Mixotrophic Plankton in the Polar Seas: A Pan-Arctic Review

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Polar marine ecosystems are characterized by low water temperatures, sea ice cover, and extreme annual variation in solar irradiance and primary productivity. A review of the available information from the Arctic suggests that mixotrophy (i.e., the combination of photosynthetic and phagotrophic modes of nutrition in one cell) is wide spread among plankton. In the central Arctic Ocean (AO) in summer, mixotrophic flagellates such as *Micromonas* and *Dinobryon* can account for much of bacterivory. Planktonic ciliates with acquired phototrophy form the bulk of microzooplankton biomass in both the ultra-oligotrophic deep basins of AO and its productive shelf seas. With the exception of the diatom bloom in the marginal ice zone, mixotrophic ciliates often dominate total chlorophyll in the mixed layer in summer taking advantage of the 24-h insolation. Their relatively high growth rates at low temperatures indicate that they are an important component of primary and secondary production. The key Arctic copepod species preferentially feed on chloroplast-bearing ciliates, which form an important link in the planktonic food web. The limited available year round data indicate that mixotrophic plankton persist in the water column during the long polar winter when irradiance is low or absent and ice cover further reduces light penetration. These observations suggest that at high latitudes an alternative food web based on mixotrophy may dominate the pelagic lower food web during much of the year.

Keywords: mixotrophy, Arctic plankton, mixotrophic flagellates, mixotrophic ciliates, Arctic Ocean

INTRODUCTION

Mixotrophy, defined as the combination of phagotrophy and photosynthesis in an individual cell, is increasingly recognized as an important trophic mode among planktonic protists, both "phytoplankton" and "microzooplankton," in the global ocean (reviewed in Caron, 2017; Leles et al., 2017; Selosse et al., 2017; Stoecker et al., 2017) but in polar waters mixotrophy has not received much attention. In fact, this mixed mode of nutrition is so wide-spread that the above dichotomy may be no longer suitable for an accurate description of the role of unicellular eukaryotes in the ocean (Flynn et al., 2013). Ecosystem models that include mixotrophy indicate that this trophic mode has profound effects on biogeochemical cycling, including increasing carbon fixation, decreasing loss of dissolved organic carbon and increasing vertical carbon flux (Mitra et al., 2014; Ward and Follows, 2016). Mixotrophy also influences the structure and function of food webs. Modeling indicates that mixotrophy can increase mean organism size and trophic transfer, potentially resulting in increased production at upper levels in the food web (Mitra et al., 2014; Ward and Follows, 2016).

It is particularly important to understand the effects of mixotrophy in the Arctic because its marine environment is changing rapidly. The Arctic Ocean may have lost over 50% of its sea ice volume (Kwok and Rothrock, 2009), with the largest decreases in the Barents, Kara, and Siberian sectors, particularly over the continental shelf (Pabi et al., 2008). In just 12 years, the open-water growing season has increased by 45 days, promoting a pan-Arctic 20% increase in net primary production (Brown and Arrigo, 2012). Climate change is causing a patchwork of altered environmental conditions in the Arctic. Decreases in sea ice thickness, extensions in the length of the ice free season, increased water temperatures, and freshening have led to increased stratification in some seas, whereas increased mixing due to storms have been observed in other areas (Metfies et al., 2016; Blais et al., 2017; Oziel et al., 2017). Although the rising trend in primary production (Slagstad et al., 2011) may be hindered by stronger stratification and nutrient limitation in offshore areas (Ardyna et al., 2011, 2017; Brown and Arrigo, 2012), these changes are expected to bolster the pelagic system at the expense of the benthic components, with profound impacts on trophic structure and carbon fluxes (Wassmann and Reigstad, 2011). Recent studies in the Arctic indicate that a major portion of pelagic primary production is channeled to the higher trophic levels through unicellular grazers such as ciliates and dinoflagellates (Olson and Strom, 2002; Verity et al., 2002; Calbet et al., 2011b; Sherr et al., 2013; Stoecker et al., 2014; Franzè and Lavrentyev, 2017). This warrants investigation of the effects of climate change on microbial plankton as even minor effects at the base of food webs could be amplified through trophic chains (Sarmento et al., 2010). Given the rapid changes in Arctic ecosystems, it is increasingly important to determine the trophic modes of plankton in Arctic seas and predict how trophic modes may change with the environment and how this may affect ecosystem processes.

The Objectives and Material

Few attempts have been made to directly examine the physiological rates of mixotrophic plankton in the Arctic due to logistical and methodological constraints (Putt, 1990; Sanders and Gast, 2012; Franzè and Lavrentyev, 2014). Nevertheless, there is evidence in the literature that mixotrophic plankton play an important role(s) in the Arctic marine ecosystems. Our objectives are to review existing data, identify data gaps, and present hypotheses about the roles of mixotrophy in Arctic Seas and how these may be altered due to changes in the physical environment.

In this review we primarily focus on the following contrasting regions of the Arctic: the deep oligotrophic Canada Basin of the Arctic Ocean, the relatively shallow and productive Barents and Kara shelf seas, and the main entrance for the Atlantic water into the Arctic Ocean, the Fram Strait (**Figure 1**). In addition we consider data from the productive shelf of the sub-Arctic Bering Sea, which has been subjected to similar climatic changes as the Arctic shelf seas (Hunt and Megrey, 2005). Each of the above polar regions is unique in terms of bathymetry, circulation, sea-ice cover, and food webs (Carmack and Wassmann, 2006). Thus, they are ideally suited for a pan-Arctic comparison.
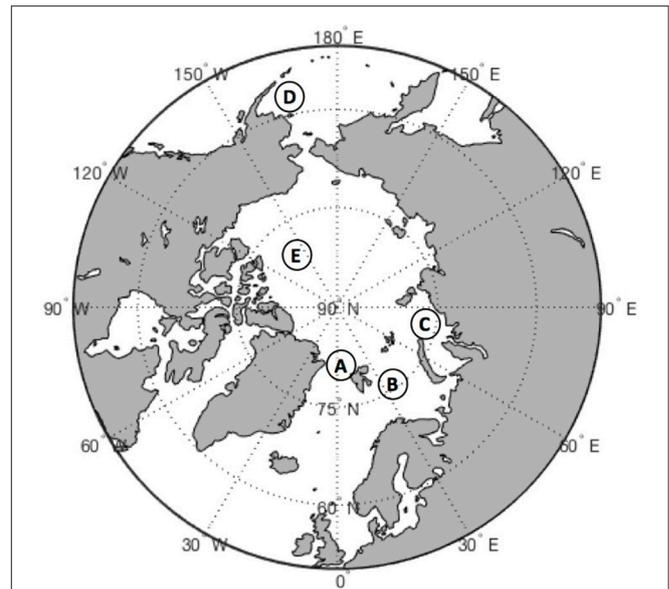

FIGURE 1 | Map of the Arctic Ocean showing the main study locations: A, Fram Strait; B, Barents Sea; C, Kara Sea; D, Bering Sea; E, Canada Basin.

REVIEW

Evidence for Mixotrophy Among Arctic Plankton

Although mixotrophy among planktonic protists is well documented in temperate and tropical waters, less is known about mixotrophy in Arctic seas. Phagotrophy by phytoflagellates is usually underestimated, particularly in remote locations such as the Arctic, where field experiments are logistically difficult or which are difficult to sample in all seasons. Ingestion of prey by small, pigmented cells is difficult to detect and is often underestimated, even in experimental studies designed to measure it (Anderson et al., 2017). Ciliates with plastids are more readily distinguished from heterotrophs than phagotrophic phytoflagellates from strict autotrophs. Measurements of feeding and photosynthesis in both mixotrophic flagellates and ciliates are rare. However, there are ample reasons to hypothesize that mixotrophy is common among Arctic plankton. Below we list mixotrophic flagellate and ciliate taxa reported from Arctic Seas and provide evidence that the taxa are mixotrophic. The evidence for mixotrophy ranges from observation of food vacuoles or plastids in preserved specimens to field or laboratory measurements of feeding and photosynthesis. For some species the evidence is very limited, whereas other species have been studied intensively. For well-studied species, we have included only a few key references.

Chrysophyta

Arctic plankton assemblages include nanoplanktonic chrysophytes such as *Ochromonas* spp. that are often bacterivorous as well as photosynthetic (Estep et al., 1986; Andersson et al., 1989; Keller et al., 1994). The colonial

chrysophyte, *Dinobryon balticum*, is a common component of the microplankton in Arctic and sub-Arctic seas (**Table 1**) and is often associated with low irradiance and the deep chlorophyll maximum (DCM) layer (McKenzie et al., 1995). The colonies are a significant contributor to particle flux during summer in the Barents Sea (Olli et al., 2002) and probably other coastal Arctic seas. Although *D. balticum* has plastids and requires light, this species supplements it nutrition with bacterivory (McKenzie et al., 1995).

Cryptophyta

Cryptophytes are another algal group often associated with low light conditions and that are known to contribute to bacterivory (**Table 1**). In phytoplankton investigations and *in situ* studies of phagotrophy by algae, cryptophytes have rarely been identified to species. *Teleaulax amphioxeia*, a widespread species found in temperate and Arctic waters (**Table 1**) has been shown to be mixotrophic (Yoo et al., 2017).

Haptophyta (Prymnesiophyta)

Although many haptophytes are mixotrophic and often dominate the mixotrophic phytoplankton assemblage in temperate waters (Unrein et al., 2014), the dominant haptophyte in Arctic waters, *Phaeocystis pouchetii*, is yet to be shown to be phagotrophic. Another photosynthetic prymnesiophyte genus found in Arctic water is *Chrysochromulina* (**Table 1**). At low irradiances, feeding can enhance growth in some *Chrysochromulina* species (Hansen and Hjorth, 2002).

Chlorophyta

A well-documented case of mixotrophy among Arctic chlorophyte flagellates is bacterivory by *Micromonas* sp. This picoplankton-sized member of the Prasinophyceae is widely distributed and abundant in the Arctic (Not et al., 2005). During autumn, when the Beaufort Sea and Canada Basin were highly oligotrophic, photosynthetic picoflagellates numerically dominated the phytoplankton and accounted for as much or sometimes more bacterivory than heterotrophic flagellates (Sanders and Gast, 2012). Genetic analysis indicated that *Micromonas* was a common and probably abundant component of the picoflagellate assemblage (Sanders and Gast, 2012). In laboratory experiments with a culture of Arctic *Micromonas*, McKie-Krisberg and Sanders (2014) observed the greatest bacterivory under conditions of high light and inorganic nutrient limitation, conditions similar to the oligotrophic polar seas in summer.

Dinophyta

Dinoflagellates possess feeding structures that allow them to consume prey of equal to or greater than their own cell size. Most plastidic dinoflagellates are probably mixotrophic (reviewed in Jeong et al., 2010; Hansen, 2011). Mixotrophic as well as heterotrophic dinoflagellates are common in the Arctic (**Table 1**). Nanoplanktonic dinoflagellates have often been overlooked, but they appear to be important components of the polar plankton. For example, plastidic nano-sized gymnodiniids formed 55–85% of total dinoflagellate abundance in the Barents Sea (Franzè and Lavrentyev, 2017). Among the small size mixotrophic dinoflagellates are *Karlodinium* and small *Gymnodinium*-like

spp. Some taxa, like *Karlodinium*, can ingest prey most of the time although inorganic nutrient limitation often stimulates feeding (Li et al., 1999, 2000; Calbet et al., 2011a). A small photosynthetic dinoflagellate that occurs in the Arctic as well as in temperate low salinity waters is *Heterocapsa rotundata* (**Table 1**). In temperate waters it blooms in winter and is stimulated to feed by light limitation (Millette et al., 2017). *H. rotundata* may be an important mixotrophic alga in low salinity, turbid waters, such as the coastal Beaufort Sea and Kara Sea. Among the larger thecate photosynthetic dinoflagellates, many species have been observed to capture and digest prey about their own size or larger, including diatoms, other flagellates, and ciliates (reviewed in Hansen, 2011). This group includes *Alexandrium* and *Tripos (formerly Ceratium)* spp. that have been observed in the Arctic (**Table 1**). Mixotrophic *Dinophysis* spp. prey on ciliates and obtain their plastids from ingestion of photosynthetic *Mesodinium* spp. (Park et al., 2006; Hansen, 2011) and are reported in Arctic Seas (**Table 1**).

Ciliophora

Phagotrophic protists that feed on phytoplankton can also be mixotrophic due to acquired phototrophy; among marine ciliates this usually involves sequestration of plastids and sometimes other organelles from their algal prey (reviewed in Stoecker et al., 2009). In field studies, presence of plastids in ciliates is easier to recognize than phagotrophy in phytoplankton. Epifluorescence microscopy is used to detect the chlorophyll (plastids) in fresh or aldehyde fixed samples that have been stored under conditions (refrigeration and darkness) that minimize chlorophyll degradation. However, many field studies of microzooplankton rely solely on acid Lugol's fixed samples. Thus, mixotrophy among the ciliates often is overlooked.

Among the oligotrich ciliates, plastid-retention is a species-specific attribute. In investigations that lack data from epifluorescence microscopy, the presence of certain species is a good indicator of mixotrophy among the oligotrichs. *Laboea strobila*, a very distinctive plastid-retaining species, several plastidic *Strombidium* spp. and *Tontonia* spp. which always seem to be plastidic, are reported from many Arctic Seas (**Table 2**). In addition, several plastidic prostomatid and haptorid ciliates such as *Askenasia*, *Cyclotrichium*, *Didinium*, *Prorodon,* and *Urotricha* occur in ice-covered waters and open waters of the Barents Sea and Kara Sea (Lavrentyev, 2012; Franzè and Lavrentyev, 2014, 2017). In field studies in which epifluorescence microscopy is utilized, plastid-retaining oligotrichs usually comprise 30–40% of the oligotrich assemblage in the euphotic zone (Stoecker et al., 2017), but in the Arctic they often dominate the ciliate assemblage (**Table 3**).

Contributions of mixotrophic ciliates to chlorophyll are highly variable even in ecosystems in which they are abundant (**Table 3**), partially because of the large variations in total chlorophyll *a*. Putt (1990) estimated that mixotrophic ciliates contributed ~15% of the total chlorophyll *a* at 2 m in the Barents Sea. In the deep chlorophyll maximum (DCM) of the Barents Sea, Franzè and Lavrentyev (2017) estimated that mixotrophic ciliates (predominantly plastidic oligotrichs) contributed between 0.5 and 46% of the chlorophyll *a*. The contribution of mixotrophs to ciliate abundance and

TABLE 1 | Common mixotrophic flagellates in the Arctic.

Taxa	Arctic regions	Evidence for mixotrophy
CHRYSOPHYTA		
Ochromonas crenata, Ochromonas marina, Ochromonas sp.	Barents Sea (Olli et al., 2002; Franzè and Lavrentyev, 2017); Kongsfjorden, Svalbard (Iversen and Seuthe, 2011)	Ingestion of prey (Estep et al., 1986; Andersson et al., 1989); Ingestion of fluorescently labeled bacteria (Keller et al., 1994)
Dinobryon balticum	Barents Sea (Olli et al., 2002; Rat'kova and Wassmann, 2002); Kongsfjorden, Svalvard (Keck et al., 1999; Iversen and Seuthe, 2011); Beaufort Sea (Ardyna et al., 2017); Arctic Ocean NW of Svalbard (Johnsen et al., 2018)	Ingestion of beads (McKenzie et al., 1995)
CRYPTOPHYTA		
	Kongsfjorden, Svalvard (Iversen and Seuthe, 2011); SE Bering Sea (Olson and Strom, 2002); Beaufort Sea (Ardyna et al., 2017); Barents Sea (Rat'kova and Wassmann, 2002; Franzè and Lavrentyev, 2017); Arctic Ocean NW of Svalbard (Johnsen et al., 2018)	Ingestion of beads by *Geminigera cryophilia* (McKie-Krisberg et al., 2015); Ingestion of prey by *Teleaulax amphioxeia* (Yoo et al., 2017); Ingestion of bacteria (Unrein et al., 2007, 2014)
HAPTOPHYTA		
Chrysochromulina spp.	Beaufort Sea (Ardyna et al., 2017)	Ingestion of prey (Jones et al., 1993)
CHLOROPHYTA		
Pyramimonas spp.	Beaufort Sea (Estrada et al., 2009; Ardyna et al., 2017); Arctic Ocean NW of Svalbard (Johnsen et al., 2018)	Ingestion of beads by *P. tychotreta* (McKie-Krisberg et al., 2015)
Micromonas spp.	Barents Sea (Not et al., 2005; Franzè and Lavrentyev, 2017); Beaufort Sea (Estrada et al., 2009); Beaufort Sea & Canada Basin (Sanders and Gast, 2012); Central Arctic Ocean, Fram Strait (Metfies et al., 2016)	Ingestion of fluorescently labeled bacteria and beads (Sanders and Gast, 2012); Ingestion of beads (McKie-Krisberg and Sanders, 2014)
DINOPHYTA		
Alexandrium tamarense	Chukchi Sea (Yokoi et al., 2016)	Ingestion of small phytoplankton (Jeong et al., 2005); Ingestion of *Skeletonema costatum* (Yoo et al., 2009)
Dinophysis acuminata, D. norvegica	Kongsfjorden, Svalbard (Seuthe et al., 2011a); Barents Sea (Franzè and Lavrentyev, 2014, 2017)	Photosynthetic *Dinophysis* spp. obtain plastids and other organelles from ciliate prey (reviewed in Hansen, 2011; Stoecker et al., 2017)
Heterocapsa triquetra, H. rotundata	Beaufort Sea (Ardyna et al., 2017)	*H. triquetra*, ingestion of bacteria (Legrand et al., 1998); *H. triquetra* & *H. rotundata* ingestion of prey (Jeong et al., 2005); *H. rotundata* ingestion of beads & bacteria (Millette et al., 2017)
Karlodinium veneficum (syn. Karlodinium micrum, Gyrodinium galatheanum)	Kongfjorden, Svalbard (Seuthe et al., 2011a)	Ingestion of cryptophytes (Li et al., 1999, 2000; Calbet et al., 2011a)
Prorocentrum minimum	Chukchi Sea (Yokoi et al., 2016)	Ingestion of cryptophytes (Johnson, 2015)
Tripos arcticus (syn. *Ceratium arcticum, C. longipes*), *Tripos fusus* (syn. *C. fusus*), *Tripos macroceros* (syn. *C. macroceros*)	Kongsfjorden, svalbard (Seuthe et al., 2011a); Barents Sea (Franzè and Lavrentyev, 2014, 2017); Kara Sea (Lavrentyev, 2012)	*T. arcticus,* observation of food vacuoles with ingested prey (Jacobson and Anderson, 1996)

total chlorophyll *a* peaked at the Polar Front primarily due to populations of the large mixotrophic oligotrichs *L. strobila, Strombidium conicum*, and *S. wulffi* (**Figure 2**). In the productive eastern Bering Sea during summer, mixotrophic ciliates abundance (also predominantly plastid oligotrichs) and their estimated contribution to total chlorophyll *a* was also very variable. The contribution of mixotrophs to ciliate abundance was relatively low at stations near the shelf edge and in upwelling around the Pribilof Islands. However, mixotrophic ciliate abundance was greatest and estimated contribution of ciliates to total chlorophyll was often 50% or more in highly stratified waters in the middle of the northern shelf (Stoecker et al., 2014). Similarly, in the shallow waters of the Kara Sea, mixotrophic ciliates were responsible for up to 46% of total chlorophyll *a* (Lavrentyev, 2012). In the western Fram Strait, mixotrophic oligotrichs formed a spring bloom in the mixed layer

within the Atlantic Drift ($>200\,\mu g\,C\,L^{-1}$, Lavrentyev and Franzè, 2017); this is the highest ciliate biomass recorded so far in the Arctic.

The above estimates of mixotrophic contributions are conservative. Mixotrophic chlorophyll *a* content was calculated based on ciliate volume (Montagnes et al., 1994), assuming that the volume to chlorophyll *a* relationship is similar to that in autotrophic plankton (Dolan and Perez, 2000). The chlorophyll *a* cellular quota calculated based on these assumptions for *S. conicum* (30,000 μm^3, 55 pg chlorophyll cell^{-1}) was similar to that measured directly in the Barents Sea (48 pg chlorophyll *a* cell^{-1}, Putt, 1990). However, oligotrich chlorophyll *a* content can be much higher (Stoecker et al., 1988; McManus et al., 2012). Laboratory and field studies have demonstrated that plastidic ciliates graze on pico- and nano-phytoplankton, can have about the same biovolume specific chlorophyll *a* content

TABLE 2 | Common mixotrophic ciliates in the Arctic.

Ciliophora	Arctic regions	Evidence for mixotrophy
Laboea strobila	Iceland/Greenland Seas & N. Svalbard/Barents Sea (Putt, 1990); Greenland Sea (Möller et al., 2006); W. Arctic Ocean (Lovejoy et al., 2002, 2007; Sherr et al., 2009); East Siberian Sea & Chukchi Sea (Jiang et al., 2015); Disko Bay, Greenland (Levinsen et al., 2000a); Eastern Bering Sea (Olson and Strom, 2002; Strom and Fredrickson, 2008; Stoecker et al., 2014); Barents Sea (Rat'kova and Wassmann, 2002; Franzè and Lavrentyev, 2014, 2017); Kara Sea (Lavrentyev, 2012)	Detection of plastids with epifluorescence microscopy, measurement of chlorophyll *a* /ciliate (Putt, 1990); Measurement of chlorophyll *a*/ciliate and photosynthesis in cultures (Stoecker et al., 1988); Detection of plastids with epifluorescence microscopy (Franzè and Lavrentyev, 2014)
Mesodinium rubrum/M. major (syn. *Myrionecta rubra*)	Iceland/Greenland Seas & N Svalbard/Barents Sea (Putt, 1990); Barents Sea (Hansen et al., 1996; Rat'kova and Wassmann, 2002; Franzè and Lavrentyev, 2014, 2017); East Siberian Sea & Chukchi Sea (Jiang et al., 2015); Disko Bay, Greenland (Levinsen et al., 2000a); NW Fram Strait (Seuthe et al., 2011b); Barents Sea & Bering Sea (Johnson et al., 2016), Kongsfjorden, Svalbard (Seuthe et al., 2011a), Kara Sea (Lavrentyev, 2012)	Growth, photosynthesis and feeding experiments with cultures (Gustafson et al., 2000; Park et al., 2007; Smith and Hansen, 2007).
Strombidium acutum	East Siberian Sea & Chukchi Sea (Jiang et al., 2015)	Measurement of chlorophyll *a*/ciliate and photosynthesis in cultures (Stoecker et al., 1988/1989)
Strombidium capitatum	East Siberian Sea & Chukchi Sea (Jiang et al., 2015)	Measurement of chlorophyll *a*/ciliate and photosynthesis in cultures (Stoecker et al., 1988/1989)
Strombidium conicum	NW Fram Strait (Seuthe et al., 2011b); Barents Sea (Franzè and Lavrentyev, 2014, 2017); Kongsfjorden, Svalbard (Seuthe et al., 2011a); Kara Sea (Lavrentyev, 2012)	Measurement of chlorophyll *a*/ciliate and photosynthesis in cultures (Stoecker et al., 1988/1989); Detection of plastids with epifluorescence microscopy (Franzè and Lavrentyev, 2017)
Strombidium wulffi	Kongsfjorden, Svalbard (Seuthe et al., 2011a); Barents Sea (Franzè and Lavrentyev, 2017)	Detection of plastids with epifluorescence microscopy (Franzè and Lavrentyev, 2017)
Strombidium spp. *A and B*	Iceland/Greenland Seas & N Svalbard/Barents Sea (Putt, 1990)	Detection of plastids with epifluorescence microscopy, measurement of chlorophyll *a*/ciliate and photosynthesis (Putt, 1990)
Tontonia spp.	East Siberian Sea & Chukchi Sea (Jiang et al., 2015); Iceland/Greenland Seas & N Svalbard/Barents Sea (Putt, 1990); Chukchi Sea (Yokoi et al., 2016); Kongsfjorden, Svalbard (Seuthe et al., 2011a); Barents Sea (Franzè and Lavrentyev, 2014)	Detection of plastids with epifluorescence microscopy, measurement of chlorophyll *a* /ciliate (Putt, 1990). Many (all?) *Tontonia* spp. have plastids (reviewed in Stoecker et al., 2009).

as their phytoplankton prey and are photosynthetic (reviewed in Stoecker et al., 2009, 2017). One of the few field studies in which chlorophyll *a* content and photosynthesis were measured in oligotrichs from natural assemblages was conducted by Putt (1990) in Arctic seas. In *Strombidium* sp. "A," carbon: chlorophyll ratios varied from 87 to 103 and in *L. strobila* from 200 to 232. In *Strombidium* sp. "A," light saturated photosynthetic rates (P_{max}) averaged 2.1 pg C (pg chlorophyll a)$^{-1}$h^{-1}, which was equivalent ~2.8% of body carbon h^{-1} (Putt, 1990; **Table 3**).

The "red" ciliates *Mesodinium rubrum* and *M. major* are important mixotrophic ciliates in coastal and upwelling waters globally (Johnson et al., 2016). In Arctic waters they are a common component of the microplankton (**Table 2**). *M. major* was described as a separate species from *M. rubrum* relatively recently (Garcia-Cuetos et al., 2012) so in **Table 2** we refer to them together. In some cases, red *Mesodinium* are responsible for dense blooms in the Arctic (Johnson et al., 2016). In contrast with the plastid retaining oligotrichs, that can retain plastids from several algal taxa (reviewed in Stoecker et al., 2009; McManus et al., 2012), the red *Mesodinium* spp. are specialized and primarily retain plastids, nuclei and other cell components from phycoerythrin-containing cryptophytes in the *Teleaulax*

and *Plagioselmis* species complex (Johnson et al., 2016). The metabolism of *M. rubrum/M. major* is primarily photosynthetic, although polar strains are capable of survival in the dark for long periods (Johnson and Stoecker, 2005). *M. rubrum* is often considered to be more a component of the phytoplankton than the microzooplanktkon because of their high chlorophyll content, high rates of photosynthesis and ability to form blooms (reviewed in Crawford, 1989). In the Arctic, as elsewhere, red *Mesodinium* spp. are routinely a significant component of the protist plankton in meso- and eutrophic waters, particularly under low light conditions which also favor their cryptophyte prey. Blooms are usually associated with fronts or upwelling events and can be "hotspots" of primary and secondary production which influence biogeochemical cycling (Herfort et al., 2012).

Factors Influencing Mixotrophy in the Arctic

Although there have been fewer studies of mixotrophy in the Arctic than in temperate seas, the environmental conditions in the Arctic should often favor mixotrophs over strict heterotrophs or autotrophs. Mixotrophy is advantageous in environments in which resource availability is highly variable and/or does

TABLE 3 | Relative contributions of mixotrophic ciliates to ciliate abundance, biomass, and total chlorophyll a (chl a) in the Arctic during summer.

Location	% Ciliate Abundance	% Ciliate Biomass	% Total chlorophyll a	References
Iceland/Greenland Seas	Meso-Avg. 6% PO-Avg. 52%	Avg. 63% of aloricate ciliates	Estimated 4%	Putt, 1990
Barents Sea/N. Svarbard	Meso-Avg. 25% PO-Avg. 40%	Avg. 59% of aloricate ciliates	Estimated 15%	Putt, 1990
Disko Bay, Greenland	Range 45–85% of oligotrich ciliates	ND	ND	Levinsen et al., 2000a
Barents Sea	Range 22–73% of total ciliates	Avg. 54% (Range 12–93%) of total ciliates	Estimated range, DCM (0.5–46%)	Franzè and Lavrentyev, 2017
Pechora (SE Barents) & Kara Seas	Avg. 48% (Range 30–60%) of total ciliates	Avg. 69% (Range 47–91%) of total ciliates	Estimated 22% (Range 7–46%) mixed layer	Lavrentyev, 2012
Eastern Fram Strait and AO Eurasian Basin slope north of Svalbard	Avg. 25% (Range 12–49%) of total ciliates	Avg. 71% (Range 40–99%) of total ciliates	ND	Lavrentyev and Franzè, 2017
Eastern Bering Sea	Range 68–75% on shelf	~65%	Variable; Estimated >50% at some stations on middle shelf	Stoecker et al., 2014

Meso, Mesodinium rubrum/major; PO, plastidic oligotrich ciliates; ND, no data; AO, the Arctic Ocean; DCM, deep chlorophyll maximum; MIZ, marginal ice zone; Avg., Average.
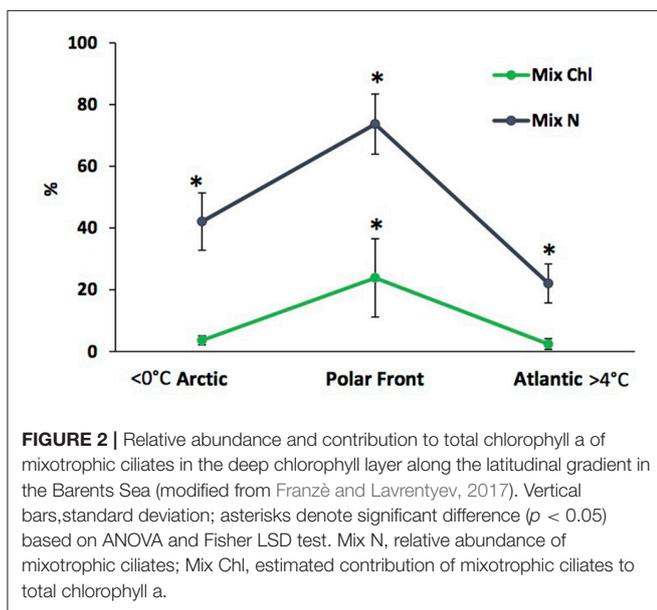

FIGURE 2 | Relative abundance and contribution to total chlorophyll a of mixotrophic ciliates in the deep chlorophyll layer along the latitudinal gradient in the Barents Sea (modified from Franzè and Lavrentyev, 2017). Vertical bars, standard deviation; asterisks denote significant difference ($p < 0.05$) based on ANOVA and Fisher LSD test. Mix N, relative abundance of mixotrophic ciliates; Mix Chl, estimated contribution of mixotrophic ciliates to total chlorophyll a.

low (Terrado et al., 2017). The same strategy may occur in some marine *Ochromonas* spp. However, at least one marine *Ochromonas* sp. is primarily photosynthetic and is stimulated to feed by low light and low nutrients (Keller et al., 1994). In the marine dinoflagellate *H. rotundata*, light limitation stimulates ingestion of bacteria (Millette et al., 2017) but it is unclear how common this response is in photosynthetic dinoflagellates. Interaction of light and inorganic nutrient availability is important in regulating the relative contributions of phototrophy and phagotrophy to survival and growth in most mixotrophic flagellates. For example, species-specific responses of both photosynthesis and feeding to light and nutrients were observed in cultured Antarctic mixotrophic flagellates (McKie-Krisberg et al., 2015).

Among the microzooplankton with acquired phototrophy (which in the Arctic plankton, is primarily mixotrophic ciliates), most use photosynthesis as a carbon and energy supplement (reviewed in Stoecker et al., 2009). Except in the case of *M. rubrum*, which has nitrate reductase, most plastidic ciliates obtain most of their nitrogen from food. In the plastidic oligotrichs, photosynthate is used primarily to cover respiratory demands for carbon and thus can increase survival times during starvation and, particularly when prey are limiting, increase gross growth efficiency and growth rate (McManus et al., 2012; reviewed in Stoecker et al., 2017).

Environmental parameters, including temperature, inorganic nutrient availability, and light availability are all expected to influence mixotrophy among both "phytoplankton" and "microzooplankton" mixotrophs in Arctic Seas.

Temperature

Sub-zero sea temperatures typical for the Arctic Ocean may be conducive to mixotrophy, particularly among microzooplankton such as ciliates, because photosynthetic plankton are thought to be less constrained by low temperatures than their heterotrophic consumers (Rose and Caron, 2007). The latitudinal trends in

not support balanced growth (reviewed in Mitra et al., 2016; Stoecker et al., 2017). Mixotrophic strategies vary among planktonic protists (Mitra et al., 2016). For example, many small phytoflagellates and photosynthetic dinoflagellates can grow as strict autotrophs, using light and dissolved inorganic nutrients for growth, but nitrogen (N), phosphorus (P), and iron limitation or skewed N:P ratios induce or increase phagotrophy (Maranger et al., 1998; Li et al., 2000; Smalley et al., 2003). Less well-known are marine phytoflagellates and photosynthetic dinoflagellates that are stimulated to feed by light or carbon limitation. A freshwater mixotrophic *Ochromonas* sp. (chrysophyte) primarily obtains carbon and nitrogen from ingestion of bacteria and only assimilates inorganic nutrients to appreciable degree when bacterial abundances are very

mixotrophic ciliate growth rates in the Barents Sea seem to support this idea (Franzè and Lavrentyev, 2014). However, mixotrophic ciliates also peaked at relatively warm summer temperatures in the Kara (Lavrentyev, 2012) and Bering Seas (Stoecker et al., 2014). In the Fram Strait the highest concentration of ciliates in the Arctic was found in the Atlantic drift warm core (Lavrentyev and Franzè, 2017).

Little information is available on latitudinal or temperature gradients in mixotrophy among phytoflagellates. Laboratory experiments with a freshwater mixotrophic flagellate suggest that some mixotrophs become more heterotrophic with increases in temperature (Wilken et al., 2013). However, it is not clear that this is a general response among mixotrophic flagellates.

Oligotrophy

Oligotrophic conditions favor bacterivorous pico- and nanoplankton in tropical and temperate seas (Zubkov and Tarran, 2008; Hartmann et al., 2012; Mitra et al., 2016). In temperate seas, mixotrophic flagellates are often most abundant during summer stratification which can result in inorganic nutrient limitation of phytoplankton growth in the surface mixed layer (Mitra et al., 2014). Oligotrophic conditions are common during the ice-free season in some parts of the Arctic including the central Arctic Ocean, Beaufort Sea and parts of the Amundsen Sea.

Seasonally low phytoplankton biomass and small phytoplankton cell size can, in turn, select for mixotrophic oligotrich ciliates over strictly heterotrophic microzooplankton (Mitra et al., 2016). In large ciliates, photosynthetic carbon could cover a significant fraction of their metabolism (reviewed in Stoecker et al., 2009, 2017) due to relatively low volume-specific respiration rates (Dolan and Perez, 2000). The Barents Sea Polar Front, where the relative abundance of mixotrophic ciliates peaked, has relatively low phytoplankton biomass in summer compared to receding ice edges and does not stimulate phytoplankton productivity in summer (Reigstad et al., 2011; Erga et al., 2014). However, large mixotrophic oligotrichs are not restricted to oligotrophic conditions in the Arctic. *Laboea strobila* was abundant under phytoplankton bloom conditions in the Bering Sea (Olson and Strom, 2002), Kara Sea (Lavrentyev, 2012), and the Fram Straight (Lavrentyev and Franzè, 2017). In the Gulf of Ob, *M. rubrum* reached its maximum of 75 μg C L^{-1} at total chlorophyll *a* >17 μg L during a cyanobacterial bloom (Lavrentyev, 2012). Mixotrophs contributed up to 46% of total chlorophyll *a* in the deep chlorophyll maximum (DCM) at the pycnocline in the Barents Sea, where phytoplankton accumulate in summer (Franzè and Lavrentyev, 2017).

Light

In contrast to temperate and especially low latitudes, the Arctic is characterized by extremes in solar irradiance. During the polar day, 24-h insolation may favor mixotrophic metabolism over strictly heterotrophic metabolism in planktonic protists. For example, given the same prey concentration, a mixotrophic oligotrich grew faster under luxury light (McManus et al., 2012). The combination of high irradiance and low inorganic nutrients stimulates phagotrophy in many mixotrophic flagellates
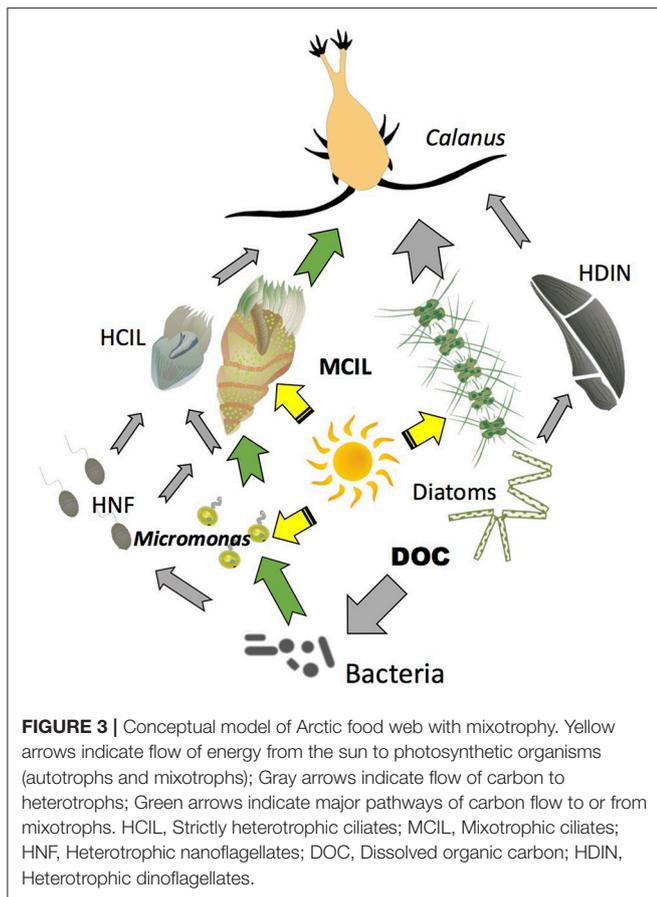
and dinoflagellates (reviewed in Stoecker et al., 2017). The proportion of phagotrophic and autotrophic-derived carbon in a mixotrophic dinoflagellate diet changed dynamically in response to light conditions and food availability (Riisgaard and Hansen, 2009). Mixotrophic ciliate abundance often peaks in the upper part of the mixed layer (Putt, 1990; Rat'kova and Wassmann, 2002; Lavrentyev, 2012; Franzè and Lavrentyev, 2014; Jiang et al., 2015). Some mixotrophic ciliates and dinoflagellates can migrate between prey or nutrient rich deep chlorophyll maximum layers and well-lit surface waters (Crawford and Lindholm, 1997; Ji and Franks, 2007).

During winter and in/under sea-ice, prolonged dark or low irradiance may also favor mixotrophic phytoplankton over strict autotrophs. Many mixotrophic phytoflagellates and some dinoflagellates use phagotrophy to supplement carbon budgets when light limited (Czypionka et al., 2011; McKie-Krisberg et al., 2015; Millette et al., 2017). Phagotrophy has been hypothesized to be an important mechanism supporting survival and limited growth of phytoflagellates during the polar winter (Zhang et al., 2003).

Although mixotrophy would not appear to be an advantage in ciliates during the dark polar winter, the plastidic ciliates *L. strobila* and *M. rubrum* persist under the ice in West Greenland (Levinsen et al., 2000a). The advantages of mixotrophy during the summer may outweigh the disadvantages of obtaining and maintaining chloroplasts during the winter. Levinsen et al. (2000a) suggested that mixotrophic ciliates survive long periods of darkness due to reduced metabolic demands at low winter temperatures. During the polar winter, photo-degradation is non-existent or minimal, which may contribute to long survival times of plastids in the ciliates. Although mixotrophic oligotrichs have been thought to require both algal prey and light (reviewed in Stoecker et al., 2017), under winter conditions some species may be able to survive and grow as heterotrophs. McManus et al. (2012) observed that a temperate mixotrophic ciliate could grow for several weeks in the dark when supplied with a small dinoflagellate as food, although the dinoflagellate did not support good growth of the ciliate in the light.

Role of Mixotrophy in the Pelagic Food Webs

Mixotrophy has important consequences for primary and secondary production and transfer of carbon to upper levels in Arctic planktonic food webs. Major differences between an Arctic food web with mixotrophy and the microbial loop sensu Azam et al. (1983) are conceptualized in **Figure 3**. In the traditional microbial loop, bacteria are consumed by heterotrophic nanoflagllates, which are then consumed by larger grazers such as ciliates. Most carbon collected by bacteria is respired in the subsequent trophic steps. In the mixotrophic microbial loop bacteria are consumed by both photosynthetic (exemplified by mixotrophic *Micromonas*) and heterotrophic nanoflagellates. The flagellates then become food for ciliates, which in addition to phagotrophy also use functional chloroplasts acquired from their photosynthetic prey. Thus, at each trophic step, energy dissipated through respiration is partially or

FIGURE 3 | Conceptual model of Arctic food web with mixotrophy. Yellow arrows indicate flow of energy from the sun to photosynthetic organisms (autotrophs and mixotrophs); Gray arrows indicate flow of carbon to heterotrophs; Green arrows indicate major pathways of carbon flow to or from mixotrophs. HCIL, Strictly heterotrophic ciliates; MCIL, Mixotrophic ciliates; HNF, Heterotrophic nanoflagellates; DOC, Dissolved organic carbon; HDIN, Heterotrophic dinoflagellates.

completely replaced by solar energy. This is particularly important under oligotrophic conditions, when inorganic nutrient supply limits primary production. With mixotrophy among the photosynthetic plankton, primary production at the base of the food web can be enhanced (Zubkov and Tarran, 2008; Mitra et al., 2014). Studies in freshwater ecosystems indicate that mixotrophy can stabilize the stoichiometry (C:N:P) of the primary producers, which may in turn stabilize the efficiency of trophic transfer to secondary producers under varying nutrient regimes (Moorthi et al., 2017). Another benefit may be enhanced survival of plastidic ciliates and flagellates in a physiologically active state during the polar winter (Levinsen et al., 2000a; Zhang et al., 2003). When light becomes available, mixotrophic plankton can rapidly respond with high growth rates despite low sea temperatures (Franzè and Lavrentyev, 2014).

Laboratory studies indicate that plastidic oligotrichs ingest and digest phytoplankton and, at least in temperate waters under moderate light intensities, derive much of their carbon, and probably almost all of their nitrogen and phosphorus from phagotrophy (Stoecker et al., 1988; McManus et al., 2012; Schoener and McManus, 2012). Particularly under prey limitation, photosynthesis can increase their gross growth efficiency (McManus et al., 2012) probably because photosynthesis can cover all or part of their respiratory demand for carbon in the light (Stoecker and Michaels, 1991). In the food

web with mixotrophy, the sun's energy is directly transferred to relatively large size microzooplankton (the mixotrophic ciliates) as well as to traditional phytoplankton (such as diatoms and phytoflagellates). This augments microzooplankton production, which is important because microzooplankton are a large component of the diet of large size Arctic copepods, such as *Calanus* spp. (Campbell et al., 2009; Saiz et al., 2013). Mixotrophic ciliates in particular are a preferred prey of copepods (Levinsen et al., 2000b; Dutz and Peters, 2008). Such mixotrophic interactions have the potential to temporarily sustain mesozooplankton under low phytoplankton biomass conditions such as occur pre- and post-bloom in many polar seas. Modeling indicates that mixotrophy has the potential to increase food web transfer efficiencies, help retain inorganic nutrients (nitrogen and phosphorous) in the upper water column, and enhance transfer of carbon to larger size organisms (Mitra et al., 2014; Ward and Follows, 2016).

Potential Significance of Mixotrophy in the Changing Arctic

Below we outline three specific examples in which mixotrophs may be affected by changing climate and or how this could affect Arctic ecosystems now and in the future:

1. McMinn and Martin (2013) have suggested that phytoplankton will need to survive the same period of seasonal darkness, but at higher temperatures in the future, thus exhausting stored metabolic resources more quickly. In dark survival, phagotrophic phytoflagellates can have an advantage over diatoms (Zhang et al., 2003; Millette et al., 2017). This could result in changes in the composition of spring blooms, with an increase in phytoflagellates over diatoms.
2. Some areas of the Arctic are becoming more oligotrophic due to increased stratification. For example, offshore areas in the Western Arctic Ocean are becoming more oligotrophic. These changes have already resulted in the phytoplankton composition shift toward small sized-taxa in the Canada Basin (Li et al., 2009). Under such conditions, the presence of mixotrophy among photosynthetic flagellates and ciliates may moderate the negative climate change impacts on energy transfer to higher trophic levels and on particle flux out of surface waters (**Figure 3**).
3. Mixotrophy can facilitate blooms of unpalatable or harmful algae (Burkholder et al., 2008). Incursions of warmer waters, containing potentially bloom-forming, harmful species, already occur in the Arctic. Toxic *Alexandrium, Dinophysis, Karlodinium,* and *Chrysochromulina* spp. are all mixotrophic taxa that often proliferate in highly stratified or freshened waters and have been reported from the Arctic (**Table 1**).

To understand plankton dynamics in a changing Arctic environment, we obviously need information on the magnitude and spatial distribution of the physical and chemical changes. To understand and predict how these changes will alter the structure and function of Arctic planktonic food webs, we need information about alterations near the base of

the food web, among the microbial plankton (bacteria and protists) because these changes will affect higher trophic levels through prey availability, palatability and size and alterations to biogeochemical cycles. In the Arctic, as elsewhere in aquatic food webs, many planktonic protists are not strict autotrophs or heterotrophs and this can have profound effects primary production and secondary production. We need to incorporate mixotrophy into our thinking, into our work on cruises and laboratory studies of Arctic "phytoplankton" and "microzooplankton," and into models of Arctic marine ecosystems.

CONCLUSIONS AND QUESTIONS FOR FUTURE RESEARCH

In summary, many mixotrophic flagellates are found in Arctic waters, but there is only one reported field investigation (Sanders and Gast, 2012) of mixotrophy from Arctic Seas. Most of the data on Arctic phytoplankton relate to bloom-forming diatom species and *Phaeocystis pouchetti* but little data exist on the distribution and abundance of potentially mixotrophic phytoflagellate taxa. Mixotrophy by taxa that are traditionally categorized as "phytoplankton" has been overlooked in most Arctic seas where it may be particularly important in oligotrophic waters during summer and in light limiting conditions for phytoplankton growth year round. Under-ice phytoplankton blooms appear to be increasing in the Arctic (Arrigo et al., 2014); mixotrophs as well as diatoms may be a component of some of these blooms. Field investigations in the Antarctic have shown that mixotrophic flagellates are an important component of sea-ice algal assemblages (Moorthi et al., 2009) but the role of mixotrophs in this habitat in the Arctic appears to be unexplored.

An important task for future research is to determine if mixotrophy among flagellates is widespread in the Arctic and its role in planktonic food webs. For example, in the study by Sanders and Gast (2012), *Micromonas* and other mixotrophic flagellates preferred inert beads over the commonly used fluorescently labeled bacteria. In real life, they may consume a variety of prokaryotic and eukaryotic microorganisms. Genomic techniques for identification and quantification of populations will need to be combined with innovative measurements of both feeding and photosynthesis to accomplish this task (Anderson et al., 2017; Terrado et al., 2017). The degree of mixotrophy in protists (i.e., phagotrophy vs. photosynthesis) can be difficult to establish and its investigation requires novel approaches, involving both field and laboratory experiments. One important question is the effect of warming water temperatures and stratification on the balance between heterotrophy and autotrophy both within species and within assemblages of phytoplankton. Will mixotrophic flagellates increase in dominance because they can survive winter darkness better than strictly autotrophic phytoplankton at higher temperatures? Will stronger stratification and oligotrophy in summer in some regions increasingly favor mixotrophs over strictly autotrophic phytoplankton? How will this influence zooplankton populations and higher trophic levels?

Mixotrophic ciliates are undoubtedly a major component of pelagic food webs across the Arctic and surprisingly, also a major component of photosynthetic biomass. The routine methods of chlorophyll *a* collection need to be revised in the light of recent data showing the importance of green ciliates in total photosynthetic biomass. Specifically, vacuum filtration through membrane filters may result in significant losses of mixotrophic chlorophyll as fragile plankton cells are destroyed and release their cellular content to the filtrate. We still know little about the physiological ecology of mixotrophs in polar waters and a number of important questions remain to be answered. Is high mixotrophic ciliate biomass linked to blooms of particular types of phytoplankton as a source of nutrients and plastids? Are *Micromonas* sp. and other mixotrophic flagellates such as cryptophytes the primary prey and source of plastids for ciliates? This appears to be true for *Mesodinium* spp. which consume certain cryptophytes (Johnson et al., 2016), but is it true for plastid-retaining oligotrichs as well? *Micromonas* is a good source of plastids for at least some species of plastid-retaining oligotichs (Stoecker et al., 1988/1989). How does seasonal 24-h light or darkness influence their survival and growth? What effects do mixotrophs have on primary and secondary production in the Arctic? How does mixotrophy among protistan prey influence trophic transfer efficiencies to macrozooplankton and fish? Does a mixotrophic microbial food web, starting with small mixotrophic flagellates that are in turn consumed large mixotrophic ciliates, support zooplankton production during most of the year? To answer these questions will take a variety of approaches: field sampling to quantify populations of mixotrophic and non-mixotrophic planktonic protists, laboratory and field experiments to determine the contributions of phagotrophy and photosynthesis to the metabolism and growth of Arctic mixotrophs, experimental manipulations to determine the effects of temperature, irradiance, and inorganic nutrient concentrations and ratios on the balance of heterotrophy and autotrophy within mixotrophs as well as the contribution of strict heterotrophs, strict autotrophs and mixotrophs to plankton assemblages. Modeling will be necessary to understand the effects of mixotrophy on food webs and biogeochemical cycling in Arctic planktonic ecosystems and to predict what effects climate change might have on mixotrophs and their roles in Arctic Seas.

AUTHOR CONTRIBUTIONS

DS and PL co-wrote the manuscript. DS had primary responsibility for constructing the tables, PL for drafting the figures.

ACKNOWLEDGMENTS

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