



REVIEW

Diatoms and fatty acid production in Arctic and estuarine ecosystems — a reassessment of marine food webs, with a focus on the timing of shorebird migration

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ABSTRACT: This review highlights diatoms and their production of fatty acids at Arctic ice edges and temperate estuaries as strategic in initiating high spring productivity. As important as their energy production is their synthesis de novo of omega-3 long-chain polyunsaturated fatty acids (LCPUFAs), which are bioactive molecules fundamental to maintaining ecosystem processes, and are necessary for reproduction and growth for the entire marine food web. Without these fatty acids, consumers can suffer poor reproduction and growth even with sufficient energy intake, and shorebirds may need LCPUFAs for nonstop long-hop migration. Timing of high energy fatty acid and LCPUFA production by diatoms coincides with growth and reproduction of consumer populations, with the arrival of seabirds in the Arctic and staging of shorebirds in estuaries. The switch from diatom production of carbohydrates to fatty acids is triggered by changes in chemical and physical environmental factors, which can be muted by factors such as climate change or habitat modification. Higher ocean temperatures and lower pH from climate change alters the ability of diatoms to make LCPUFAs, and habitat degradation reduces the numbers of diatoms in the area, subsequently reducing the amounts of LCPUFA produced. Changes in LCPUFA output could impact functionality of ice-edge and estuarine ecosystems, impacting shorebird migration and consumer productivity. Research is scarce on marine consumer reproduction and growth comparing quantity vs. quality of ingested saturated, monounsaturated, and omega-3 LCPUFAs, and nonexistent for seabirds and shorebirds. Future studies of marine food webs should include the role of diatoms and their contribution of not just energy, but also LCPUFAs to the food web.

KEY WORDS: Marine and estuarine food webs · Essential fatty acids · Diatoms · Shorebirds · Seabirds · Migration · Climate change

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1. INTRODUCTION

1.1. Background

The contribution of energy from diatoms within food webs is well known, and their role as a source of omega-3 long-chain polyunsaturated fatty acids (LCPUFAs) for heterotrophs, from copepods to sea-

birds, has been summarized over the past few decades. The function of these fatty acids has been discussed widely over vastly different fields, e.g. oceanography, invertebrate physiology, shorebird migration and physiology, reproductive performance of seabirds, zooplankton, and fish. This review paper is a first attempt to bring these disparate fields together, summarizing LCPUFA production, use, and

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importance for many marine taxa. The review details how these molecules are used in estuarine and Arctic food webs, and presents studies with contrasting perspectives of their importance. The review also suggests which hypotheses should be tested in the future, and frames use of LCPUFAs against a background of climate change.

1.2. Overview

The role of diatoms in temperate estuaries and Arctic ice-edge ecosystems is briefly summarized with emphasis on their importance in the production of energy and LCPUFAs. The review highlights the significance of diatoms in marine food webs and their energy contribution to diets of marine species, highlighting shorebirds and seabirds. Production of omega-3 fatty acids by diatoms is compared with their production by other taxa, and the chemical and physical factors that influence production of these high-energy omega-3 fatty acids are described, including the energy quantity vs. quality of LCPUFAs. Next, the similarities of diatom bloom and long-chain fatty acid production in temperate estuaries and at the Arctic ice edge are compared, and the path of these LCPUFAs through the food web is discussed.

The bioactivity of these LCPUFAs in many species groups is then discussed, with examples of effects on species from deficits in omega-3 fatty acids. Examples are given showing that ingestion of LCPUFAs for some species might be essential, and comparing others that show the opposite. Gaps in our knowledge of effects of these omega-3 molecules and suggestions of possible *in vivo* testing to determine their importance are then discussed. A short review of climate change effects on LCPUFAs is then provided, with implications for species that rely on diatoms for both energy and for the bioactive molecules. Suggestions for further studies that are necessary to test these hypotheses are then proposed.

2. METHODS

This review is derived from a synthesis of literature on: (1) productivity in Arctic and estuarine food webs in spring, (2) shorebird foraging before nonstop migration, (3) food web structure in the Arctic and in estuarine mudflats in spring (relationships among microphytoplankton, zooplankton, fish, seabirds, and shorebirds), (4) physiology of diatoms in both exponential (growth/cell division) and stationary (lipid

production) stages, (5) LCPUFAs, in particular eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), their synthesis and functions in animal physiology (see Table 1 and Fig. 1), (6) biochemistry of fatty acid metabolism, analysing stoichiometry and energy derivation, (7) bioactivity of LCPUFAs in heterotrophs, (8) effects of a lack of LCPUFAs in diets of many species, and (9) effects of climate change on the production of LCPUFAs and the potential lack of these molecules for consumers. I reviewed the literature of the above topics from both marine and freshwater research worldwide, from the mid-20th century until the present. This synthesis is limited to articles published in English.

For definition, the Arctic marine environment is considered to be areas surrounded by sporadic to continuous permafrost and also areas including the 10°C historical isotherm in order to incorporate important seabird and shorebird areas in the subarctic. Discussion is limited to the marine trophic web, mainly the ice edge, during the spring–summer when seabirds return to nest, and to temperate estuarine mudflats where migratory shorebirds stage to refuel before long-distance nonstop flights, either in spring or in fall.

3. SYNTHESIS AND INTERPRETATION

3.1. Diatoms—the foundation of the marine food web

Annual cycles of Arctic and estuarine ecosystems revolve around diatoms as the hub because diatoms initiate the high productivity of these ecosystems, by transferring energy and lipids to consumers via copepods and other zooplankton (Falk-Petersen et al. 1990, Marshall et al. 1999, 2000, Parrish 2013). Diatoms (microalgae of the Class Bacillariophyceae) flourish in both freshwater and saltwater environments (Fenchel 1988, Parris 2011, Krause et al. 2018) and are the most abundant phytoplankton in estuaries and at the Arctic ice edge, although chrysophytes, flagellates, and cryptophytes occasionally occur in large numbers in low-salinity Arctic waters at the ice edge (Sakshaug 2004). In Arctic, pelagic, and estuarine ecosystems, diatoms are the main food of the predominant primary consumers, copepods (Scott et al. 2002, Dahl et al. 2003, Falk-Petersen et al. 2009). In estuaries, diatoms, including the microphytobenthos in biofilm, are prey of zooplankton, invertebrate larvae (e.g. abalones; Kawamura et al. 1995), fish larvae, and shorebirds (Kuwaie et al. 2008). Copepods are prey of heterotrophs from other zooplankton, e.g.

amphipods (*Themisto*) (Dalpadado et al. 2001, Noyon et al. 2011, Kohlbach et al. 2016), to macroinvertebrates, e.g. molluscs or polychaetes (Fidalgo e Costa et al. 2000), to fish larvae, e.g. larval cod (*Gadus* spp.) (Kane 1984, Jónasdóttir et al. 1998), to shorebirds, e.g. western sandpipers *Calidris mauri* (Elner et al. 2005, Kuwae et al. 2008, Beninger et al. 2011), and seabirds, e.g. dovekies (also known as little auks) *Alle alle* (Mehlum & Gabrielsen 1993, Węśławski et al. 1999). Consequently, the quality and abundance of diatoms affect the entire trophic web, from surface to benthic areas as well as pelagic, and from primary consumers to apex predators.

3.2. Energy and fatty acids

The energy output of diatoms is highest when they begin to produce fatty acids after a major change in physical and chemical factors, often in spring, e.g. increased light, turbulence, an influx of cold and less saline water, and a depletion of inorganic nutrients (Brown et al. 1996, Henson et al. 2006). Lipids are more energy-dense than carbohydrates and proteins, yielding $37.65 \pm \text{kJ g}^{-1}$ versus $16.74 \pm \text{kJ g}^{-1}$ for carbohydrates or proteins (Silverthorn 2019). Diatom communities contribute up to 30 % of the early spring primary productivity at the edges of Arctic sea ice (Mikkelsen et al. 2008), and up to 50 % of the energy intake of western sandpipers at their spring staging sites in estuaries (Kuwae et al. 2008). Diatoms contribute 60–90 % of the diet of ice-associated heterotrophs (Gosselin et al. 1997, Kohlbach et al. 2016) and 45–59 % of mass in the diet of western sandpipers at their final staging sites before long-distance migration (Kuwae et al. 2008). Birds primarily metabolize fats to fuel flight and exercise, unlike other animals (Jenni & Jenni-Eiermann 1998, Price 2010, Kuzmiak et al. 2012), and fat is especially important in long-distance flight. The high-energy and physiologically important fatty acids, especially polyunsaturated omega-3 fatty acids, from microphytobenthos at their staging at estuaries are necessary for this nonstop migration (Beninger et al. 2011, Parrish 2013, Budge et al. 2014). Similarly, in the fall before their nonstop flights south, shorebirds consume high amounts of fat and LCPUFAs in invertebrate larvae and amphipods from tundra ponds, or from estuaries, which were not available in spring due to ice cover (Holmes & Pitelka 1968, Senner et al. 1989, Hamilton et al. 2003).

Carbon compounds are not qualitatively equal, and although previous research has focussed on high amounts of energy from diatom lipid production, which

stimulates high reproduction and growth in marine food webs (Marshall et al. 1999, Parrish 2013), the production of quality LCPUFAs may be as important as energy (Klein Breteler et al. 2005, Tocher 2010, Twining et al. 2016). Earlier research has shown that even with adequate energy measured in terms of amount of fat or mass of prey, secondary production can still be low if high-quality food is not provided (Massias & Becker 1990, Kadin et al. 2012). Recent studies have demonstrated that this quality of food, the amount of long-chain fatty acids, might indeed be more important for development and growth than total energy, measured in calories or kJ (Budge et al. 2014, Galloway & Winder 2015, Twining et al. 2018). Controlled feeding studies in riparian species, comparing effects of consuming omega-3 LCPUFAs vs. high-energy food to a consumer (tree swallow *Tachycineta bicolor* chicks), have demonstrated that food quality, not energy quantity, is better for growth and reproduction in this species (Twining et al. 2016). Similar studies should be carried out on other species, especially for long-distant migrants. Because reproduction and cellular division in all heterotrophs are dependent on fatty acids for energy, for their roles as ligands in various physiological cascades, and as biomembranes in cell growth and repair, results of controlled studies such as these are necessary to demonstrate whether omega-3 LCPUFAs have a greater effect on productivity and growth than does total energy. Examples of effects of LCPUFA levels on a variety of taxa are provided in Section 3.5, with studies presented of both positive and negative or neutral effects of these molecules.

3.3. Synthesis of fatty acids

Diatoms are among the few species groups able to produce omega-3 LCPUFAs de novo (Table 1), especially EPA, yet only certain diatom species make them in large amounts (Brett & Müller-Navarra 1997, Liang et al. 2000, Tocher 2010). Of these, EPA (20:5n-3) and DHA (22:6n-3) are the most important physiologically in heterotrophs, and DHA can be synthesized from EPA using either the Sprecher shunt or in the presence of the enzyme delta-4 desaturase (Sprecher 2000, Monroig & Kabeya 2018). Marine algae other than diatoms can produce omega-3 fatty acids de novo; for example, Cryptophyceae (cryptomonad algae) and Dinophyceae (dinoflagellates) produce DHA, but these classes do not dominate marine ecosystems (Henson et al. 2006, Gladyshev et al. 2013, Galloway & Winder 2015), or if they are abundant,

Table 1. Fatty acids (FAs) discussed in this review. Cn:x n-y notation – Cn: no. of carbons; x: no. of double bonds; n-y (sometimes written as ω -y): which carbon from the omega (methyl) end has the most recent double bond. For example, C18:1 n-9 has 18 carbons and 1 double bond on the ninth carbon from the methyl—the omega (ω)—end (also written as C18:1 ω -9). SAT: Saturated, 0 double bonds; MUFA: monounsaturated FA, 1 double bond; PUFA: polyunsaturated FA, >1 double bond and ≥ 18 C; LCPUFA: omega-3 long-chain PUFA; HUFA: highly unsaturated FA, >3 double bonds and >20C

English name	Notation	Meaning and type
Palmitic acid	C16:0	Saturated FA (SAT)
Stearic acid	C18:0	Saturated FA (SAT)
Oleic acid	C18:1 n-9	Monounsaturated (MUFA)
Linoleic acid (LIN)	C18:2 n-6	PUFA omega-6 FA (LCPUFA)
Alpha-linolenic acid (ALA)	C18:3 n-3	PUFA omega-3 FA (LCPUFA)
Arachidonic acid (ARA)	C20:4 n-6	PUFA omega-6 FA (LCPUFA)
Eicosapentaenoic acid (EPA)	C20:5 n-3	HUFA omega-3 FA (LCPUFA)
Docosahexaenoic acid (DHA)	C22:6 n-3	HUFA omega-3 FA (LCPUFA)

they can be harmful or distasteful despite being primary producers with intermittent high carbon output (Wassman et al. 1990, Smith et al. 2021). Most heterotrophs, including zooplankton, fish, birds, and mammals require linoleic acid (LIN, 18:2n-6) and alpha linolenic acid (ALA, 18:3n-3) (see naming of fatty acids, Table 1) because they lack the delta-12 and delta-15 desaturase enzymes needed to insert double bonds beyond the ninth carbon, essential to make these LCPUFAs from saturated (SAT) or monounsaturated fatty acids (MUFAs) (Fig. 1; Parrish 2009, Gladyshev et al. 2010, Brenna & Carlson 2014). Some

species of insects are able to make the polyunsaturated LIN, an 18-carbon PUFA (Stanley-Samuelson et al. 1988, Bell & Tocher 2009), and several species within the Cnidaria, Rotifera, Mollusca, Annelida, and Arthropoda have genes encoding desaturation and elongation enzymes; however, their ability to desaturate MUFAs to the PUFAs LIN and ALA is uncertain (Kabeya et al. 2018, Monroig & Kabeya 2018, Boyen et al. 2020). However, most marine consumers are dependent on algae like diatoms as direct sources of LCPUFAs.

It is generally agreed that most heterotrophs cannot synthesize EPA and DHA efficiently, and synthesis of LCPUFAs from LIN or ALA is possible in

some consumers to fulfill their needs, but at an energetic cost (Plourde & Cunnane 2007, Bell & Tocher 2009, Gladyshev et al. 2013). Vertebrates cannot synthesize LCPUFAs de novo as they lack the $\Delta 12$ and $\Delta 15$ ($\omega 3$) desaturases (Jing et al. 2013) and are dependent on dietary input in order to synthesize EPA and DHA. A few fish species, for example, can elongate fatty acids (Monroig et al. 2009, Oboh et al. 2017, Ferraz et al. 2019), and there is discussion on how well any of the fish elongase enzymes can synthesize PUFAs (Castro et al. 2016, Monroig et al. 2016). Laboratory testing has been done in rabbits or

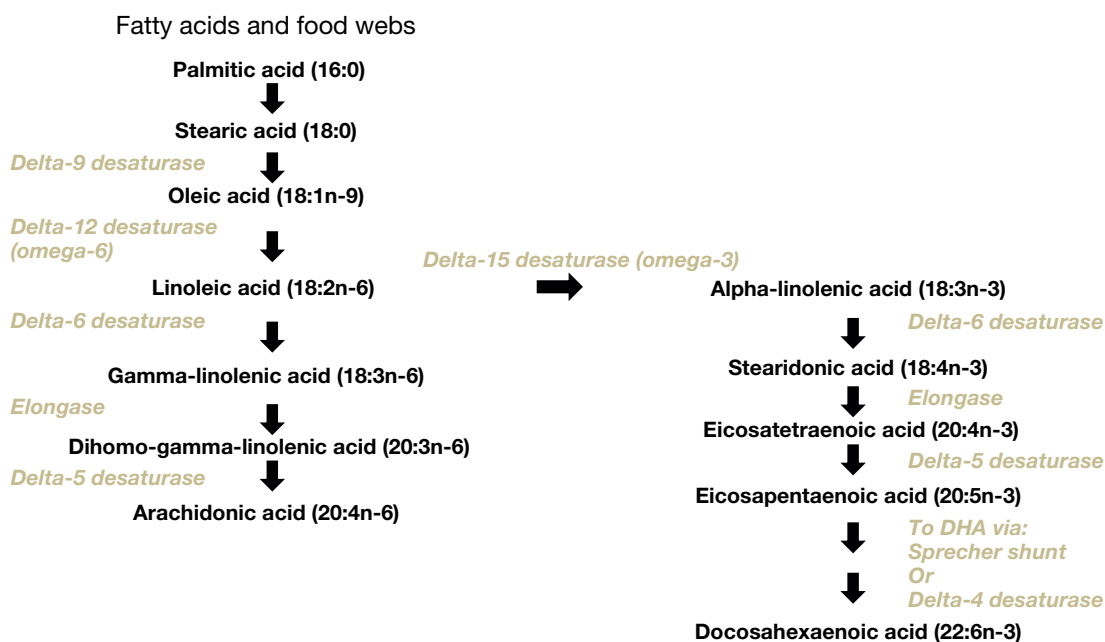


Fig. 1. Synthesis of long-chain fatty acids discussed in this review: saturated to monounsaturated to polyunsaturated. Synthesis from linoleic acid to arachidonic acid and from alpha-linolenic acid to docosahexaenoic acid from Miles & Calder (2017)

rats fed artificial diets, and the genes to express elongation have sometimes been found to be upregulated with low input of ALA or LIN, but no quantitative data on amounts or synthesis efficiency were given (Igarashi et al. 2007, Mattioli et al. 2019). Heterotrophic thraustochytrids can synthesize LCPUFAs using an unusual $\Delta 4$ desaturase pathway, and the harpacticoid copepods *Tisbe holothuriae* and *Tisbe* sp. were found to have 'substantial amounts' of EPA and DHA when fed microalgae with ALA, indicating synthesis (Bell & Tocher 2009). A small number of invertebrates and a few fish have a limited ability to synthesize EPA and DHA from LIN and ALA, but only with high energy input and very low efficiency and output (Van Horn et al. 2008, Gladyshev et al. 2010, Twining et al. 2018). In fish, differences were seen *in vitro* and *in vivo*, and expression of the delta 5 and 6 desaturase enzymes to produce EPA and DHA from LIN and ALA were higher in fish fed vegetable oil, vs. those fed fish oil, indicating production of these molecules (Bell & Tocher 2009). More research needs to be done to understand this (Bell & Tocher 2009). Humans have been found to be polymorphic in expressing genes to desaturate and elongate shorter-chain PUFAs (Kothapalli et al. 2016). Diatoms, however, do provide the majority of these compounds to the marine food web, and probably to the freshwater food web, and therefore to terrestrial consumers. Thus, diatoms also benefit consumers that are able to make LCPUFAs, thereby relieving them of the need to direct their energy towards synthesis. For this review, long-chain fatty acids, especially EPA and DHA, are called 'vital' because heterotrophs usually must obtain these molecules from their diet (Tocher 2010, Chen 2012, Brenna & Carlson 2014).

3.4. Factors influencing production of fatty acids in estuaries and the Arctic ice edge

Fatty acid chain length, degree of unsaturation, and placement of double bonds determine physiological properties of fatty acids; their 'quality' and specific configurations are furthermore affected by nutrient availability, salinity, temperature, and pH (Viso & Marty 1993, Stevens 1996, Galloway et al. 2012, Parrish 2013). These factors change seasonally. Superficially, Arctic ice edge and temperate estuarine ecosystems appear very different, but in spring, they share similar increases in sunlight, depletion of nutrients, and changes in salinity, temperature, and pH, and these have profound effects on their food webs, and production of LCPUFAs by diatoms (Hen-

son et al. 2006, Hu et al. 2008). In spring, increased solar irradiance melts Arctic ice and snow packs near rivers, producing freshets in estuaries, and adding fresh water into both ecosystems. Growth of diatoms increases rapidly with more light, and even though surface nutrients might be low, nutrients necessary for exponential growth can enter from outside the photic zone through upwelling and mixing of nutrient-rich deep water and from river input and turbulence that mixes deeper water at estuaries (Fenchel 1988, Howarth 1988, Sakshaug 2004). Due to differences in salinities, turbulence is important to assist this mixing.

These annual changes in chemical factors (salinity, pH, nutrients) and physical factors (temperature, light) trigger both benthic and planktonic diatoms, including sympagic, to switch their physiology from the exponential growth phase to the stationary phase (Hu et al. 2008). The 2 production phases are the cell division (growth) phase producing carbohydrates and the stationary phase producing fatty acids (Fisher & Schwarzenbach 1978, Sharma et al. 2012, Schwenk et al. 2013).

The exponential growth phase persists in the early spring in cold waters with high salinity when inorganic molecules, e.g. nitrogen, become available due to convective mixing in the Arctic as solar radiation increases (Brown et al. 1996, Henson et al. 2006, Schwenk et al. 2013). In this phase, from experimental conditions *in vitro*, mimicking *in vivo* abiotic seasonal factors, their lipid content is low: 5–20% dry weight (Fisher & Schwarzenbach 1978, Sharma et al. 2012, Scholz & Liebezeit 2013). The rapid increase in cell division and exponential growth due to an increase in solar radiation depletes inorganic nutrients, also limited in the Arctic by stratification of surface water, and the growth phase slows (Leu et al. 2015). Diatoms then switch to the stationary stage as a response not only to lack of nutrients (Reitan et al. 1994, Guschina & Harwood 2009, Yodsuwan et al. 2017), but also to temperature changes, osmotic or pH stress (Thompson et al. 1992, Renaud et al. 2002, Li et al. 2011), and light (Brown et al. 1996). Depletion of nutrients, increase of fresh water with ice melt and spring freshet, and concomitant changes in solar radiation, usually in spring, inhibit cell division and start the stationary phase (Sharma et al. 2012, Solovchenko 2012, Scholz & Liebezeit 2013), producing lipids (Sakshaug 2004). *In vitro* studies suggest that the switch to fatty acid production is a protective reaction to an accumulation of free radicals produced when cell division decreases due to depletion of nutrients, changes in temperature, pH, and light (Hu et al. 2008, Sharma et al. 2012), although Piepho

(2011) and Guschina & Harwood (2009) stated that at high light intensity, occurring in the spring and summer, diatoms produce more carbon and their production of triacylglycerols is a way to store excess carbon that cannot be used immediately for new cell structures. Salinity, higher before snow melt in estuary systems or ice melt in the Arctic, also affects this switch (Henson et al. 2006).

Sea ice supports a complex and diverse algal community, especially ice and under-ice diatoms (Ryan et al. 2004), and with spring ice melt, diatoms proliferate. When their exponential growth slows down, they produce high levels of LCPUFAs, especially EPA, e.g. sea ice diatoms *Nitzschia frustulum*, *N. frigida*, *N. closterium*, under-ice diatoms, e.g. *Melosia arctica*, and Arctic pelagic diatoms, e.g. *Coscinodiscus centralis* and *Thalassiosira* spp. (Horner 1985, Pinckney et al. 1998, Tremblay et al. 2006). In the stationary phase, the lipid content of diatoms increases to 20–50% of dry weight with ~33–45% LCPUFAs (Orcutt & Patterson 1975, Liang et al. 2000, Renaud et al. 2002, Guschina & Harwood 2006). This contribution of energy and LCPUFAs to the ecosystem in the Arctic is mainly from ice-associated (sympagic) and pelagic diatoms, and in estuaries from benthic diatoms, the microphytobenthos in biofilm. In the Arctic, benthic diatoms have only a minor contribution, yet in shallow coastal areas benthic production is very important (MacIntyre et al. 1996, Gattuso et al. 2006, Glud et al. 2009). In estuaries, the microphytobenthos in biofilm is the crux of benthic estuarine ecological food webs (Hope et al. 2020). In estuaries, there is also a variety of vertical and horizontal distribution of diatoms in the sediment, and benthic diatoms can become resuspended and are then available throughout the water column, depending on water flow (Colijn & Dijkema 1981). Output of energy and LCPUFAs, especially EPA, by benthic diatoms in an estuarine system can be high (Scholz & Liebezeit 2013), and the microphytobenthos are significant contributors to estuarine productivity and trophic dynamics.

Diatoms are an early energy and quality nutrient source for zooplankton and forage fish in this ecosystem, and their associated food webs flourish at a time when millions of seabirds start arriving to breed or forage during their Austral winter (Søreide et al. 2010, 2013, Leu et al. 2015). Seabird colonies are geographically structured by their foraging areas (Camphuysen et al. 2006, Mallory 2006, Mallory et al. 2006, Thaxter et al. 2012), and the success of colonies depends on accessing the associated prey which exist because of the rich food web in spring (Hipfner 2008, Watanuki et al. 2009).

In estuaries, as in the Arctic, changes in nutrients and other chemical and physical conditions trigger growth of estuarine diatoms that also start producing high-energy lipids and LCPUFAs in abundance, similarly initiating an explosion of productivity in that food web, at levels 3–7 times those in winter (Caffrey et al. 2014, Schnurr et al. 2020). Populations of consumers there such as zooplankton and fish subsequently reproduce and begin to increase as shorebirds arrive at temperate estuaries in spring. Estuarine diatoms in spring have very high levels of LCPUFAs (Duerksen et al. 2014, Schnurr et al. 2020) (e.g. North Sea *Amphora exigua*, *Gyrosigma spenceri*, *Pleurosigma angulatum*, *G. littorale*, all >30%). In estuaries, the presence of diatoms with high-quality fatty acids (longer length and greater desaturation, especially the omega-3 LCPUFAs), depend on both temperature and salinity (Scholz & Liebezeit 2013, Galloway & Winder 2015). The timing of reproduction, development, and growth of zooplankton and fish coincides with the stationary fatty acid production phase of diatoms, as does the timing of shorebird staging in estuaries before nonstop legs of migration, as well as arrival of seabirds at colonies and foraging areas in the Arctic. EPA, DHA, and other omega-3 LCPUFAs are important in reproduction in all consumers for gamete and embryo development, membrane synthesis, and cell growth (Arts et al. 2001, Broadhurst et al. 2002, Stevens 1996), and DHA is necessary in neurogenesis and neurotransmission (Innis 2005, 2008). Specific effects of LCPUFAs on the marine food web from copepods to birds is discussed in Section 3.5 in greater detail.

3.5. Effects of dietary LCPUFAs on marine food webs—positive, negative, and neutral

The transfer of energy from diatoms up the food web has been well documented, and it has been established that most heterotrophs, from zooplankton to fish larvae to birds, need LCPUFAs for normal growth and survival of due to the fact that they lack the enzymes to synthesize the essential fatty acids LIN and ALA (Parrish 2009, Gladyshev et al. 2010, Brenna & Carlson 2014). LIN and ALA, when desaturated and elongated, respectively form arachidonic acid (ARA, 20:4n-6), or EPA and DHA (Fig. 1).

A majority of studies on LCPUFA intake over a wide variety of taxa indicate that consumers fare poorly when they do not acquire LCPUFAs from food, and the consequences of not having enough in the diet suggest that LCPUFAs are bioactive mole-

cules and have critical physiological functions (Arts et al. 2009) in consumers to ensure growth, survival, and successful reproduction (Kattner et al. 2007). The following sections review studies of the positive and negative effects of adequate or scarce dietary LCPUFAs on different taxa in marine estuarine and Arctic ecosystems, from primary consumers, copepods, to zooplankton, invertebrates, fish, and birds. This is by no means a comprehensive discussion, but it contrasts many examples of species showing the need for LCPUFAs with a smaller number of species that might not need LCPUFAs. For shorebirds especially, there is much debated research on their hypothesized need to consume prey with LCPUFAs to enable them to make their long-distance nonstop migrations, 'the doping hypothesis' (e.g. Nagahuedi et al. 2009, Dick & Guglielmo 2019). The results of these studies have equivocal outcomes.

3.5.1. Copepods and other zooplankton: primary and secondary consumers

The transfer of LCPUFAs from diatoms to the rest of the food web parallels the transfer of energy and begins with accumulation of these molecules by primary consumers such as copepods, the prey of many heterotrophs. In the Arctic, transfer of large amounts of energy to primary and secondary consumers up the food web from ice algae (e.g. *Nitzschia frigida*, *Melosia arctica*) and from diatoms in biofilm in temperate estuaries to consumers is well documented, as is transfer of LCPUFAs (Kohlbach et al. 2016). In the Arctic, calanoid copepods and the amphipod *Themisto libellula* furthermore transfer these molecules pelagically (Kohlbach et al. 2016).

The major prey of zooplankton, fish, and a seabird, the dovekie, are Arctic and boreal copepods *Calanus glacialis* and *C. hyperboreus*, respectively 1.4 and 2.0× larger than the warmer water *C. finmarchicus* with a 9.5 and 25.75% higher lipid content, containing high levels of EPA and DHA (Kohlbach et al. 2016). Their lipid content more than triples after the spring stationary phase, during which they obtain 48% (*C. glacialis*) and 40% (*C. hyperboreus*) of their EPA from ice diatoms (Kattner & Hagen 2009, Kohlbach et al. 2016).

Primary consumers like copepods bioaccumulate (concentrate) lipids from microalgae (Sakshaug 2004, Kattner & Hegner 2009) and Arctic amphipods (*Themisto libellula* and *Gammarus wilkitzkii*) that prey on high-LCPUFA *C. hyperboreus* and *C. glacialis*, have a greater fatty acid content than their copepod prey, and have high levels of EPA and DHA (Kohlbach

et al. 2016) (see Section 3.7), and their lipid content subsequently doubles by the end of summer (Pinchuk et al. 2013). Ice diatoms have been found to contribute up to ~50% and ~90% of the energy and EPA in the diets of these copepods and amphipods, respectively (Kohlbach et al. 2016). Amphipods in turn are preferred prey for juvenile herring *Clupea harengus*, capelin *Mallotus villosus*, and seabirds, e.g. thick-billed murre (Brünnich's guillemots) *Uria lomvia*, and dovekies (Mehlum & Gabrielsen 1993, Dalpadado et al. 2001, Kraft et al. 2013).

To understand how LCPUFAs travel through the food web, controlled experiments in a closed system could be conducted, using labelled fatty acids fed to copepods which would be traced to determine their uptake and transfer to higher trophic levels such as amphipods and larval fish. Adding shorebirds to the mix would be difficult, but larval fish and copepods could be a proxy for them in this system. The amount of the original LCPUFAs could be determined, and this would demonstrate the bioaccumulation of LCPUFAs. If diatoms could be grown in a medium where the carbon was labelled, and if diatoms could be triggered to produce LCPUFAs, tracing could begin from primary producers and not primary consumers such as copepods. Research labelling carbon available to diatoms, triggering them to produce LCPUFAs, or labelling LCPUFAs fed to primary consumers, and then tracing this through the food web, would create a better understanding of what and how much is transferred from copepods or other primary consumers to secondary and other consumers, e.g. larval fish.

Estuarine systems in spring have a food web structure similar to early summer ice food webs (Figs. 2 & 3). At staging areas, diatoms that make up the microphytobenthos contribute energy and fatty acids not only to shorebirds (Kuwae et al. 2008, Beninger et al. 2011), but also to estuarine zooplankton. For example, EPA and DHA from diatoms comprise 45% of the fatty acids in the amphipod *Corophium volutator* in the Bay of Fundy that is then consumed by shorebirds staging for fall migration (Hamilton et al. 2003, Maillet & Weber 2006, MacDonald et al. 2012). These amphipods accumulate and biosequester fatty acids from diatoms (Noyon et al. 2011) and pass them up the food web. Labelling EPA and DHA in this system and following their transfer is needed to fully understand the estuarine food web and the importance of diatoms for energy and for LCPUFAs.

Diatom production of LCPUFAs is important for zooplankton egg production, hatching, growth, and function in both estuaries and the Arctic (Conklin & Provasoli 1977, Støttrup & Jensen 1990, Jónasdóttir

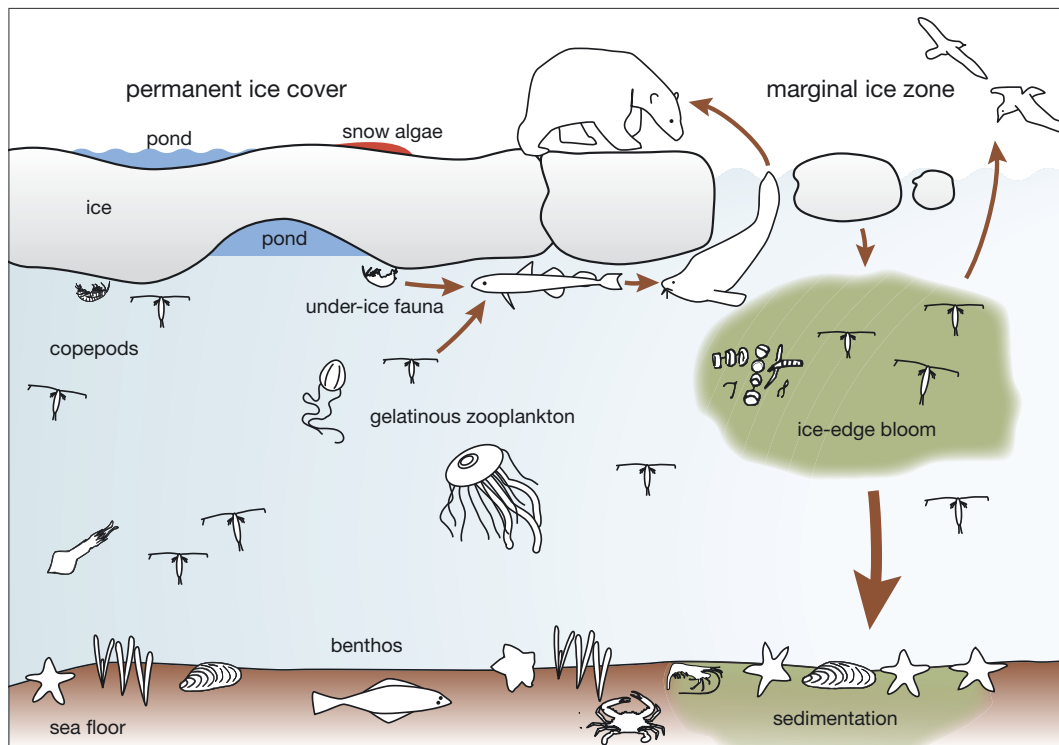


Fig. 2. Arctic ice edge food web (© Conservation of Arctic Flora and Fauna [CAFF], www.caff.is); Hugo Ahrenius cartographer, GRID-Arendal <https://www.grida.no/>

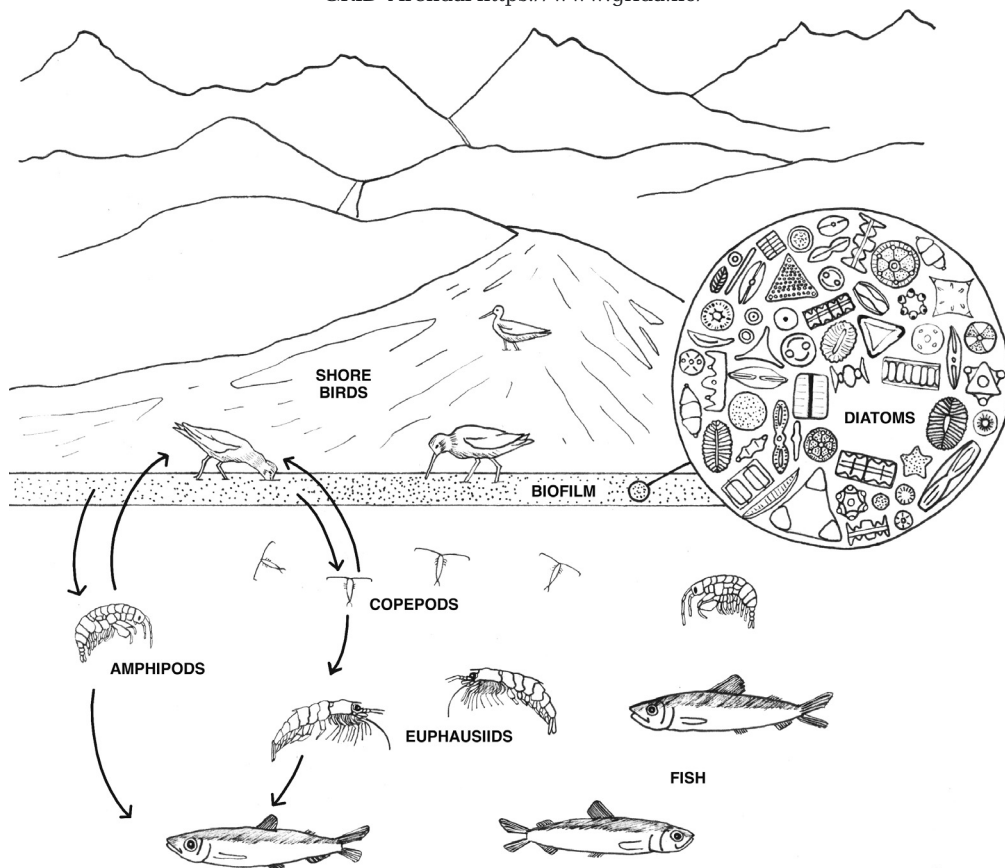


Fig. 3. Estuary food web (© Gillian Trotter, 2022)

1994). When primary consumers do not ingest these fatty acids in adequate amounts, many do not reach maturity, and subsequently their numbers available to predators decrease (Klein Breteler et al. 2005). Some studies have shown that copepod egg production increases with increasing concentrations of diatoms and LCPUFAs (Jónasdóttir 1994, Irigoien et al. 2002, Duerksen et al. 2014), although a review of experimental studies from 1970–1998 suggests that high densities of diatoms can result in low productivity for calanoid copepods (Paffenhöfer 2002). For calanoid copepods fed diets containing either no LCPUFAs, a mixture of LCPUFAs, mainly EPA, or mainly DHA, the fatty acid DHA had the highest partial correlation coefficient for egg production rate, whereas hatching success was significantly correlated with 3 omega-3 LCPUFAs: ALA, EPA, and DHA (Chen et al. 2012). Heterotrophs that eat zooplankton will have low amounts of these lipids if their prey are depauperate in LCPUFAs (Pond et al. 1996, Klein Breteler et al. 2005, Müller-Navarra 2008, Brett et al. 2009).

3.5.2. Invertebrates— not zooplankton

The effects of PUFAs and highly unsaturated fatty acids on invertebrates are well studied (Milke et al. 2004). Dietary LCPUFAs are retained and enriched (Brett et al. 2006, Gladyshev et al. 2011, Koussoroplis et al. 2013) and are correlated with better growth in juvenile bivalves and other invertebrates, which are prey of shorebirds (Milke et al. 2004, Parrish 2013). Sea urchins are sometimes seabird prey and they have increased gonad development if their consumption of omega-3 PUFAs is high (Carboni et al. 2013). With a normal kelp diet (32% omega-3, 20.9% MUFAs, 16.2% omega-6), vs. an experimental pellet diet (12.4% omega-3, 39.4% MUFAs, 27.3% omega-6), the omega-3 LCPUFAs make up 32% of their gonads (Carboni et al. 2013). In wild-caught sea urchins, EPA and DHA have been reported as ~7.9–10.7% in gonads (Kelly et al. 2008) and EPA from 9 to 12.6% in gametes of laboratory-raised urchins (Carboni et al. 2013). Parrish (2013) suggested that the need for ARA has been underestimated, especially in sea urchins. Polychaetes, which are common shorebird prey, eat diatoms, invertebrate larvae (e.g. *Artemis*), and copepods, i.e. prey that usually have high levels of EPA and DHA in the wild if they consume high amounts of these omega-3 LCPUFAs. In a laboratory setting, when polychaetes were fed high levels of EPA and DHA, they had higher survival and growth rates (Fidalgo e Costa et al. 2000).

3.5.3. Marine fish

Estuaries are nurseries and breeding grounds for fish, and the high spring productivity there provides necessary energy and fatty acids for fish reproduction. LCPUFA production is high in late spring through summer, when anadromous fish larvae migrate to estuarine nursery areas and consume euphausiids, amphipods (e.g. *Themisto libellula*), and other fish (Hewitt et al. 2009, Kasai et al. 2018, Jungbluth et al. 2021). As in other consumers, the importance of omega-3 LCPUFAs for growth in fish larvae and for overall productivity is well established. DHA and EPA are necessary for the structural components of biomembranes, and DHA is critical for larval vision, survival, and pigmentation (Bell et al. 1995, Copeman et al. 2002, van Anholt 2004). High omega-3 LCPUFAs have been associated with elevated fish egg production, larval development, growth, and viability (Jónasdóttir et al. 1998, Ballantyne et al. 2003). For example, fish fed rotifers raised on high-LCPUFA diets had higher growth rates and survival than fish fed rotifers with LCPUFA-poor diets (Watanabe et al. 1983, Copeman et al. 2002, Park et al. 2006). Salmon fed EPA also showed better growth than those fed other fatty acids (Hixson et al. 2017), and fish that eat prey with low LCPUFAs have reduced lipid reserves, decreased mass, lower in-river survivorship, fewer eggs produced, and poor embryo quality (Todd et al. 2012). However, in experimental feedings of larval North Sea cod reared on different algal food chains, St. John et al. (2001) found that concentration of LCPUFAs was highest in larval fish fed the dinoflagellate *Heterocapsa triquetra*, a typical harmful algal bloom species that grows during the winter in Chesapeake Bay (USA), and lowest when fed the diatom *Thalassiosira weissflogii*, a widespread generalist species. However, these are not species of microalgae usually found in large numbers in temperate estuaries or at the ice edge (von Quillfeldt 1997). More studies need to investigate LCPUFAs in different microalgae and their effects.

Abundance and quality of plankton prey of Atlantic salmon *Salmo salar* decrease with ocean warming, affecting reproduction and growth (Boehme et al. 2014). In Canada, Fraser River chum salmon *Oncorhynchus keta* have poor reproduction when their copepod prey consume diatoms raised in acidic ocean waters where they produce small amounts of LCPUFAs, and thus copepods that consume the diatoms subsequently have only ~5% LCPUFAs (Rossoll et al. 2012). Similar examples from climate change studies are further addressed in Section 3.8.

Fish with diets devoid of LCPUFAs can suffer from intestinal steatosis (abnormal retention of lipids), fin erosion, bleeding from gills, lordosis (excess curvature of the spine), reduced reproductive potential, and shock syndrome (Sargent et al. 2003, Glencross 2009). Van Anholt (2004) and Tocher (2010) suggested that only a diet with essential long-chain fatty acids can prevent these deficiency symptoms.

3.5.4. Migrating shorebirds staging at estuarine mudflats

Nutrient acquisition is of pivotal importance for long-distance migrating shorebirds that travel thousands of kilometres from wintering to breeding grounds and back annually. Foraging habitat choice is complex and based on many factors, including food quality, substrate, energy balance, heat and water balance, danger or presence of predators, social interactions such as competition and facilitation or presence of other species or conspecifics, or behaviour of the prey (Hicklin & Smith 1984, Piersma 2012). The conventional understanding is that shorebirds forage in areas where they can accumulate fuel and increase their muscle mass and fat stores for their long-distance flights (Piersma 2011), and the importance of fuelling up at staging areas is shown by how large a proportion of their active hours away from the non-breeding grounds is spent at staging areas (Battley et al. 2012). However, quality of prey vs. total energy of prey, obtained by analysis of fatty acids or other factors, has not been studied in a direct comparison in the field, and because shorebirds on migration are known to consume food high in LCPUFAs, such studies would be important to understand whether LCPUFAs are critical for migration and reproduction.

Observational studies linking consumption of high-LCPUFA prey to shorebird populations that fly long nonstop migratory legs suggest that fat quality consumed by shorebirds at these stopovers is important for long-distance legs (e.g. Scheiffarth 2001, Domingo et al. 2007, Duijns et al. 2009). For example, long-distance migrants such as western sandpipers consume diatoms in biofilm at the Fraser River delta before their nonstop long hop to Alaska (Kuwaie et al. 2008, Beninger et al. 2011, Jardine et al. 2015), and this was discussed in Section 3.2. Schnurr et al. (2020) also found a positive relationship between high LCPUFAs and western sandpiper abundance at this staging area before the long nonstop leg, suggesting that the quality of prey measured by their fatty acid content should be incorporated in studies of shorebird

habitat use. Foraging by other sandpiper species reflects the same sort of pattern. Before flying >1200 km south to the Bay of Fundy from their breeding grounds in Canada and Alaska, semipalmated sandpipers *Calidris pusilla* feed on insect larvae and crustaceans high in LCPUFAs (e.g. tipulids, chironomids, amphipods) (Holmes & Pitelka 1968, Senner et al. 1989, Würzberg et al. 2011, Fernández et al. 2015). They then stage at the Bay of Fundy and graze on diatoms in biofilm, eating amphipods (*Corophium volutator*) as well as polychaetes and molluscs, high in LCPUFAs, before their flight to South America, 3200–4000 km away (Hicklin & Smith 1979, Gratto et al. 1984, Hamilton et al. 2003, Quinn & Hamilton 2012, Quinn et al. 2017). On their northbound non-stop leg of >1300 km to their nesting grounds, they stage at Delaware Bay (USA) and consume eggs of horseshoe crabs *Limulus polyphemus* (Castro et al. 1989, Tsipoura & Burger 1999) that have eaten diatoms (Botton 1984), and they also eat molluscs (e.g. *Mulinia lateralis*), polychaete worms, and larval invertebrates, all high in DHA and EPA (Sellmer 1967, Würzberg et al. 2011). Likewise, black-bellied plovers *Pluvialis squatarola* on northward migration forage in elevated salt marshes in the Bay of Fundy where they eat dipteran larvae, e.g. soldier flies and horse flies, which have over 41 % dry weight of the LCPUFAs LIN and ALA (Hicklin 1987). On southbound migration, these plovers forage in mudflats in the Bay of Fundy (Hicklin & Smith 1979), and consume high-EPA larvae of horseflies, soldier flies, and beetles, polychaetes, *Nereis diversicolor* and *N. virens* (Hicklin & Smith 1979), and the amphipod *C. volutator*, all high in LCPUFAs.

Studies of 2 subspecies of bar-tailed godwits (*Limosa lapponica taymyrensis* and *L. l. lapponica*) that forage on mudflats in the Wadden Sea but on different prey or prey of different sizes, showed that the population of one subspecies migrated nonstop and much farther than the other to their breeding areas (Scheiffarth 2001, Duijns et al. 2009). This suggested looking into the different amounts of LCPUFAs in those prey to speculate if LCPUFAs are implicated in the ability to fly longer distances. Both species consume polychaetes, but only *L. l. taymyrensis* that travels the longer distance to breeding grounds in Siberia (3000 km) eats the most LCPUFA-rich prey: the largest polychaetes and crane flies in coastal meadows (Duijns et al. 2009). Similarly, red knots *Calidris canutus* all consume prey high in omega-3 LCPUFAs before their long nonstop migratory hops, but those that have long nonstop flights to South America (e.g. Argentina and Brazil) stage in a separate part of the

outer Cape Cod peninsula, North Pleasant Bay (Massachusetts, USA), and consume blue mussels *Mytilus edulis* with high omega-3 content (Fernández et al. 2015). Red knots which travel shorter distances to the SE USA and the Caribbean (Harrington et al. 2010) eat gem clams *Gemma gemma* in South Pleasant Bay; these clams are low in omega-3 fatty acids (Domingo et al. 2007). The migration studies and the prey analysis studies are unrelated, but bring up an interesting hypothesis of how LCPUFAs might affect shorebird migration distances. Additionally, on fall migrations, some shorebird species eat blueberries, high in the omega-3 PUFAs LIN and ALA (Cramp & Simmons 1983, Klavins et al. 2016, Zorzi et al. 2020). Blueberry consumption is not restricted to migratory shorebirds; migratory thrushes also consume blueberries with high PUFAs before long-distance migration (Zurovchak 1997).

Sandpipers' tongues have spines that trap biofilm, and various configurations of spines are found in 70 shorebird genera, from small *Calidris* sandpipers to larger genera such as ruffs *C. pugnax*, turnstones (*Arenaria* spp.), redshanks and greenshanks (*Tringa* spp.), and plovers (*Charadrius* spp.) (Elner et al. 2005, Kuwae et al. 2008). This characteristic might indicate that feeding on biofilm, and its main component, diatoms, is important for shorebird fitness, whether for fuel or for LCPUFAs, or it could simply be an exaptation.

The diversity of prey and foraging techniques of shorebirds present an opportunity to compare different species, quality of food consumed, and distances travelled. Presence or absence of diatoms or invertebrates with LCPUFAs at staging sites of shorebirds, along with their foraging density, could be used as a marker for high amounts of energy in each habitat, or as proxies for high-quality food affecting their ability to migrate nonstop. Sampling of the total energy available (i.e. the fatty acid profiles of shorebird prey), while concurrently sampling the fatty acid intake of shorebirds per habitat, would clarify this relationship. Exactly which fatty acids shorebirds are ingesting, and the origins of those nutrients, are as important to know as what the characteristics of the foraging sites are compared to shorebird density.

3.5.5. Seabirds in the Arctic

Tens of millions of seabirds forage or breed at high latitudes, including Arctic-breeding alcids (e.g. murres [*Uria* spp.] and dovekeys) and larids (e.g. ivory gulls *Pagophila eburnea* and glaucous gulls *Larus*

hyperboreus), as well as populations of some Southern Hemisphere-breeding seabirds (e.g. short-tailed shearwaters *Ardenna tenuirostris*) (Schneider & Shuntov 1993). Colonial seabird colonies are usually situated near areas of high productivity and abundant prey (Gaston 1985, Huettmann & Diamond 2001, Davoren et al. 2003), and the success of these colonies is linked to prey quality as well as prey abundance (Wanless et al. 2005, Kadin et al. 2012, Divoky et al. 2015).

Seabirds in the Arctic and subarctic occupy a wide range of trophic levels and forage in all zones, littoral to pelagic, and range from planktivores, e.g. dovekeys and thick-billed murres, that feed on coldwater Arctic and boreal zooplankton high in LCPUFAs (respectively copepods, *Calanus glacialis*/*C. hyperboreus*, and amphipods, *Themisto libellula*), to piscivores, e.g. black guillemots *Cephus grylle* and glaucous gulls which feed on coldwater fish high in LCPUFAs, such as Arctic cod *Boreogadus saida*, Pacific or Atlantic cod (*Gadus* spp.), herring (*Clupea harengus* and *C. pallasii*), and anchovies *Engraulis encrasicolus* (Bradstreet 1982, Mehlum & Gabrielsen 1993, Dahl et al. 2003). Some planktivores, e.g. dovekeys and thick-billed murres, also feed on these coldwater fish which themselves eat copepods and amphipods (Belopol'skii 1961, Bradstreet & Cross 1982).

Because seabirds consume marine prey, they theoretically have high levels of LCPUFAs, and thus these molecules should not be limiting, as they could be for shorebirds. The one issue that could be a problem for seabirds for both energy and LCPUFAs is when diatom growth and synthesis of LCPUFAs is low in the ocean, which could result from changes in physical factors (light, temperature, turbulence) or chemical factors (salinity, nutrients, pH). Climate change is affecting all of these factors, and changes in output of LCPUFAs from climate change are addressed in Section 3.9.

The importance of LCPUFAs for reproduction in seabirds has not been investigated in the field. Successful seabird reproduction is attributed to the abundance and quality of their prey. Quality of prey is a proxy for fat or energy, and prey with low fat/low energy have been associated with breeding failures in alcids (Harris & Hislop 1978, Monaghan et al. 1994, Kadin et al. 2012), larids (Massias & Becker 1990, Monaghan et al. 1992, Wanless et al. 2005), and among sympatric species foraging on prey with different amounts of fat (Baird 1990, Furness & Camphuysen 1997). When cold water high-LCPUFA fish like herring are available, productivity and chick growth are high (Massias & Becker 1990). There is an

absence of seabird foraging studies that look at fat quality vs. quantity in the experimental way that Twining et al. (2016) did with tree swallow chicks and LCPUFAs. The most similar research reports poor reproduction in seabirds linked to prey low in fat yet high in carbohydrate and protein biomass (Massias & Becker 1990, Wanless et al. 2005, Harris et al. 2008).

3.6. Arguments supporting LCPUFAs as critical nutrients for all taxa: selective uptake of LCPUFAs and bioaugmentation

The high transfer efficiency (bioaugmentation) of EPA and DHA between trophic levels points to their importance as qualitatively different fatty acids from SATs and MUFAs (Gladyshev et al. 2010, 2013, Koussoroplis et al. 2013, Budge et al. 2014). Additionally, their low amounts in adipose tissue point to uses other than solely for fuel, and support their role as ligands and bioactive molecules (Section 3.8). They are sequestered, and their selective uptake and storage is found throughout the marine food web (Gladyshev et al. 2010, 2011). Bulk carbon, including carbohydrates and SATs, are used for energy, and are transferred up aquatic food webs at ~5–10% efficiency, whereas transfer rates for LCPUFAs can be 2–3 times higher (Gladyshev et al. 2010, 2013, Koussoroplis et al. 2013, Budge et al. 2014). Various small grazing invertebrates preferentially accumulate LCPUFAs, suggesting there is selection pressure to retain them from diets (Brett et al. 2006, Gladyshev et al. 2011, Koussoroplis et al. 2013), and LCPUFAs from diatoms are transferred and bioaugmented up the food web (Falk-Petersen et al. 1990, Sakshaug 2004, Brett et al. 2006). For example, LCPUFAs have been found in 10–20% of the dry mass of phytoplankton and in 50–70% of herbivorous zooplankton (Falk-Petersen et al. 2007). In birds, grey herons *Ardea cinerea*, for example, concentrate EPA and DHA in their muscles at levels twice as high as in their fish prey (Gladyshev et al. 2010), and herring gulls *Larus argentatus* bioaccumulate them from fish (Käkelä et al. 2005).

3.7. Summary of the physiological functions of LCPUFAs in the marine food web

Fatty acids have a number of roles in many taxa; for example, they can be stored for future fuel as triglycerides and can be metabolized when needed, and they can be changed into structural biomembranes,

e.g. phospholipids, for cellular repair in the consumer or in egg and embryo formation. Notably, LCPUFAs such as EPA and DHA are ligands, biologically active metabolites which are signals that can turn genes in cells on or off. Many marine and estuarine animals, except a small number of invertebrates and a few fish, have a limited ability to elongate and desaturate LIN and ALA to produce the LCPUFAs EPA and DHA (Stryer 1995), and moreover, this production is inefficient, with high energy input and very low output (Van Horn et al. 2008, Gladyshev et al. 2010, Twining et al. 2018).

3.7.1. Fuel

Long-chain fatty acids are not as efficient a fuel as shorter-chain SATs or MUFAs due to their multiple *cis*-double bonds, which twist them and configure the side chains tightly. This crowded configuration makes access difficult for catabolic enzymes to break the bonds for fuel (Berg et al. 2002, Silverthorn 2019), and thus LCPUFAs need an enzyme-coupled reaction requiring energy to shift the bonds from *cis* to *trans* for enzymatic access (Ball et al. 2012, Mehta 2013). The *cis* isomer is also more stable than the *trans*, needing more energy to go from *cis* to *trans* than for the reverse reaction (Whitesell & Fox 2004, Engelking 2015). Because of this stability and physical hindrance of LCPUFA *cis* bonds, SATs and MUFAs produce more net energy when oxidized, and are better fuel sources (Sargent et al. 2003). Supporting this, Dick & Guglielmo (2019) tested fatty oxidation *in vivo* on migratory songbirds in the fall, kept in artificially manipulated light cycles simulating spring migration, and fed them MUFAs or LCPUFAs. Fatty acid composition in adipose storage tissues, no matter which diet, was 95–96% SATs and MUFAs, the fuel-efficient fatty acids.

3.7.2. Ligands

In addition to providing energy, free fatty acids are also ligands, and have major roles as messengers and regulators of gene transcription. LCPUFAs are most importantly signalling molecules (Arts et al. 2001, Guschina & Harwood 2006), and fatty acid ligands, once bound to their receptor on the cell membranes, initiate physiological cascades in organisms (Guglielmo et al. 1998, 2002, McFarlan et al. 2009). Unlike nutrients used for fuel, LCPUFAs often bypass the normal route of fat breakdown for storage and are

transported directly to the plasma membrane of cells where they bind to and activate fatty acid binding proteins (FABPs), part of the cell signalling system (Desvergne & Wahli 1999, Budge et al. 2006, Falomir-Lockhart et al. 2019). When activated by fatty acid ligands, their signalling regulates the environment within cells (Schmitz & Ecker 2008), affecting metabolic pathways (Price 2010, Butler 2016). Effects on FABPs activated by fatty acids include an increase in fatty acid transport across the membrane and a delivery of high-energy fuel to muscles (e.g. to aid in migration) (Guglielmo 2018). During migration, birds can increase their FABPs in pectoral muscles by 70–110% above wintering levels, especially the kind necessary for high uptake of fatty acids.

Small but critical amounts of LCPUFAs, especially EPA and DHA, and ARA, have unique roles in controlling and regulating cellular metabolism and animal physiology for all members of the marine, estuarine, and Arctic food webs (Tocher 2010, Fu et al. 2017, Falomir-Lockhart et al. 2019). EPA and DHA especially affect gene expression in many species, initiating physiological cascades throughout the organism (Arts et al. 2001, Arts & Kohler 2009, Parrish 2013). Intracellularly, they bind to and activate peroxisome proliferator-activated receptors, nuclear transcription factors that regulate the expression of genes of metabolism and signalling (Schmitz & Ecker 2008). These modulate and regulate genes affecting blood clotting, immune and inflammatory responses, cardiovascular tone, renal and neural functions, reproduction (Schmitz & Ecker 2008, Tocher 2010), and development, metabolism, neural development, and homeostasis in general (Olefsky 2001, Falomir-Lockhart 2019, Silverthorn 2019).

The physiological significance of EPA and DHA at the cellular level can be found throughout heterotroph tissues; in endotherms, these molecules are present in high concentrations in cerebral cortex, retina, testis, and sperm, despite low levels in blood plasma (Opstvedt 1985). DHA especially has important structural and functional roles in all membranes, but particularly in neural membranes (Innis 2008, Wassall & Stillwell 2008), and it regulates the function of several neurotransmitters (Arts & Kohler 2009, Hixson et al. 2015). Furthermore, PUFAs, such as LIN and ALA, are bioactive precursors of prostaglandins, leukotrienes, thromboxanes, resolvins, protectins, and endocannabinoids which help modulate regional blood flow to tissues, control blood pressure, and regulate contraction of smooth muscles in bronchial passages, the alimentary canal, and blood vessel walls (Thompson 2018).

3.7.3. Adjuvant roles

Below is a short summary of some of the other potential benefits of mainly the omega-3 (n-3) LCPUFAs. Note that compounds other than LCPUFAs also fulfill these functions, and LCPUFAs are not uniquely responsible for them. However, they may act in an adjuvant role for inhibition of inflammation, for immunity, or for fuel regulation. More research is needed on these possible roles of LCPUFAs.

Inflammation inhibition and immunity. Inflammation from injury, disease, or stress has negative effects on the success of migration and reproduction of shorebirds and seabirds, and thus, consuming nutrients that suppress inflammation would aid energy costs of migration and reproduction. With inflammation produced by pathogens or injury, EPA and DHA are both anti-inflammatory and inflammation-resolving (Calder 2013) and could be considered adjuvant mechanisms to decrease inflammation. Pathogens elicit an inflammatory immune response, and EPA and DHA suppress this in part by down-regulating inflammatory genes and modulating the production of eicosanoids and cytokines, as well as producing resolvins and protectins (Calder 2003, 2013). In contrast, the n-6 ARA is pro-inflammatory (Calder 2013), and EPA and DHA antagonize it, turning off production of eicosanoids, reactive oxygen, and cytokines (Schmitz & Ecker 2008, Calder 2013).

Fuel regulation and muscle efficiency. Migration and reproduction are energy demanding, and the ability to move fuel into cells is critical during these periods. Omega-3 fatty acids bind to and increase activity of peroxisome proliferator-activated receptors on cells involved in transport of fatty acids (Guglielmo 2018), regulating genes of energy metabolism (Desvergne & Wahli 1999). Migrating birds such as western sandpipers increase their FABPs for EPA and DHA in their flight muscles (levels can double) before migration (Guglielmo et al. 2002, McFarlan et al. 2009, Butler 2016).

There has been some controversial research that has yet to be resolved regarding the ability of LCPUFAs to boost flight enzymes. In one study on bobwhite quail *Colinus virginianus*, which are not long-distance migrants, those fed high doses of EPA and DHA increased the amount of oxidative enzymes in their flight muscles by 58–90%, a level only seen in migrating shorebirds (Nagahuedi et al. 2009), some mammals, red-eyed vireos *Vireo olivaceus* (Pierce et al. 2005), and European starlings *Sturnus vulgaris* (Hall et al. 2014). *In vitro*, bird muscle EPA and DHA increase the mitochondrial respiratory chain efficiency and also the basal and maximal oxygen con-

sumption in muscles (Young 2019) which allow more complete utilization of fuel and a more efficient oxidation. Further *in vitro* evidence of the assistance of LCPUFAs in migration is an increased mitochondrial proton leak (Young 2019), which, especially in muscle mitochondria, is thought to aid in thermogenesis and help limit production of free radicals and cellular oxidative harm (Jastroch et al. 2010, Divakaruni & Brand 2011, Young 2019). No *in vivo* testing of this has been done to detect if a boost in fuel efficiency is actually effected by LCPUFAs via these mechanisms.

3.8. Alterations in marine trophic structure from climate change

Marine systems are experiencing the effects of climate change, and current global temperatures are changing faster than these food webs can adapt (Pörtner et al. 2019). The speed at which changes are taking place in the Arctic is unprecedented (Reid et al. 2007, Meier et al. 2014, Box et al. 2019). Arctic marine ecosystems are structured by seasonal and permanent sea ice (Eicken 1992, Kattner et al. 2007, Vancoppenolle et al. 2013), and the productivity and growth cycle in late spring/early summer in the Arctic follows the timing of this structure that has been in place for a very long time. Hixson & Arts (2016) modelled climate change and LCPUFAs in phytoplankton and predicted a reduction in global n-3 LCPUFAs of 8.2% for EPA and 27.8% for DHA if water temperature increased 2.5°C. Early ice melt from climate change would affect chemical and physical triggers for diatoms to produce LCPUFAs (Kattner et al. 2007). Further, as warmer temperatures advance ice melt and decrease thickness and extent of ice cover, premature transmission of light to under-ice diatoms stimulates their early proliferation and release of nutrients into the water column, and there could be a potential mismatch between consumers and diatom production of LCPUFAs (Cushing 1990, Søreide et al. 2010, Dezutter et al. 2019).

Warming conditions influence the suite of micro-phytoplankton species in an ecosystem, reduce their total output of LCPUFAs, and affect consumer abundance and reproduction (Kohlbach et al. 2016). LCPUFAs decrease significantly in response to higher amounts of CO₂ (Bermúdez et al. 2015), and loss of omega-3 fatty acids has been found experimentally in zooplankton such as rotifers raised at higher temperatures (Copeman et al. 2002). Field studies have shown that increases in ocean temperatures have decreased zooplankton numbers and size, causing

lower survival of young Atlantic cod *Gadus morhua* in the North Sea (Beaugrand et al. 2003). Likewise, in a warming ocean, coldwater-adapted high-LCPUFA prey are often displaced by poorer-quality prey, creating growth and reproductive issues for consumers (Beaugrand et al. 2003, 2009, Beaugrand 2004, Weijerman et al. 2005, Fossheim et al. 2015).

Anomalous warm years reduce spring phytoplankton biomass, resulting in lower abundances of seabird prey such as large-bodied fatty zooplankton and forage fish with high energy (Stabeno et al. 2012, Duffy-Anderson et al. 2017), and seabird productivity decreases during these times. Warmer subarctic water and its associated food web have slowly been entering the Arctic since the 1990s, and Arctic zooplankton and fish with high amounts of fat are being replaced by warmer subarctic species (Berge et al. 2005, 2015, Beaugrand et al. 2009, Gilg et al. 2012). Subsequently, Arctic seabirds deliver less energy to chicks, and often seabird colonies fail (Jakubas et al. 2007, Provencher et al. 2012, Meier et al. 2014).

Recent intrusion of warm water and the associated food web into the Arctic might portend what the effects of climate change could bring. The traditional copepod prey of dovekies, the large high-lipid Arctic *Calanus hyperboreus* and *C. glacialis* in the Norwegian, Greenland, and Barents Seas, are being replaced by the smaller subarctic *C. finmarchicus* and subarctic gammarid amphipods that have 10–25 times lower lipid content (Węśławski et al. 2018, Kristiansen et al. 2019). This has resulted in lower dovekie productivity (Mehlum & Gabrielsen 1993, Węśławski et al. 1999, Falk-Petersen et al. 2007). Similarly, in Hudson Bay, the fish prey of thick-billed murre, Arctic cod, has been declining since the mid-1980s, as warmer water intruded (Gaston et al. 2003). In addition, the traditional amphipod prey of murre, high-lipid *Themisto libellula*, has decreased with entry of warmer water, and lower-fat smaller marine amphipods such as *T. abyssorum* or *T. compressa* have replaced them (>16 mm smaller; mass 5–8% of *T. libellula*) (Gaston et al. 2003, 2005, Noyon et al. 2011). Poor reproductive success and low chick growth from low-fat diets are also found in subarctic seabird species (see Section 3.5.5) (Massias & Becker 1990, Wanless et al. 2005).

Many seabirds are already in decline, e.g. Cassin's auklets *Ptychoramphus aleuticus* (Morrison et al. 2011) and tufted puffins *Fratercula cirrhata* (Gaston et al. 2009, Hart et al. 2018), and wide-ranging and persistent marine warming could push population numbers down alarmingly. The ultimate mechanisms driving food-web-wide shifts in forage fish species distribu-

tion and population decreases in zooplankton in the Pacific and Atlantic Oceans and Bering and North Seas need to be studied. At the very least, suites of diatom species and their amounts of energy and LCPUFAs should be addressed in all studies on climate change. If some of these shifts in seabird prey become permanent, this will affect seabird productivity.

Widespread climate change, sea level rise, and ocean acidification and warming will also create vast changes to estuarine ecosystems in the way that climate change will affect the ice edge (Bindoff et al. 2019, Pörtner et al. 2019). Coastal ecosystems and estuarine mudflats have already contracted, and many have lost biodiversity and functionality, as well as large shorebird population declines at the estuaries due to anthropogenic disturbances. Rising temperatures from climate change are affecting the timing of snow melt most rapidly in coastal mountains, where snow is predicted to melt a month earlier than historically (Evan & Eisenman 2021). Further, snow melt in coastal mountains, like ice melt in the Arctic, is predicted to begin up to a month earlier than historically (Evan & Eisenman 2021), and river outflow carrying important nutrients for phytoplankton, with input of fresh water and turbulence, might trigger the stationary phase earlier than normal in diatoms. Thus the timing of the diatom stationary phase might be mismatched with consumer abundance, as in the Arctic, with deleterious impacts on entire estuarine ecosystems (Tremblay et al. 2006, Dugdale et al. 2012). The microphytobenthos in biofilm in estuaries are the important productive class of diatom under these conditions (Hope et al. 2020), and the species producing LCPUFAs could be replaced by other species more adapted to the new conditions. Worldwide, large decreases in population numbers of migratory birds have already occurred due to modification or destruction of their flyways (Goss-Custard et al. 1995, Amano et al. 2010, Clemens et al. 2016), and if the presence of high-energy fatty acids as well as production of biologically active LCPUFAs in diatoms is a critical factor for shorebird migration, then mismatch of nutrients plus habitat losses could impact shorebird migration at an even greater rate.

3.9. Seabird die-offs

Changes in ocean conditions could influence seabird population abundance and species of prey, not just at the breeding grounds or in the Arctic, but throughout their ranges (Gaston et al. 2005, Stabeno et al. 2012, Jones et al. 2018). The open ocean where

many seabird species forage includes plankton communities which are adapted to the physical and chemical conditions of each region, yet with increased ocean temperature and acidity, the communities of microphytoplankton will most probably change, theoretically affecting the food web dependent on them. Over the past 40 yr, there have been many examples of seabird die-offs, both coastal and pelagic, and they are increasing in frequency. Starvation is most frequently the cause (Blake 1984, Furness & Tasker 1999), and is frequently linked to low availability of their traditional prey (Furness & Tasker 1999, Jones et al. 2018). Storms are sometimes implicated, but this should not be an issue for murre and other pursuit divers (Bourne 1976). Pollutants are sometimes suggested as causes, yet often verification tests are not run, or are inconclusive (Bourne 1976). Die-offs are not restricted to the Arctic; there have been mass mortalities of seabirds from starvation in temperate oceans, many along the Pacific coast since 2014, with mortalities of 400 000 Cassin's auklets and more than 500 000 common murre in 2014 and 2015, respectively (Jones et al. 2019).

Most seabird die-offs have been linked to decreases in zooplankton species, and the causes for this decrease point to a warming climate. In future studies on this phenomenon, change in food quality due to such temperature changes, especially extreme heat waves, and movement of warm water or warm-water species into the area of die-off, should also be considered (Bond et al. 2015, Jones et al. 2018, 2019). For example, prior to the Pacific die-off of Cassin's auklets, there was an unseasonal heat wave and an intrusion of warm water into their winter foraging area (Jones et al. 2018), and a similar die-off of Cassin's auklets off British Columbia (Canada) in 2007 was linked to consumption of invasive low-fat warmwater copepods after a marine warming episode (Jones et al. 2018). However, none of these reports documented diatom abundance, species, or energy and LCPUFA content either in diatoms or in the consumers. Events like these point to the need to assess the energy and LCPUFA content of members at the bottom of food webs in any foraging or population study.

3.10. Ocean acidification and fatty acids

When atmospheric CO₂ increases, oceans warm, dissolved CO₂ concentrations increase, and oceans become more acidic (Doney et al. 2009). The oceans have been acidifying since the late 1980s, with surface water pH declining 0.017–0.027 pH units per decade (Pörtner et al. 2019), altering nutrient cycles

and having a regionally variable impact on microphytoplankton (Pörtner et al. 2019). Acidification could change the fatty acid energy content of diatoms as well as their quality measured by LCPUFAs. For example, McLaskey et al. (2019) found *in vitro* that low oceanic pH and high temperatures were 2 factors that significantly decreased fatty acid concentration and composition of the cryptophyte plankton *Rhodomonas salina*. Copepods that consumed these low-LCPUFA cryptophytes exhibited low growth and reproduction similar to that of copepods consuming low-LCPUFA diatoms (Section 3.6.1); at high CO₂, there was a 10-fold decline in LCPUFAs and a 3-fold increase in SATs (Rossoll et al. 2012). Research like this that measures LCPUFA content in microphytoplankton and their consumers under different seawater acidities needs to be conducted to determine if there is an effect of poor productivity and growth up the food web. If the presence of high LPUFA diatoms is a critical factor for reproduction and growth of the marine community or for shorebird migration, then a warmer and more acidic ocean that would depress this output by diatoms could impact the marine food web at an even greater rate.

4. CONCLUSION AND FUTURE DIRECTIONS

This review focussed on the production of LCPUFAs by diatoms in the Arctic and in temperate estuaries mainly in spring, on what triggers their LCPUFA production, and on the contrasting effects of LCPUFAs on various taxa in the marine food web, with an emphasis on shorebird and seabird ecology and their trophic webs. Climate change will continue to have strong effects on marine communities, and probably could affect the Arctic and temperate estuaries in similar ways by altering many abiotic factors e.g. the timing of release of inorganic nutrients or input of fresh water (i.e. ice melt or freshet), or cold water (i.e. oceanic upwelling). These factors normally launch productivity in both Arctic and estuarine ecosystems by stimulating diatoms to change their metabolism from the exponential growth stage to the high-energy and high-LCPUFA-producing stationary stage.

Climate change thus has the potential to alter the timing of the suite of factors that initiate productive food webs, affecting not only phytoplankton at the base of the food web, but also consumers, increasing mismatches of spring bloom and consumer growth and reproduction. Effects might reverberate throughout the food web if high-energy fatty acids and bioactive LCPUFAs are indeed necessary for consumer

growth and reproduction. The timing of both the arrival of seabirds in the Arctic and the staging of shorebirds in temperate estuaries corresponds with this high production in those ecosystems, suggesting that resources containing omega-3 LCPUFAs produced by diatoms may be important for these birds.

When research data from the fields of oceanography, marine biology, climate change, ecology of phytoplankton primary producers (mainly diatoms), and reproduction, growth, and food web relationships of zooplankton, fish, shorebirds, and seabirds, as well as shorebird migration, are reviewed together as one whole entity, the results suggest that climate change depresses phytoplankton populations, lowers historical prey populations, and increases the abundance of poor-quality prey. Evidence suggests that there may be additional effects of climate change due to the replacement of high-energy and high-LCPUFA diatoms by low-energy and low-LCPUFA-producing ones, or from the inability of these high-quality diatoms to start production in warmer waters without a trigger. If the presence of high-LPUFA diatoms is a critical factor for reproduction and growth of the marine community or for shorebird migration, then a warmer and more acidic ocean that would depress this output by diatoms could impact the marine food web at an even greater rate, especially at the Arctic ice edge where climate change is more accelerated than in the rest of the marine ecosystem. Likewise, if LCPUFAs are important for estuarine communities and for shorebird migration, further destruction of estuaries containing LCPUFA-producing microphytobenthos would decrease LCPUFA production and impact this system negatively.

Future research on shorebird and seabird ecology and Arctic and estuarine food webs, as well as studies on climate change or habitat destruction of shorebird staging areas, should include assessments of fatty acid content of co-occurring diatoms, and the types of fatty acids transferred from them to their food web. In sum, fatty acid composition and availability from primary producers like diatoms, transferred up the food web from zooplankton to invertebrates to fish and birds, play a definitive role in food web structure in estuarine and Arctic ecosystems, potentially influencing growth rates and secondary production over many taxa including shorebirds and seabirds. Future research on growth and reproduction of marine consumers at the Arctic ice edge and in estuaries, and more explicitly, on seabird and shorebird prey, should investigate fat quality in the respective food webs to understand the potential contribution of fatty acids.

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