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Marine-terminating glaciers sustain high productivity in Greenland fjords

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Abstract

Accelerated mass loss from the Greenland ice sheet leads to glacier retreat and an increasing input of glacial meltwater to the fjords and coastal waters around Greenland. These high latitude ecosystems are highly productive and sustain important fisheries, yet it remains uncertain how they will respond to future changes in the Arctic cryosphere. Here we show that marine-terminating glaciers play a crucial role in sustaining high productivity of the fjord ecosystems. Hydrographic and biogeochemical data from two fjord systems adjacent to the Greenland ice sheet, suggest that marine ecosystem productivity is very differently regulated in fjords influenced by either land-terminating or marine-terminating glaciers. Rising subsurface meltwater plumes originating from marine-terminating glaciers entrain large volumes of ambient deep water to the surface. The resulting upwelling of nutrient-rich deep water sustains a high phytoplankton productivity throughout summer in the fjord with marine-terminating glaciers. In contrast, the fjord with only land-terminating glaciers lack this upwelling mechanism, and is characterized by lower productivity. Data on commercial halibut landings support that coastal regions influenced by large marine-terminating glaciers have substantially higher marine productivity. These results suggest that a switch from marine-terminating to land-terminating glaciers can substantially alter the productivity in the coastal zone around Greenland with potentially large ecological and socio-economic implications.

KEYWORDS
climate change, fjords, glaciers, Greenland ice sheet, oceanography, phytoplankton, primary production

1 | INTRODUCTION

Air temperatures in the Arctic have increased substantially in recent years leading to a reduction in sea ice and the melting of glaciers at unprecedented rates (Bamber, Van Den, Ettema, Lenaerts, & Rignot, 2012; Comiso, Parkinson, Gersten, & Stock, 2008). While the ecological consequences of the decreasing sea ice have received attention (Wassmann & Reigstad, 2011), the impact of increased glacial melting on Arctic marine ecosystems remains largely unstudied. The Greenland ice sheet currently discharges ~1000 Gt year^{-1} of freshwater into the coastal ocean, originating from both meltwater runoff and solid ice discharge (Bamber et al., 2012). The fjords and shelves surrounding Greenland are strongly impacted by this freshwater runoff from Greenland ice sheet, which has doubled over the last two decades. At the same time, some of these coastal ecosystems sustain a high productivity, and the associated fisheries generate a large part of Greenland national income (Berthelsen, 2014; ICES, 2015; Jensen, Pedersen, Burmeister, & Hansen, 1999), thus calling for a better understanding of the links between coastal productivity and glacial melting.

The role of glacial runoff on the productivity of high-latitude coastal ecosystems is currently the subject of debate. It has been proposed that runoff from the Greenland ice sheet could provide a source of organic matter and mineral nutrients, thus positively influencing primary production by providing an additional supply of nitrogen, phosphorus, iron and silica throughout the melt season (Bhatia et al., 2013; Hawkings et al., 2015; Wadham et al., 2016). However, a large proportion of the incoming nutrients are in particulate form (Hawkings et al., 2016), and so their fate and role in productivity of the fjord systems remain uncertain. Moreover, a recent study has questioned the direct fertilization effect, revealing that glacial meltwater is an important source of dissolved silica, though only supplies low amounts of nitrate and dissolved phosphate to the photic zone, which are the limiting nutrients for primary productivity in the fjords (Meire et al., 2016).

The melting of Greenland ice sheet is currently accelerating, and this freshwater input is expected to substantially increase with ongoing climate change (Fettweis et al., 2013). Yet, our understanding of how glaciers and glacial meltwater impact the biogeochemistry and productivity of the coastal region around Greenland is currently limited, which makes it difficult to predict how this region will be affected by future climate change. Here we present data from two different fjord systems adjacent to Greenland ice sheet that are influenced by either land-terminating or marine-terminating glaciers. We find that ecosystem productivity during summer is higher in the fjord with marine-terminating glaciers compared to the fjord which only has land-terminating glaciers. Despite differences in geographical location, sea ice regime in winter and total meltwater input between fjords, our dataset demonstrates that nutrient upwelling caused by rising subsurface meltwater plumes at the marine-terminating glaciers which entrain deep ambient fjord water, is the critical factor explaining the difference in ecosystem productivity between these fjords during summer. With the ongoing melting of the Greenland ice sheet, marine-terminating glaciers are retreating and might eventually transform into land-terminating glaciers. The resulting impact on the productivity of the coastal zone around Greenland could have large socio-economic implications.

2 | MATERIALS AND METHODS

2.1 | Sampling sites

Hydrographic and biogeochemical data were collected in two fjord systems adjacent to the Greenland ice sheet, Godthåbsfjord and Young Sound. Godthåbsfjord is a large sub-Arctic fjord system located on the southwest coast of Greenland with a length of ~190 km and covering an area of 2013 km^2 (Figure 1). The inner-part of the fjord system (generally from station GF13) is covered by sea ice for ~7 months. Three grounded marine-terminating glaciers deliver glacial ice and meltwater to the fjord: Kangiata Nunaata Sermia (KNS), Akullersuup Sermia (AS) and Narsap Sermia (NS). KNS is the largest marine-terminating glacier in Godthåbsfjord and has a grounding depth of ~250 m (Mortensen et al., 2013; Motyka et al., 2017). The grounding line of AS is ~140 m and the depth of the NS is ~160 m (Mortensen, Bendtsen, Lennert, & Rysgaard, 2014; Motyka et al., 2017). Meltwater also drains from three land-terminating glaciers: Qamanaarsuup Sermia (QS), Kangilinnguata Sermia (KS) and Saqqap Sermersua (SS), which drains through Lake Tasersuaq (LT). Recent hydrological simulations for the period 1991–2012 estimate a total annual freshwater input of 20 km^3 year^{-1} and a solid ice discharge of 8 km^3 year^{-1} from KNS to Godthåbsfjord (Motyka et al., 2017; Van As et al., 2014). The Young Sound-Tyrolerfjord is a 90 km long high Arctic fjord system located in northeast Greenland, which covers an area of 390 km^2 (Figure 1). Young Sound is the outer part of the fjord system connected with the Greenland Sea via an entrance sill at 45 m depth with a basin depth of 220 m, while the Tyroler fjord is narrow and deeper with a maximum depth of 360 m. The fjord is covered by sea ice for 8–9 months (Rysgaard & Glud, 2007). In summer, two meltwater rivers (Tyroler and Zackenberg river) are fed by land-terminating glaciers and discharge into Young Sound with an annual discharge of 0.6 to 1.6 km^3 year^{-1} (Rysgaard & Glud, 2007).

2.2 | Sample collection and analysis

Data from Godthåbsfjord was collected during a cruise in August 2013 along a length-transect that covers the entire fjord and the adjacent continental shelf (20 CTD stations of which water samples were collected at 10 stations; Figure 1). The presence of a dense ice mélange in inner Godthåbsfjord made sampling impossible beyond station GF15 towards the KNS terminus, though samples were taken close to the NS terminus (i.e., within ~10 km) (Figure 1). Monthly sampling at station GF10, located in the inner part of the fjord, between January 2013 and December 2013 further complemented the dataset. Samples in Young Sound were collected in August 2011 (30 CTD stations of which water samples were collected at 10 stations) along a length-transect from the inner fjord to the open sea. In both fjord systems, conductivity, temperature and depth profiles were obtained using a CTD (Seabird SBE19plus) equipped with additional sensors for fluorescence (Seapoint chlorophyll fluorometer), turbidity (Seapoint) and Photosynthetic Active Radiation (Biospherical QSP-2350L Scalar sensor). Water samples from discrete depths (1, 5, 10, 20, 30, and 40 m) were collected using 5 L Niskin bottles. To calibrate the fluorescence sensor, water samples (0.5–1 L) were filtered through 25 mm GF/F Whatman filters (nominal pore size 0.7 μm) for chlorophyll *a* analysis. Filters were placed in 10 ml of 96% ethanol for 18 to 24 hour and chlorophyll *a* fluorescence in the filtrate was analyzed using a fluorometer (TD-700, Turner Designs) before and after addition of 200 μl of a 1 M HCl solution. Subsamples (10 ml) for nutrients were filtered through 0.45 μm filters (Q-Max GPF syringe filters) and directly frozen at −20°C until analysis. Nitrate

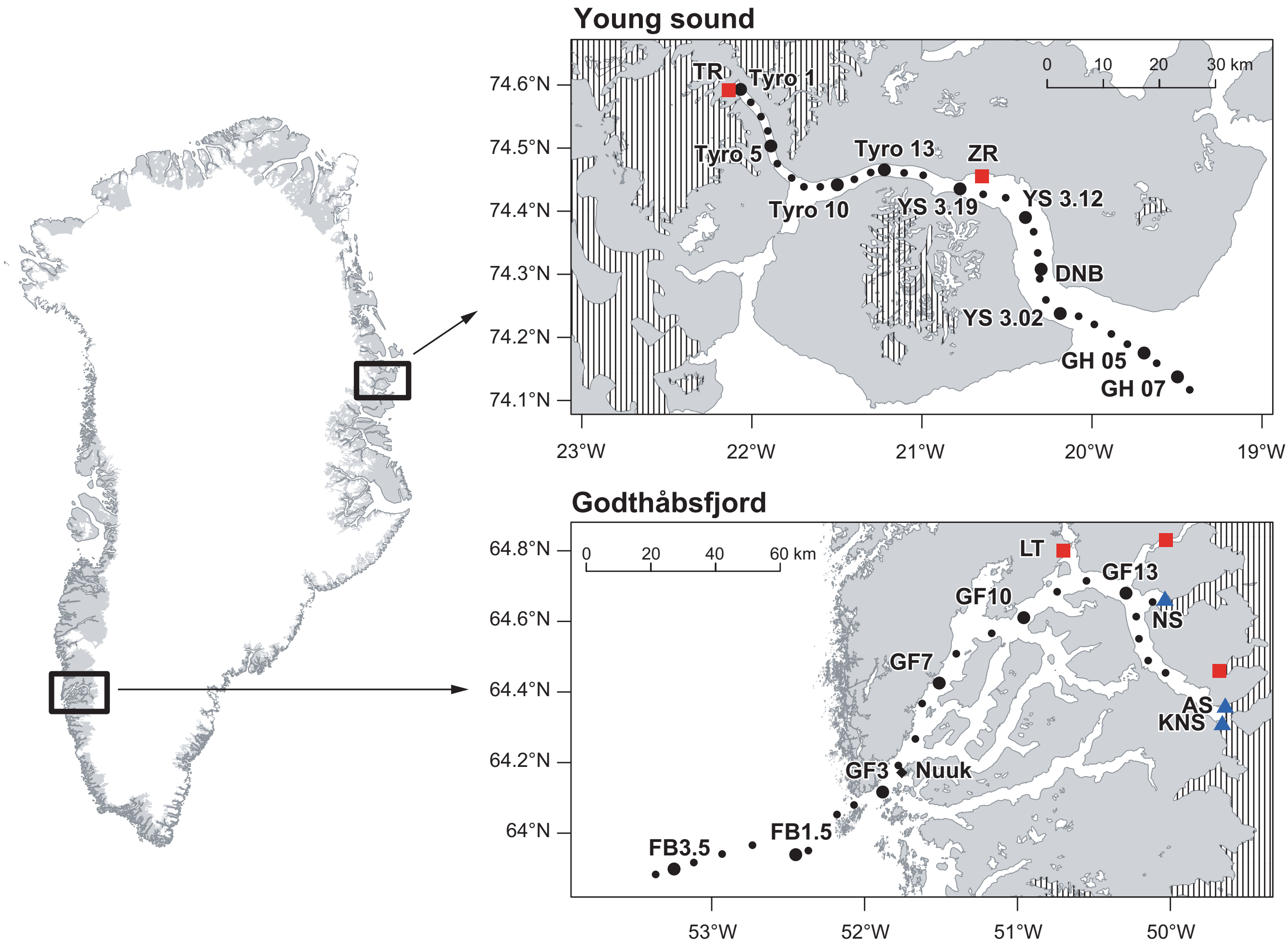

FIGURE 1 Map of Young Sound and Godthåbsfjord indicating the stations (solid dots) along a transect from the Greenland Ice Sheet (shaded area) towards the mouth of fjord region. Marine-terminating glaciers in Godthåbsfjord are indicated by blue triangles (NS, KNS and AS), major meltwater rivers in Godthåbsfjord and Young Sound by red squares (Lake Tasersuaq LT; Zackenberg river ZR; Tyroler river TR)

concentrations were measured using standard colorimetric methods on a Seal QuAAtro autoanalyzer.

Primary production (PP) was measured by ^{14}C incubations using photosynthesis-irradiance (PI) curves and in situ incubations. Euphotic depth was calculated as 1% of surface irradiance. During the transect study in Godthåbsfjord, PI-curves were obtained from samples at 5, 10, 20 and 30 m depth. Furthermore at station GF10, PI-curves were recorded monthly at 5 and 20 m depth to assess the seasonality of productivity. Unfiltered seawater (55 ml) from a given water depth was transferred to incubation bottles, spiked with 175 μL $NaH^{14}CO_3$ (20 μCi mL^{-1}) and incubated for two hours (ICES incubator, Hydro-Bios, Germany). At the monitoring station (GF3) in Godthåbsfjord and the Young Sound transect, samples from 5, 10, 20, 30 and 40 m depth were incubated in situ in glass bottles (two light and one dark bottles at each depth) for *c.* 2 hr around mid-day. Samples were filtered through 25 mm GF/C filters (Whatman), 100 μl of 1 M HCl was added to remove excess $NaH^{14}CO_3$ and the filters were left open for 24 hr in a fume hood. Subsequently, 10 ml of scintillation cocktail (Ultima Gold, Perkin Elmer) was added to the samples before counting them on a scintillation counter (Liquid Scintillation Analyzer, Tri-Carb 2800TR, PerkinElmer). Gross primary production rates were calculated based on measured dissolved inorganic carbon concentrations, after subtracting CO_2 fixation rates obtained from the dark incubations. Primary production rates were calculated from the obtained PI-curves using the light attenuation coefficient from the measured PAR profile. Solar irradiance was obtained from the meteorological survey in Nuuk (Meteorological station 522, Asiaq Greenland Survey). Annual productivity at station GF10 was estimated by calculating daily productivity over the entire year assuming that light extinction and PI-curves remain the same in the two-week period before and after the sampling dates. For the in situ primary production estimates, daily rates were calculated by multiplying the production value from the two hours in situ incubation with the ratio between the incoming PAR during the deployment period (*c.* 2 hr) and the entire day of sampling (24 hr).

The stratification parameter (φ, J m^{-3}) was calculated based on the water density profiles in the upper 60 m and represents the amount of energy required to homogenize the water column through vertical mixing (Simpson, Crisp, & Hearn, 1981).

2.3 | Statistical analysis of the halibut landings

Greenland halibut (*Reinhardtius hippoglossoides*) is a common fish along the west coast of Greenland, and forms a socio-economically important resource, as it sustains one of the largest commercial fisheries in Greenland responsible for 42% of total fishery income (Boje, Neuenfeldt, Sparrevohn, Eigaard, & Behrens, 2014). Commercial halibut landing data were retrieved for 37 fjord systems on the west coast of Greenland based on stock assessments by the Fishery Department at the Greenland Institute of Natural Resources (GINR). This dataset consists of the total annual halibut landings for the years 2012 to 2015, which are specified on a geographical grid for different regions in Greenland (Fig. S4 shows the different grid cells in the Ilulissat fjord). The total halibut landing, H, in a fjord was calculated by summation of the landings in all grid cells belonging to that fjord (for delineation of the fjord systems see Sup. Mat.). The total area, A, of the fjord was calculated by summation of individual grid cell areas, accounting only for the sea surface area (due to tortuous fjord geography, some grid cells consist partly out of water and partly land). The mean area-based halibut landing in a fjord (kg km^{-2} year^{-1}) was finally calculated as H/A, and this statistic was correlated with a set of environmental parameters for each fjord (presence of glacier termini, length of sea ice period, glacial freshwater input and bathymetry; supplementary material). As no in-fjord fishery data were available from East Greenland, the fjord systems on the East coast were not included in the analysis.

The glacial freshwater input to the different fjord systems was obtained from a hydrological water-flow model embedded in the Greenland ice sheet model of Huybrechts et al. (2011). This estimate only includes runoff from the Greenland ice sheet and not from peripheral glaciers. Consequently, our values may underestimate the total meltwater runoff to the fjord systems. The glacial freshwater input originates from both surface runoff and basal ice melt, with a minor contribution from summer rainfall (solid ice discharge is not quantified). Basal melting occurs far inland depending on basal temperature conditions while near the margins surface melt is dominant. Only a part of the surface melt contributes to surface runoff as a fraction refreezes (30% of the surface melt averaged over the entire ice sheet) and is stored in the snowpack (Janssens & Huybrechts, 2000). The hydrological model assumes that all water reaches the bottom of the ice sheet, where it is routed further towards the ice-sheet margin according to the steepest gradient of the hydraulic potential. This allows determining the total basal water flux that exits at any given location along the margin of the Greenland ice sheet. The calculations were made on a 5 km numerical grid using the bedrock topography from Bamber et al. (2013) and a routing algorithm similar to Le Brocq, Payne, Siegert, and Alley (2009). Figure S2 shows an example of the integrated meltwater flux to the Ilulissat fjord. For all selected fjord systems, the hydraulic catchment (i.e., the collection of grid cells that deliver meltwater to a given fjord) was delineated based on topography. The meltwater runoff to individual marine or land terminating glaciers within the fjord catchment was derived based on the delineation of the hydrologic subbasin on the ice sheet by Lewis and Smith (2009) (Fig. S3). The total meltwater runoff to the fjord is the sum over all glaciers in the fjord. In this way a difference can be made between melt that is routed towards marine or land terminating glaciers discharging into the fjord.

Processing of data was done in the open-source programming language R (R Core Team, 2013). Interpolation of the data and contour plots were produced using the OceanView package.

3 | RESULTS

3.1 | Hydrography during summer

Godthåbsfjord (SW Greenland) is a sub-Arctic fjord influenced by meltwater discharge from three land-terminating and three large marine-terminating glaciers, while Young Sound (NE Greenland) is a high Arctic fjord exclusively fed by land-terminating glaciers. The hydrography and water column chemistry of both fjord systems were surveyed during hydrographic cruises covering transects from the inner fjord to the adjacent continental shelf (Figure 1). This was done in summer, when maximum melting of the ice sheet occurs. Both Young Sound (August 2011) and Godthåbsfjord (August 2013) are strongly impacted by glacial meltwater during summer, as indicated by the low salinities (<5) in the surface layer (Figure 2a,b). In both fjords, this surface freshening is most pronounced in the inner parts of the fjords close to the glacier discharge points and the incoming meltwater induces a strong stratification, creating a low saline surface layer that is separated from deeper waters by a pycnocline at 5–10 m depth (Figure 2g,h). The meltwater input into Godthåbsfjord (~20 km^3 year^{-1}) is considerably larger than for Young Sound (~1.6 km^3 year^{-1}), but the ratio of meltwater discharge over surface area is similar in both fjord systems, which explains the comparable freshening and stratification in the two fjords. The inflow of glacial meltwater at the head of the fjord drives an estuarine circulation (Bendtsen, Mortensen, & Rysgaard, 2014; Mortensen, Lennert, Bendtsen, & Rysgaard, 2011), where the surface layer is transported downstream. Despite the higher latitude, maximum surface water temperatures were higher in Young Sound (~11.2°C) than in Godthåbsfjord (~6.3°C) as the melting of icebergs, calved from the marine-terminating glaciers, reduces the surface water temperature in Godthåbsfjord (Figure 2c,d). While Young Sound exclusively receives a surface meltwater input, Godthåbsfjord is also affected by subglacial freshwater discharge from its marine-terminating glaciers. Surface meltwater that percolates to the glacier bed via fractures and channels enters the fjord at submarine levels (Chu, 2014). When this freshwater enters the fjord at depth, it rises to the surface as a buoyant plume and entrains large volumes of ambient saline fjord water on its way up. These rising buoyant plumes create a region of turbulent upwelling immediately adjacent to the terminus of the marine-terminating glaciers (Supplementary Video). We observed the upwelled water mass originating from subglacial freshwater discharge as a cold water anomaly (0–1°C) between 10 and 30 m depth in the inner region of Godthåbsfjord (Figure 2c).

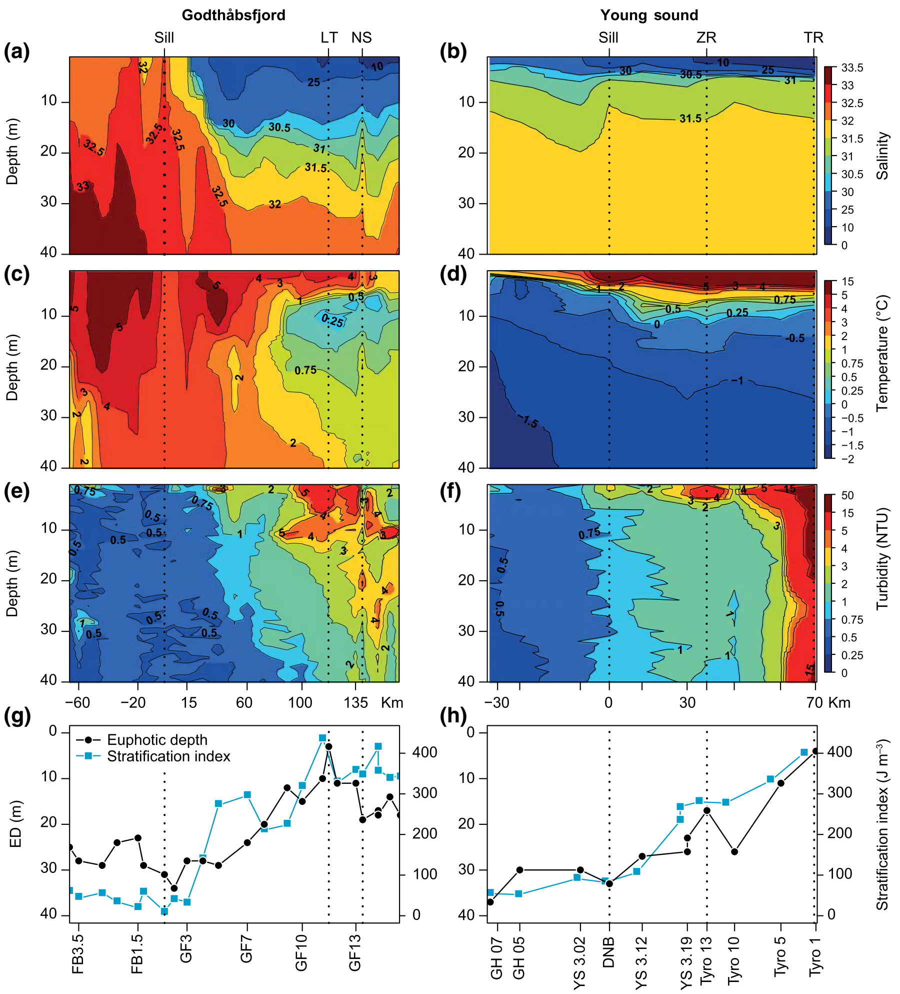

FIGURE 2 Hydrographic data from two fjords in Greenland in summer (Left column: Godthåbsfjord, right column: Young Sound). Length sections of salinity (a, b), temperature (°C) (c, d) along fjord transects showing the upper 40 m of the water column. Impact of glacial meltwater on turbidity (NTU) (e, f), euphotic depth (ED, m) and stratification index (Ψ, J m^{-3}) (g, h). To enable comparison, the depth transects in both fjords are plotted in the same direction (left = downstream, mouth of fjord; right = upstream, glacier region). The entrance sills of the fjords, glaciers and incoming rivers are indicated by the dashed lines and on the top axis of the panel

3.2 | Impact of glacial meltwater on turbidity and light regime

Concomitant with the input of glacial meltwater, both fjord systems also receive a high input of glacially derived particles, which leads to a high turbidity close to the glacier outlets (Figure 2e,f). The coarse particle fraction generally falls out quickly, forming deltas and submarine fans as observed close to the Tyroler river mouth in Young Sound (Figure 2f). The finer particles are transported further downstream before settling out of the surface layer. While land-terminating glaciers only supply turbid meltwater to the surface layer, marine-terminating glaciers also increase turbidity at depth due to subglacial discharge (Figure 2e). The suspended particles in the surface waters strongly impact the light penetration, thus limiting photosynthesis (Figure 2g,h). In Young Sound, the euphotic depth, defined as the depth at which the photosynthetic active radiation equals 1% of the surface value, is shallow (around 5 m) at the meltwater river inlets. Due to gradual settling of suspended particles, light penetration increases to 20–30 m in the central and outer part of the fjord (Figure 2h). Similarly, in Godthåbsfjord, input of turbid meltwater reduces the light penetration in the inner part of the fjord, especially close to the glacial outlet points as Lake Tarsarsuaq (Figure 2g). Generally, the euphotic depth lies ~10 m in the inner fjord but then increases to 30 m towards the mouth of the fjord (Figure 2g).

3.3 | Impact on biogeochemistry

In Young Sound, meltwater rivers show low nitrate concentrations (Meire et al., 2016) and observed nitrate concentrations in the surface layer of the fjord were low (Figure 3b). The pronounced stratification impedes nutrient supply from deeper waters, while high turbidity limits light penetration (Figure 2h). This combination of light limitation and low nutrient supply explains the low chlorophyll *a* concentrations (<0.5 μg L^{-1}) and low primary production (PP) rates (<40 mg C m^{-2} day^{-1}) in the inner and central parts of Young Sound during summer (Figure 3d,f). The light does not penetrate sufficiently deep in the central part of the fjord (i.e., beneath the nutrient-depleted surface layer) to allow the development of a deep chlorophyll maximum (Figure 3d). Only within the sill region and further onto the continental shelf, we observed a slight increase in phytoplankton biomass (chlorophyll *a* of 2–3 μg L^{-1} and PP of 200 mg C m^{-2} day^{-1}), likely resulting from an extended euphotic depth combined with an enhanced nutrient supply, due to a combination of tidal mixing within the sill region and coastal upwelling at the shelf break (Figure 3b,d,f).

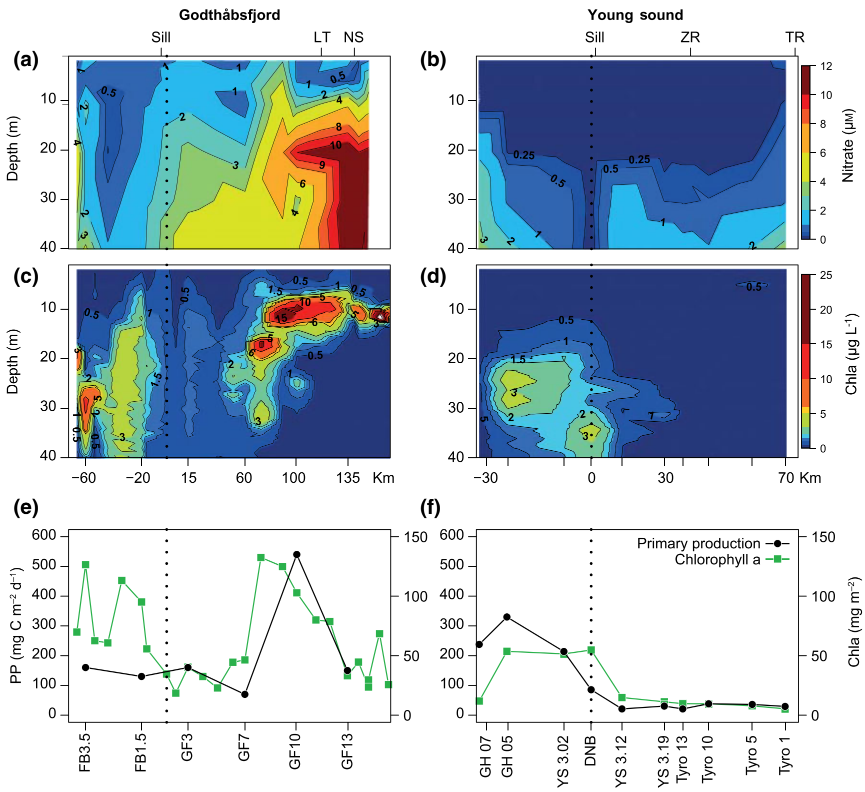

FIGURE 3 Biogeochemical data from two fjords in Greenland in summer (Left column: Godthåbsfjord, right column: Young Sound). (a, b) Length sections of nitrate (NO_3^-, μmol L^{-1}) and (c, d) fluorescence calibrated by chlorophyll a (Chl a, μg L^{-1}) along the fjord transect showing the upper 40 m of the water column. Gross primary production (mg C m^{-2} day^{-1}) and area-integrated chlorophyll a inventory (mg m^{-2}) along the fjord transects (e, f). To enable comparison, both fjords are plotted in the same direction (left = downstream, mouth of fjord; right = upstream, glacier region). The entrance sills of the fjords are indicated by the dashed lines

On the continental shelf adjacent to Godthåbsfjord (station FB3.5 to FB1.5), we observed a similar coastal upwelling and tidal mixing, resulting in a resupply of nutrients and higher biomass (Figure 3c,e). However, conditions are different inside Godthåbsfjord, as primary production rates and algal biomass were substantially higher compared to Young Sound (Figure 3a,c). Matching the cold water anomaly (Figure 2c), we observed high nitrate concentration and a high productivity suggesting that the nitrate was supplied by subglacial upwelling. Due to the rising buoyant meltwater plumes from the marine-terminating glaciers, large volumes of deep nutrient-rich water are entrained, which settle below the low-saline surface layer between 10 and 40 m (Figure 3c).

The idea that nutrient upwelling caused by subsurface meltwater discharge stimulates summer production is further supported by data from the monthly sampling campaigns at a station in the inner part of Godthåbsfjord (GF10). Figure 4 compares the situation in mid-May (at the end of the spring bloom and before the glacial melt season) to mid-August (during peak glacial melt). At the start of the summer, nitrate was depleted in upper 30 m, after being used up by the spring bloom (Figure 4d,e). During this period, glacial melting is limited, so the fjord received limited freshwater runoff (surface salinity ~32.4; Figure 4c) and subglacial freshwater discharge was not yet active. In contrast, in mid-summer, the fjord was impacted by large surface runoff (surface salinity ~13.5; Figure 4c) and subglacial discharge causes strong upwelling close to the terminus of the glaciers (supplementary video). Higher nitrate concentrations coincided with a pronounced subsurface temperature anomaly between 8 and 35 m, suggesting that subglacial upwelling resulted in an increased nitrate supply to the surface layers during summer (Figure 4b,e). This fueled a high primary production, as indicated by the subsurface chlorophyll maximum of 17 μg chlorophyll *a* L^{-1} at 10 m depth in GF10 (Figure 4d) and similar subsurface chlorophyll maxima along the transect in inner and central fjord (10–25 μg L^{-1} between GF9 to GF17; Figure 3c). Productivity was highest at GF10 (PP of 550 mg C m^{-2} day^{-1}; Figure 3e), where glacially derived silt had settled and the euphotic depth has increased. In central Godthåbsfjord, the subsurface chlorophyll maximum gradually migrated deeper (~10 μg L^{-1} at 20 m depth in GF8; Figure 3c) due to nutrient depletion and increasing light penetration. At the mouth of the fjord, strong tidal mixing creates a density gradient between the outer sill region and the main fjord (Mortensen et al., 2011). This drives the intermediate baroclinic circulation which was observed as an inflow in the depth range between 30 and 60 m and below (Mortensen et al., 2014) (Figure 4a,c). In the water mass referred to as sill region water, nitrate concentrations were lower (5–8 μM) compared to the subglacial discharge layer (10–12 μM) (Figure 4e).

The production during summer plays an important role for the annual primary production. Figure 5 shows the annual primary production for Godthåbsfjord and Young Sound. Seasonal measurements in station DNB in Young Sound show an annual pelagic primary production of ~10 g C m^{-2} $year^{-1}$. Annual pelagic primary production in Godthåbsfjord was 139 g C m^{-2} $year^{-1}$ at station GF3 in 2011 with an average of 104 ± 7 g C m^{-2} $year^{-1}$ for the period 2008–2012 (Juul-Pedersen et al., 2015). For station GF10, in the inner part of the fjord, the annual production in 2013 was 120 g C m^{-2} $year^{-1}$.

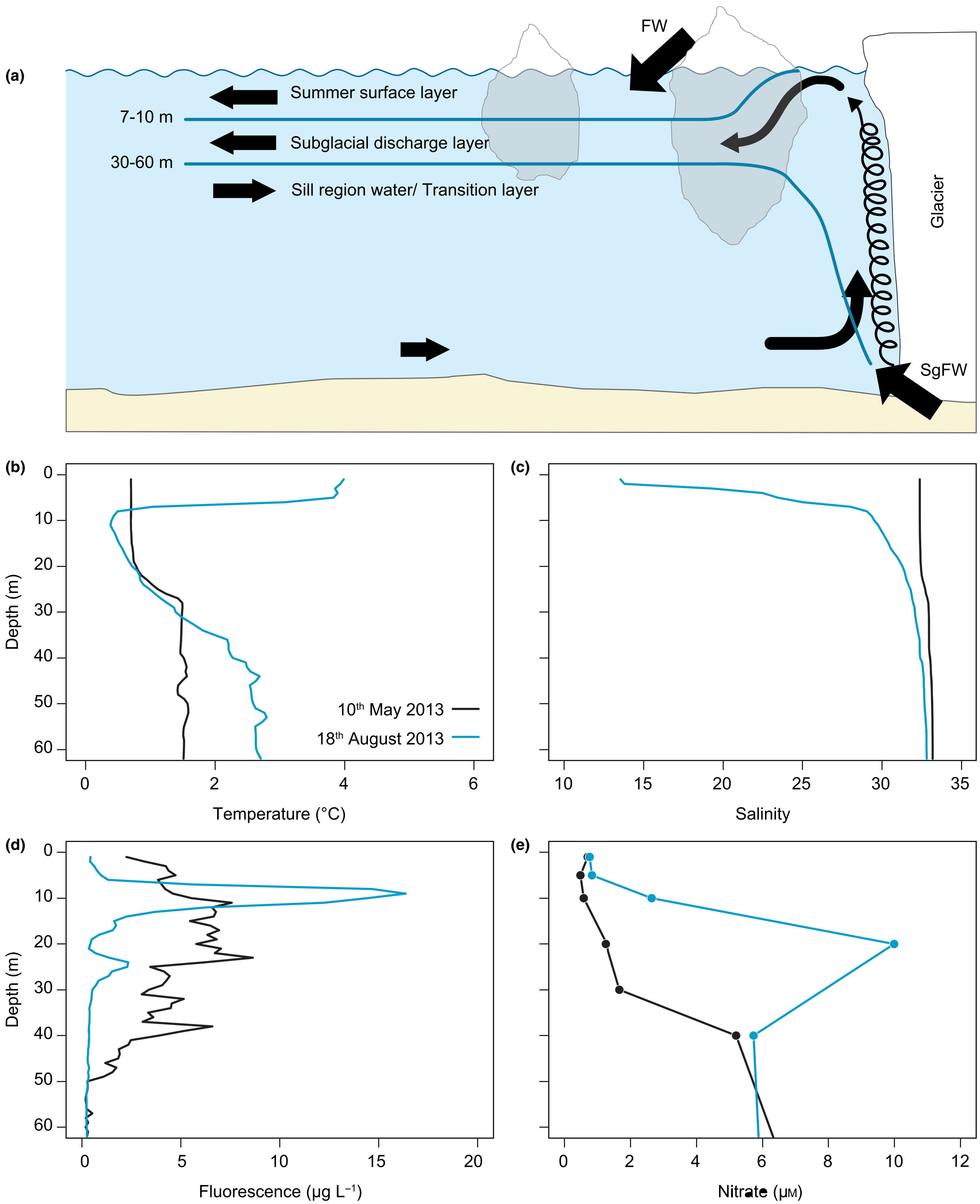

FIGURE 4 (a) Conceptual scheme of hydrodynamic circulation during summer months in inner part of Godthåbsfjord as described earlier by Mortensen et al. (2013). The lines indicate the border between different water masses in the surface layer during summer (glacial melting season) (FW: Freshwater, SgFW: Subglacial Freshwater). (b, c, d, e) Data for station in inner part of Godthåbsfjord (Station GF10) in May 2013 and August 2013. Depth profiles of temperature (°C) (b), salinity (c), fluorescence (μg L^{-1}) (d) and nitrate (μM) (e)

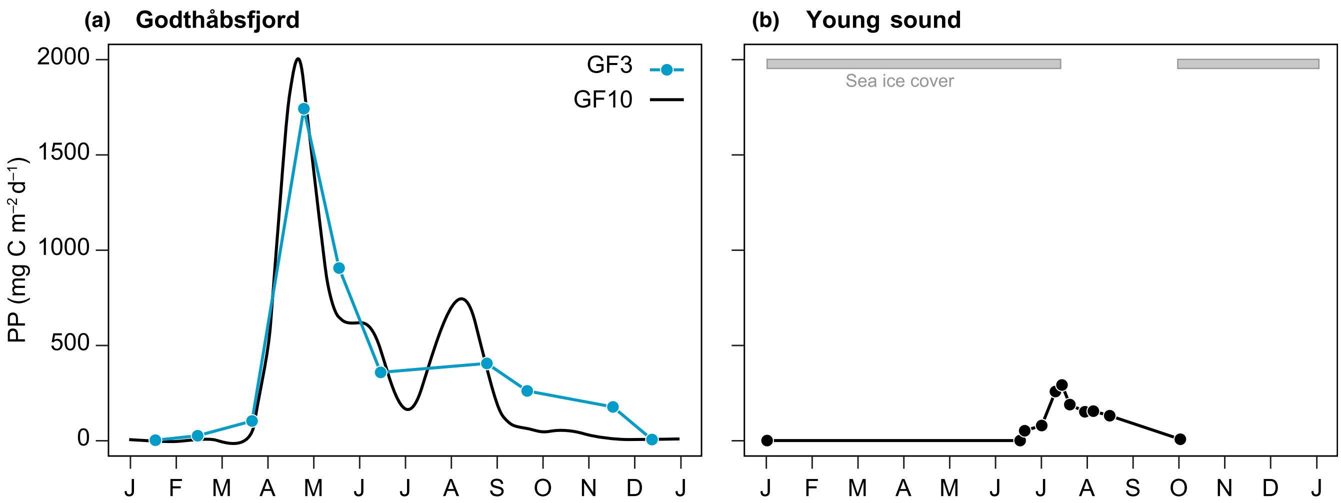

FIGURE 5 Seasonal evolution of the gross primary production (GPP, mg C m^{-2} day^{-1}) in Godthåbsfjord (a) and Young Sound (b; redrawn from Rysgaard et al., [1999]). GPP was recorded at two separate stations in Godthåbsfjord: GF3 (mouth of the fjord) measured in situ (redrawn from Juul-Pedersen et al., [2015], year 2011) and GF10 (close to marine-terminating glaciers, year 2013). In Young Sound, GPP was recorded at one station (DNB, close to the mouth of the fjord) and the period with sea-ice cover is indicated

3.4 | Halibut landings

When inspecting the geographical distribution of the halibut landing data in Greenland, it is noticeable that regions close to the marine-terminating glaciers termini show important fisheries activity (e.g., Disko Bay and Uummannaq in Figure 6). The resulting hypothesis that marine-terminating glaciers correlate with high productivity and important fisheries was quantitatively examined via statistical analysis. Halibut landings (HL) differed significantly (Wilcox test; p-Value = .002) between fjords with marine-terminating glaciers (HL = 1029 ± 376 kg km^{-2} year^{-1}) compared to fjords with only land-terminating glaciers (HL = 131 ± 44 kg km^{-2} year^{-1}).

Furthermore, halibut landings showed a significant positive correlation with meltwater runoff of marine-terminating glaciers (Pearson p-Value < 10^{-4}, df = 16; Figure 6). The correlation between halibut landings and runoff of land-terminating glaciers was not significant (Pearson p-value = 0.3, df = 35). Halibut landings for fjords with only land-terminating glaciers are low and do not increase with increasing total meltwater runoff (Figure 6e).

A multiple regression analysis was used to investigate the correlation of the halibut landings with available environmental parameters for each fjord (presence of glacier type, length of sea ice period, meltwater runoff to land- terminating glaciers, runoff to marine terminating glaciers and bathymetry) (Supp. Material). This showed that the runoff originating from the marine terminating glacier, which can be regarded as a proxy for subglacial discharge, is the most important explanatory variables for halibut landings (Figure 6d) (Model F-statistic: 26.3, $p < 10^{-4}$). Although the meltwater runoff to the marine-terminating glaciers includes both surface and subglacial discharge, marine-terminating glaciers characterized by a high total meltwater runoff are likely also characterized by a larger subglacial discharge, which can then sustain a higher productivity in the fjord through nutrient upwelling.

4 | DISCUSSION

4.1 | Glaciers impact on the nutrient dynamics in fjords

Our data suggest that fjords only influenced by land-terminating glaciers (like Young Sound) show a distinct nutrient dynamics and primary production compared to fjords with large marine-terminating glaciers (like Godthåbsfjord) (Figure 7). During the summer months, Godthåbsfjord is characterized by intense summer bloom with high primary production, while in contrast, Young Sound has a low summer productivity. These summer blooms in Godthåbsfjord suggest an additional input of nitrate to the surface waters, which is the limiting nutrient for primary production (Juul-Pedersen et al., 2015; Meire et al., 2016). Following the spring bloom, nitrate is depleted in the photic zone (Figure 4e), and consequently, a high summer production must be fueled by an additional input of nitrate. Both Young Sound and Godthåbsfjord are steep-side fjords, and so nutrient effluxes from sediments to the surface waters are small, implying that nitrate must be supplied either from lateral input by meltwater rivers or by upwelling from below (Tremblay & Gagnon, 2009). It has been suggested that meltwater runoff from Greenland ice sheet contains significant concentrations of specific bioavailable nutrients (Hawkings et al., 2015, 2016), and that such a direct input of these nutrients along with the glacial meltwater could stimulate primary production during the melt season in summer. However, direct measurements of nutrient concentrations in glacial ice and meltwater rivers show that they are an important source of silica, but only to a limited extent of nitrate (Meire et al., 2016). This idea that glacial meltwater does not stimulate production through direct nutrient fertilization is corroborated by our data from Young Sound, which only receives surface meltwater input from land-terminating glaciers. The freshening of the surface waters (Figure 2b) coincided with low nitrate

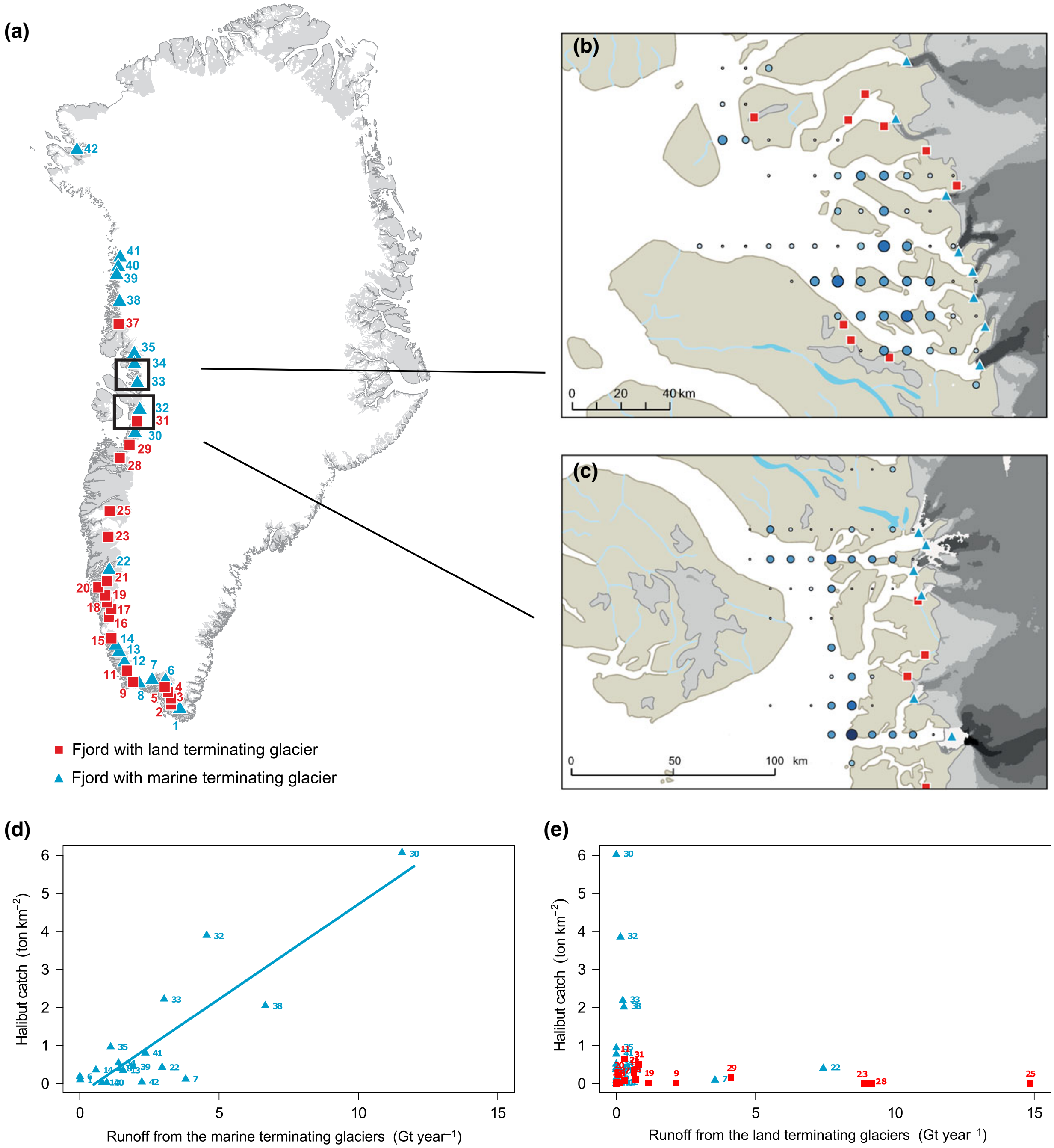

FIGURE 6 (a) Halibut landings for different fjord systems in West Greenland impacted by marine and/or land-terminating glaciers. (b, c) Location of large halibut fishery in two different regions (b: Uummannaq 70°40′N 52°07′W, c: Ilulissat 69°13′N 51°06′W). Halibut landings from 2013 are shown in the different regions together with the presence of marine-terminating glaciers (blue triangles) and land-terminating glaciers (red squares). Grey shading of the Greenland Ice Sheet shows ice velocity (m year^{-1}). (d) Relation between meltwater runoff originating from the marine-terminating glaciers in the fjord (in Gt year^{-1}) and fishery catchment (ton km^{-2}) in the different areas indicated as dots on overview map (a, dots) (e) Relation between meltwater runoff originating from land-terminating glaciers in the fjord (in Gt year^{-1}) and fishery catchment (ton km^{-2}) in different areas indicated as dots on overview map (a, dots)

concentrations (Figure 3b) and low productivity (Figure 3d), suggesting a limited nitrate input in summer. In addition to low meltwater nitrate concentrations, surface runoff will tend to decrease primary productivity, because it induces a poor light climate due to high turbidity resulting from the high suspended material in the meltwater (Murray et al., 2015; Figure 2f), and it enhances stratification (Figure 2h) which prevents a nitrate supply from deeper water. The absence of suitable supply mechanism for nitrate explains why summer production remains low in Young Sound after the exhaustion of the surface nitrate by the spring bloom.

Likewise, the summer bloom in Godthåbsfjord cannot be explained by surface meltwater runoff. In addition to surface

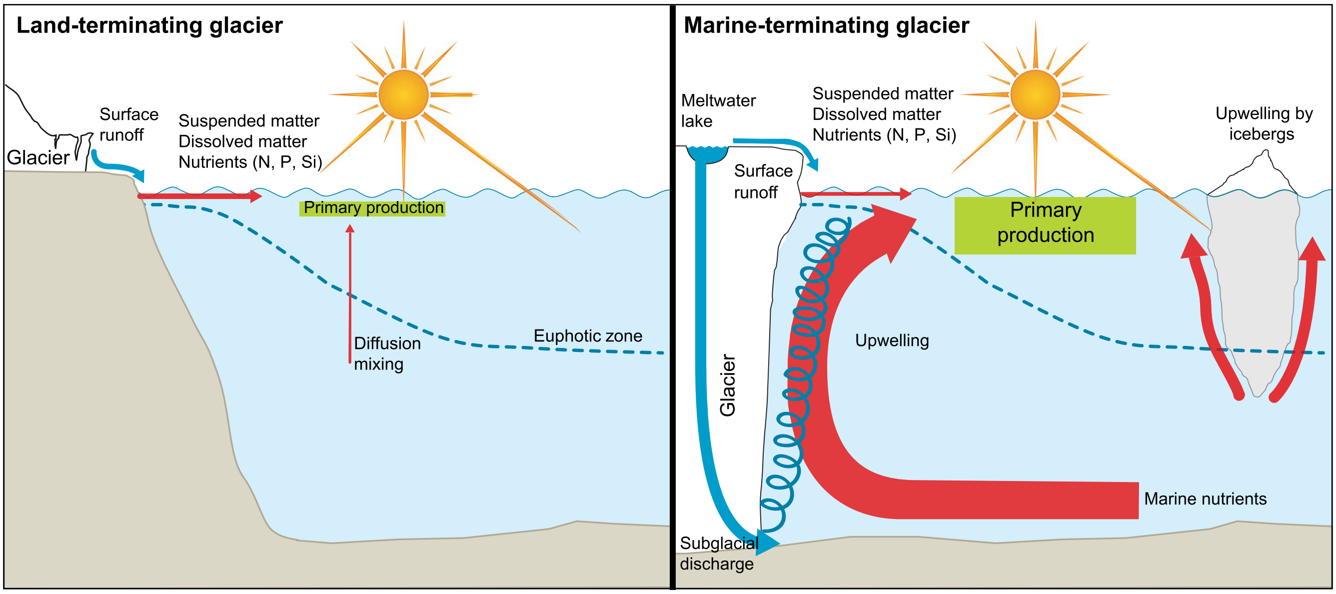

FIGURE 7 Conceptual model of the hydrodynamic circulation and its impact on the biogeochemistry in a fjord affected by marine-terminating glaciers (e.g., Godthåbsfjord) and a land-terminating glacier (e.g., Young Sound)

runoff, fjords with marine-terminating glaciers are influenced by subglacial discharge (Kjeldsen et al., 2014; Straneo & Cenedese, 2014). Here we argue that subglacial discharge could be an important mechanism to resupply nutrients to the surface layer, hereby sustaining summer primary production in fjords with marine-terminating glaciers. Hydrographic observations have previously shown that during summer months, subglacial freshwater discharge drives a strong upwelling in the inner part of Godthåbsfjord (e.g., Bendtsen, Mortensen, Lennert, & Rysgaard, 2015; Bendtsen, Mortensen, & Rysgaard, 2015; Kjeldsen et al., 2014; Mortensen et al., 2013). This leads to a buoyant plume (Figure 2c), which entrains large volumes of nutrient rich saline ambient fjord water on its way up (typically 10 to 30 times the initial volume of the subglacial freshwater plume) (Bendtsen et al., 2015; Mortensen et al., 2013; Sciascia, Straneo, Cenedese, & Heimbach, 2013). In Godthåbsfjord, this buoyant water mass settles below the low saline surface layer (Mortensen et al., 2013) and generates a subsurface cold water anomaly as it is advected out of the fjord (Figure 2c). Our study links this subglacial upwelling to a resupply of nitrate to the surface layers, which results in elevated nitrate concentrations in the water layer between 10 and 30 m depth (Figures 3a, 4e), and pronounced subsurface chlorophyll maxima (Figure 3c), thus explaining the sustained phytoplankton bloom from July to September (Figure 5). An artificial upwelling experiment performed in Norwegian fjords resulted in a similar strong increase in chlorophyll concentrations (Aure, Strand, Erga, & Strohmeier, 2007), of which the subglacial discharge observed here forms the natural analogue. Note that nitrate concentrations in the deeper waters of Godthåbsfjord (~11 μM) and Young Sound (~12 μM) are similar (Fig. S1). Accordingly, both fjords have a similar overall nitrate content, and hence a similar potential to stimulate primary production, if a suitable upwelling mechanism were present. Yet only in Godthåbsfjord, such nutrient upwelling is realized by subglacial freshwater discharge taking place throughout summer.

A nutrient budget confirms that the nitrate upwelling induced by subglacial freshwater discharge can account for the observed summer production in Godthåbsfjord. The rate of subglacial discharge (Q_{SD}) can vary substantially during summer months and generally consists of a lower baseline discharge rate, on top of which rapid increases occur over short periods of time. Analysis of the subglacial plume at the KNS glacier in Godthåbsfjord provides a baseline subglacial discharge rate of ~10 $m^3\ s^{-1}$ (Bendtsen et al., 2015). Glacial lake drainage induces strong percolation of meltwater to the glacier bedrock, and during such episodic events, the Q_{SD} in Godthåbsfjord has been observed to increase by a factor of 10 to 100 (Kjeldsen et al., 2014). Details on the frequency and amplitude of such episodic drainage are, however, lacking, and consequently, the mean Q_{SD} of the different glaciers in Godthåbsfjord is currently not well constrained. Here, we use a range of 10 to 100 $m^3\ s^{-1}$ for the Q_{SD} of KNS. This is likely a conservative estimate as other studies estimated a much larger average discharge for KNS (Slater et al., 2017) and even a discharge of ~100 $m^3\ s^{-1}$ for a smaller glacier (Mankoff et al., 2016). When the subglacial freshwater enters the fjord, it rises to the surface and entrains large volumes of ambient fjord water. Previously, entrainment factors (ratio of total upwelling over subglacial freshwater discharge) have been proposed in the range of 10 to 30 (Bendtsen et al., 2015; Mankoff et al., 2016; Mortensen et al., 2013). A recent heat budget model at the KNS glacier in Godthåbsfjord estimated an entrainment factor of 14, thus generating an upwelling rate of 140 to 1400 $m^3\ s^{-1}$ (Bendtsen et al., 2015). For the other two marine-terminating glaciers in Godthåbsfjord (NS and AS), no information on subglacial discharge is available, but these glaciers are similar in size as KNS, and so we adopted the same parameter values as for KNS.

The deep water in Godthåbsfjord has nitrate concentration of ~11 μM (Fig. S1), thus providing an upwelling flux of nitrate: $J_{NO3} = 0.4 \times 10^6$ to 4.0×10^6 mol N day^{-1}.

New production takes place in central and inner part of Godthåbsfjord, (surface area ~650 km^2), of which 20% is covered by icebergs during summer (Mortensen et al., 2013), yielding a surface area of 520 km^2 available for light penetration and primary production. Using the Redfield ratio (106C:16N), the upwelling nitrate $J_{NO3} = 0.4 \times 10^6$ to 4.0×10^6 mol day^{-1} thus provides an area-based rate of potential new production of 70–700 mg C m^{-2} day^{-1}, which aligns with the values measured at station GF10 (~550 mg C m^{-2} day^{-1}).

The importance of subglacial discharge can be illustrated by upscaling to all 210 marine-terminating glaciers in Greenland with calving fronts wider than 1 km (Howat & Eddy, 2011). Assuming subglacial freshwater discharge is active for approximately two months per year and using a subglacial discharge of 10–100 m^3 s^{-1} per glacier, this results in a nitrate flux of 1.7–17 Gmol year^{-1} to the surface layer. Comparing this to the direct input of dissolved inorganic nitrogen with glacial meltwater of 0.3–0.7 Gmol year^{-1} (Hawkings et al., 2015), the entrainment associated with subglacial discharge has potentially a far larger impact on the nitrogen supply to the surface layer of Greenland coastal waters.

The transport of icebergs through fjord systems with marine terminating glaciers could add an additional nutrient supply, as iceberg movement leads to local upwelling and increased productivity (Smith, Sherman, Shaw, & Sprintall, 2013; Vernet et al., 2012). Yet, the relative importance of iceberg-induced nutrient upwelling is currently unconstrained, and hence, its impact on productivity is not further quantified here. In addition to the impact of glaciers, other mechanisms such as tidal mixing at the fjord mouths and coastal upwelling at the continental shelf break can also resupply nutrients to the surface layer that sustains productivity on the shelf (Figure 3e,f).

4.2 | Importance of marine-terminating glaciers for the marine ecosystem

Young Sound has an overall annual pelagic primary production of ~10 g C m^{-2} year^{-1} (Rysgaard, Nielsen, & Hansen, 1999), which is 12 times lower than Godthåbsfjord, which has an estimated annual primary production of ~120 g C m^{-2} year^{-1} (Juul-Pedersen et al., 2015; Meire et al., 2015). One factor that could explain this large difference is the presence of sea ice in fjords, which reduces the productive period window, thus leading to a lower annual production (Arrigo, Van Dijken & Pabi, 2008; Rysgaard & Glud, 2007). Although Young Sound experiences a longer and more extensive sea ice cover than Godthåbsfjord, this only explains part of the observed differences in annual primary production as production during the ice-free summer is substantially lower than in Godthåbsfjord. Sea ice is typically present in Young Sound until early July, after which there is a single short phytoplankton bloom (Figure 5) (Rysgaard et al., 1999). The predicted increase in the ice-free period from 80 days at present to 160 days by the end of the twenty-first century, potentially can lead to a threefold increase in annual production to ~30 g C m^{-2} year^{-1} as projected by Rysgaard and Glud (2007). So even without sea ice limitation, the annual primary production in Young Sound would remain substantially lower than in Godthåbsfjord. In addition to the typical spring bloom, the inner part of Godthåbsfjord also shows a sustained summer productivity (Figure 3a), which accounts for 35%–40% of the annual production (Juul-Pedersen et al., 2015; Meire et al., 2015). This summer bloom has been observed to reoccur annually and coincides with the maximum meltwater runoff from Greenland ice sheet (Calbet et al., 2011; Juul-Pedersen et al., 2015) As substantiated above, this increased summer productivity is not due to a direct fertilization from nutrients contained in glacial meltwater, but runs through an indirect impact of the meltwater input on the physical oceanography, as nutrient upwelling is stimulated by rising meltwater plumes from marine-terminating glaciers.

The high productivity in Godthåbsfjord during both spring and summer has a direct effect on higher trophic levels, as confirmed by the sustained zooplankton production that is observed throughout summer (Arendt, Juul-Pedersen, Mortensen, Blicher, & Rysgaard, 2013; Tang et al., 2011). This high zooplankton biomass is an important food source for crustaceans (krill) and small pelagic fish (polar cod, arctic cod and capelin) (Bergstrøm & Vilhjalmarsson, 2007), which are preyed upon by Greenland halibut, seals and whales that seasonally migrate into Godthåbsfjord (Boye, Simon, & Madsen, 2010). In contrast, Young Sound is characterized by low pelagic biomass (Arendt, Agersted, Sejr, & Juul-Pedersen, 2016), and instead, the limited primary production is mainly channeled to slow growing benthic filter-feeding organisms (Sejr, Blicher, & Rysgaard, 2009). Consequently, the dominant top predators in Young Sound (walruses and eider ducks) rely primarily on benthic biomass that has accumulated over decades (Sejr et al., 2002). These observations hence suggest that subglacial discharge, or equally the presence of marine-terminating glaciers, acts as a structuring factor for the marine food web in the fjords.

The coastal and fjord waters of west Greenland are productive with net primary production rates of 70–320 mg C m^{-2} day^{-1} (Jensen et al., 1999) and this productivity sustains important fisheries, which contributes up to 92% of Greenland's total export income, and forms the basis for the traditional hunting of marine mammals. Halibut fisheries occur within or at the mouth of the fjord systems (ICES, 2015) and are of particular economic importance for Greenland (Berthelsen, 2014), accounting for 42% of the total fisheries income. Our statistical analysis reveals that high halibut landings spatially correlate with the presence of large marine-terminating outlet glaciers (Figure 6b,c). Moreover, in fjords with marine-terminating glaciers, the halibut landings correlate with the glacial freshwater input, while this is not the case for fjords with only land-terminating glaciers (Figure 6d). To explain this, we hypothesize that larger glaciers systems induce a higher subglacial discharge, which in its turn sustains a higher productivity. Major inshore halibut fishing grounds are found in the inner Disko Bay, where primary production rates of 1200 to 3200 mg C m^{-2} day^{-1} have been recorded in summer (Andersen, 1981; Jensen et al., 1999), as well as in the Uummannaq and Upernavik regions. These are all areas with major marine-terminating glaciers (Figure 6). Notwithstanding the risks and difficulties of fishing in these areas (calving glaciers and icebergs), fishermen do sail into these glacier fjords, as these are known to provide rich fishing grounds, generating high landings (Nygaard, 2014). A similar reasoning could explain the foraging behavior of narwhals, which feed on squid, shrimp and fish, and are found close to the marine-terminating glaciers during summer (Laidre et al., 2016). The connection between subglacial discharge and sustained summer productivity is not limited to Greenland, but has been observed in other parts of the Arctic. Earlier works have observed similar upwelling events in other marine-terminating glacier fjords in the Arctic (Greisman, 1979; Hartley & Dunbar, 1938). Tracking data of sea-birds and marine mammals (seals and whales) in Svalbard also reveal that regions near marine-terminating glaciers are important feeding grounds (Lydersen et al., 2014).

4.3 | Outlook

Our results indicate that glaciers strongly impact the biogeochemistry and productivity of marine fjord ecosystems in Greenland. The impact of glaciers on marine productivity is not direct, in the sense that meltwater is not a significant source of nitrate which is the main limiting nutrient. Rather, the effect on productivity is indirect via the impact of glaciers and icebergs on the hydrography. Marine-terminating glaciers drive substantial upwelling of nutrient-rich deep water, thus sustaining a high primary production throughout the summer while this mechanism is absent for land-terminating glaciers. In recent decades, a widespread retreat and thinning of marine-terminating glaciers has been observed along the Greenland ice sheet, with an average retreat of 110 m year^{-1} over 2000–2010, resulting from increasing submarine and atmospheric melt (Carr, Stokes, & Vieli, 2013; Howat & Eddy, 2011). Glaciers along the northeast and north coast of Greenland typically have submerged beds that extend far inland, and are less likely to become land-terminating. However, marine-terminating glaciers in other parts of Greenland may well retreat above sea level in the near future (Howat & Eddy, 2011), a transition that as shown here, may drastically reduce summer productivity. Yet, as long as glaciers remain marine-terminating, increased surface melting may stimulate increased meltwater percolation, leading to higher subglacial discharge, enhanced nutrient upwelling and increased summer productivity. Overall, we expect that the shrinking of the Greenland ice sheet will cause fundamental changes in the hydrography, biogeochemical cycling and marine productivity of the fjord ecosystems around Greenland.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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