels from the other treatments directly after being fed; likely reflecting the total higher amount of food added in this treatment. The CI significantly decreased over time during the experiment regardless of treatment, and also significantly decreased over time for the mussels collected in the field (Fig. 2d, Table S1).

The scope for growth (SFG, Fig. 2g, Table S1) was negative at the start of the experiment ($-0.9 \text{ J h}^{-1} \text{ g}^{-1}$ mussel dw) and was low or negative throughout the experimental duration for mussels fed diatoms (median across time points: $-2.5 \text{ J h}^{-1} \text{ g}^{-1}$ mussel dw), intermediate for mussels fed the mix (median: $6.9 \text{ J h}^{-1} \text{ g}^{-1}$ mussel dw), and higher for mussels fed cyanobacteria (median: $33.4 \text{ J h}^{-1} \text{ g}^{-1}$ mussel dw). The clearance rate (CR) was higher for mussels fed cyanobacteria during the experiment (median: $65.0 \text{ J h}^{-1} \text{ g}^{-1}$ mussel dw), compared with mussels fed the mix (median: $48.0 \text{ J h}^{-1} \text{ g}^{-1}$ mussel dw), with intermediate values for mussels fed diatoms (median: $53.6 \text{ J h}^{-1} \text{ g}^{-1}$ mussel dw; Table S1). The respiratory expenditure (ΔO_2) was similar for the three treatment (median: $6.9 \text{ J h}^{-1} \text{ g}^{-1}$ mussel dw; Table S1). The assimilation efficiency (AE) was low in the diatom treatment (13%), high in the cyanobacteria treatment (62%) and intermediate in the mix treatment (34%). The energy lost as faeces (F, similar values were measured at t10 and t50 for each treatment) was similar between treatments ($0.038 \pm$

$0.001 \text{ J h}^{-1} \text{ g}^{-1}$ mussel dw).

3.2. Food sources characteristics

As expected, the $\delta^{15}\text{N}$ signal was well discriminated between the two food sources, with positive values for the diatom material ($9.1 \pm 0.2\text{‰}$) and negative values ($-0.8 \pm 0.2\text{‰}$) for the cyanobacteria material (Fig. 3a, Table S1). Similarly to the bulk $\delta^{15}\text{N}$, the $\delta^{15}\text{N}$ signal of the source amino-acid Phenylalanine (Phe- $\delta^{15}\text{N}$, Fig. S3) was positive for diatom material (10.7‰) and negative for cyanobacteria (-1.5‰). $\delta^{13}\text{C}$ also differed between both food sources with more negative values for cyanobacteria material ($-27.2 \pm 0.1\text{‰}$) compared with diatoms ($-23.2 \pm 0.1\text{‰}$; Fig. 3a, Table S1). Carbon, nitrogen and phosphorus contents were comparable for both food materials ($21.1 \pm 0.6\%$ C, $3.6 \pm 0.1\%$ N, and $0.42 \pm 0.01\%$ P for diatom; $24.6 \pm 3.2\%$ C, $4.8 \pm 0.6\%$ N, and $0.28 \pm 0.04\%$ P for cyanobacteria; Table S1).

A total of 21 and 27 FAs (8 to 23 in carbon chain length) were identified in the diatom and cyanobacteria material respectively, with similar FA content (diatom: $15.5 \text{ mg} \pm 1.0 \text{ FA g}^{-1}$ sample dw; cyanobacteria: $15.0 \text{ mg} \pm 1.3 \text{ FA g}^{-1}$ sample dw) for both food materials (Table S2). In both food materials, the saturated FAs (SFA) 14.0 and 16.0 constituted the largest proportion of the total FA (sum of ca. 42 to 57% for cyanobacteria and diatoms, respectively). The diatom material was characterized by high proportions of monounsaturated FAs (MUFA, ca. 33%), especially 16:1 $\omega 7$ (ca. 27%). Cyanobacteria had high proportions of polyunsaturated FAs (PUFA, ca. 46%), especially 18:3 $\omega 3$ and 18:2 $\omega 6$ (ca. 37%, and ca. 7% respectively) compared with diatoms (PUFAs of ca. 9%, no 18:3 $\omega 3$, <0.5% for 18:2 $\omega 6$). Regarding the essential FAs (EFA), 20:4 $\omega 6$ (arachidonic acid, ARA) was only found in cyanobacteria and in very small proportions (<1%), while 20:5 $\omega 3$ (eicosapentaenoic acid, EPA) and 22:6 $\omega 3$ (docosahexaenoic acid, DHA) were higher in diatoms (ca. 4 and 1.3% respectively) than in cyanobacteria (<1% for both). The $\omega 3/\omega 6$ ratio was 20.7 for diatoms compared with 5.0 for cyanobacterial material. Bacterial FAs (BAFA) were <1% in both food materials.

3.3. Elemental and isotope ratios of blue mussels

During the experiment, $\delta^{13}\text{C}$ significantly increased for all treatments (between 0.7 and 1.3‰ increase) and there were significant $\delta^{15}\text{N}$ changes over time depending on treatment (Fig. 2f and 3c, Table S1). The mussels fed cyanobacteria material had significantly lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values compared to the two other treatments (Fig. 2e,f and 3c). Similarly to the bulk-values, the $\delta^{15}\text{N}$ -Phe was lower at the end of the experiment for the mussels fed cyanobacteria compared with the two other treatments (Fig. S3). There were no significant differences in C, N and P content nor ratio over time and/or among treatments in the mussels from the experiment (Fig. 2a,b,c and S4).

For the mussels collected in the field, the C and P % were significantly lower in July compared to previous months (Fig. S4, Table S1) and generally lower compared to the values for experimental mussels. The $\delta^{13}\text{C}$ values were more enriched in July compared to previous months and to the experimental mussels (Fig. 2f and 3b). There were no significant differences over time in N content, C:N, or bulk- $\delta^{15}\text{N}$ in the mussels collected in the field (Fig. 2a,e and S4), but a decrease in Phe- $\delta^{15}\text{N}$ over time in the field was apparent (Fig. S3).

3.4. Fatty acid profiles of blue mussels

A total of 33 FAs was identified in the mussels' tissue (Table S2) with an absolute amount of total FA per mussel ranging from ca. 50 to 120 mg FA g^{-1} sample dry weight. Generally, mussels were rich in PUFAs which constituted ca. 55% of total FA. Beside SFAs (ca. 26%), mussels were rich in EFAs (ca. 26% of total FA), especially EPA (ca. 9%) and DHA (ca. 16%). Overall, FA profiles significantly differed in time between field months, between experimental t0, t20 and t50 mussels and also between treatments for the experimental mussels (NMDS, Fig. 4, stress = 0.08,

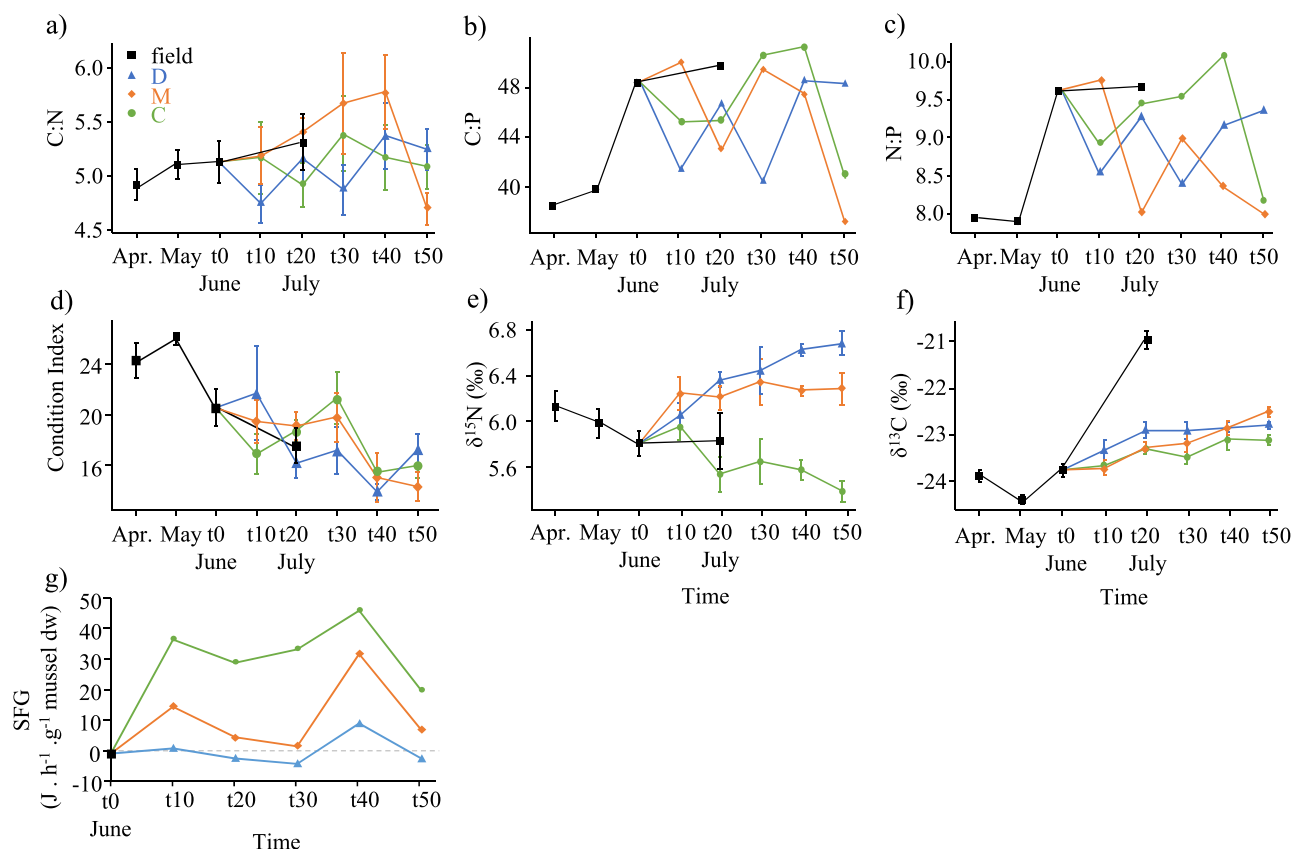


Fig. 2. a - g: Elemental (C:N, N:P, C:P) and isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) ratios, condition index (CI) and scope for growth (SFG) of mussels over time for field (black squares) and for the experiment, D: diatom (blue triangles), C: cyanobacteria (green circles), M: mix (orange diamonds). Mussels sampled in June correspond to t0, and July to t20 in the experiment. When present, error bars represent the standard error. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

PERMANOVA tests in caption). There were 11 FAs contributing up to 80% of the overall dissimilarity (SIMPER, Fig. 4), especially the EFAs EPA and DHA, the 16:1 ω 7 (marker of diatoms), and the precursors of ω 3 and ω 6 long-chain PUFAs 18:3 ω 3, 18:2 ω 6.

During the experiment, significant changes in the mussels' FA compositions were observed over time, some with treatment (Fig. 5, Table S2 and S3). The absolute amount of total FA was significantly lower in the mussels at the end of the experiment independently of the treatment (Fig. 5a). The relative proportions of SFAs and PUFAs did not change significantly over time or with treatment (Fig. 5b,d). MUFAs were higher for the mussels fed diatoms only while BAFA were higher in the mussels fed cyanobacteria compared to other treatments (Fig. 5c). The EFA content (low in the cyanobacterial material) was significantly lower in the mussels fed cyanobacteria (Fig. 5e). The FA ARA (20:4 ω 6) decreased over time for all treatments (Fig. 5l) while EPA (20:5 ω 3) increased but EPA was lower for mussels fed cyanobacteria compared to the other treatments (Fig. 5k). The FA marker of diatoms, 16:1 ω 7, was significantly higher in mussels fed diatoms only (Fig. 5h), while the FA 18:3 ω 3, abundant in the cyanobacteria material, was significantly higher in mussels fed cyanobacteria (Fig. 5i). There was a significant decrease in the ω 3 precursor 18:3 ω 3 over time except for the cyanobacteria treatment where it instead increased over time (Fig. 5i). The ω 3/ ω 6 ratio increased over time for all treatments, with higher values for the mixed treatment (Fig. 5g).

For the mussels collected in the field, the absolute amount of total FA in mussels' tissues, the relative contribution of SFAs and MUFAs, varied over time with the highest values in May compared to April and June (Fig. 5). The proportion of PUFAs showed an opposite pattern with the lowest values in May (Fig. 5d). There was a significant increase in both ω 3 and ω 6 precursors: 18:3 ω 3 and 18:2 ω 6 (Fig. 5i,j). The EFAs were

significantly higher in mussels sampled in April: EPA decreased while ARA and DHA increased (Fig. 5e,k,l,m). Mussels tissues' ω 3/ ω 6 ratio significantly decreased over time (Fig. 5g).

3.5. Compound specific isotopes, assimilation and trophic niche

Food assimilation calculated based on bulk $\delta^{15}\text{N}$ data suggests only slightly higher assimilation of the diatom-derived N (16%) compared to cyanobacterial N (10%) at the end of the experiment, despite the 50% higher amount of diatoms given compared to cyanobacteria. However, this was not seen for the $\delta^{15}\text{N}$ values in the source AA Phenylalanine where values from diatom and mixed treatments remain similar to t0 values at t50, while the cyanobacteria fed mussels showed a clear decrease (Fig. S3). Regarding isotope niche size, at t50, the niche size was ca. 33% larger in the mixed treatment compared with the cyanobacteria and diatom treatments (Fig. S6).

Regarding $\delta^{13}\text{C}$ -FAs, there was generally negligible enrichment between diatom material and mussels fed diatoms (ca. 0.1‰), especially for the diatom marker 16:1 ω 7, while enrichment was large between cyanobacteria and mussels fed cyanobacteria (ca. 3.4‰, Fig. 6a,b; see also Fig. S5, Table S4). Generally, for the identified FAs, the $\delta^{13}\text{C}$ -FAs of the mussels fed the (diatom dominated) mix were closer to diatom material than to cyanobacteria material (Fig. 6c, Table S4). The difference in $\delta^{13}\text{C}$ -FAs between mussels at t0 and t50 for each treatment was high for diatoms and mix (ca. 1.1‰) compared with cyanobacteria (ca. 0.6‰; Fig. S5).

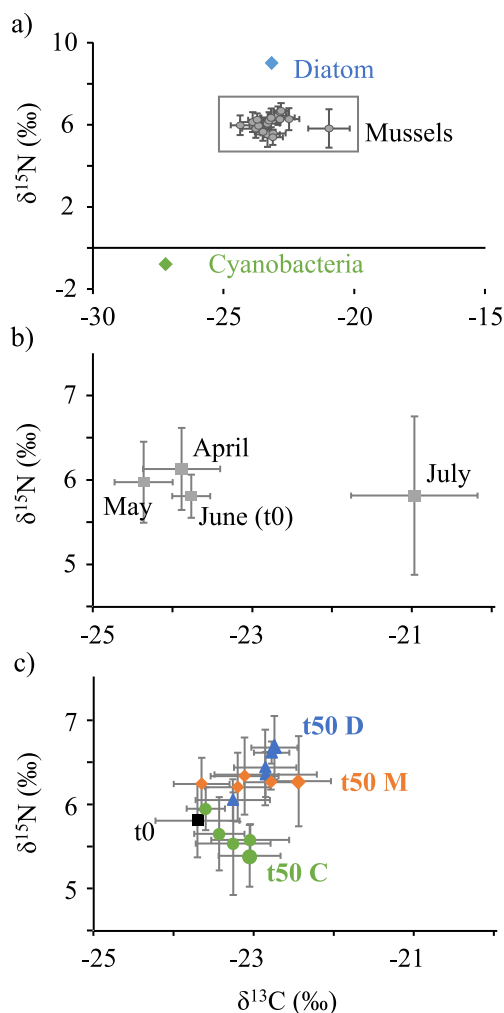


Fig. 3. Biplots of carbon and nitrogen isotope composition of a) food sources (blue and green diamonds) and all mussels (grey circles), the rectangle indicates the focus of the two other panels: b) mussels collected from the field from April to July (squares), c) mussels used in the experiment from t0 (black square, corresponds to June) to t50 for the three treatments, D: diatom (blue triangles), C: cyanobacteria (green circles), M: mix (orange diamonds). Error bars represent the standard deviation, and are not visible for diatom and cyanobacteria food sources (0.1‰ for $\delta^{13}\text{C}$ and 0.2‰ for $\delta^{15}\text{N}$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.6. Correlations between diet biomarkers, growth and condition proxies in mussels

Significant correlations are presented in Table 1 and briefly described here.

Among the various diet biomarkers in the mussels, bulk- $\delta^{15}\text{N}$ was positively correlated with proportions of essential FAs. The $\delta^{15}\text{N}$ -Phe was positively correlated to proportions of MUFAs and more specifically to the diatom marker 16:1 ω 7, while it was negatively correlated to proportions of PUFAs. In the experimental mussels, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were positively correlated. Total FA content was negatively correlated with $\delta^{13}\text{C}$ (i.e., the more negative the $\delta^{13}\text{C}$, the more the absolute amount of total FAs) while the proportions of essential FAs were positively correlated to $\delta^{13}\text{C}$ (i.e., the more negative the $\delta^{13}\text{C}$, the less the % of EFA).

The associations between proxies for mussels' condition status and diet biomarkers were observed through the following correlations: The CI was negatively correlated with $\delta^{13}\text{C}$, the more enriched ^{13}C values the lower CI, i.e., lowest in July and in the end of the experiment

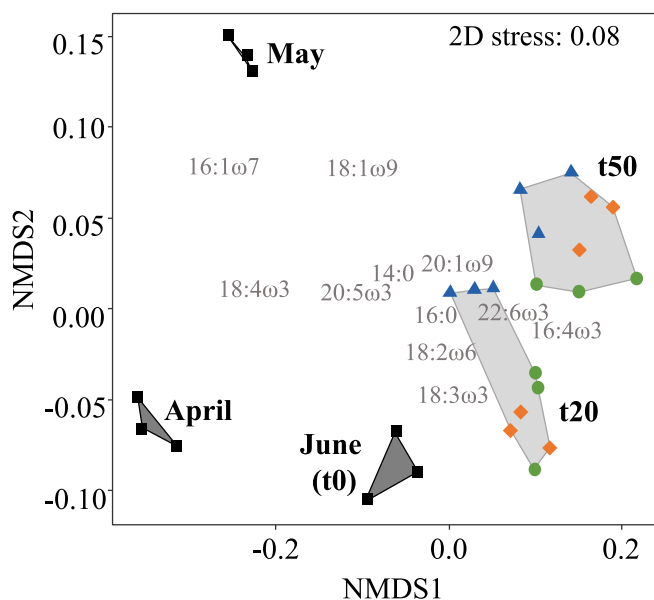


Fig. 4. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity matrix calculated on fatty acids (FA) % for blue mussels from the field (black squares, dark grey polygons; April, May, June) and the different treatments of the experiment at t20 and t50 (light grey polygons), D: diatom (blue triangles), C: cyanobacteria (green circles), M: mix (orange diamonds). Mussels from July were not measured for FAs. The factor 'time' is represented with the hulls since significant difference was found (PERMANOVA, $p = 0.0001$; Table S3). There was also significant difference in the factor 'treatment', D: Diatoms (blue), C: cyanobacteria (green), M: mix (orange) for the experiment mussels (PERMANOVA, $p = 0.012$; Table S3). The 11 FAs shown in the NMDS are the main FAs explaining up to 80% of the average dissimilarity (SIMPER analyse). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(correlation remained if focusing on experimental mussels only). Mussels' CI was also negatively correlated with PUFAs, especially ω 3 and the essential FA 22:6 ω 3, and positively correlated with the absolute amount of total FAs and relative amounts of MUFAs and to the diatom marker 16:1 ω 7.

Associations between proxies for growth and diet biomarkers were inferred from the positive correlations between N:P and 18:2 ω 6, 20:4 ω 6 and ω 6. During the experiment, the SFG, which was generally high for the mussels from the cyanobacteria treatment, was negatively correlated to $\delta^{15}\text{N}$ and with 16:1 ω 7, while positively correlated with SFAs and BAFAs proportions, the latter group being higher in the mussels from the cyanobacteria treatment.

4. Discussion

During the 50 days of the experiment, we observed a low mortality rate (<3%) in all treatments. However, the condition index (CI) and total fatty acid (FA) content of the mussels started decreasing in all treatments after 30 and 20 days respectively. A possible explanation can come from increased respiration rate of the mussels due to suboptimal temperatures in late summer which reduces body condition in mussels (Hiebenthal et al., 2013). At this time of the year, late summer, blue mussels in the Baltic also have their lowest growth rate, probably partly from high temperatures and hence high energy requirements, but also lower food availability (Kautsky, 1982). Indeed, there was a temperature increase $>5^\circ\text{C}$ in the air and surface water at the Askö field station area between day 20 and 30 of our experiment (Fig. S7a, b). Despite water temperature being controlled throughout the experiment, there was 1°C increase in water temperature for all raceways during feeding sessions (when our water system was turned off to allow feeding).

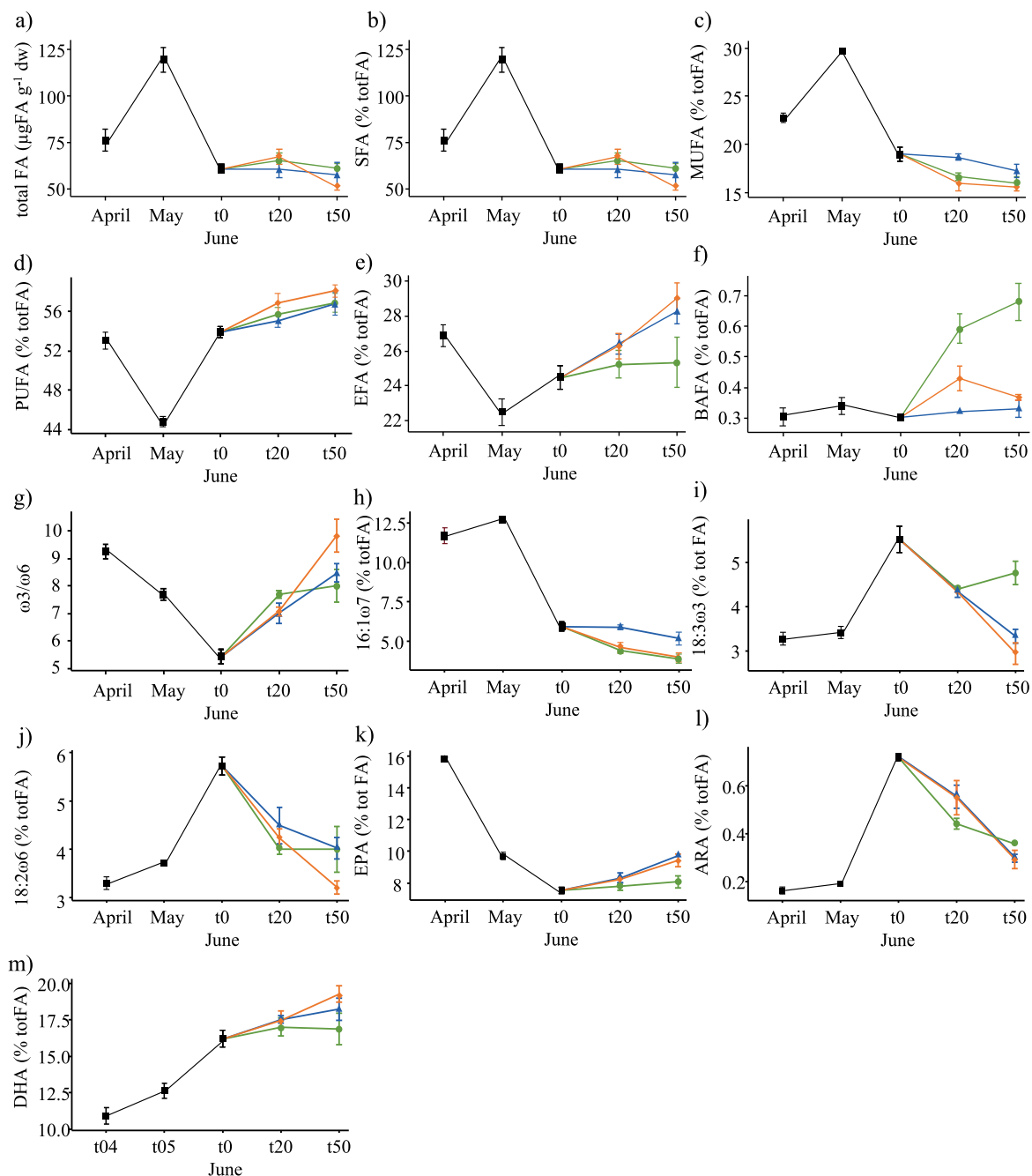


Fig. 5. a) Fatty acid total absolute amount (in $\mu\text{g g}^{-1} \text{dw}$), and b-m) relative content of the different groups or individual FAs (in % of total FA) in mussels' soft tissue over time for field mussels (black squares) and for the different treatments in the experiment, D: diatom (blue triangles), C: cyanobacteria (green circles), M: mix (orange diamonds). Mussels sampled in June correspond to t0. Error bars represent the standard error. Data are shown also in Table S2. EPA is 20:5 ω 3, ARA is 20:4 ω 6, DHA is 22:6 ω 3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Moreover, the mussels could have been food limited in the second half of the experiment (partly from increased respiration with higher water temperature). Hence, our results will be discussed, when there is a difference for a given endpoint, in relation to both the first half and the second half of the experiment. The three food materials (treatments) of our experiment were diatom-dominated spring bloom material (highest food quantity), cyanobacteria-dominated summer bloom (lowest food quantity), and a mix of both that is dominated by diatoms (approximately 75% diatoms, intermediate food quantity).

4.1. Evidence for assimilation of cyanobacteria and diatoms and potential preferences

4.1.1. Nitrogen and amino acids

In support of hypothesis 1 (i.e., the mussels' $\delta^{15}\text{N}$ would reflect that of each food type), we observed a decrease of 0.4‰ in the $\delta^{15}\text{N}$ for the mussels fed cyanobacteria (depleted in ^{15}N), and an increase of 0.9‰ in $\delta^{15}\text{N}$ for the mussels fed diatoms (enriched in ^{15}N in our experiment) during the experiment, demonstrating assimilation of N from both food types. A recent feeding experiment from Berezina et al. (2021) also showed decreasing bulk- $\delta^{15}\text{N}$ signal in different invertebrates (e.g., copepod, cladocerans, isopods, amphipods) exposed to the the same,

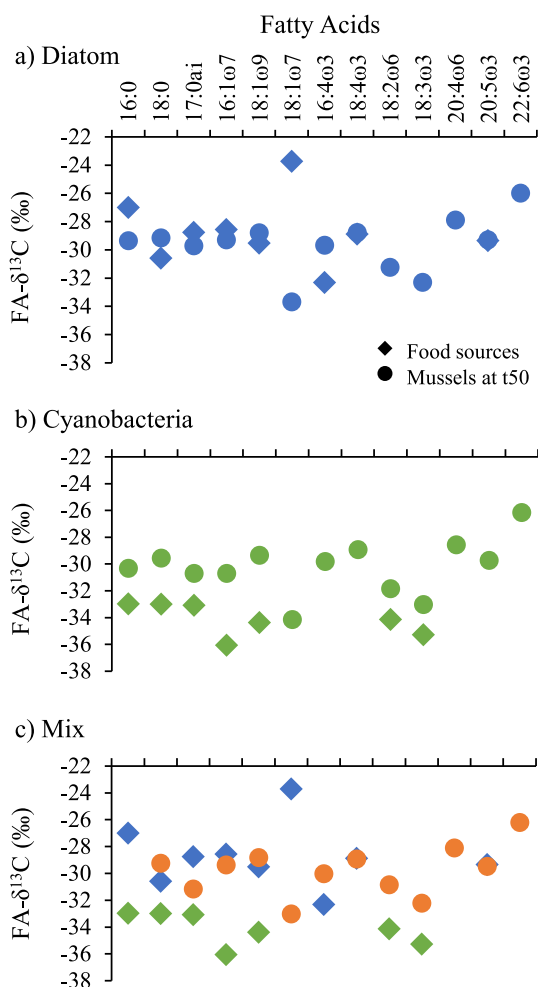


Fig. 6. $\delta^{13}\text{C}$ values of the different fatty acids (FA- $\delta^{13}\text{C}$, in ‰) for the food sources; diatom (blue diamonds) and cyanobacteria (green diamonds) and mussels at t50 (circles) in the three treatments a) diatom (blue circles), b) cyanobacteria (green circles), c) mix (orange circles). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

non-toxic *Aphanizomenon* as used in our study. Our results were further supported at the end of the experiment by the low $\delta^{15}\text{N}$ of the source amino acid (AA) Phenylalanine ($\delta^{15}\text{N}$ -Phe) in mussels fed cyanobacteria (even more pronounced ^{15}N depletion compared to bulk values; Fig. S3). Also, $\delta^{15}\text{N}$ -Phe of mussels sampled in the field in July (during the cyanobacteria peak, see Fig. S7c) were approaching the cyanobacteria $\delta^{15}\text{N}$ -Phe signal (Fig. S3), demonstrating that mussels assimilate Phenylalanine from cyanobacteria in summer, which was partly masked in the bulk $\delta^{15}\text{N}$ -signal in field mussels, supporting observations from long-term monitoring data in the same area (Liénart et al., 2022). The $\delta^{15}\text{N}$ -Phe in mussels fed diatoms and the mix were however similar and rather unchanged from field mussels in May and June (start of the experiment). This was unexpected since diatom-Phe was enriched (similar to bulk $\delta^{15}\text{N}$ for diatoms), suggesting that N sources other than Phenylalanine (i.e., other AAs) are responsible for the observed increase in bulk $\delta^{15}\text{N}$ values over time for mussels fed diatoms. Differences in specific AAs incorporation rates (Loick-Wilde et al., 2012) may explain the difference between bulk and Phe $\delta^{15}\text{N}$ patterns in mussels fed diatoms. The contrasting pattern between bulk and Phe precludes testing hypothesis 2 (i.e., mussels fed on mixed diet selectively assimilate some compounds from one food type according to food preferences) on selective assimilation of diatom or cyanobacteria N in the mix treatment. The 30% larger niche size in the mixed treatment relative to the single

diets (Fig. S6) indicates that mussels fed on both food sources in the proportions they were given in the mix (ca. 75 diatom - 25 cyanobacteria), suggesting no diet selection.

4.1.2. Carbon and fatty acids

Our bloom materials differed in FA composition, with more PUFAs but less essential FAs in the cyanobacteria. Similar FA patterns between diatoms and cyanobacteria have been reported by Nascimento et al. (2009) comparing *Nodularia spumigena* with diatom-dominated spring bloom. Mussels fed diatoms (diatom only and the diatom-dominated mix) showed a higher proportion of 16:1 ω 7, a diatom-biomarker (Dalsgaard et al., 2003), and EPA (an essential FA), both abundant in our diatom material. There was also higher proportion of DHA in mussels fed diatoms, a marker of dinoflagellates, indicating that dinoflagellates species were present in the spring bloom material (see section 2.1) and might be selectively assimilated since they were not visually dominant. High proportions of MUFAs and essential FAs in diatoms were generally reflected in diatom-fed mussels. Mussels sampled in the field in spring (April and May) also showed high proportions of the diatom marker and EPA demonstrating diatom assimilation from the spring bloom (similarly as in Irisarri et al., 2014). In contrast, mussels fed cyanobacteria showed higher proportions of 18:3 ω 3 (a precursor of the essential FAs EPA and DHA, Fig. S8), which was the dominant FA in our cyanobacteria material. The mussels collected in the field in June, corresponding to the onset of the cyanobacterial bloom at this time of the year (see Fig. S7), also showed a high proportion of 18:3 ω 3 and more PUFAs relative to spring.

Traditionally, $\delta^{13}\text{C}$ is used as a diet tracer since the trophic enrichment is smaller than for ^{15}N , however, physiological processes can also influence $\delta^{13}\text{C}$ values in consumers. During the experiment, $\delta^{13}\text{C}$ of mussels fed diatoms shifted towards the diatom $\delta^{13}\text{C}$ value, supporting an assimilation of diatom material, but mussels fed cyanobacteria also showed enriched ^{13}C values at the end of the experiment, despite the low $\delta^{13}\text{C}$ values of cyanobacteria and the evidence of utilization of cyanobacterial N (see above). Such enrichment in bulk- $\delta^{13}\text{C}$ values in mussels fed cyanobacteria can be explained by the larger ^{13}C enrichment of the individual FAs (FAs consist of a chain of carbon atoms and is an important C pool in living cells) between mussels and the cyanobacteria diet (Fig. 6b) relative to the negligible enrichment in the same FAs between mussels and diatoms diet (Fig. 6a). The $\delta^{13}\text{C}$ values of individual FAs also support a preferential assimilation of diatoms when mussels were offered both diatoms and cyanobacteria (hypothesis 2, i.e., mussels fed on mix diet selectively assimilate some compounds from one food type according to food preferences) since the FA- $\delta^{13}\text{C}$ values of the mussels fed the diatom dominated mix was often identical to diatom material (Fig. 6c, see e.g., FAs 16:1 ω 7 and 18:1 ω 9).

Our $\delta^{13}\text{C}$ -FA results hence indicate that mussels fed diatoms likely acquire FAs directly from their food, while metabolic steps exist for mussels fed cyanobacteria (i.e., FA biosynthesis); the average difference in FA- $\delta^{13}\text{C}$ between cyanobacteria and mussels was larger (3.4‰) than between diatoms and mussels (0.1‰). A low fractionation between the $\delta^{13}\text{C}$ -FA of diet and a consumer generally result from direct FA assimilation (i.e., negligible physiological transformation of these FAs), while a larger fractionation (whether it is an enrichment or a depletion) is observed in a mix of both dietary and synthesized molecules in consumers' tissues (Mathieu-resuge et al., 2022; Traugott et al., 2013). As an example, our diatom marker 16:1 ω 7, which is ca. 27% of total FA in diatom material but <3% of total FA in cyanobacteria but is still present in similar proportions in mussels regardless of treatment, showed ^{13}C enrichment of 0.7‰ between diatom and mussels (direct assimilation of this abundant FA), while it has an enrichment of 5.4‰ between cyanobacteria and mussels (indicating synthesis from precursor FAs).

An alternative explanation for the larger ^{13}C enrichment between cyanobacteria and mussels FAs is that an intermediate trophic step exists between the cyanobacteria food source and the mussels. Microorganisms colonizing cyanobacterial filaments is a possible pathway

for cyanobacterial N and P assimilation by macrofauna as shown for zooplankton and deposit-feeders in the Baltic Sea (Eglite et al., 2018; Karlson et al., 2015; Ploug et al., 2011). In our experiment, mussels fed cyanobacteria had higher proportions of bacterial FAs (BAFAs) in their tissues compared with mussels fed other diets (Fig. 5f), although these FAs were surprisingly low in the cyanobacteria material (Table S2). Specific bacteria in mussels' gut microbiome may help in degrading cyanobacterial filaments as an adaptation mechanism to toxic cyanobacterial blooms, as shown for zooplankton (Gorokhova et al., 2021).

4.2. Effect of food quality on mussels physiological status and growth

According to hypothesis 3, we expected a better health status, reflected in higher condition index, total FA and essential FA content, and higher scope for growth for mussels exposed to the mixed-diet, due to complementarity in micronutrients between the two food materials. No such clear effects were seen here and comparisons were complicated by the fact that the mixed treatment was not a 50:50 mix. In fact, there was a positive effect of cyanobacteria as assessed from the scope for growth (and negative correlation between $\delta^{15}\text{N}$ and SFG, the more cyanobacterially derived N assimilated by mussels, the better SFG). The SFG was always low or negative for the mussels fed diatoms, which indicates less favourable energetic status (likely growth limited) and the use of body reserves, despite the higher total amount of food added as well as the higher proportion of essential FA observed in these mussels.

Filamentous cyanobacteria are known to be rich in N, P and AAs (Ahlgren et al., 1992; Loick-Wilde et al., 2012; Walve and Larsson, 2007), which are essential compounds for consumers to maintain basal metabolic functions and good growth (e.g., Li et al., 2008; Peltomaa et al., 2017). During the experiment, the mussels maintained a relatively constant elemental composition independently of the lower diet quantity and quality, which reflect the generally high degree of homeostatic control of N and P of consumers (in our bloom materials, % N was somewhat higher in cyanobacteria, but % P higher in diatoms, with a similar % C for both food sources, Table S1). However, the N:P ratio were on average higher for the cyanobacteria-fed mussels and lowest for the diatom-fed mussels (Fig. 2c). Mussels are N limited in the Baltic since N is required for short-term osmoregulation (NH_4 and free amino acids are excreted during low salinity conditions, Tedengren and Kautsky, 1986). Elemental requirements of the mussels likely vary with season and biological processes (Smaal and Vonck, 1997), and it is possible that the somewhat higher N:P ratio of the cyanobacterial material is better for mussels at this time of the year, despite generally lower quantity of cyanobacteria than diatoms in the experiment.

On a similar note, even though the essential FA proportions and especially EPA and DHA were higher in diatoms compared to cyanobacteria, which generally indicates diatoms as superior in terms of food quality, the cyanobacteria material was very rich in 18:3 ω 3 (37%), a precursor of EPA and DHA (see Supplemental material Fig. S8 for a summary of biosynthesis pathways). In mussels fed diatoms and the mix, the proportions of EPA were high and increased over time indicating a selective retention of this EFA from diet, especially from day 20 when thermal stress or food limitation may have occurred. Such selective accumulation has previously been observed for other bivalve species (Ezgeta-Balić et al., 2012; Ventrella et al., 2008). In mussels fed cyanobacteria, the proportions of 18:3 ω 3 increased after 20 days while EPA and DHA proportions remained stable over time, indicating that, despite low proportions in the food, mussels were able to cover their EFAs requirements and maintain a certain threshold in EPA and DHA. Mussels are likely capable of biosynthesis of long-chain ω 3 EFAs from dietary precursors (Alkanani et al., 2007; Fernández-Reiriz et al., 2015). Indeed, according to the $\delta^{13}\text{C}$ -FA results, 18:3 ω 3 in the cyanobacteria material was likely biotransformed by the mussels to maintain essential EPA levels (as shown by the large fractionation between $\delta^{13}\text{C}$ of this FA in cyanobacteria and in the mussels, Fig. 6b, see 4.1.2). Other invertebrate taxa also show such endogenous capacity for long-chain PUFAs synthesis

(De Troch et al., 2012; Hall et al., 2006; Kabeya et al., 2018), suggesting that de novo production or biosynthesis from precursors of EFAs might be more common than previously thought. Also, copepods sampled during a large cyanobacterial bloom in the Baltic were able to cover their energy requirements, despite the lipid-poor cyanobacterial food source (Eglite et al., 2019). Hence, consumers can cope with suboptimal food sources if given enough low quality food by adjusting their biosynthetic pathways.

4.3. Mussels diet and physiology in natural environmental conditions

Elemental composition (C:P and N:P) of mussels from the field varied significantly over time reflecting the effect of natural physiological processes (i.e., reproduction cycle) on mussels' stoichiometry (Smaal and Vonck, 1997). The drop in absolute amount of total FA and in condition index from May to June, together with ^{13}C enriched values of mussels sampled in July, indicate that the mussels have spawned. Indeed, lipid content increase during bivalve gametogenesis, then decrease rapidly during spawning (Martínez-pita et al., 2012; Zandee et al., 1980), where mussels can lose up to half of their body mass (Kautsky, 1982). Since lipids (i.e., C rich molecules) are depleted in ^{13}C relative to protein and carbohydrates (Post et al., 2007), the loss of tissue rich in fat such as gametes is likely reflected into a high $\delta^{13}\text{C}$ signal, as observed in field mussels in July. In the Baltic, mussel spawning first consists of a release of 80% of the gametes before mid-June, and later on a release of the 20% remaining (Kautsky pers. com.). The mussels were purposefully sampled for our experiment in end June (26th) supposedly after the largest spawning peak had already happened. During the experiment, there was a depletion in ^{13}C in mussels' tissues for the three treatments and, besides the dietary effects on $\delta^{13}\text{C}$ values (see section 4.1.2.), it could possibly be that mussels released the remaining part of their gametes during the experiment, as observed in the field (i.e., mussels were fully spawned mid-July) which could contribute to explain decreases in body condition.

The CI of the mussels also decreased in the field from May to July, but experimentally feeding them cyanobacteria or a diet-mix seemed to improve the post-spawning recovery after a month (from t_0 to t_{30} , highest CI for cyanobacteria treatment and lowest for diatoms, despite the fact that diatoms were given in higher quantity). Cyanobacteria as food resulted in better growth conditions (SFG). Hence, the nutritional quality provided by cyanobacteria at this time of the year after the main spawning occurred (i.e., mussels sampled in late June), seems to better match mussels physiological requirements, while in spring (i.e., April) the diatom bloom (see Fig. S7d) provides more EFAs to build up lipid and P-rich gametes (without the need for energy-costly biosynthesis).

4.4. Ecological perspectives and concluding remarks

Our results add to the growing body of literature demonstrating utilization of diazotrophic nitrogen in the Baltic food webs (e.g., Karlson et al., 2015), previously not tested for blue mussels, only indicated from spatio-temporal correlations (Liénart et al., 2022). As far as we know, our study provides the first long-term feeding experiment demonstrating how blue mussels assimilate N and FAs from cyanobacteria and diatoms and shows the physiological response to these food types. The mussels were able to cope with different food qualities either by preferentially taking up and retaining essential FAs or other compounds (e.g., amino acids), or through biosynthesis of these essential FAs from precursors, when available in diet. Despite cyanobacteria was added in lower quantities, a diet based on them resulted in a better scope for growth and higher N:P ratios in mussels, likely matching their physiological requirements, i.e., post-spawning recovery, at this time of the year.

Our study demonstrates that imbalances in diet biochemical composition can largely be overcome by consumers through biosynthesis of essential FAs. The results of our experiment that was conducted using *Aphanizomenon* bloom are however not necessarily translatable to

the toxic cyanobacteria *N. spumigena*. Still, *Aphanizomenon* constitute 80% of the cyanobacterial biomass in the Baltic Sea, and can be even more dominant in the coastal regions (Högländer et al., 2004; Olofsson et al., 2020) where blue mussels are abundant. Cyanobacterial blooms are increasing worldwide in frequency and duration and understanding the biological effects of such changes in the quality of the production base is critical, especially in the current context of climate change.

Authors contribution statement

CL (0000-0001-5945-9869): Conceptualization, Methodology, Investigation, Formal analysis, Project administration, Writing – Original Draft

MT (0000-0002-1087-6714): Conceptualization, Methodology, Writing – Review & Editing

AG (0000-0002-3105-8059): Investigation, Writing - review & editing

HL: Investigation, Writing - review & editing

MC: Investigation, Formal analysis, Writing - review & editing

CR: Investigation, Writing - review & editing

TM (0000-0003-2142-6441): Investigation, Writing - review & editing

AMLK (0000-0001-6493-9533): Conceptualization, Methodology, Formal analysis, Project administration, Funding acquisition, Writing – review & Editing.

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Ethical approval

This study was carried out in accordance with the current laws in Sweden. There are no legal or ethical restrictions for invertebrates.

Consent to participate

All authors agreed on being co-authors of this manuscript.

Consent for publication

All authors agree on publishing the paper.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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