

## The land–sea interface: A source of high-quality phytoplankton to support secondary production

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### Abstract

Coastal-estuarine systems are among the most productive marine ecosystems and their special role in producing harvestable fish and shellfish has been attributed to high primary production fueled by nutrient runoff from land and efficient trophic transfer. Here we ask if phytoplankton species composition and their food quality based on the percentage of long-chain essential fatty acids (LCEFA) is another factor contributing to high secondary production in these ecosystems. We used long-term measurements of major phytoplankton taxonomic groups and estimated their content of LCEFA along the salinity gradient in coastal-estuarine ecosystems, with emphasis on Chesapeake Bay and the Baltic Sea, and an oceanic transect. Our data show that cyanobacteria with low nutritional quality often dominate at low-salinity regions, while intermediate to higher salinity regions produce diatoms and dinoflagellates that have a higher content of LCEFA and are thus a higher-quality food resource for consumers. Higher salinity regions have less pronounced seasonal changes in the percentage of phytoplankton LCEFA compared to low salinity regions, providing a stable supply of nutritious phytoplankton to consumers. The phytoplankton LCEFA content is similarly high in coastal upwelling systems and it decreases further offshore in oligotrophic oceanic regions dominated by picophytoplankton. Our results from a broad range of coastal-ecosystem types show that ecosystems at the land-sea interface provide a valuable service by producing phytoplankton enriched in the biochemicals essential for consumers. High primary production, coupled with high quality of that production, explain why the production of fish and shellfish is high where land and sea meet.

Land–sea transitional ecosystems, such as coastal waters, estuaries, bays, lagoons, fjords, river plumes, and inland seas are special places on Earth as they are uniquely influenced by processes from both land and sea (Cloern and Jassby 2012 and references therein). These are some of the world's most productive ecosystems (Nixon 1988) and they play an

important role in fish and aquaculture production (Houde and Rutherford 1993; Nixon and Buckley 2002), providing at least 40% of the value of the world's ecosystem services (Costanza et al. 1997; Barbier et al. 2011). These ecosystems are also among those most at risk from increasing human pressures and climate change (Halpern et al. 2008; Cloern et al. 2016), threatening the provision of essential proteins and oils from fish and shellfish (Halpern et al. 2008; Turchini et al. 2009). Maintaining the functioning of these ecosystems is important for human welfare since secondary production expressed as fish yield per unit primary production is 10 times higher in marine systems, particularly in estuaries and coastal upwelling systems, compared to freshwater systems (Nixon 1988). High productivity in coastal-estuarine ecosystems has been attributed to two factors: (1) the large supply of carbon (energy) fixed by primary producers fueled by nutrient runoff from land (Nixon and Buckley 2002; Österblom et al. 2007), and (2) efficient transfer of this energy to higher

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trophic levels driven by physical (tidal) energy inputs (Nixon 1988). Shallow depths that promote efficient nutrient recycling, physical variability, and the omnivorous diet of many estuarine animals are thought to contribute to efficient transfer of energy from primary producers to consumers in these ecosystems (Costanza et al. 2007).

Here, we explore another potential explanation for the high trophic efficiency in coastal-estuarine systems, namely the combination of high primary productivity and production of phytoplankton taxa having higher nutritional quality, based on their content of essential biochemicals, than those in freshwater or open-ocean ecosystems. Primary productivity is one determinant of biological productivity at higher trophic levels (Ware and Thomson 2005). The quality of this primary resource regulates trophic efficiency because consumers require an adequate intake of all necessary building blocks to fulfill their nutritional needs (Mueller-Navarra et al. 2000; Dickman et al. 2008; Sommer et al. 2012), and their growth and reproduction can be limited when food quality is poor (Brett and Müller-Navarra 1997; Sterner and Elser 2002). Moreover, phytoplankton nutritional quality affects the efficiency with which herbivores use plant energy and the production of multiple upper trophic levels (Dickman et al. 2008).

Accumulating evidence indicates that fatty acids are important nutritional components that can limit consumer growth or reproduction (Mueller-Navarra et al. 2000; Vargas et al. 2006; Hixson 2014). In particular, long-chain essential fatty acids (LCEFA), largely produced by phytoplankton, play a critical role for secondary production because consumers are limited in their ability to synthesize these molecules (Dalsgaard et al. 2003). Of particular importance are several polyunsaturated fatty acids with 20 or more carbon atoms, such as eicosapentaenoic acid (EPA; 20 : 5 $\omega$ 3), arachidonic acid (ARA; 20 : 4 $\omega$ 6), and docosahexaenoic acid (DHA; 22 : 6 $\omega$ 3), which fulfill important structural and physiological functions in animals (Arts et al. 2001; Parrish 2009). Accordingly, consumer growth and production are not only constrained by the quantity of carbon fixed by phytoplankton, but also by their synthesis of essential fatty acids (Mueller-Navarra et al. 2000).

The relative composition of fatty acids varies across major taxonomic phytoplankton groups (Ahlgren et al. 1990; Brett et al. 1992), and this between-group variability is larger than variability caused by environmental factors such as temperature, nutrients, light, and salinity (Brett et al. 1992; Dalsgaard et al. 2003; Galloway and Winder 2015). Some taxa, such as cyanobacteria and chlorophytes, lack or have only small proportions of LCEFA, while others, such as diatoms, cryptophytes, and dinoflagellates, are rich in these essential compounds (Taipale et al. 2013; Galloway and Winder 2015). Consequently, phytoplankton community composition can determine whether consumers are provided an adequate supply of essential biochemicals for efficient energy conversion to herbivores and then to upper trophic levels

(Vargas et al. 2006; Dickman et al. 2008), independent on environmental conditions. For example, change in phytoplankton abundance and composition along a salinity gradient in a fjord-like estuary was related to sixfold differences in seston LCEFA concentrations (Lowe et al. 2016). The importance of phytoplankton species composition for trophic efficiency is further demonstrated by the contrasting food web architectures between upwelling systems and eutrophic lakes (Brett and Müller-Navarra 1997). The former are primarily dominated by diatoms and often characterized by high ratios of consumer : phytoplankton biomass, or inverted pyramids (higher consumer than producer biomass), while the latter are dominated by cyanobacteria and a steep decrease of consumer biomass with trophic level.

Our goal was to understand the extent to which nutritional quality of primary producers varies between freshwater and seawater. A recent meta-analysis of phytoplankton communities in the world's coastal-estuarine ecosystems showed systematic changes in taxonomic composition of blooms along the salinity gradient, with prominence of cyanobacteria and chlorophytes at low salinity and of diatoms and dinoflagellates at higher salinities (Carstensen et al. 2015). This suggests the potential for spatial gradients of phytoplankton food quality along the land-ocean continuum. We explored this hypothesis by converting measurements of phytoplankton taxonomic composition into an index of food quality based on the content of LCEFA, and then searched for patterns along salinity gradients. Therefore, we compiled information from ca. 19,000 phytoplankton and water quality samples collected in two extensively monitored regions influenced by connectivity to land, and less geographically focused global analysis consisting of an additional 11,000 samples. We report nutritional quality of the phytoplankton food resource based on taxon-specific LCEFA for each algal group (e.g., Galloway and Winder 2015). To place these results in a broader context, we compared phytoplankton LCEFA composition along the salinity gradient of coastal-estuarine waters with an oceanic transect between productive upwelling regions and oligotrophic open ocean systems. We further conducted a literature synthesis on coastal-estuarine organisms to illustrate the ecological importance of the dietary LCEFA content for consumer growth. Our study reveals a common pattern of increasing food quality, and increasing provision of LCEFA for upper trophic levels, along the gradient from fresh to seawater.

## **Materials and methods**

We conducted a literature synthesis of studies that measured growth performance of consumer organisms (e.g., growth, egg production, survival) as a function of the LCEFA content of their diet. We selected studies that (1) cover a wide range of diet LCEFA, including data points with diet low in LCEFA since most consumer responses show a saturation level

or are humped shaped, and (2) include consumers that feed on phytoplankton and are common in coastal-estuarine systems. In addition to the original performance data, we standardized data to zero mean and unit standard deviation in order to compare studies that reported different response variables over a range of different %LCEFA levels and species that have different threshold responses, and grouped the analysis by organism type (bivalves,  $n=3$  studies; crustaceans,  $n=6$  studies; fish,  $n=6$  studies). We tested the relationship between species performance and dietary %LCEFA using quadratic regressions for grouped organism type but not for individual species as these studies include few data points.

Phytoplankton and water quality data were provided from different coastal-estuarine monitoring programs. Samples were collected year-round covering all seasons and multiple years for 21 locations in the Chesapeake Bay (1984–2009) and for 36 locations in the Baltic Sea (1966–2013) (Supporting Information Table S1). In order to investigate phytoplankton patterns across salinity gradients at larger scale, additional 31 locations from the North Sea region, Neuse River Estuary, San Francisco Bay, and Patos Lagoon (Brazil) were included. Details about the time period, number of stations and samples, and the data sources for each region are given in Supporting Information Table S1. Phytoplankton biomass was analyzed using standard techniques of Lugol's fixed samples (Utermohl 1958) and described in detail in the different national monitoring programs. Phytoplankton was identified to species or genus level and size class and biomass reported as either carbon content or biovolume (North Carolina and San Francisco Bay). In the latter case, biovolumes were converted to carbon biomass using conversion factors for diatoms and non-diatoms (Strathmann 1967; Edler 1979). We focused on nano- and micro-phytoplankton ( $> 2 \mu\text{m}$ ) that dominate biomass in coastal waters (Carstensen et al. 2015) and are the main food resource for pelagic and benthic primary consumers that are key trophic links to fish (Alpine and Cloern 1992; Sommer et al. 2002). Total nitrogen (TN) and total phosphorus (TP) were analyzed according to standard methods for the Baltic Sea (HELCOM 2014) and the Chesapeake Bay (EPA 1996). For the oceanic transect, we used a phytoplankton dataset from the Southern Indian Ocean, covering nutrient-rich upwelling sites and nutrient-poor open water sites (for site description, see Fig. 6 legend and Supporting Information Table S2). Here, phytoplankton was identified using pigment analysis of samples collected on filters and included picophytoplankton ( $0.2\text{--}2 \mu\text{m}$  diameter) as they dominate in open oligotrophic oceans, and biomass was calculated based on a proxy of taxon specific chlorophyll *a* concentration (Schlüter et al. 2011). For all datasets, phytoplankton carbon biomass was aggregated for six major taxonomic groups (autotrophs and mixotrophs only): Chlorophyta, Cryptophyta, cyanobacteria, diatoms, dinoflagellates, and other species (mostly haptophytes); for the Southern Indian Ocean also for haptophytes.

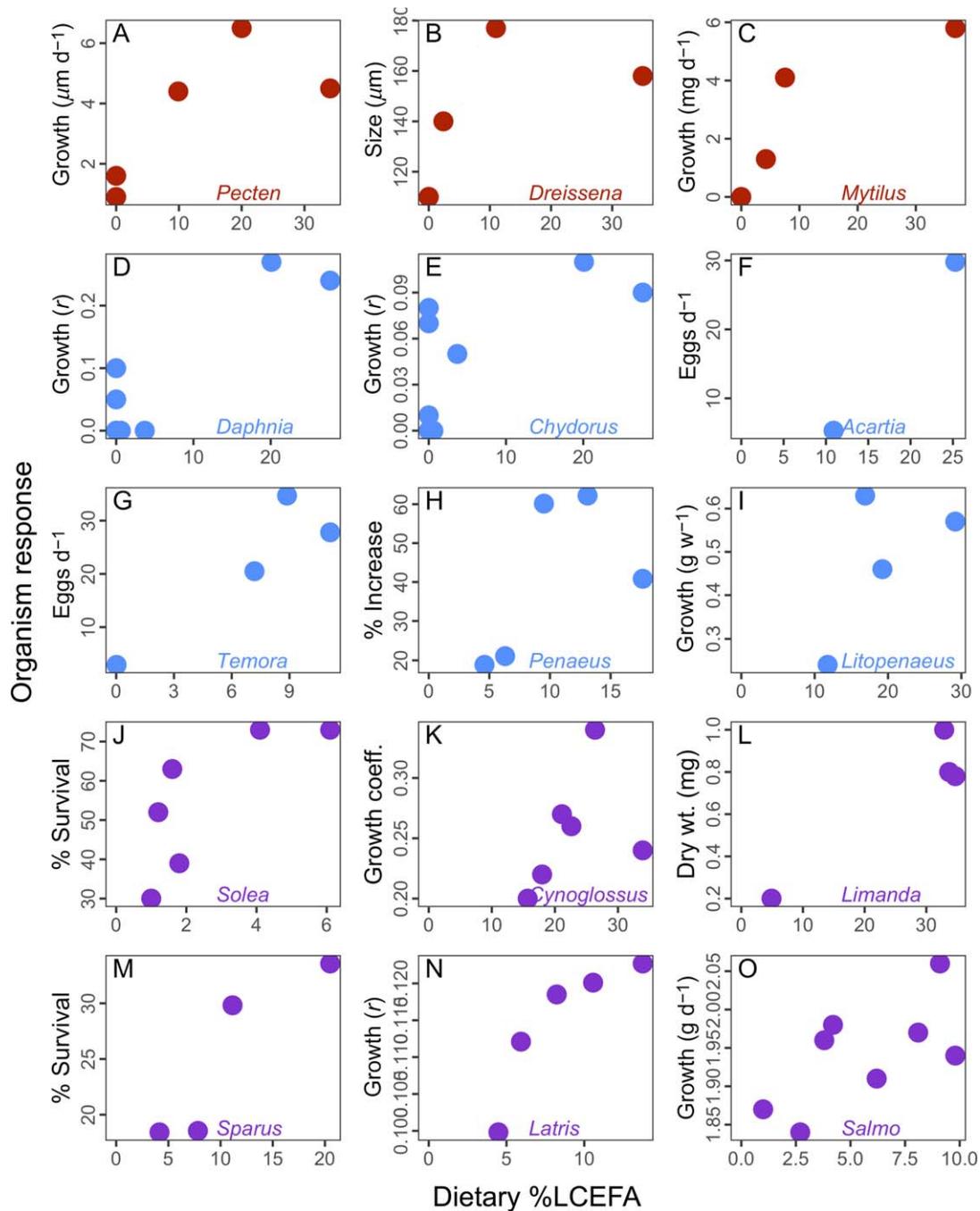
To investigate whether phytoplankton FA composition varies along the salinity gradient, we calculated nutritional quality based on biomass and the percentage of LCEFA (sum of ARA, EPA, and DHA) of the different algal groups according to Galloway and Winder (2015). We calculated phytoplankton derived percentage of LCEFA to total fatty acid (%LCEFA) by multiplying phytoplankton biomass of the six major taxonomic groups with the respective %LCEFA for that group (Galloway and Winder 2015), and summing the products across all groups. The %LCEFA is based on a meta-analysis across six algal groups (diatoms, dinoflagellates, chlorophytes, cryptophytes, cyanobacteria, haptophytes), including 1145 published fatty acid profiles from 208 species in diverse culture conditions. Average LCEFA content for all unique phytoplankton taxa was calculated within these six groups across all culture conditions ensuring that often studied model taxa were not biasing the group level LCEFA values (Galloway and Winder 2015). Dinoflagellates and diatoms have the highest levels of LCEFA; cryptophytes and haptophytes are intermediate in LCEFA content; and chlorophytes and cyanobacteria have very low LCEFA content (Supporting Information Table S3 and Galloway and Winder 2015). For the unspecified phytoplankton grouped as "Others" in our datasets, we used the %LCEFA for haptophytes, which constituted a substantial proportion of this group in our phytoplankton datasets.

To describe land-sea gradients, location-specific means for %LCEFA as well as salinity, TN, and TP were first estimated using a general linear model (GLM) with month and year as categorical factors (separate for each location) to derive location-specific means and account for unbalanced sampling across time in the monitoring data (Carstensen et al. 2006). TN and TP were log-transformed prior to the GLM analysis and the resulting means were back-transformed. Subsequently, relationships between location-specific means of %LCEFA and nutrients versus salinity were investigated using generalized additive models (GAMs). The GAMs included both linear and nonlinear components, and non-significant components were iteratively removed.

To investigate seasonal patterns across the land-sea gradient, monthly means of %LCEFA were calculated by grouping all phytoplankton %LCEFA into five salinity bins of 0–5, 5–10, 10–15, 15–20,  $> 20$ , and employing a GLM with location, month, and year as categorical factors within each bin to calculate monthly means. The monthly means from the GLM describe the seasonal variation common to all observations within the salinity bin after accounting for differences between sites and years of sampling.

## Results

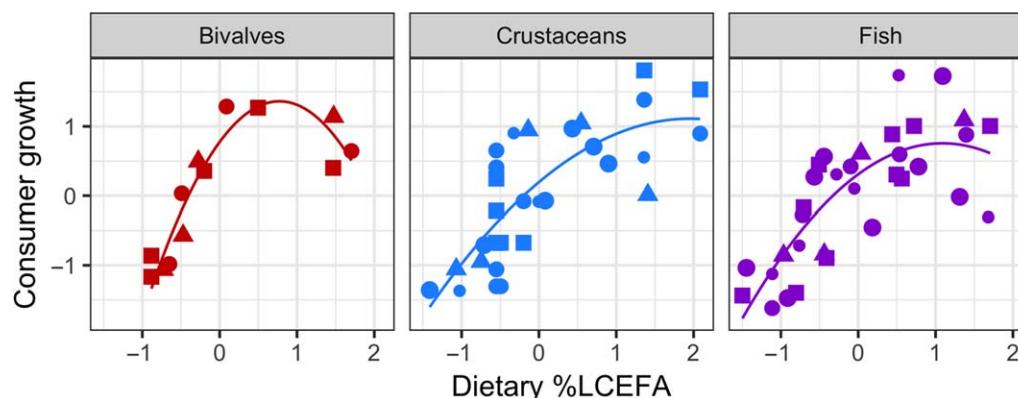
A data survey of studies that measured consumer growth performance as a function of the dietary LCEFA content indicates that growth rate, egg production, and survival



**Fig. 1.** Consumer growth and survival performance responses of diverse bivalves, crustaceans, and fish as function of diet %LCEFA of total fatty acid. Diet %LCEFA is the sum of the fatty acids ARA, EPA, and DHA. Red symbols are bivalve, blue are crustacean, and purple are fish species. Data sources: (A) Delaunay et al. (1993), (B) Wacker et al. (2002), (C) Pleissner et al. (2012), (D, E) Ahlgren et al. (1990), (F) Rossoll et al. (2012), (G) Arendt et al. (2005), (H) Rees et al. (1994), (I) Ju et al. (2009), (J) Navarro-Guillén et al. (2014), (K) Yuan et al. (2015), (L) Copeman et al. (2002), (M) Salhi et al. (1994), (N) Bransden et al. (2005), (O) Glencross et al. (2014).

increase with increasing %LCEFA in their diet in diverse aquatic consumers that feed on phytoplankton (Fig. 1). Species performance data suggest a saturation or optima level for dietary %LCEFA, which likely differs between consumers. Increasing growth performance and a saturation or optima

performance level are supported by the scaled original data merged by organism type with a significant quadratic or linear effect of dietary %LCEFA on species performance for bivalves (linear term (lt):  $b = 2.41$ ,  $t = 7.05$ ,  $p < 0.001$ , quadratic term (qt):  $b = -1.98$ ,  $t = -5.78$ ,  $p < 0.001$ ), crustaceans



**Fig. 2.** Consumer growth and survival data performance as a function of diet %LCEFA of total fatty acid grouped by bivalves (species  $n = 3$ ), crustaceans ( $n = 6$ ), and fish ( $n = 6$ ). Data are from empirical studies that report consumer growth performance across the sum of diet LCEFA, including ARA, EPA, and DHA (see Fig. 1). The fitted growth curves were estimated using a polynomial function, which performed better compared to a linear function. Data are standardized to zero mean and unit standard deviation. Different symbols indicate different studies.

(lt:  $b = 3.89$ ,  $t = 6.53$ ,  $p < 0.001$ , qt:  $-1.09$ ,  $p = 0.08$ ), and fish (lt:  $b = 3.76$ ,  $t = 6.52$ ,  $p < 0.001$ , qt:  $b = -1.72$ ,  $-2.98$ ,  $p = 0.006$ ) (Fig. 2).

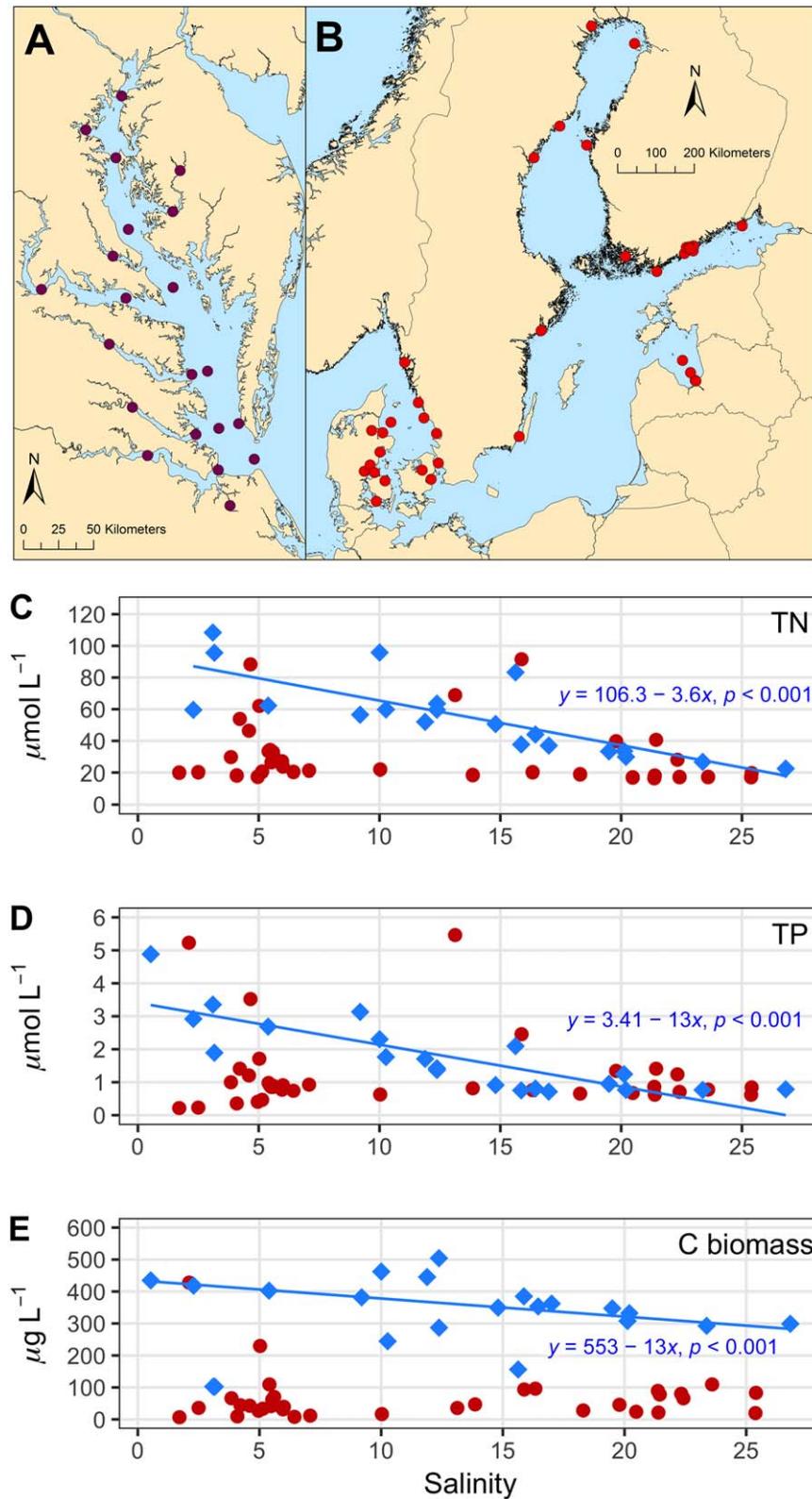
For phytoplankton taxonomic observation along salinity gradients, our study focused on Chesapeake Bay and the Baltic Sea because they are intensively sampled and represent a broad range of habitats (57 locations) along salinity gradients from near-freshwater to near-seawater (salinity  $> 25$ ) (Fig. 3A,B). Nutrient concentrations along the salinity gradient differ substantially between the two ecosystems. Averaged decadal measurements ( $> 15$  yr) of TN and TP concentration in Chesapeake Bay were characterized by a pronounced spatial gradient with highest nutrient levels at low salinity and dilution toward the ocean (Fig. 3C,D). Decadal averaged nutrient concentrations were more variable along the salinity range in the Baltic Sea, with an overall weak gradient and elevated concentration in specific locations driven by high local nutrient inputs. Similar to nutrients, phytoplankton biomass declined with increasing salinity in Chesapeake Bay, but it showed no consistent pattern along the salinity gradient in the Baltic Sea (Fig. 3E).

Long-term measurements of phytoplankton taxonomic composition showed a general pattern along the salinity gradient, which was especially pronounced in the Baltic Sea and less in Chesapeake Bay. Chlorophytes and cyanobacteria contributed substantial fractions to total phytoplankton biomass at lower salinities in both ecosystems (Fig. 4). These two groups dominated at salinities below 5 and were absent, or present in low proportions, at salinities above 20. In the Baltic Sea, cyanobacteria and chlorophytes contributed more than 60% to total phytoplankton biomass, and in Chesapeake Bay up to 30%, at salinities below 5. In Chesapeake Bay, diatoms also contributed a high fraction of biomass at low-salinity sites. Diatoms and dinoflagellates dominated phytoplankton biomass in both ecosystems at salinities above 5. At salinities above 15, these two groups contributed

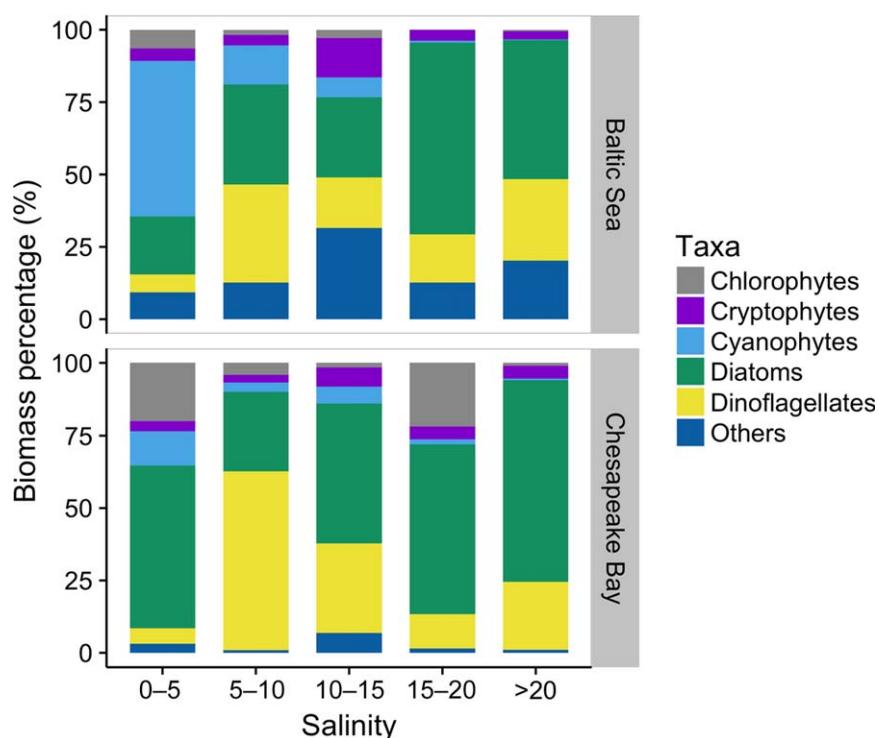
almost 80% of overall mean phytoplankton biomass. Cryptophytes contributed a small fraction of phytoplankton biomass and were most abundant at intermediate salinities of 10–15.

The %LCEFA of the phytoplankton taxonomic composition based on the biomass and relative proportion of LCEFA of different algal groups revealed a systematic changes along the salinity gradient (Fig. 5A). Phytoplankton %LCEFA was smallest in the low-salinity zones and increased with salinity in both ecosystems. In Chesapeake Bay, %LCEFA increased from 12% to 17%, reaching a plateau at salinity of around 10. The %LCEFA increased linearly with salinity in the Baltic Sea, displaying high variability ranging between 9% and 15% at low salinity. These %LCEFA values were also generally lower than in Chesapeake Bay, whereas levels were similar for the two ecosystems at salinity above 15. The Baltic Sea data included few measurements around salinity of 10, thus the possibility of an inflection point in %LCEFA of phytoplankton, similar to that in Chesapeake Bay, cannot be excluded. This pattern of increasing %LCEFA at higher salinity is supported with individual measurements from coastal-estuarine sites in the North Sea region, Neuse River Estuary, San Francisco Bay, and Patos Lagoon, representing combined a wide salinity range; however, continuous land-sea gradients could not be analyzed separately for these ecosystems. Overall, the phytoplankton derived %LCEFA of total fatty acid in these systems increased from less than 12% to more than 17%.

Analysis of phytoplankton %LCEFA revealed a pronounced seasonal pattern at low salinities, while seasonal variability was smaller in high salinity regions (Fig. 5B). This seasonal pattern was especially pronounced in the Baltic Sea, where high proportions of cyanobacteria at salinities below 10 explain low phytoplankton %LCEFA during summer (Supporting Information Fig. S1). This decrease in summer phytoplankton %LCEFA was absent at salinities above 10



**Fig. 3.** Sampling locations in the Chesapeake Bay (**A**) and the Baltic Sea (**B**), and site-specific means of TN (**C**), TP (**D**) and phytoplankton carbon (**E**) vs. salinity for the Chesapeake Bay (blue diamond symbols) and the Baltic Sea (red circle symbols). Regression lines are only included for significant relations. The nonlinear GAM component was not significant for any of the relationships.



**Fig. 4.** Biomass distribution for the major phytoplankton taxonomic groups across different salinity classes for the Chesapeake Bay and the Baltic Sea.

(Fig. 5B and Supporting Information Fig. S2), where cyanobacteria are absent (Supporting Information Fig. S1).

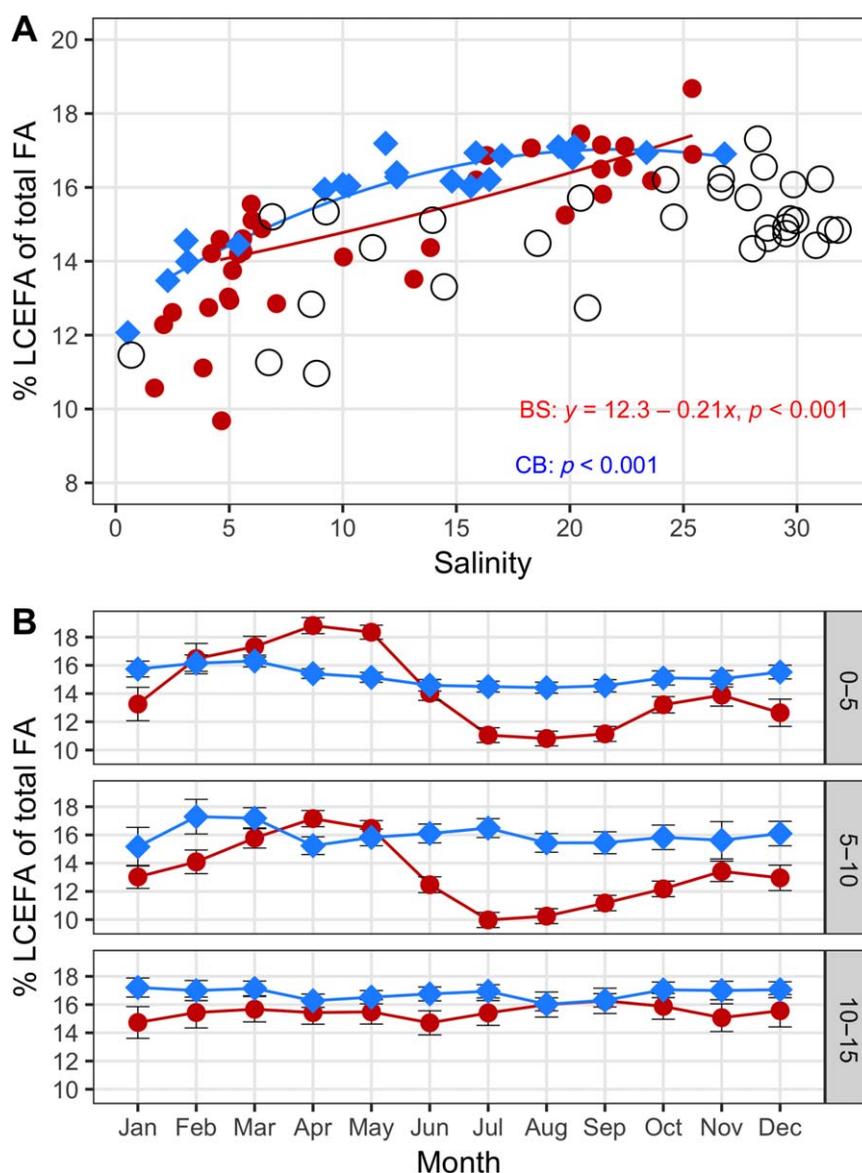
A transect across the Southern Indian Ocean revealed that diatoms and haptophytes dominated phytoplankton biomass at coastal sites influenced by upwelling (sites 1 and 2 in Fig. 6A), whereas picophytoplankton taxa (0.2–2  $\mu\text{m}$  diameter) such as prochlorophytes and chlorophytes contributed most to the phytoplankton biomass in open ocean regions (Fig. 6B). The corresponding phytoplankton %LCEFA was highest ( $\sim$  15–20% LCEFA) at the two coastal upwelling sites and decreased to 7%LCEFA offshore (Fig. 6C).

## Discussion

We combined two large data sets to address global-scale questions along the salinity continuum: (1) is there a general pattern of increasing phytoplankton food quality along the transitional zones between fresh and seawater? and (2) do these transitional zones produce phytoplankton biomass of higher nutritional quality than in freshwater and nutrient-poor open ocean ecosystems, thus supporting high production efficiency of consumers in coastal-estuarine habitats? We included one exceptionally robust data set that measured seasonal and spatial patterns of phytoplankton taxonomic composition along the salinity gradient between fresh and seawater. The second dataset was based on a meta-analysis that measured over 1000 phytoplankton fatty acid profiles comprising more than 200 species under various

environmental conditions (Galloway and Winder 2015), which allowed us to transform measures of phytoplankton taxonomic composition into an index of phytoplankton food quality for consumers. Our analyses reveal a general pattern of increasing phytoplankton food quality based on %LCEFA as we move from rivers toward the sea, and that phytoplankton food quality in coastal-estuarine ecosystems is higher than in the freshwater and nutrient-poor open ocean they bridge.

Coastal-estuarine systems with salinities above 10 produce phytoplankton with high LCEFA proportions in the form of nutritious diatoms and dinoflagellates, while the LCEFA proportion decreases at lower salinity sites and in nutrient-poor open ocean regions. Chesapeake Bay illustrates the characteristic high phytoplankton production of nutrient-rich coastal sites and systematic gradient of increasing food quality in terms of LCEFA content along the transition from rivers to sea. This diatom-dominated ecosystem (Carstensen et al. 2015) supports a productive oyster fishery at higher salinities, although the production has declined significantly over the last decades due to human pressures (Rick et al. 2016). The land–sea patterns of nutrients and phytoplankton biomass were less clear in the Baltic Sea, where nutrient inputs vary greatly from the boreal watersheds in the north to agriculturally dominated watersheds in the south. This system shows a striking shift from a cyanobacteria dominated phytoplankton biomass at low salinity to a diatom and dinoflagellate dominated biomass at salinities above 10. Nutrient

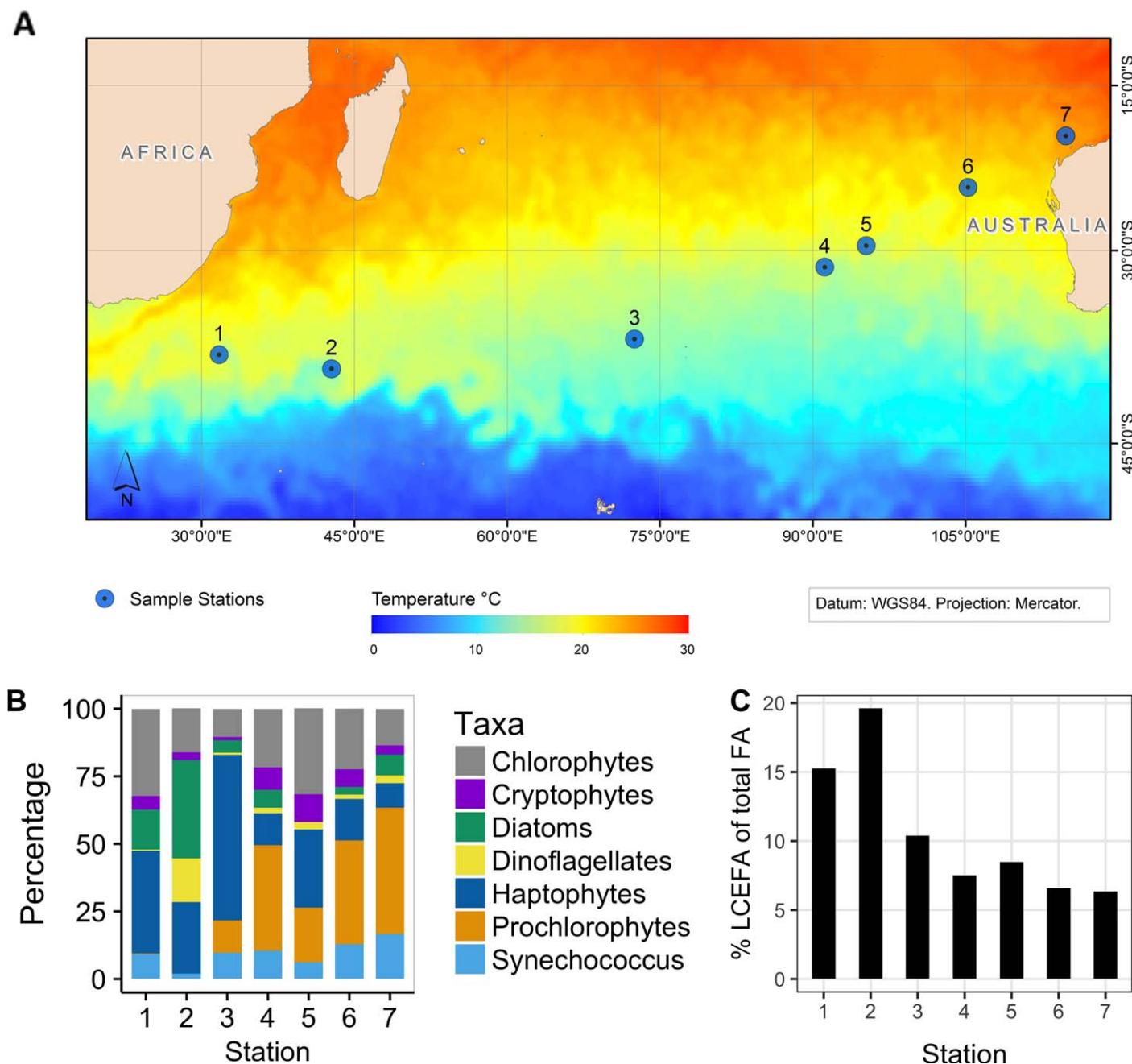


**Fig. 5.** Phytoplankton food quality based on percentage of LCEFA of total FA across **(A)** the salinity gradient and **(B)** month for different salinity ranges in Chesapeake Bay (blue diamond symbols) and the Baltic Sea (red circle symbols). In **(A)**, other sites are included (see “Materials and methods” section; open circles). Seasonal variations for salinities above 15 are shown in Supporting Information Fig. S2. Error bars display the standard error of the monthly means.

enrichment and subsequently increasing phytoplankton production over the last five decades have increased fisheries production in this system, with the southern Bornholm Basin at a salinity range of 7–10 and other basins at similar or higher salinity being productive areas for commercial fisheries (Hansson et al. 2007; Köster et al. 2016). Diatoms and dinoflagellates, rich in LCEFA, dominate the phytoplankton community at this and higher salinity ranges, likely contributing to high fish production in these basins. The southern Indian Ocean shows a typical coast-offshore phytoplankton gradient (Schlüter et al. 2011) with peak biomass of diatoms and haptophytes, high in LCEFA at the nutrient-rich

upwelling sites transitioning to offshore dominance by picophytoplankton with lower LCEFA content. Copepod abundance and fecal pellet production was highest at the upwelling sites along the transect (Møller et al. 2010), confirming that high secondary production occurs at sites with high concentration of LCEFA-rich phytoplankton taxa.

Phytoplankton LCEFA content can also show contrasting seasonal variation in low- and high-salinity zones. At salinities below 10, poor-quality cyanobacteria and chlorophytes (Dalsgaard et al. 2003; Taipale et al. 2013; Galloway and Winder 2015) can dominate over the summer period, resulting in high seasonal variability of phytoplankton LCEFA.



**Fig. 6.** Sampling stations for an open-ocean transect across the Southern Indian Ocean (**A**) and corresponding phytoplankton proportions based on pigment analysis (**B**) and recalculated into phytoplankton %LCEFA of total fatty acid (**C**) for the different stations. Sta. 1 and 2 are situated where the Agulhas Current is retroflected at the subtropical frontal zone (Beal et al. 2011) and represent nutrient-rich upwelling sites. Sta. 3–7 are situated in nutrient-poor ocean waters, with Sta. 3–5 located in the sup-tropical gyre of the southern Indian Ocean, Sta. 6 in the tropical waters of the Indonesian Throughflow, and Sta. 7 at the Northwest Australian Shelf (Visser et al. 2015).

This seasonal pattern was especially pronounced in the Baltic Sea, where high proportions of cyanobacteria explain low phytoplankton %LCEFA at salinities below 10 during summer. At salinity above 10, the phytoplankton %LCEFA content was consistent over the seasons and was dominated by diatoms and dinoflagellates. Zooplankton fatty acid

composition and growth generally follow the seasonal variability in phytoplankton, and thus the transfer of LCEFA to higher trophic levels (Vargas et al. 2006; Strandberg et al. 2015), with increased egg production during periods of diatom and dinoflagellate dominance (Kiørboe and Nielsen 1994; Peters et al. 2006; Vargas et al. 2006). Large seasonal

variability of food quality in low-salinity zones can be challenging for consumers if their growth and reproductive cycles do not match the cycles of high-nutritious food availability (Cushing 1990). In comparison, seasonal variability of food quality is less pronounced at salinities above 10, where diatoms (rich in EPA) or dinoflagellates (rich in EPA and DHA) are the largest components of biomass. Therefore, consumers in high-salinity regions have a more stable supply of phytoplankton LCEFA than those in low-salinity regions, allowing more flexibility in consumer life history strategies and likely contributing to high secondary production (Schindler et al. 2010).

The spatial pattern of phytoplankton LCEFA content has important implications for growth and reproduction of diverse aquatic consumers. A survey of different experimental studies revealed that the proportion of dietary LCEFA is a limiting factor for growth and survival in many bivalves, crustaceans, and fish (Fig. 1 and references therein). While the requirements for specific essential fatty acids differ among organisms (Ahlgren et al. 2009), these dominant aquatic consumers showed increasing growth and survival performance with increasing prey LCEFA content up to a saturation level, and decreased thereafter in bivalves. The hump-shaped response in bivalve survival is intriguing, but requires validation with more extensive surveys. Similarly, the required LCEFA thresholds in the diet for optimum growth and survival are not known for most species and likely differ between species (Fig. 1) and life stages (Ahlgren et al. 2009). The response of diverse consumers to LCEFA in the food resource and the mechanisms is an important area for future research (see also Ahlgren et al. 2009). However, indices of secondary production are sensitive to relatively small changes in LCEFA content. For example, a 5% increase in food %LCEFA more than doubled growth and reproduction in bivalves, crustaceans, and fish (Fig. 1). Similarly, replacement of a copepod diet consisting of toxic algae with a dinoflagellate diet reversed the deleterious effects of the toxic form on egg production and hatching success (Ianora et al. 2003). Thus, the grand mean increase of LCEFA proportion from about 9% to more than 17% in our data compilation may have significance both from a population and ecosystem production perspective. In addition, the content of phytoplankton LCEFA affects the amount of essential biochemicals transferred to zooplankton and eventually fish (Taipale et al. 2016), with fish having higher amounts of LCEFA in ecosystems where primary production is dominated by phytoplankton taxa high in LCEFA content. Consequently, a shift in phytoplankton species composition along the salinity gradient affects the composition of essential biochemicals at the base of the food chain and likely the magnitude of secondary production and the nutritional quality of fish and shellfish for human consumption.

Here, we considered one central component of food quality and found spatial patterns and interpreted their ecological

significance. There are other food quality properties that restrict consumer growth, such as amino acids, sterols, vitamins, elemental stoichiometry or morphological characteristics (Sommer et al. 2012; Wacker and Martin-Creuzburg 2012), and cyanobacteria, dinoflagellates and some diatoms can produce toxic substances (Prince et al. 2016). In addition, some heterotrophic protists may be able to biochemically upgrade low-quality phytoplankton (Klein Breteler et al. 1999; Martin-Creuzburg et al. 2004; Bec et al. 2006), which is however species-specific (Klein Breteler et al. 1999; Veloza and Tang 2006). It remains to be investigated if these nutritional components vary among taxonomic groups and along salinity gradients. Thus, our LCEFA-derived estimation measures only one component of food quality. However, that component is meaningful because LCEFA are essential nutrients in food webs generally and for fish in particular (e.g., Paulsen et al. 2013; Fuiman et al. 2015), and they have been shown to function as regulators of ecosystem-level production (Brett and Müller-Navarra 1997; Litzow 2006). Further, our study is restricted to temperate ecosystems, while in oligotrophic tropical oceans *Trichodesmium* sp. is a common bloom forming alga (Carpenter et al. 2004). *Trichodesmium* sp. produces some LCEFA, however, only few copepod species feed on this colony forming cyanobacteria (Post et al. 2002), thereby restricting the direct transfer of essential compounds to higher trophic levels. Thus, our results might extend to tropical systems having coastal-offshore gradients of primary production (Behrenfeld et al. 2006) and phytoplankton species composition from diatoms and dinoflagellates to cyanobacteria.

Higher food quality in coastal-estuarine ecosystems compared to freshwater and the open ocean has important implications for production at higher tropic levels, including fish and shellfish we harvest and culture as key sources of food and protein. An increased proportion of high-quality phytoplankton contributes to efficient trophic transfer efficiency to herbivores (Mueller-Navarra et al. 2000; Dickman et al. 2008), and eventually fish (Malzahn et al. 2007). Thus, phytoplankton production with high %LCEFA content, together with their high primary productivity can contribute to the higher efficiency of fish and shellfish production in coastal-estuarine ecosystems compared to freshwater systems and the open ocean as shown by Nixon (Nixon 1988).

Our study provides new insight into the question of why fisheries yield are high in many coastal-estuarine ecosystems. The production of nutritious algae in coastal-estuarine ecosystems is an important ecosystem service, contributing to the supply of proteins and essential fatty acids to billions of people worldwide and aquatic foods of high quality (Halpern et al. 2008; Turchini et al. 2009). In coastal areas, this also includes macroalgae and seagrasses, which are another source of essential fatty acids (Galloway et al. 2012) to food webs (e.g., Crawley et al. 2009). This ecosystem service is, however, at risk from dense human settlements, socioeconomic activities and climate change that have led to

nutrient enrichment and harmful substances pollution, overfishing, habitat loss, and altered thermal structure in many coastal-estuarine systems (Cheung et al. 2013; Carstensen et al. 2014; Cloern et al. 2016). These alterations threaten the production of nutritious primary producers by restructuring biodiversity and often promote the formation of harmful cyanobacteria or toxic dinoflagellate blooms (Paerl and Huisman 2008; Cloern et al. 2016) and the loss of macrophyte communities (Waycott et al. 2009). These pressures will reduce the supply of essential fatty acid produced by primary producers to the ecosystem, which at a global scale may be barely sufficient to meet global human and fish nutritional needs (Budge et al. 2014). To ensure continuous provision of essential compounds to feed a growing human population, it will be important to sustain the production of high-quality phytoplankton composition that synthesizes rich amounts of essential compounds in the face of threats from human pressures and climate change.

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### Conflict of Interest

None declared.

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